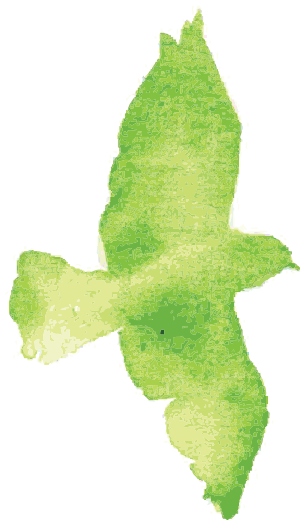


A teal background featuring several watercolor-style birds in flight. One bird is in the top left, another in the top right, and a third partially visible in the bottom right.

WHAT'S LOVE GOT TO DO WITH IT: THE EVOLUTION OF MONOGAMY

EDITED BY: Alexander G. Ophir and Nancy G. Solomon
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WHAT'S LOVE GOT TO DO WITH IT: THE EVOLUTION OF MONOGAMY

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Editorial: What's Love Got to Do With It: The Evolution of Monogamy

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Editorial on the Research Topic

What's Love Got to Do With It: The Evolution of Monogamy

Monogamy and pair-bonding are central to the human experience in the majority of cultures worldwide (Schacht and Kramer), which might explain the long-running fascination scientists have for understanding monogamy within mammals and across other taxa. The inherent interest in monogamy in western cultures, in part, may be a result of anthropomorphism and a belief that who we mate with defines us. Nevertheless, monogamy captivates the human mind and has been the subject matter in art, religion and literature for centuries. It is a topic that has brought together researchers from diverse backgrounds including anthropology, behavioral ecology, psychology, psychiatry, pediatrics, neurobiology, endocrinology, and molecular biology.

There is still much we do not understand about monogamy. A collective, systematic, and concerted effort toward answering questions surrounding the meaning of monogamy is overdue. This Research Topic aimed to bring experts, from a variety of disciplines and conceptual approaches, together to showcase our current understanding of monogamy. This issue is composed of articles focusing on the specific and general aspects of monogamy within a variety of species, and taking empirical, methodological, conceptual, or theoretical approaches to provide a deeper and more complete understanding of aspects of behavior that comprise monogamy, its evolution, and its meaning.

The term “monogamy” can be used in very different contexts or ways, emphasizing the need to carefully delineate or define terminology. This is a critical concern because not only can there be confusion between different forms of monogamy (e.g., “social” and “genetic” monogamy), but also about the particular behaviors that should be included within the concept of monogamy. Thus, consistent and clearly defined terminology is crucial, especially when conducting comparative analyses (Huck et al.; Kappeler and von Schaik, 2002). Early studies of monogamy often assumed that animals with a high degree of spatio-temporal overlap mated exclusively with each other (Wittenberger and Tilson, 1980). Since the advent of molecular techniques enabling parentage determination, it has become clear that exclusive mating with a social partner (i.e., genetic monogamy) is much rarer than social partnerships in which mating outside the pair occurs (e.g., eastern bluebirds, *Sialia sialis*, Gowaty and Karlin, 1984, indigo buntings, *Passerina cyanea*, Westneat, 1987; fat-tailed dwarf lemur, *Cheirogalus medius*, Fietz et al., 2000). Thus, the propensity for two opposite sexed individuals to live together need not relate to an exclusive mating relationship, in itself requiring a reevaluation of the common understanding of monogamy.

Social monogamy can be defined in terms of spatial overlap of one adult male and one adult female that live as a pair. Advances in methods to study such behavior in nature, particularly among cryptic subterranean species (like rodents), provide accurate and more refined determinations of behavior that can significantly improve assessment of the behaviors that define monogamy. For example, Sabol et al. demonstrated that incorporating automated radio frequency identification

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tracking (RFID) and social network analysis can provide new opportunities to measure and operationalize monogamous behavior beyond classic laboratory tests of partner preferences (Williams et al., 1992; Donaldson et al., 2010) and assessment of home ranges and spatial overlap using radiotelemetry in the field (Solomon and Jacquot, 2002; Ophir et al., 2008; Lambert, 2018).

Although the spatio-temporal relationship between mating partners provides one important way to define socially monogamous relationships (Emlen and Oring, 1977; Ophir, 2017), other conceptualizations of monogamy focus more heavily on the suites of behaviors that contribute to delineating this social system. Relying on behavioral characteristics to define monogamy (i.e., social association, formation of an attachment, mating pattern, biparental care of offspring, and selective aggression toward same-sex conspecifics) can lead to different views of monogamy because not all the behaviors that contribute to various conceptualizations of monogamy are consistently found in every socially monogamous species. For example, some of the early reviews of monogamy (Kleiman, 1977; Wittenberger and Tilson, 1980) included biparental care as a key feature of monogamy, but we now know that biparental care is not found in all monogamous animals (Brotherton and Rhodes, 1996; Whiteman and Côté, 2004, Table 2; Lambert et al., this issue Supplementary Data sheet 1). Even when biparental care is common (e.g., in avian monogamy, Mock and Fujioka, 1990), the contributions of parents are not necessarily equal and may not be constant over time. Rogers et al. examines the pattern of biparental care seen across multiple litters and finds that the mother and father appear to compensate for the time spent in parental care by the partner. Similarly, Schacht et al. investigate human paternal investment within a population of Maya living in Mexico in response to changes in socioecological factors. The authors investigate how changes in socioecological factors such as the introduction of mechanized farming, and their potential to provide stability in offspring social environments might compensate for a partner's waning parental effort or create opportunities for increased effort. For instance, mechanized farming among the Maya increases efficiency in providing subsistence, mating partnerships, and bi-parental care.

Another issue that can confound our understanding of monogamy is the acknowledgment that individuals within a population typically described as monogamous vary. Indeed, any mating system is best considered to be a collection of individual reproductive decisions, which are shaped by many internal and external factors. For example, many species that are considered monogamous contain individuals that engage in alternative mating tactics. Typically, alternative tactics within mating systems tend to take the form of (socially) monogamous residents that maintain territory, site, or nest fidelity with an opposite-sex partner, or the form of non-monogamous (often promiscuous) wandering or roaming individuals that maintain more than one nest and/or lack the site fidelity of the former. How evolution has maintained the variation in tactics is an important question that strikes at the heart of this phenomenon (Dawkins, 1980; Koprowski, 1993; Taborsky et al., 2008). In this issue, Shuster et al. used data from a 3-year study in two geographically separate populations of prairie

voles to investigate the average fitness obtained by males and females that exhibited alternative reproductive tactics. They showed that a form of balancing selection could maintain both behavioral phenotypes in the populations. Adopting a socially monogamous resident tactic does not preclude the motivation (or reproductive advantages that presumably support it) to pursue extra-pair matings. So, although the tactics are distinct from each other, an individual can switch from one tactic to another depending on which tactic results in higher fitness under particular environmental conditions. In another paper in this special topic, Rice et al. use optimal performance modeling to predict when it would be better for males that are pair-bonded to stay and guard their mates vs. seek extra-pair copulations in a population where males display alternative mating tactics. The latter would come with the cost of losing matings with their female partner to conspecific males in the population. Together, studies such as these highlight the profound individual variation between and within tactics that exists within "monogamy" and point to external factors (social or ecological) that help shape the evolution of reproductive decision-making.

There are still many unanswered questions that remain about how socially monogamous animals respond to infidelity in their partner. A number of papers in this issue explore different aspects involved in the potential for loss of genetic monogamy in socially monogamous individuals. Pultorak et al. investigates vocalizations among individuals during the formation of a pair-bond and during an "infidelity challenge," where the male and female were housed for 1 week with an unfamiliar opposite-sex conspecific. Maninger et al. used functional imaging to investigate the changes in cerebral glucose metabolism, and an array of hormones taken from brain and blood after a pair-bonded male titi monkey observed his partner in close proximity with a rival male. Maninger et al. provocatively suggest that the experience induced a neural and physiological response indicative of "jealousy" and that such responses preserve pair bonds.

In recent years, a focus on proximate studies like the latter one, and recognition for the tremendous value toward providing a complete understanding of behavior (*sensu* Tinbergen, 1963), has increased. Studies about the neurogenetic mechanisms underlying characteristics of monogamy, particularly the formation of pair bonds, have received considerable attention (Young and Wang, 2004; Klatt and Goodson, 2013; Fischer et al., 2019) and have been major contributors toward this wave of interest in proximate behavioral mechanisms. Nevertheless, the mechanistic underpinnings of monogamy are complex, and important outstanding questions remain about the relative importance and interrelationship among neurogenetic factors. In a remarkably comprehensive review, Carter and Perkeybile outline many of the behavioral, hormonal, neural and genetic/epigenetic mechanisms that contribute to mating behavior, the formation and maintenance of the pair bond, the emotion humans call "love," and the gulf between them. Similarly, Carp et al. focus on the role of dopamine in the length of time animals have been paired to assess the function of this neurotransmitter in the strength of bonds. Together, these papers provide insight into the deep evolutionary roots of shared

mechanisms that govern short-term or long-term monogamous relationships, while also demonstrating that there is no one single neurochemical recipe for social monogamy. Finally, ontogenetic effects on monogamy have received comparably little attention compared to Tinbergen's other levels of analysis, though such studies do exist. For example, rodent studies have clearly demonstrated that early-life experience can alter the propensity for monogamy (Bales et al., 2007; Ahern and Young, 2009; Prounis et al., 2015), and the neurochemical substrates that contribute to it (Hiura and Ophir, 2018; Hiura et al., 2018; Kelly et al., 2018; Prounis et al., 2018). Similarly, Al-Naimi et al. examines the effects of social and environmental disruptions in the life of young animals, and discuss how these may affect the tendency of males to behave monogamously.

Many studies of monogamy naturally lead to questions that address the adaptive value of this mating system, but the importance of understanding monogamy from the comparative evolutionary, mechanistic, and developmental perspectives (sensu Tinbergen, 1963) cannot be understated. Questions about the evolution of monogamy have been a steadfast area of interest in behavioral ecology and the study of animal behavior. In the 1980–2000s, the costs and benefits of monogamy to males and females received a lot of attention (Wittenberger and Tilson, 1980; van Schaik and Dunbar, 1990; Hames, 1996; Reavis and Barlow, 1998), and numerous hypotheses were proposed and tested in different species. Since then, great advances in phylogenetic reconstruction have paved the way for a better understanding of the evolution of social monogamy, including the causal factors that led to social monogamy and the factors that were consequences of this social/mating system (Dobson et al., 2010; Lukas and Clutton-Brock, 2013). Previous phylogenetic studies on factors influencing genetic monogamy have not reached consistent conclusions for a number of reasons, including differences and limitations in methodology and the species included in analyses (Clutton-Brock and Isvaran, 2006; Cohas and Allaine, 2009; Huck et al., 2014; Dobson et al., 2018). In this issue, Lambert et al. used phylogenetic corrections to examine factors influencing genetic monogamy within socially monogamous mammals and found that there was not one best model that explained the different ways in which genetic monogamy could be assessed. Numerous life history factors such as pair living and paternal care were important contributors to the top models. These, together with some demographic factors such as density or sex ratio, affected some measures of genetic monogamy. This conclusion is consistent with the argument made by Klug, which considered the life-history and ecological conditions that permit the evolution and persistence of monogamy, and advocated for the idea that

multiple (interacting) factors influence the display of monogamy. In a more specific example, Macdonald et al., reviewed some of the same functional hypotheses for the evolution and persistence of social and genetic monogamy in wild canids, a mammalian family in which monogamy is common. They proposed the hypothesis that the combination of particular characteristics of canids has led to both monogamy and pro-social cooperation. In another study employing the comparative approach, Kalcounis-Rueppell et al. consider the relationships between the form and function of *Peromyscus* vocalizations with ecological traits, physiological traits, and different mating systems, ranging from polygyny to monogamy, across seven species of mice.

The study of monogamy has accelerated in the past few decades, painting a nuanced, and at times perplexing yet captivating, picture for what monogamy actually is. Such work has only uncovered more exciting questions that merit investigation, and highlight that we are just beginning to understand what monogamy actually is. Love, for example, is—at best—only a small part of this larger phenotypic complex. We hope that the contributed papers contained within this collection will stimulate discussion and promote more research, which in the end, will enhance our understanding of monogamy, and lead to achieving a deeper understating of the mating system often associated with humans and many other species across the animal kingdom.

AUTHOR CONTRIBUTIONS

AO had the original idea for this topic. AO and NS collaborated on the description and organization of this special topic and wrote this introductory article together.

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Of Apples and Oranges? The Evolution of “Monogamy” in Non-human Primates

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Behavioral ecologists, evolutionary biologists, and anthropologists have been long fascinated by the existence of “monogamy” in the animal kingdom. Multiple studies have explored the factors underlying its evolution and maintenance, sometimes with contradicting and contentious conclusions. These studies have been plagued by a persistent use of fuzzy terminology that often leads to researchers comparing “apples with oranges” (e.g., comparing a grouping pattern or social organization with a sexual or genetic mating system). In this review, we provide an overview of research on “monogamy” in mammals generally and primates in particular, and we discuss a number of problems that complicate comparative attempts to understand this issue. We first highlight why the muddled terminology has hindered our understanding of both a rare social organization and a rare mating system. Then, following a short overview of the main hypotheses explaining the evolution of pair-living and sexual monogamy, we critically discuss various claims about the principal drivers of “monogamy” that have been made in several recent comparative studies. We stress the importance of using only high quality and comparable data. We then propose that a productive way to frame and dissect the different components of pair-living and sexual or genetic monogamy is by considering the behavioral and evolutionary implications of those components from the perspectives of all participants in a species’ social system. In particular, we highlight the importance of integrating the perspective of “floater” individuals and considering their impacts on local operational sex ratios, competition, and variance in reproductive success across a population. We stress that pair-living need not imply a reduced importance of intra-sexual mate competition, a situation that may have implications for the sexual selection potential that have not yet been fully explored. Finally, we note that there is no reason to assume that different taxa and lineages, even within the same radiation, should follow the same pathway to or share a unifying evolutionary explanation for “monogamy”. The study of the evolution of pair-living, sexual monogamy, and genetic monogamy remains a challenging and exciting area of research.

Keywords: monogamy, paternal care, aotus, callicebus, pithecia, primates, pair bonding, pair-living

1. INTRODUCTION

For decades, behavioral ecologists, evolutionary biologists, and anthropologists have been fascinated by the existence of “monogamy” in the animal kingdom. Thus, a large literature exists exploring the factors underlying its evolution and maintenance (Kleiman, 1977; Trumbo and Eggert, 1994; Kappeler and van Schaik, 2002; Brotherton and Komers, 2003; Møller, 2003; Reichard, 2003a; Kokko and Morrell, 2005; Lukas and Clutton-Brock, 2013; Opie et al., 2013a; Díaz-Muñoz and Bales, 2016; Tecot et al., 2016; French et al., 2018; Klug, 2018; Macdonald et al., 2019). In many animal taxa, the amount of time and energy invested in offspring is conspicuously sex-biased, with females often investing more in each reproductive opportunity than males. This is especially true among mammals, where internal fertilization, gestation, and lactation, almost *de facto*, demand greater investment by females. Under these circumstances, it is often assumed that males might improve their fitness by increasing their number of mates, whereas female fitness is presumed to be tied less directly to the number of partners they mate with and more directly to access to the resources needed to sustain pregnancy and early infant development (Bateman, 1948; Trivers, 1972; Clutton-Brock, 2007; Clutton-Brock and Huchard, 2013). As a result, “monogamy” (or more specifically, “monogyny,” where an individual male’s mating or breeding is restricted, over some time, to a single female) is seen as a paradox in need of explanation (Klug, 2018). Thus, the question is often reduced to when and why males should “settle” for defending access to and mating with only one female when, all else being equal, their reproductive output could be improved by pursuing polygynous mating. Less often discussed, though equally important, is to consider the female perspective; under what conditions is it in a female’s reproductive interest to pursue “monandry” instead of “polyandry?” These observations have motivated a number of comparative analyses (Komers and Brotherton, 1997; Brotherton and Komers, 2003; van Schaik and Kappeler, 2003; Cohas and Allainé, 2009; Shultz et al., 2011; Lukas and Clutton-Brock, 2013; Opie et al., 2013a; Huck et al., 2014); the results have generated no small amount of controversy (e.g., de Waal and Gavrilets, 2013; Dixon, 2013; Lukas and Clutton-Brock, 2014).

In this review, we provide an overview of research on the expression and evolution of “monogamy” in mammals in general and primates in particular, and we highlight a number of problems that complicate comparative attempts to understand this issue. We focus on non-human primates, the set of mammals we know best, but refer to other taxa where relevant. We start with a brief, but necessary, discourse about the muddled terminology used and the problems that arise from not paying enough attention to defining terms precisely (section 2.1) (Reichard, 2003a, 2017; Tecot et al., 2016), and we suggest a set of preferred terms which we then use throughout the rest of the manuscript (section 2.2). We follow with a short review of the major hypotheses that have been put forward (section 3) (see also Klug, 2018; Macdonald et al., 2019). Together, sections 2 and 3 provide the needed backdrop for section 4.

In section 4, we critically evaluate several recent comparative studies that have focused on investigating some of the proposed explanations for “monogamy”. We first summarize the general conclusions of these studies, concentrating on two that have arguably received the most attention (section 4.1). We then consider how well the data we have collected over the course of our own 25+ years of collective fieldwork on four different “monogamous” primates support (or not!) the assumptions made and the conclusions reached (section 4.2). Because of the multiple concerns we raise with these studies, we close the section with a set of guiding principles that, we argue, should be adhered to in comparative studies of animal social systems (section 4.3). The last of those principles calls for considering the behavioral and evolutionary implications of particular components of a taxon’s social system from the perspectives of all involved participants, not just certain classes of individuals. We devote section 5 to discussing these individual perspectives in detail. We highlight the need to consider how the interests of non-reproductive group members and “floater” animals (i.e., individuals who range unassociated with other reproductively mature individuals) change the range of theoretical evolutionary scenarios. We conclude with a few suggestions for future research directions (section 6) formulated in light of the critiques of recent comparative studies we raise and the questions that arise from explicitly considering the perspectives of all classes of individuals.

2. TERMINOLOGY MATTERS, ESPECIALLY FOR COMPARATIVE ANALYSES!

2.1. Why the Words We Use Matter

Nearly all reviews of the evolution of “monogamy” in mammals state, in one way or another, that while ~90% of bird species are classified as “monogamous” (usually citing Lack, 1968), less than 10% of mammalian species are (usually citing Kleiman, 1977). These reviews almost uniformly point out that “monogamy” is relatively more common among primates than among other mammals (e.g., 30 vs. 5% of species: Lukas and Clutton-Brock, 2013; Opie et al., 2013a). We contend that statements like these—offered at the beginning of review papers as foundational ideas upon which subsequent analyses are developed—are fundamentally problematic because comparative analyses are in danger of “comparing apples with oranges” if they do not pay careful attention to terminology (Dixon, 2013). Precise definitions matter because researchers frequently use similar terms to refer to different social situations (Table 1). This is partly related to different usage conventions for researchers working with different groups of organisms. For example, because the majority of avian taxa are pair-living, birds are often classified in broad-scale comparative analyses as “socially monogamous,” even though it has long been recognized that true “genetic monogamy” occurs in only 14% of passerine birds (Griffith et al., 2002). By contrast, many of the mammalian taxa that are classified as “socially monogamous” in reviews and comparative analyses (e.g., Lukas and Clutton-Brock, 2013; Opie et al., 2013a; Lambert et al., 2018; Macdonald et al., 2019) are decidedly not pair-living; in fact, they often live in groups containing more than

TABLE 1 | Some definitions of “monogamy” and “social monogamy” used in prior studies and reviews of primates and other animals.

Terms	Definition	References	
Monogamy	“...exclusivity in mating, i.e., a given male and female will mate only with each other.” Additionally, generally recognized as involving (1) persistent close proximity of an adult heterosexual pair both during and outside periods of reproduction, (2) mating preferences, and (3) an absence of adult unrelated conspecifics from the pair's home range.	Kleiman, 1977	Describes a mix of aspects of social organization, social structure, and the social mating system.
	A prolonged association and essentially exclusive mating relationship between one male and one female. Occasional covert matings outside the pairbond do not negate the existence of monogamy.	Wittenberger and Tilson, 1980	Describes primarily the social mating system.
	Males mate with the same female in several reproductive attempts.	Clutton-Brock, 1989	Describes the social mating system, but this definition would also apply to a polyandrous system.
	Close social association (bonding) between the members of a male-female pair.	van Schaik and Dunbar, 1990	Describes a mix of aspects of social organization and social structure.
	A social bond implying mating exclusivity.	Komers and Brotherton, 1997	Describes a mix of aspects of social structure and the social mating system.
	A pattern wherein individual females and males mate exclusively with one other partner over successive mating periods.	Fuentes, 1998	Describes primarily the social mating system.
	A single male and a single female form an exclusive association and cooperate in breeding activity.	Bull, 2000	Describes a mix of aspects of social organization, the social and genetic mating system, and the care system.
	A male mates for several breeding seasons with the same female and vice versa.	Müller and Thalmann, 2000	Describes primarily the social mating system.
	A unique social relationship between one adult female and one adult male for the purpose of reproduction.	Møller, 2003	Describes a mix of aspects of social structure and the social mating system.
	The term monogamy... can refer <i>only</i> to mating systems in which each sex has a single mate for life.	Shuster and Wade, 2003	Refers to a mating system, but under very restrictive conditions.
Social Monogamy	Individuals mate with only one partner over one or several reproductive cycles.	Hilgartner et al., 2012	Describes primarily the social mating system.
	Males and females are physically close for an extended period or share space or resources with each other.	Bull, 2000	Describes primarily social organization.
	A single adult male and female share a common “living arrangement” (e.g., share use of a territory, show behavior indicative of a social pair). Does not imply any particular pattern of interactions or reproduction.	Reichard, 2003a, 2017	Describes a mix of aspects of social organization and social structure. The mating system is explicitly not included.
	An exclusive association between a breeding male and a breeding female during the breeding season where mating is observed exclusively between these two individuals.	Cohas and Allainé, 2009	Describes a mix of aspects of social organization and the mating system.
	A single breeding female and a single breeding male share a common range or territory and associate with each other for more than one breeding season, with or without non-breeding offspring.	Lukas and Clutton-Brock, 2013	Describes the social mating system, although the definition is open to misinterpretation if not read carefully.
	A synonym for pair-living.	Opie et al., 2014	Describes the social organization, although in the supplementary table for this publication, the term is being used, inappropriately, as a character state to describe the “Mating System”.
	An adult individual has only one social adult partner of the opposite sex at a given time.	Huck et al., 2014; Fernandez-Duque, 2016	Describes primarily social organization.
	Breeding adults living in pairs.	Clutton-Brock, 2016	Describes a mix of aspects of social organization and the social and genetic mating system.
	Characterized by a number of important features, including spatial and temporal proximity of a single male–female pair, exclusion of unfamiliar adult individuals from the home range, co-rearing of offspring, and the existence of a strong social attachment (pair bond) between the adult male and female.	French et al., 2018	Describes a mix of aspects of social organization, social structure, and the care system.
	All pair-living mammals as well as group-living mammals that have a dominant breeding pair.	Lambert et al., 2018	Describes a mix of aspects of social organization and the mating system.

one reproductive age individual of one or both sexes (e.g., African wild dogs, *Lycaon pictus*; meerkats *Suricata suricatta*; marmosets, genera *Callithrix* and *Mico*; tamarins, genera *Saguinus* and *Leontocebus*). At the same time, given that they show relatively high rates of reproductive monopolization, their mating system is nonetheless called “monogamous” (Lukas and Clutton-Brock, 2013). Classifying both of these situations as “social monogamy” in a comparative study is problematic because the terms are being used differently for birds and mammals—apples and oranges! Additionally, in some other taxonomic groups (e.g., certain non-social insects), the term “monogamy” is used as a shorthand that applies to only the female’s mating perspective to mean sexual monandry, without specifying whether males also mate with a single female (sexual monogyny) or several ones (sexual polygyny) (Bybee et al., 2005; Ivy and Sakaluk, 2005).

As we have surely telegraphed by bracketing the word with quotation marks, it is our opinion that much of the confusion and frustration surrounding comparative analyses of “monogamy” is engendered by loose phrasing, a lack of precision and consistency across studies about the phenomena being described or explained (Carter and Perkeybile, 2018), and folk conceptions about what the term implies. Definitions must be made explicit, and primary data should be reviewed, clarified, and cast into consistent terms before they are used (e.g., Borries et al., 2014; Valomy et al., 2015; see also Schradin, 2017). Most obviously, and as others have also noted, uncritical compilations of comparative data risk conflating different ideas about the term “monogamy”. For birds (and often primates), the term is typically used to describe a particular social living situation where there is only one adult of each sex in a group, while mammalogists more commonly use the term to refer to either a mating pattern where a single male and female each have one another as their sole sexual partner, or a breeding pattern, where a single female and male exclusively produce offspring with each other (Tecot et al., 2016; Klug, 2018; Lambert et al., 2018).

The implication of mating or breeding “exclusivity” comes with its own fuzziness. What does it mean for a mating relationship to be exclusive? If an adult mates 90% of the time with one particular opposite-sex individual, is that relationship exclusive? What about 80%? What if a female mates 100% of the time with one male when she is in her periovulatory period, but mates with others outside of that period? What about the converse, where she mates 100% of the time with one male outside of the time when she is most likely to conceive, but has a different partner (or more than one) during the narrow window around ovulation? It is likewise unclear what time frame researchers consider important for operationalizing mating “exclusivity”. Is it over one reproductive event, or several? If litter or clutch size is large, or if the taxon under consideration reproduces only once or a small number of times in a lifetime, then researchers might be willing to classify such a taxon as “monogamous” if females are not seen to mate with more than one male during such single conceptive period or if all offspring are sired by the same male. However, that may be an unsatisfying definition for researchers studying taxa like primates that are long-lived, typically give birth to singleton offspring,

and have male-female associations that persist over multiple reproductive events.

Folk conceptions of “monogamy” also often presume that a suite of other behavioral traits tends to co-occur with an exclusive mating relationship, including co-ranging and coordination of activity by a male-female pair, some form of bonding between pair-mates, joint range defense, same-sex intolerance, and cooperative offspring care. While some researchers have conscientiously (and appropriately!) acknowledged that these traits are not necessarily all seen in all taxa that are considered “monogamous” (Wickler and Seibt, 1983; Fuentes, 1998, 2002; Tecot et al., 2016; French et al., 2018), the folk conception persists, as exemplified in the Wikipedia entry on “Monogamy in Animals”, which states that, “Monogamous pairing in animals refers to the natural history of mating systems in which species pair bond to raise offspring. This is associated, usually implicitly, with sexual monogamy” (Wikipedia, 2019).

Finally, even when we recognize that certain comparative studies (e.g., Lukas and Clutton-Brock, 2013) may be concerned primarily with the sexual or genetic mating system and others (e.g., Opie et al., 2013a) with the particular grouping pattern of pair-living, the confusing terminology is problematic, and even circular, for other analyses. For example, some studies aim to compare the degree of extra-pair paternity (EPP) in group-living “monogamous” and “non-monogamous” species (Cohas and Allainé, 2009; Lambert et al., 2018). But if “monogamy” is defined by the degree of paternity monopolization, then EPPs are, by definition, low and should therefore not be used in an analysis that tries to establish whether monogamous or non-monogamous taxa have higher rates of EPPs! One study that explicitly looked at rates of extra-group paternity in pair-living taxa found that genetic studies on pair-living mammals are still astonishingly rare, and only five of the 15 species for which data were available at the time of the study indeed showed no evidence of EPPs (Huck et al., 2014). Moreover, for most of these taxa, data on rates of extra-pair mating (which requires observation, not simply analysis of parentage) are scant or unavailable, so the extent to which, in any of these taxa, mating is restricted to within a pair is unknown.

To summarize, most researchers are likely aware that there are various definitions of “monogamy” and that—depending on the taxa being studied—a veritable menu of different behavioral traits may be considered as part of the definition. The problem is that the terms “pair-living”, “pair-bonded”, “social monogamy”, and “monogamy” are nonetheless seldom distinguished properly, even in the scientific literature, and are often used interchangeably. In no way are we ourselves exempt from being guilty of using this terminological shorthand in less than a consistent manner (e.g., Di Fiore et al., 2007; Fernandez-Duque et al., 2008; Huck et al., 2014; Fernandez-Duque, 2016).

2.2. Proposed Terminology

There have been several productive attempts to clearly define relevant terms (Wickler and Seibt, 1983; Tecot et al., 2016; Reichard, 2017; French et al., 2018; **Table 1**). Below, we follow the lead of Kappeler and van Schaik (2002) who provide some standard terminology that has influenced discussions

about primate social systems. Under their framework, the social organization (i.e., who lives with whom) of pair-living refers to situations where a single adult male and a single adult female form a two-adult group without the additional presence of other adults (Table 2). To avoid confusion, we concur that this social organization should be referred to as “pair-living” and should not be called “social monogamy”, as is often done in bird and some mammal studies. That is, the word monogamy should only be used in reference to animals’ mating and reproductive behavior, not simply their grouping pattern. Kappeler and van Schaik (2002) also make a distinction between the “social mating system” (who mates with whom), which relates to individual behavior and behavioral choices, and the “genetic mating system” (who has offspring with whom), which relates to realized reproduction. Thus, if one male and one female have an exclusive mating relationship (irrespective of the grouping pattern, or social organization), then the social mating system is monogamous. Some researchers (e.g., Reichard, 2003a, 2017; French et al., 2018) have referred to this situation as sexual monogamy, and we encourage the use of this accurate and useful term for describing such a social mating system (Table 2). As alluded to above, what is considered “exclusive”, as well as the critical time frame over which to consider “exclusivity” still needs to be defined and may depend on the taxon of interest. If a single male and a single female have offspring exclusively with each other (irrespective of whether one or both mate with other individuals, whether they associate in the same social group, whether they belong to different social groups, or whether one or both range solitarily), then the genetic mating system can be considered monogamous and the term genetic monogamy is appropriate. If a species is sexually monogamous it will, necessarily, also be genetically monogamous (because if a female mates with only one male, and the male mates with only one female, there can be no extra-pair offspring), although the reverse is not necessarily true. As for sexual monogamy, the time frame, over which genetic monogamy is determined needs to be considered carefully, depending on the mean litter size and

the lifetime number of reproductive events per individual for each species.

An additional layer of complexity relates to the degree of spatiotemporal association between male and female pair partners, an aspect of their social organization. Most pair-living mammals share a territory, spend a large proportion of their time together and have an affiliative relationship that, when properly characterized by behavioral, emotional, and endocrinological characteristics (Hinde et al., 2016; Maninger et al., 2017; Carter and Perkeybile, 2018), can be defined as a pair-bond. In contrast, in some species pair-mates do not manifest such close connections, and these dyads are sometimes referred to as “dispersed pairs” in contrast to “associated pairs” (e.g., fork-marked lemurs, *Phaner furcifer*: Schülke and Kappeler, 2003).

Species like fork-marked lemurs are perceived as odd, because, as mentioned above, folk conceptions about “monogamy”—and much of the usage of the term in the scientific literature— additionally incorporate ideas and concepts about the nature of the social relationship between pair-mates (e.g., the presence of “pair bonds”) and about the level of offspring care provided by each of the pair-partners (e.g., “biparental care”) or by older siblings or additional reproductive age adults (e.g., “cooperative breeding”). But, clearly, there can be pair-living animals that are not “pair-bonded” (e.g., fork-marked lemurs: Schülke and Kappeler, 2003), males and females can be sexually monogamous without both sexes contributing to offspring care (e.g., Kirk’s dik-dik, *Madoqua kirkii*: Brotherton et al., 1997), and males can contribute substantially to offspring care even when the mating system is sexually polygynous or polyandrous (e.g., mustached tamarins, *Saguinus mystax*: Huck et al., 2005), to name just a few situations that would require careful consideration of definitions. Thus, for comparative studies of pair-living, sexual, or genetic monogamy, it is critical for researchers to also characterize the social relationship between pair-mates, which is an element of a species’ social structure (Kappeler and van Schaik, 2002), and to document the level of care or investment provided by each pair-mate and by other non-reproductive adults, which are

TABLE 2 | Preferred terms that describe different components commonly associated with “monogamy”.

Pair-Living	A social situation in which two adults of the opposite sex live together within a home range (possibly with their non-reproductive offspring) and associate continuously or intermittently.	Describes a taxon’s social organization
Sexual Monogamy	An exclusive mating relationship between a single female and a single male, based on observations of sexual interactions during at least one reproductive season.	Describes a taxon’s social mating system
Genetic Monogamy	A female and a male reproduce exclusively with one another over a set of multiple births, i.e., over at least one reproductive season for species that producing two or more offspring per litter, and over more than one consecutive reproductive season for species with singleton births.	Describes a taxon’s genetic mating system
Pair-Bonding	A female-male pair manifest an emotional attachment as evidenced by their affiliative interactions, maintenance of spatial proximity, physiological distress upon separation from the pair-mate, and reduced anxiety following reunion with the pair-mate.	Describes aspects of a taxon’s social structure
Biparental Care	Both members of a putative sire-dam pair regularly perform behaviors with presumed positive effects on infant development, growth, well-being, and/or survival.	Describes aspects of a taxon’s care system
Cooperative Offspring Care	Other individuals, in addition to one or both of the putative parents, regularly perform behaviors with presumed positive effects on infant development, growth, well-being, and/or survival. These “helpers” can, but do not have to be related to the infant or to the breeders.	Describes aspects of a taxon’s care system

These components do not always occur together and need to be considered individually.

elements of the species’ care system (Kappeler et al., 2019). In the remaining sections of this review, we try to translate, as needed, the terminology used in the various studies we discuss so that it conforms to the definitions provided in **Table 2**. However, in some cases we deliberately continue using, in quotation marks, the fuzzy terms “monogamy” and “social monogamy” to highlight both that these were terms the authors originally used and the associated ambiguity about their precise meaning.

Our renewed call for clear terminology notwithstanding, we should remain aware that characterizing any of these components for a given taxon often involves assigning one of a set of discrete categories to traits that fall on a continuous dimension. For example, there were no EPPs detected in 35 young of Azara’s owl monkeys (*Aotus azarae*: Huck et al., 2014), extra-pair copulations (EPCs) resulted in 4% of the young of Malagasy giant jumping rats (*Hypogeomys antimena*: Sommer, 2003), and 7 and 23% of meerkat pups were born by a subordinate female and subordinate male, respectively (Griffin et al., 2003). While it may be straightforward to decide, on the basis of these results, to classify owl monkeys as genetically monogamous, decisions for the other species will be more arbitrary. Should jumping rats also be classified as genetically monogamous, despite the occasional offspring from EPCs? What about meerkats, where <80% of offspring are progeny of the main breeding pair? Ideally, if paternity data were available for more species, the proportion of EPPs would be used as a continuous variable in analyses. Still, given the paucity of data (Huck et al., 2014; Lambert et al., 2018), it may not be feasible to assign continuous values to this trait, and some authors have even argued that it might be preferable to use distinct categories for social systems (Rubenstein et al., 2016), although we disagree with that position for reasons akin to those discussed in the section 4.2. In any case, authors must make explicit the definitions and criteria they use for assigning a taxon to one category or another, with explicit reference to the primary literature where the original data were published (Borries et al., 2016). In species where there is a clear modal pattern, it might be acceptable to use the modal social organization or mating system, but for some taxa the range of variation may be so large that it warrants clearly classifying them as “variable” or polymorphic.

Among primates, the marmosets and tamarins (subfamily Callitrichinae) offer an excellent example to illustrate the problems that follow from inadequate consideration of terminology. These small Neotropical primates, particularly the tamarins (*Saguinus*, *Leontocebus*) and lion tamarins (*Leontopithecus*), have variable social organizations and mating systems. Most of the species in these genera are not pair-living, but rather live in groups that can contain up to four adults of each sex. The variation includes the remarkably uncommon mating pattern among mammals of polyandry, where a single female (even when there are other females in the group) mates with all adult males in the group who are not related to her (Heymann, 2000; Garber et al., 2016). It sometimes happens that one of the males gets the major share of paternity, even over consecutive years (Huck et al., 2005). This means that, while the social mating system is clearly sexually polyandrous, there might still be a tendency, in some groups, toward high male reproductive skew that approaches genetic monogamy. Researchers working with

wild populations of marmosets and tamarins have repeatedly stated that they should not be considered “monogamous” (Savage et al., 1996; Heymann, 2000; Díaz-Muñoz, 2011; Garber et al., 2016), and yet in recent comparative analyses, they are either expressly classified or casually referred to as such (Lukas and Clutton-Brock, 2013; Opie et al., 2013a; Lambert et al., 2018).

In a nutshell, we have argued and illustrated with a few examples that using unclear terminology can lead to ambiguity in the data upon which comparative analyses rest, which in turn can make us question the results or validity of these analyses. Furthermore, specific proposed evolutionary drivers that might be relevant for the evolution of certain aspects of social organization may not be relevant for understanding the evolution of the mating system; predictions or conclusions might differ when these components of the social system are considered separately. Tecot et al. (2016) developed specific, separate predictions for the evolution of pair-living, sexual monogamy, and pair-bonding derived from the major hypotheses for “monogamy” reviewed below; the authors pointed out that not all of these hypotheses are relevant for explaining each of these aspects of the social system. These concerns are particularly true for comparative studies that use large datasets for phylogenetic or meta-analyses, where data from many different studies by many different authors are integrated.

3. OVERVIEW OF HYPOTHESES FOR THE EVOLUTION OF “MONOGAMY”

There are seven drivers historically and regularly considered in discussions about the evolution of either pair-living or sexual monogamy (see also Tecot et al., 2016; Klug, 2018; Fernandez-Duque et al., in review) (1) The ‘infant care’ hypothesis states that the need for biparental, or communal, care of costly offspring is presumed to force males to stay with a single mate and her offspring (Kleiman, 1977; Huck and Fernandez-Duque, 2013; Rogers et al., 2018; Schacht et al., 2018; Macdonald et al., 2019). This hypothesis assumes that male care is required for the successful raising of offspring. Selective pressures encourage solitary individuals to associate with the mating partner for the period of infant raising. Once bi-parental care is established, the hypothesis also proposes pressures for sexual monogamy, if the costs of parenting are high (Tecot et al., 2016). (2) The ‘female dispersion’ hypothesis states that female scarcity, where females also do not aggregate with one another, leads to an inability of males to monopolize spatial access to more than one female (Emlen and Oring, 1977; Shuster and Wade, 2003; Schacht and Bell, 2016). Under this hypothesis, it is assumed that resources that females rely on are scarce, low quality, or highly dispersed, such that a male would not be able to defend the range of more than one female. Note that this hypothesis relates to the social organization rather than the sexual mating system or pair-bonding. (3) The ‘mate guarding’ hypothesis states that the benefits to males of guarding one female to obtain exclusive mating access outweigh the benefits of seeking additional matings with other females (Emlen and Oring, 1977; Komers and Brotherton, 1997; Fernandez-Duque, 2016).

While this hypothesis appears similar to the ‘female dispersion’ hypothesis, it predicts that males will not attempt to mate with more females, even if they are able to cover more than one home-range. It also predicts that, within a population, females will show some reproductive synchronicity, or seasonality, that limit males’ opportunities for extra-pair matings, and that both males and females will show sex-specific aggression toward same-sex intruders and that such aggression will be more pronounced in the breeding season. In contrast to the ‘female dispersion’ hypothesis, the ‘mate guarding’ hypothesis relates to both the social organization and the sexual mating system (see “Mate defense” hypothesis of Tecot et al., 2016). (4) The ‘infanticide prevention’ hypothesis (van Schaik and Kappeler, 2003) states that the pressure for females to associate with a male who can protect her, and her offspring, from aggressive and potentially infanticidal conspecifics, leads to the formation of groups consisting of male-female pairs and to sexual monogamy. The hypothesis assumes that females losing their offspring become receptive sooner than if they continue nursing current offspring. It also assumes that a female’s partner is the likely sire of her offspring and that the presence of a male increases both his and the female’s reproductive success by reducing the success rate of potentially infanticidal intruders. While this hypothesis proposes a selective pressure acting on the social organization, the degree of pair-bonding and the sexual mating system (Tecot et al., 2016), it more strongly relates to pair-living than to sexual monogamy in otherwise group-living species, since one of the assumed counter-strategies of females against infanticide is to mate with multiple males (e.g., Chakrabarti and Jhala, 2019). (5) The ‘predation prevention’ hypothesis states that the pressure of predation leads to a male associating with a single female if their joint permanent presence helps to protect their offspring from predators. The hypothesis assumes that males (or male-female pairs) can deter predators more effectively than females can on their own. This hypothesis is related to the social organization; it does not explain pressures on the sexual mating system. (6) The ‘resource defense’ hypothesis states that pair-living has a selective advantage due to the combined defense of resources year-round. If resources are of low quality, or sparsely distributed, this will generate intra-specific competition that leads to a situation where an area cannot support larger groups. This hypothesis states that resource defense is directed by both males and females against intruders of both sexes, unless males, and females differ greatly in their requirements of specific resources. Under this scenario, pair-bonding is favored because it enhances coordinated territory defense (Rutberg, 1983; Tecot et al., 2016). This hypothesis does not address the social mating system (i.e., the issue of sexual monogamy). (7) Lastly, according to the ‘optimal group size’ hypothesis, pair-living is favored if the costs and benefits of group living in general [not just for defending resources, as in Hypothesis (6)] lead to an optimal group size of only two adults (plus a few offspring). The hypothesis does not presume a link between pair-living and sexual monogamy, because it only refers to the social organization, nor does it presume that two adult group members will be pair-bonded (Tecot et al., 2016). The hypothesis does suggest that changes in predation pressure or resource availability may shift the social organization

toward, or away from, an optimal adult group size of two animals. In certain taxa, or under certain conditions, some of these hypotheses (e.g., the ‘mate guarding’ hypothesis) might be sex-reversed. For example, if males are a scarce resource for parental care, females may benefit by guarding a single male from other females.

4. COMPARATIVE ANALYSES OF THE EVOLUTION OF “MONOGAMY”

4.1. Overview of Recent Work

Over the past few decades, a number of influential studies have investigated one or more of the hypotheses outlined above using broad, comparative data, either for mammals or for particular mammalian groups. For example, two early comparative studies of ungulate mating systems concluded that female dispersion, *per se*, does not provide a general explanation for the evolution of “monogamy” in mammals (Komers and Brotherton, 1997; Brotherton and Komers, 2003). Rather, the authors concluded that it is the necessity and feasibility of guarding independently ranging females (whose home ranges might nonetheless overlap) that promote its evolution. They also proposed that paternal care has more likely evolved as a consequence of a “monogamous” mating system, and not as its cause.

Another early comparative study of the evolution of “monogamy” focused on primates and used parsimony-based phylogenetic comparative methods to reconstruct the ancestral states from which the social organization of pair-living may have arisen (van Schaik and Kappeler, 2003; see also Kappeler, 2014). The authors suggested that it is important to distinguish two different types of pair-living in primates: “associated” pairs (where pair partners show coordinated activity and spend substantial amounts of time in spatial proximity to one another) and “dispersed pairs” (where pair partners share a home-range, but show little coordination of their activity and do not regularly rest together). Based on presumed phylogenetic relationships and the distribution of behavioral patterns across extant taxa, the study concluded that these two types of pair-living arose from different ancestral social organizations, with associated pairs evolving from ancestors where females lived in mixed-sex groups, and dispersed pairs (which are seen only among strepsirrhine primates) arising from ancestors where females maintained solitary ranges. Thus, for example, pair-living in (almost) genetically monogamous indris (*Indri indri*; Bonadonna et al., 2019) is proposed to have evolved from a social organization such as that exhibited by ring-tailed lemurs (*Lemur catta*) or Verreaux’s sifakas (*Propithecus verreauxi*), while co-sleeping in fat-tailed dwarf-lemurs (*Cheirogaleus medius*) would have evolved from a solitary social organization, such as that exhibited by mouse lemur (*Microcebus*; Kappeler, 2014). In a more recent study, Shultz et al. (2011) compared four competing models for the evolution of social organization across all primates and concluded that pair-living in all primates—including in those strepsirrhines living in dispersed pairs—evolved from ancestors living in multimale-multifemale social groups rather than from ancestral taxa where females were solitary.

More recently, two ambitious analyses have explored the evolutionary history of “monogamy” among mammals in general (Lukas and Clutton-Brock, 2013) and among primates in particular (Opie et al., 2013a), using comparative phylogenetic methods (Lukas and Clutton-Brock, 2013; Opie et al., 2013a). In the following, we focus mainly on these two studies because they are highly cited, reached somewhat contrasting conclusions, and refer explicitly, for some aspects of the analyses, to primates, the group of mammals on which our own work is based. Both studies analyzed the correlated evolution between “social monogamy” (as both research groups referred to it) and some of its candidate drivers (e.g., the need for male care, female grouping and ranging patterns, and the risk of infanticide). The data used for each of these studies were extracted, primarily, from previously published reviews or encyclopedias, supplemented with additional information compiled by the authors from primary sources, as explained in the supplementary materials. Lukas and Clutton-Brock (2013) classified ~2,545 mammalian species “for which information was available” as either solitary, “socially monogamous”, or group-living, and as showing male care or not. Importantly, their category of “socially monogamous” included many taxa that are pair-living, as well as several taxa that are group-living, but where breeding is largely or exclusively restricted to a single male-female pair. Thus, their study was concerned with the evolution of sexual monogamy rather than the social organization. They likewise compiled data on several ecological and life history variables (e.g., gestation and lactation length, home-range size and overlap) for each taxon. Opie et al. (2013a) compiled a similar dataset on ~230 primate species, scoring each species’ mating system as “polygynous”, “polyandrous”, “monogamous”, or some combination thereof. However, despite using these terms that describe mating patterns in their supplementary table, the definition of “monogamy” that Opie et al. (2013a) used in their text (**Table 1**) suggests that they are referring to the social organization of pair-living rather than to the mating system of sexual monogamy. They also characterized, for each species, whether male care is present or absent and whether female ranges are discrete or overlapping, and they calculated an index of theoretical “infanticide risk” based on how quickly a female who loses an infant may be expected to return to breeding. Both studies then used phylogenetically explicit comparative methods to reconstruct inferred trait conditions at ancestral nodes in the phylogeny and examined whether and how transitions to “social monogamy” (i.e., pair-living in the case of Opie et al., 2013a, and sexual monogamy in Lukas and Clutton-Brock, 2013) were associated with particular female grouping patterns, with patterns of male care, and with changes in infanticide risk.

These two analyses show some consensus with respect to the timing of the evolution of the character state of “social monogamy” in relation to the character state of male care. Transitions to pair-living (in the study by Opie et al., 2013a) and sexual monogamy (in the study by Lukas and Clutton-Brock, 2013), typically preceded or co-occurred with, rather than followed, an increase in male involvement in infant care. Once intense male care evolved, the likelihood of lower rates of extra-pair paternity increased, potentially leading to more

strict genetic monogamy. This evolutionary sequence may then contribute to the persistence of sexual monogamy once it arises (Lukas and Clutton-Brock, 2013). The two studies, however, reached rather different conclusions with regard to the ultimate causes of the evolution of “monogamy”. Lukas and Clutton-Brock (2013) concluded that “social monogamy” (i.e., sexual monogamy) evolves most commonly when females are solitary and when males are unable to defend reproductive access to more than one female. They additionally concluded that the evolution of sexual monogamy does not seem to be associated with a high risk of infanticide by males. Opie et al. (2013a), by contrast, claim that “social monogamy” (i.e., pair-living), at least among primates, evolved in response to increased infanticide risk; indeed, they emphasize that position in the title of their article: “Male infanticide leads to social monogamy in primates.”

4.2. Methodological Considerations in Comparative Analyses

While the studies reviewed above have indeed contributed to a broader discussion of mating system variation in mammals and have been both influential and widely cited, many of them suffer from some of the concerns that we are raising here, including the problem of terminology discussed in section 2, as well as others we highlight below. For example, the definition of “monogamy” used by Komers and Brotherton (1997) and Brotherton and Komers (2003) is not clear; the illustrations that accompany the analyses seem to point to pair-living, but the species included in their analyses are often group-living, raising the possibility that the authors actually refer to sexual monogamy instead (**Table 1**). Likewise, the studies by Lukas and Clutton-Brock (2013) and Opie et al. (2013a) utilized rather different definitions for “social monogamy” (**Table 1**), which complicates direct comparison of their results. Additionally, all studies have relied heavily on data compiled from the secondary literature and from review articles, which raises concerns about both data quality and comparability. Not surprisingly, there has been controversy and critique by other researchers who have questioned some of the conclusions and methods of analysis used in these studies (e.g., de Waal and Gavrilets, 2013; Dixon, 2013; Opie et al., 2013b, 2014; Lukas and Clutton-Brock, 2014).

We would like to stress that we are fervent supporters of using comparative phylogenetic analyses for examining social system evolution, one of us having published one of the first such studies on primates (Di Fiore and Rendall, 1994). But we are skeptical about the value of some published conclusions about the evolution and maintenance of “monogamy”, given our concerns about the process by which the data have been compiled, analyzed, and findings interpreted. We are not alone in trying to highlight the fact that comparative analyses are only as good as the data and measurements they are based upon (Gittleman, 1989; Smith and Jungers, 1997; Houle et al., 2011; Patterson et al., 2014; Sandel et al., 2016).

As field biologists who work with a suite of taxa that are characterized as “monogamous” in many of these analyses, we are of course intimately interested in the questions being considered. Thus, below we illustrate some of the problems with data used

in comparative studies specifically for the four taxa of platyrrhine primates (monkeys from South and Central America) on which we have worked and published extensively (e.g., Huck et al., 2004a,b, 2007; Carrillo-Bilbao et al., 2005; Di Fiore et al., 2007; Fernandez-Duque et al., 2008, 2013; Fernandez-Duque, 2016; Spence-Aizenberg et al., 2016; Van Belle et al., 2016, 2018). The four taxa we refer to are owl monkeys (genus *Aotus*), western and southwestern Amazonian titi monkeys (genus *Plecturocebus*), tamarins (genera *Leontocebus* and *Saguinus*), and saki monkeys (genus *Pithecia*). All are usually classified as “monogamous” and three of them (owl monkeys, titi monkeys, and tamarins) as showing male care. We focus here on the studies by Opie et al. (2013a) and Lukas and Clutton-Brock (2013), not because we think the problems are exclusive to them, but because the central questions being examined are the ones on which we have worked for decades and for which we know data the best. Similar concerns have been raised about a host of other broad-scale comparative analyses, whether they focus on behavioral, ecological, or morphological traits (e.g., Patterson et al., 2014; Rubenstein et al., 2016; Sandel et al., 2016; Powell et al., 2017; Schradin, 2017; Tanaka et al., 2018), with some interesting follow ups as well (Lukas and Clutton-Brock, 2017; Dey et al., 2019). A more complete analysis of our data in view of recent evaluations of the factors driving the evolution of pair-living, sexual monogamy and biparental care is provided elsewhere (Fernandez-Duque et al., in review).

In addition to issues of terminology, comparative studies have been hampered by an over-reliance on secondary (and sometimes out-of-date) sources, as well as by serious questions about data quality and comparability. We tackle each of these inter-related concerns in turn below.

4.2.1. Concerns About Bibliographic Sources

Judging from the references provided, the raw data used in a number of influential comparative analyses are based heavily on review articles (some of which are 20–40 years old), on encyclopedic summaries, and, partly, on studies done in captivity (e.g., Jolly, 1966; Kleiman and Malcolm, 1981; Kinzey, 1997; Komers and Brotherton, 1997; Nowak, 1999; Shultz et al., 2011; Lukas and Clutton-Brock, 2013; Opie et al., 2013a). Based on our own review of the primary literature and of the references cited in these studies, we think the choice of many of these sources is questionable. We document the extent of the problem in more detail elsewhere (Fernandez-Duque et al., in review). There we present the results of a thorough review of cited references, where we find that more than two-thirds of the references used by Opie et al. (2013a) for classifying parental care for the four taxa of owl monkeys, titi monkeys, sakis, and tamarins—and all but two of the references used by Lukas and Clutton-Brock (2013)—do not support the category assigned for the trait. It is frequent, and unfortunate, that researchers trying to compile data for hundreds or thousands of species seem to rely on previous compilations instead of the primary literature that reports the original data. It is equally problematic if editors request that authors of order-wide analyses reduce the associated reference list, as Lukas and Clutton-Brock (2017) assert happened with their submission.

We acknowledge that checking the original data is time consuming; but, when time is limited, the solution should be to consider fewer taxa or take longer to publish, not to compromise the quality of the analyses (Borries et al., 2016; Schradin, 2017). Whether the inclusion of data of unknown quality is a problem that can influence the main conclusions will depend on the amount of dubious data, and how central those data are to the analysis (Symonds, 2002). When researchers have access to a comparative dataset where all of the data have been carefully vetted, it is then possible to explore the consequences of including or not certain data through simulation and permutation. Such sensitivity analyses should be standard for any comparative analysis.

4.2.2. Concerns About Data Quality and Comparability

Further problems associated with data quality and the lack of clarity in how candidate traits are classified are also apparent when we look at the examination of alternative hypotheses for the evolution of pair-living or sexual monogamy. The infanticide prevention hypothesis is among the most contentious ones (Brotherton and Komers, 2003; van Schaik and Kappeler, 2003; Lukas and Clutton-Brock, 2013; Opie et al., 2013a) and offers an illustrative example to unpack. The challenges begin with identifying a measure of acceptable internal validity (Smith, 2019), given the difficulty of operationalizing the “risk of infanticide”, followed by the limited data available on infanticide across the primate order outside of a handful of well-studied species (Dixon, 2013). Because infanticide itself is difficult to directly observe and quantify (van Schaik and Janson, 2000), several broad-scale comparative studies focused instead on quantifying “infanticide risk” and then explored how changes in mating systems may have coevolved with changes in that risk across primate phylogeny (van Schaik, 2000; Lukas and Clutton-Brock, 2013; Opie et al., 2013b). These studies use as a proxy for infanticide risk the ratio between the duration of lactational amenorrhea (i.e., the period from birth to the resumption of ovulatory cycles) and the combined duration of gestation and amenorrhea. The rationale for such a proxy is that when this ratio is high (i.e., lactation is long compared to the total period of maternal investment), infanticide offers higher potential benefits to males since they can substantially reduce females’ time to resumption of cycling. Since there are hardly ever adequate data to determine lactational amenorrhea, the length of the lactation period (or, rather, the age at weaning; McNeilly, 2006) is used instead. Opie et al. (2013a) operationalize infanticide risk as $L/(L+G)$ (where L = duration of lactation and G = gestation length). While “gestation length” is a trait that can be reliably defined and accurately measured (given that it is relatively inflexible), the “duration of lactation” is much more difficult to measure, as it is challenging to define the end of weaning (Borries et al., 2014). Therefore, it is not surprising that reported “weaning” ages vary widely between different studies. For example, Goeldi’s monkeys (*Callimico goeldii*) are reported to finish weaning at 112 days of age (Carroll, 1982), to begin weaning at 14–21 days of age but continue to suckle frequently up to 92 days (Jurke and Pryce, 1994), and to have a nursing

period that lasts ca. 60–70 days (Lorenz and Heinemann, 1967). When considering this species, Opie et al. (2013a) use a number that is 2 weeks shorter than the longest reported weaning age. For cotton-top tamarins (*Saguinus oedipus*), while Opie et al. (2013a) use a gestation period of 168 days, a different study suggests that gestation lasts 182–197 days (Ziegler et al., 1987).

Apart from these problems with accurately characterizing the lactation period, the validity of the $L/(L+G)$ proxy for infanticide risk is only informative for species that do not have a circumscribed birth season, have interbirth intervals (IBIs) longer than 1 year, or do not show rapid postpartum ovulation. Species with a circumscribed birth season, that give birth annually, or that can conceive again shortly after parturition, are unlikely to experience substantial risks of sexually selected infanticide, given the impossibility of speeding up female receptivity. Moreover, even if adequate data on gestation and lactation length were available for some taxa within the radiation of interest, it is unjustified to presume that data that are available for one species can be assigned to different species of the same genus or to different genera, however closely related. For example, gestation length for saddle-back tamarins, *Leontocebus fuscicollis* (mean female body mass = 358 g; Smith and Jungers, 1997) is 150 d (Heistermann and Hodges, 1995), while for cotton-top tamarins, *S. oedipus* (mean female body mass = 404 g; Smith and Jungers, 1997) it is much longer at 183 d (Oerke et al., 2003). Furthermore, it challenges extensive knowledge on the biology of reproduction to use data on weaning age from captive primates, who have consistent, predictable access to adequate food, for developing evolutionary scenarios in an ecological context. For example, weaning was completed at 19–21 months of age in wild white-headed langurs (*Trachypitecus leucocephalus*), while in captivity they are reported to be weaned when they are only 6 months of age (Zhao et al., 2008). We have presented elsewhere more detailed analyses of the problems associated with the misuse of gestation length and weaning age data on owl monkeys, titi monkeys and sakis for examining the infanticide prevention hypothesis (Fernandez-Duque et al., in review).

The data on seasonality used in tests of the ‘infanticide prevention’ hypothesis are likewise problematic. For example, Opie et al. (2013a) classify some owl monkey species (*A. lemurinus*, *A. nancymae*, *A. trivirgatus*) as aseasonal breeders based on reports from studies of captive populations, when field data, even if very limited, suggest that, in most owl monkey species, the majority of birth occur over only a limited number of months (Fernandez-Duque, 2011). When taxa are misclassified for a test of a crucial aspect of a hypothesis, conclusions ought to be considered tentative, even if the analysis itself may be statistically sophisticated and appropriate. We suggest that researchers should start abandoning the dichotomous classification of traits (e.g., seasonal vs. aseasonal) in favor of quantifications, such as the number of weeks or months when births are observed. Even when the quantification of traits might raise new considerations (e.g., how to treat outliers), we think it will improve the quality of the comparative analyses. This change will obviously require that fine-grained natural history data be available for more taxa.

The quality and comparability of the data used in comparative studies to test the ‘female dispersion’ and ‘mate guarding’

hypotheses are likewise concerning. Examining these hypotheses requires knowledge about the spatio-temporal distribution of females, including estimates of home range size and overlap. Compiling appropriate data on these traits is challenging; methods used to determine home ranges vary widely, and, by extension, estimates of the degree of home range overlap between groups and population densities vary as well. Additionally, often no distinction is made between territories (i.e., defended areas) and home ranges (i.e., the area used by an animal for its “normal” activities such as foraging, resting, mating or caring for young: Burt, 1943), but for consideration of some of the hypotheses discussed above, this distinction is quite relevant. The choice of home range estimator, or of overlap metrics, can also profoundly influence estimated sizes and degree of overlap (Fieberg and Kochanny, 2005; Getz et al., 2007; Huck et al., 2008). The problems surrounding appropriate and comparable estimation of home range sizes are not trivial, given that socioecological theory traditionally assumes that a primary driver determining the spatial distribution of females is the distribution of food resources needed to support survival and reproduction, while the main driver of males’ spatial distribution is the distribution of females (Emlen and Oring, 1977; van Schaik, 1989; Altmann, 1990; Mitani et al., 1996; Sterck et al., 1997; Schülke and Ostner, 2012).

The data on home-range sizes used in Lukas and Clutton-Brock’s (2013) comparative analysis come from PanTHERIA (<http://esapubs.org/archive/ecol/E090/184/default.htm>), a publicly-accessible species-level database of life history, ecological, and geographical traits of mammals (Jones et al., 2009). When we compared the data on the four taxa we work with, as extracted from PanTHERIA, with our own review of the primate literature, our estimated median home range sizes were approximately twice, three, and seven times larger for tamarins, owl monkeys, and titis and sakis, respectively (Fernandez-Duque et al., in review). Such a discrepancy is both striking and concerning.

Given our apprehensions about the appropriateness and quality of the data that are being used in comparative analyses, we also examined the data on home range size reported in a recent study re-evaluating the link between brain size and behavioral ecology in primates (Powell et al., 2017). The authors obtained home range (HR) size data from “dataset 1”, which they describe as a previously unpublished dataset compiled from the literature. The dataset, available online as Supplementary Information, consists of 289 rows of data, one row for each primate taxon considered. We focused on the 19 rows providing data on “HR size average” and “HR range” for different species of owl monkeys, titis, and sakis. For only nine species were data reported on average home range size, and for only eight species were data reported on the range of home range sizes.

To consider the quality of these data, we compared the values used in Powell et al.’s (2017) analyses with values we extracted ourselves from the references cited by the them (Table 3). At time of submission we were not able to check Sussman (2000), a review reference on platyrrhine primates. Of the 15 comparisons we were able to make between data reported in the comparative study and data in the cited sources, we found exact agreement

TABLE 3 | Information on average home range size and range of home range sizes for all listed species of the genera *Aotus*, *Callicebus*, and *Pithecia* from Powell et al. (2017) and from our own search of the references cited therein.

Species	Average home range size			Range in home range size			Notes
	Value from Powell et al. (2017)	Value from Our Search	Agree?	Value from Powell et al. (2017)	Value from Our Search	Agree?	
<i>Aotus miconax</i>	1.4	NA in cited source	NO		1.2–1.4		Shanee and Shanee, 2011 in Rowe and Myers, 2011
<i>Aotus azarae</i>	7	NA in cited source	NO	4–12	4–12	YES	Fernandez-Duque, 2007
<i>Aotus nigriceps</i>	8.55	NA in cited source	NO	3.1–14	7–14	NO	Fernandez-Duque, 2007
<i>Callicebus moloch</i>	9.25	NA in cited source	NO	6–18	6–8	NO	Norconk, 2007
<i>Aotus trivirgatus</i>	10	NA in cited source		6–12	NA in cited source		Sussman, 2000 (not checked); Wright, 1996
<i>Pithecia pithecia</i>	12.8	NA in cited source	NO	10.3 –15, 34.6	10.3–34.6	YES	Vié et al., 2001; Norconk, 2007 in Rowe and Myers, 2012
<i>Callicebus lugens</i>	14.2	NA in cited source	NO	9–22	NA in cited source	NO	Norconk, 2007
<i>Callicebus torquatus</i>	15.9	NA in cited source		4–30	4–30	YES	Sussman, 2000; Norconk, 2007
<i>Pithecia monachus</i>	24.9	NA in cited source	YES	9.7–40	9.7–42	NO	Soini, 1986 (reports <i>P. hirsuta</i>)
<i>Callicebus brunneus</i>					1.4		Norconk, 2007
<i>Aotus vociferans</i>					6.3		Fernandez-Duque, 2011
<i>Aotus brumbacki</i>					17.5		Fernandez-Duque, 2011
<i>Pithecia albicans</i>		172.4			147–204		Norconk, 2007
<i>Callicebus cupreus</i>					3.5–14		Norconk, 2007
<i>Callicebus personatus</i>					4.7–24		Norconk, 2007

(i.e., the data fully match) on only four. Two additional concerns arose about how the data included in the table were decided upon. First, we found information on four additional taxa in some of the sources cited that, for unspecified reasons, were not included in Powell et al.’s (2017) dataset. Second, even when the authors report average home range sizes, only one of the original sources cited provided an average home range size, and we could not find information on how the averages were then derived by the study’s authors nor what average they computed (i.e., mean or median). To illustrate the possible problems associated with reducing variation in a presumably evolved trait, we focus on the data used from Soini (1986). This source reports home range size estimates from three different groups as 9.7, 24, and 40–42 ha, and Powell et al.’s (2017) dataset then reports an average of 24.9 ha, presumably calculated as $(9.7 + 24 + 41)/3$. Is there much information of biological value in such an average?

With all these issues in mind, we are concerned that many contemporary considerations of hypotheses for the evolution of “monogamy” assume—maybe too readily—that these inferential analyses are solid and robust.

4.3. Suggested Guiding Principles

To summarize this section thus far, we have reviewed a number of comparative studies that have tried to test, in mammals and primates, several of the hypotheses outlined in section 3. Then, with a particular focus on a few recent, large-scale analyses, we have highlighted a number of concerns we have with respect to issues of data classification and compilation and have further examined the issue of data quality by comparing the data used in those studies with our own compilation of information from the primary literature for the four primate genera that we know best. This exercise leads us to suggest a few guiding principles around data quality for comparative analyses (see also Borries et al., 2013).

First, we cannot stress enough the importance of researchers more carefully assessing the quality and sources of the data used in their comparative analyses, including explicitly addressing the possible implications of changes in taxonomy. Second, we all need to be more careful to ensure that definitions are used consistently and are comparable between studies, or, at minimum, that we “translate” the terms applied in different

studies into a common vocabulary. Third, we must be willing to rigorously exclude taxa for which no relevant field data exist, or to show that data from captive populations are representative of conditions in the wild. Similarly, data for potentially unusual and “atypical” populations should be clearly highlighted as such (e.g., island or provisioned populations). Fourth, we should strive to use only primary peer-reviewed sources for each trait and, as much as possible, not rely on just one reference per species or genus of interest. Fifth, as much as possible, for continuous data we should provide not just the mean or median value for a trait but also some measure of variation, range, number of studies included, and sample size. Moreover, if data from several studies are combined, it should be clearly stated how the “average” value was obtained. Sixth, it is essential that editors and reviewers agree to adhere to, and begin enforcing these minimal standards, to help ensure the quality of the data being used in comparative studies. We suggest that societies and journals consider requesting that authors certify that they have followed adopted standards; this could be done in the same manner that has become common practice for certifying adherence to animal ethics and data sharing guidelines. Finally, with respect to the particular topics of pair-living and sexual monogamy that we are concerned with here, we argue that researchers ought to explore their evolution considering perspectives of all of the different kinds of individuals (e.g., males, females, residents, floaters, helpers, etc.) that comprise those systems (e.g., Jennions and Petrie, 2000; Gowaty, 2004). It is to that topic that we shift our attention below.

5. THE IMPORTANCE OF THE “INDIVIDUAL” PERSPECTIVE

Sexual monogamy and pair-living obviously cannot be fully explained by focusing solely on why members of one, or the other sex, might benefit from having only one opposite-sex mating partner or group mate. That is, pair-living and sexual monogamy can only be understood as consequences of the interaction of male and female mating strategies and of the compromises that interaction engenders (Gowaty, 1996; Shuster and Wade, 2003; Hosken et al., 2009). Indeed, mathematical models continue to incorporate factors influencing the variance of reproductive success in both males and females (Shuster and Wade, 2003; Kokko and Morrell, 2005; Port and Johnstone, 2013). Modeling approaches have indicated, for example, that the question of whether mate-guarding by males can be an evolutionary stable strategy (ESS) is also likely to depend, not only on the spatial distribution of females, but on the propensity of females to seek extra-pair copulations (Kokko and Morrell, 2005). In this context, the relevance of the extent of female synchrony of oestrous, which can strongly affect whether males are able to monopolize females, has not been considered in the same way as spatial dispersion in recent comparative phylogenetic analyses (but see Lambert et al., 2018). It is also important to consider the interaction between the spatial distribution of females, their relative oestrous lengths, and the daily travel distances of both males and females. For example, a breeding season of 1 month

may be ample time for males, or females, to mate with multiple partners if home ranges are fairly small and close together; on the other hand, in a species with large home ranges, where females are spaced far apart, a month may not be sufficient time for individuals to mate with more than one partner.

Despite these considerations, there is still sometimes a tendency to consider quite different aspects for males and for females—namely distribution of females for males, but variation in clutch size or number of broods for females (Shuster and Wade, 2003). This may often be adequate, but not necessarily always. Additionally, while it is common to point out that not all males will reproduce, this possibility is seldom considered for females. This omission is particularly problematic in systems where reproducing individuals mate with only one partner, since in these systems (e.g., sexually monogamous species) it is often assumed that there will be minimal variance in mate numbers for either males or females (e.g., Table 6.1 in Shuster and Wade, 2003). However, in territorial species with limited breeding spaces, such as many territorial birds or mammals, variance in reproductive success can be high when comparing territory holders and floaters (e.g., Fernandez-Duque and Huck, 2013). Thus, in the following sections, we consider the behavioral, adaptive and evolutionary implications of pair-living and sexual monogamy from the perspectives of the breeding female and the breeding male, as well as from the perspectives of both reproductive and non-reproductive adults. We recognize, of course, that the social system outcome reflects an integration of all of these different perspectives (Gowaty, 1996; Shuster and Wade, 2003; Hosken et al., 2009).

5.1. The Breeding Female’s Perspective

We consider three questions in exploring why a female lives in a pair or is sexually monogamous. First, why are there no other females sharing a home range with a given female? Second, why does only one of them breed when several females share a home range? And third, why does a breeding female not mate with several males, either from her own social group or from other groups?

5.1.1. Why Don’t Females Share Home Ranges?

Asking why females do not share home ranges relates fundamentally to the social organization of a species—in other words, who groups with whom and why? When females range and breed independently, it can result in either a solitary or a pair-living social organization (or, much more rarely, in a one-female, multi-male group). All these systems are characterized by relatively small group sizes. The fact that females do not share home-ranges with other females is most likely related to the distribution of resources needed to support female survival and reproduction (Emlen and Oring, 1977; Sterck et al., 1997; Lukas and Clutton-Brock, 2013); if resource distribution were not part of the explanation, one would expect to at least sometimes see large groups comprising a single female ranging with multiple males. Still, among mammals, we see numerous examples of the reverse: very large groups consisting of a single male associating with multiple females (e.g., Hanuman langurs, *Semnopithecus entellus*, with harem sizes of up to nine females: Newton, 1994;

Southern elephant seals, *Mirounga leonina*, with harem sizes of up to 90 females: Fabiani et al., 2004). However, among primates, there are no taxa in which a single female lives with many males in rather large groups, nor are we aware of cases of strongly male-skewed social groups in other mammalian taxa. Among the callitrichine primates, and among some hylobatids (gibbons and siamang), there are cases of single females living with several males, but in these cases the number of adult males is invariably small (≤ 4), and total group size is usually smaller than 10 individuals, including offspring (Heymann, 2000; Reichard and Barelli, 2008; Digby et al., 2010; Garber et al., 2016). Sometimes these groups are referred to as “polyandrous”, although we caution that that word—just like “monogamy”—carries with it connotations about patterns of mating or reproduction and should be eschewed unless it is being used, explicitly, to refer to either the social or genetic mating system.

Explicitly considering the point of view of the breeding male (see section 5.2) might be important for explaining apparent limits to the number of males present in these one-female, multi-male groups. Females may not object to the presence of more than one adult male; still, the selection pressure on males to reject other males may be higher than for the females to encourage them. It is worth mentioning that in several primates with either a modal pair-living social organization or a modal sexually monogamous mating system, sometimes other adults of either sex occasionally reproduce (Digby, 1995; Reichard and Barelli, 2008; Thompson, 2016; Porter et al., 2017).

5.1.2. Why Don't Other Females in the Group Breed?

If females live together with other females but only one of them reproduces, the question arises of why other females do not breed. In most group-living mammals all adult females regularly reproduce (e.g., cercopithecine primates, carnivores, Perissodactyla, and Artiodactyla, bats, elephants, and rodents: Ebensperger et al., 2012; but see Rubenstein et al., 2016). However, in some primates, and in some other group-living mammals, reproduction is highly skewed toward a dominant male-female pair. That is, even when there is more than one reproductively mature female, most females do not normally reproduce. This pattern occurs in several group-living carnivores (e.g., coyotes, *Canis latrans*: Hennessy et al., 2012; wolves, *Canis lupus*: vonHoldt et al., 2008; meerkats: Griffin et al., 2003; Young et al., 2007; see also Macdonald et al., 2019) and rodents (e.g., common mole-rats, *Cryptomys hottentotus*: Bishop et al., 2004; hoary marmots, *Marmota caligata*: Barash, 1981; Kyle et al., 2007). It is also seen in marmoset and tamarin primates, where reproduction by more than one female is very uncommon (e.g., golden lion tamarins, *Leontopithecus rosalia*: Dietz and Baker, 1993; saddleback tamarins, *Saguinus weddelli*, and several other members of the genus *Saguinus*: Garber et al., 2016).

In some cases, when subordinates are closely related to the opposite-sex adult in the group, inbreeding avoidance seems a likely explanation, and has been demonstrated in female Damaraland mole-rats (*Cryptomys damarensis*: Cooney and Bennett, 2000). However, in groups where females are not related to the dominant male, other explanations are necessary. Breeding being restricted to, or heavily skewed toward, a single dominant female suggests that some limited resources other than food

(e.g., allomaternal infant care) constrain female reproductive output. In primates, group-living in association with true sexual or genetic monogamy is actually quite rare or, arguably, absent. Callitrichines are a special case. They show such high intra-specific variability in their social organization and mating patterns that researchers are reluctant to classify any species as either definitely pair-living or sexually monogamous (Garber et al., 2016). Some taxa tend to be pair-living (e.g., pygmy marmosets, *Cebuella pygmaea*: Soini, 1982; de la Torre et al., 2009), some may have several females breeding simultaneously (e.g., common marmosets, *Callithrix jacchus*: Garber et al., 2016), and yet others show monopolization of parentage by one pair despite polyandrous or polygynandrous mating (e.g., mustached tamarins: Huck et al., 2005). Still, what all callitrichine taxa have in common is a high degree of alloparental care of the infants (Garber, 1997; Erb and Porter, 2017). It has been hypothesized that competition for infant care explains the monopolization of reproduction by one female (e.g., Digby, 2000; Yamamoto et al., 2010).

In contrast, it is less clear why subordinate females do not reproduce. The topic remains rather understudied, and “proof” for hypotheses is hard to come by. At a proximate level, there are some hypotheses based on physiological and behavioral mechanisms. For callitrichines, studies of captive individuals suggest that the reproductive cycles of subordinate females are hormonally suppressed by the dominant female (French et al., 1984; Ziegler et al., 1987; Snowdon et al., 1993; Puffer et al., 2004). However, the few studies of wild callitrichines that have examined physiological suppression have failed to find similar evidence (Lötker et al., 2004; Sousa et al., 2005). There are alternative mechanisms, besides physiological ones, that may be regulating the suppression of subordinate females or otherwise reducing their reproductive output. Subordinate females may be prevented behaviorally from copulating, or their offspring may be killed by dominant females (e.g., Abbott, 1984, 1987; Digby, 1995; Digby and Saltzman, 2009). Ultimate explanations for the lack of reproduction in subordinates are not as well understood. It is possible they are “making the best of a bad job”, with the costs of foregoing reproduction being ameliorated by kin-selection benefits or by direct benefits from group living, as has been suggested for male tamarins (Huck et al., 2004a).

5.1.3. Why Do Females Mate Monandrously?

When females are mating with only one male, this can simply be related to a scarce distribution of males. In otherwise famously promiscuous domestic cats (*Felis silvestris catus*), a population on Kerguelen Island showed a monogamous genetic mating system when cat density was so low that it was not beneficial for males to attempt finding more than one female (Say et al., 2002). Despite the potential genetic benefits of mating with several males (Jennions and Petrie, 2000), and despite possible advantages accrued through confusing paternity (e.g., securing additional male investment or reducing the risk of infanticide: Hrdy, 1979; van Noordwijk and van Schaik, 2000; van Schaik et al., 2000; Soltis, 2002), it is unlikely that the benefits of finding several partners are generally as high for females as they are for males, while the costs could be higher. These higher costs can occur through harassment (e.g., normally monandrous

parasitoid wasps, *Nasonia vitripennis*, had reduced longevity if exposed to more males during oviposition: Boulton and Shuker, 2015) or through acquiring sexually transmitted diseases that might have potentially higher costs in females (Thrall et al., 2000). An intriguing exception could be lekking species. There is some indirect evidence that female blue-crowned manakins (*Lepidothrix coronata*) visit multiple leks before mating, seeking out leks that are beyond their usual home-range and further away than the nearest lek (Durães et al., 2009). While considering lekking strategies of females in more detail is beyond the scope of this review, the possibility warrants further exploration.

Still remaining is the question of why, if several unrelated adult males live in a group, a breeding female mates with only one of them. Influenced, possibly, to an unjustified extent by Bateman's (1948) study of intra-sexual selection and reproductive output in *Drosophila*, it has long been presumed that females cannot increase their fitness by mating with multiple males. However, even if that were true (but see Jennions and Petrie, 2000), and important challenges to Bateman's paradigm notwithstanding (Tang-Martinez et al., 2000; Drea, 2005; Tang-Martinez and Ryder, 2005; Gowaty et al., 2012), the argument against mating polyandrously is still weak, unless there are actual costs associated that would select against mating with several partners (e.g., Wigby and Chapman, 2005). It is also possible that it is not a female's choice to mate with only one male, but rather that a given male might prevent other ones from mating with her (see section 5.2). Alternatively, females may indeed actively choose to mate with only one male to give him more reason to be monogynous due to increased paternity certainty. This can in turn increase the benefits of male care, since multiple matings by females and the resulting decrease in paternity certainty select against male care (Kokko and Jennions, 2008).

5.2. The Breeding Male's Perspective

By analogy to the female's perspective, we consider here three parallel questions relevant to understanding pair-living and monogyny from the point of view of the breeding male: (1) why does a male live in a group or occupy a home range that contains no other males; (2) when there are several males in a group or several males with largely overlapping ranges, why might only one of them mate or breed; and (3) why doesn't a male mate with several females, either from his own social group or from other groups?

5.2.1. Why Are There No Other Males Present?

As for females, this first question refers to the social organization of the species. When other males are breeding, but are not residing in the same group, this results in a solitary, pair-living, or one-male, multi-female (“harem”) organization. All these possible social arrangements may result from resource distribution and availability and from female dispersion (see section 5.1). Behaviorally, males may actively prevent other males from entering the group. In Azara's owl monkeys (*Aotus azarae*), males, and indeed females as well, fiercely try to prevent solitary intruding floater males from entering a group (Fernandez-Duque and Huck, 2013). In itself, the ability to prevent other males from

entering a group might depend partly on aspects of the species' ecology (Krüger et al., 2014).

5.2.2. Why Don't Other Males in the Group Breed?

In groups with more than one male, however, an almost genetically monogamous mating system may result even when the sexual mating system is polyandry, as shown for mustached tamarins (Huck et al., 2005). In these cases, the question arises why some males do not reproduce. Incest avoidance may be one explanation, as it may be a mechanism preventing males from mating with their mother or a sister. Intriguingly, in an intensely studied (>3,000 h of observation) group of mustached tamarins, the son of the breeding females was the only adult male that was never observed to mate with her (Huck et al., 2005). For males unrelated to the breeding female other explanations are necessary. If the breeding male prevents, or the female refrains from, copulations between the female and other males, at least during the female's fertile period, this results in a polygynous or a genetically monogamous mating system. Another reason could be that in pair-living mammals, females tend to be the same size as males, or slightly larger (ungulates: Loison et al., 1999; canids: Macdonald et al., 2019; primates: Smith and Jungers, 1997). Males, therefore, find it more difficult to actively prevent females from mating with other males than males in taxa with substantial body size sexual dimorphism. In the latter case, males may employ more subtle strategies, such as mate guarding. One of the phylogenetic comparative analyses discussed above suggested that a lack of sexual size dimorphism is actually not a consequence of, but rather a prerequisite for, sexual monogamy (Lukas and Clutton-Brock, 2013). Mathematical modeling also suggests that the propensity of females to seek extra-pair copulations strongly affects how worthwhile a mate-guarding strategy may be to males (Kokko and Morrell, 2005). The mate guarding strategy of the male can consist of preventing other males from approaching the female, more than preventing the female from mating with other males. When the female's reproductive status is assessed through olfactory mechanisms, males may try to prevent other males from getting close enough to a female to assess her reproductive status, as has been suggested for Kirk's dik-dik (*Madoqua kirkii*: Brotherton et al., 1997), Azara's owl monkeys (*Aotus azarae*: Spence-Aizenberg et al., 2018), and mustached tamarins (*Saguinus mystax*: Huck et al., 2004a).

5.2.3. Why Do Males Mate Monogynously?

Given the profound differences in the reproductive biology of male and female mammals, understanding why males might not attempt to mate with several females remains a challenging question. We consider separately the situation of males in solitary, pair-living, and group-living species.

If females are widely dispersed and solitary, there might be conditions where it becomes difficult for males to assume a roving strategy that has higher fitness benefits than staying with one female and guarding her (e.g., cats on Kerguelen Island; Say et al., 2002; prairie voles, *Microtus ochrogaster*: Rice et al., 2018). Lukas and Clutton-Brock's (2013) study suggested that the ancestral state for extant mammals with a “monogamous”

system, whether pair-living or group living, were solitary females. However, a study focusing only on primates, and distinguishing between "dispersed" and "associated" pairs, concluded that the ancestral state for primates living in "associated" pairs (like all haplorhine pair-living primates) was group living, while species with "dispersed pairs" (e.g., pair-living strepsirrhines) usually had solitary ancestors (van Schaik and Kappeler, 2003). Given that there are no extant solitary haplorhine primates, and that pair-living occurs in a variety of independent haplorhine branches, the most parsimonious proposition for the ancestral state of haplorhines is indeed group-living species.

Living in pairs does not necessarily preclude males, or females, from seeking extra-pair copulations. Among fat-tailed dwarf lemurs (*Cheirogaleus medius*), who usually live in dispersed pairs, nearly half of the offspring were conceived through EPCs (Fietz, 1999; Fietz et al., 2000). This result raises the question of what prevents males in other pair-living species, such as Azara's owl monkeys (Huck et al., 2014), from mating with females in other groups. Emlen and Oring's (1977) ecological model for the evolution of mating systems suggests that the spatial distribution of females might make it impossible for males to seek EPCs. Yet, the home-ranges of females in pair-living species tend to be smaller, rather than larger, than those of solitary females with a potentially promiscuous mating system (Komers and Brotherton, 1997; Lukas and Clutton-Brock, 2013). In Azara's owl monkeys, home ranges average 6.2 ha (Wartmann et al., 2014), groups regularly travel several hundred meters (300–500 m) in a few hours (Fernandez-Duque, unpublished data) and the ranges of floaters are larger than those of established groups (Huck and Fernandez-Duque, 2017). Thus, male owl monkey can easily transverse several females' ranges in a short time. Similarly, titi monkeys and sakis (Van Belle et al., 2018), as well as gibbons (Reichard, 2003b), all have home-range sizes that are sufficiently small relative to day range length, such that a male should be able to cross several female ranges per day, potentially gaining reproductive access to more than one of them. That extra-pair copulations and paternities have been reported in several species of hylobatids (Reichard, 1995; Kenyon et al., 2011; Barelli et al., 2013) suggests that pair-living males, and females, sometimes do pursue successfully mating opportunities outside the pair.

When multiple females live in a group, it is even more difficult to understand why males do not attempt to mate with several of them. Callitrichines are the only primate clade where males often live with several unrelated adult females and do not normally mate with more than one of them. During more than 3,000 h of observations of a group of mustached tamarins, none of the adult males attempted to copulate with either of the two non-breeding females, while all males unrelated to the breeding females did mate: with her (Huck et al., 2005). However, in the same population, one of us observed a copulation by a subordinate female with a male from a neighboring group (Huck et al., 2005). Furthermore, very occasionally, more than one female may attempt to breed in the same group (Culot et al., 2011). This indicates that tamarin males might not say "no" if the opportunity arises. In no other group-living primate taxon are males known to be sexually monogynous.

Similar strategies as discussed for females (active defense and mate-guarding) may prevent other males from achieving copulations with a guarded female. Another reason why males do not mate polygynously may be that females are preventing it through physical or hormonal mechanisms. That this is more than just a theoretical possibility has been shown for burying beetles (*Nicrophorus defodiens*), where females try to coerce males into mating monogamously by preventing them from advertising through pheromones to other females (Eggert and Sakaluk, 1995). Although traditionally we have not considered female mammals as having a high potential for coercing sexual monogamy in males, the previously discussed lack of dimorphism that characterizes most pair-living primate taxa can reasonably allow females to have influence over their partner's mating strategies. Additionally, dominant females may also be able to exert control over a male's interest in mating with other females indirectly, by suppressing the ovulation of subordinates.

More generally, it remains necessary to explain how the benefits to a male from staying with a particular female may be higher than the alternative strategy of trying to find and mate with additional females. The relative payoffs will depend on both the costs of mate search, the probability of encountering potential mates (Fromhage et al., 2005) and the accrued benefits from increasing the female's fitness. For example, by reducing the costs of raising offspring for a female, a male might increase the likelihood of future reproduction with the same partner, and male care could likewise directly increase infant survival. Taking at face value the evidence from recent comparative phylogenetic analyses that pair-living typically evolves before extensive parental care (Lukas and Clutton-Brock, 2013), this explanation obviously must be a secondary step that drives extra-pair paternity rates down once an association has been established, rather than being the primary cause. Mathematical modeling investigating situations where male mate-guarding and sexual monogamy are likely to evolve, indicate that important factors are the adult sex ratio (ASR), where an increasingly male-biased sex-ratio would increase a male's mate-guarding time, and the female's likelihood of seeking EPCs, where either very high or very low rates of female EPCs reduce a male's guarding effort (Kokko and Morrell, 2005; Harts and Kokko, 2013). These findings lead to further questions as to why, in some taxa, the ASR can be, or could have been in the past, more male-biased than is typically seen in mammalian systems.

5.3. Non-breeders' and Floaters' Perspectives

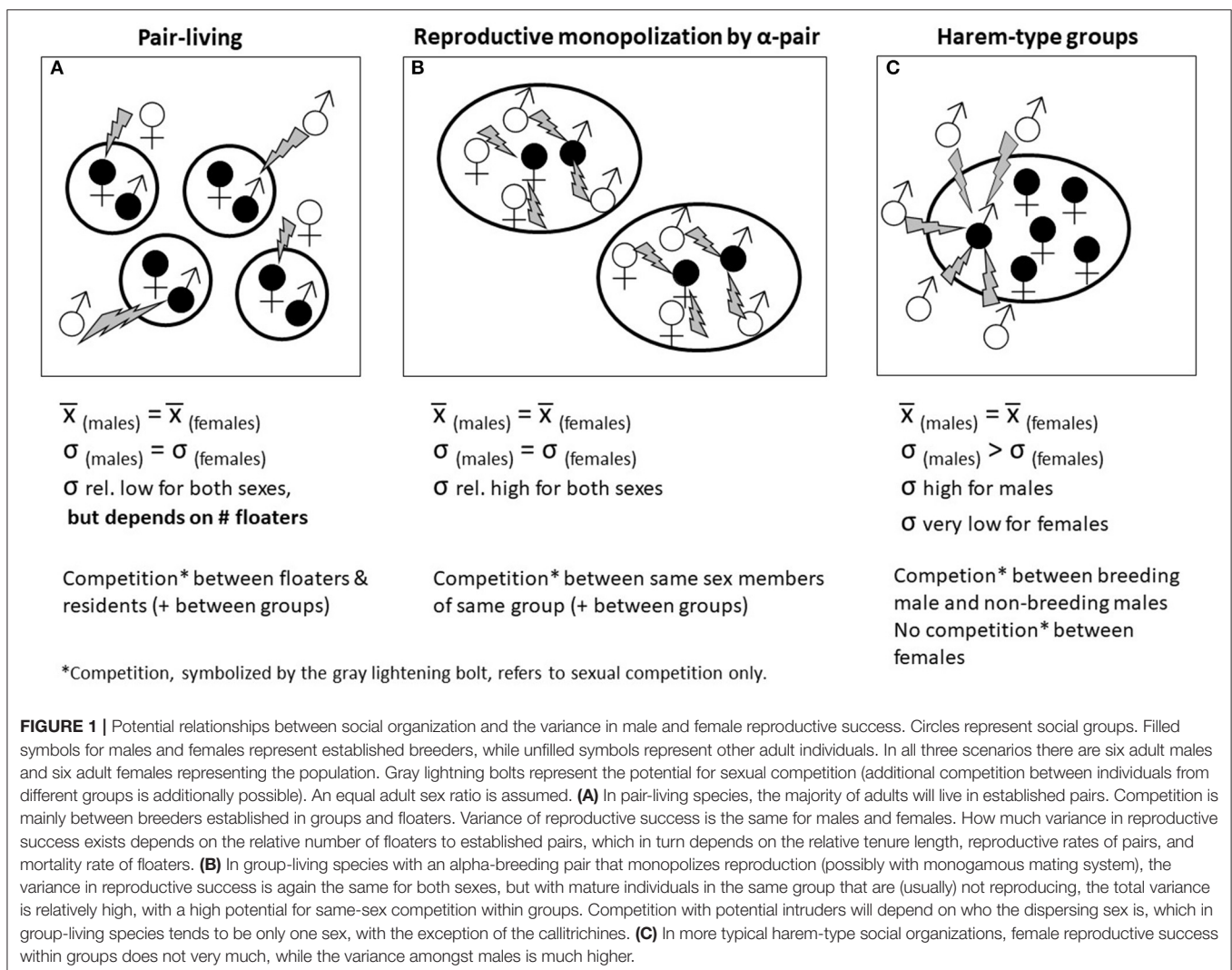
While it is hard enough to understand why males or females refrain from mating with others than their partners, it is even more difficult to understand why some individuals do not reproduce at all, a phenomenon that occurs in group-living species, as well as in pair-living ones (Figure 1). Unless otherwise stated, we consider the arguments for male and female non-breeders and floaters to be similar in pair-living species and in species with sexual monogamy. In both cases, unless there is a strong difference in the adult sex ratio, non-breeders and floaters can be of either sex. This should be the case in pair-living

species, while in group-living species that are usually sexually monogamous the sexes might differ more strongly, because one sex might find it easier to “sneak in” breeding possibilities. For example, in callitrichines, it might be easier for males to mate with the dominant female while the dominant male is not watching than for a subordinate female to rear offspring in the presence of a dominant one.

Non-breeders would do better holding a breeding position themselves. In the case of cooperative breeders, or when subadults show natal delayed dispersal, the costs of non-breeding might be partly offset by direct or indirect fitness benefits. Quite commonly, non-breeders seem to be making the best of a bad job. For example, non-breeding turkey (*Meleagris gallopavo*) males participate in the displays of breeders to attract females in a manner that fits expectations from Hamilton's rule. While dominant males clearly have higher fitness, the benefits through indirect fitness for the related non-reproductive males appear to be higher than their probability of successful breeding (Krakauer, 2005). If indirect benefits to subordinate males are

suboptimal, then it follows that they should be a constant threat to breeders.

Additionally, floaters, or non-breeders, of both sexes will affect the operational sex ratio, which can fluctuate locally and temporally (Fernandez-Duque and Huck, 2013). A large population of floaters will lead to intense intra-sexual competition. The role of floaters in the social organization and mating system of species needs urgent addressing; this is particularly true in pair-living species, where they are not so conspicuous as bachelor groups or subordinate males are in group-living species (Fernandez-Duque and Huck, 2013). The role of floaters in the formation of communal breeding in group-living species has been previously modeled (Port et al., 2011, 2017; Port and Johnstone, 2013), but not their impact on population dynamics when breeders are usually pair-living. Furthermore, but beyond the scope of this review, it would be interesting to evaluate how various models of reproductive skew (such as queuing or tolerance models: Clutton-Brock, 1998; Reeve et al., 1998; Johnstone, 2000), originally proposed



for hymenopteran insects (e.g., Reeve and Ratnieks, 1993) but also applied to studies on group-living primates (Port and Kappeler, 2010; Snyder-Mackler et al., 2012; Port et al., 2018), could be developed to help understand the dynamics of interactions between floaters of both sexes and breeding pairs, e.g., by examining the extent of deviations from pair-living or sexual monogamy in relation to different levels of alloparental care behavior.

Floaters can potentially have a strong impact on population dynamics and on the operation of sexual selection. Given an equal sex ratio, the mean number of offspring must be the same for males and females (Houston and McNamara, 2002; Wade and Shuster, 2002; Kokko and Jennions, 2003). Thus, all else being equal, the variance in reproductive success should be similar for males and females under sexual monogamy, but higher for males than females in a polygynous system (Trivers, 1972; Clutton-Brock, 1988). But what has not been pointed out before is that the magnitude of the variance in reproductive output might differ between pair-living species with sexual monogamy, and group-living species with the same mating system (Figure 1). This would most definitely be the case if the population includes floaters, since floaters also contribute to the variance in reproductive success in a population.

In owl monkeys, the majority of adults live in stable pairs, such that a majority of adult males and a majority of adult females hold reproductive positions. However, there is a substantial number of young adults who after emigrating from their natal groups remain in the population, ranging over the home ranges of several pair-living residents (Figure 1A). These floaters either challenge the same-sex individuals of established pairs to try to gain a breeding position or take advantage of vacancies in resident positions that arise through natural deaths (Fernandez-Duque and Huck, 2013; Huck and Fernandez-Duque, 2017). It has proven difficult to quantify precisely the frequency of those challenges. Over the years, we have quantified the frequency of successful takeovers by floaters (27 female and 23 male replacements in a total of 149 group-years: Fernandez-Duque and Huck, 2013), but the frequency of their failed attempts is likely to go unnoticed by researchers. Equally, while there should be the possibility of sneaky copulations with individuals from neighboring groups, the opportunity of EPCs should be relatively low in closely associated pairs, such as owl monkeys. Male and female owl monkey partners are constantly in very close proximity to each other; they should therefore be able to ward off attempts to copulate with other individuals. Thus, we expect variance in fitness to be similar for males and females, and similarly low amongst breeding individuals of both sexes. However, differences between breeding male and female variance in reproductive success will also depend on the relative numbers of male and female floaters in the population, and variance in reproductive success amongst all adults, i.e., including floaters that never obtain a breeding position, will be much higher than often assumed (e.g., in Table 6.1 in Shuster and Wade, 2003).

By contrast, in group-living species with several potentially reproductively active males and females, and where one alpha male manages to monopolize reproduction, there will be several

mature adults of both sexes present on a daily basis that could compete for reproductive opportunities. A large proportion of the population will live in groups, but only a small number will hold a main reproductive position. The total variance of reproductive success should, on a population level, be therefore higher, and opportunities for competition should be more frequent (Figure 1B). Naturally, these arguments focus on a snapshot in time. Conditions might differ if dominance is, for example, age-dependent, so that if skew is measured over a multi-year window, the variance will be actually lower and approach that of the "less competitive" sex. In groups, there will likely not only be competition between group members, but additional interactions with dispersing individuals or neighboring groups could also take place, as in the case of pair-living species. In one-male multi-female groups, essentially all females should reproduce, so there should be very little variance among females (and less than among pair-living females, where floating females might never gain a reproductive position), but very high variance among males (Figure 1C). We find it important to reiterate that pair-living need not imply lack of competition; indeed, competition can be frequent and/or intense, depending on the characteristics of the floater population (Fernandez-Duque and Huck, 2013). Still, competition should occur more sporadically than in group-living sexually monogamous species, and a larger proportion of the population should be able to reproduce at the same time. This might have implications for the sexual selection potential that have not been fully explored.

6. FUTURE RESEARCH DIRECTIONS

Our understanding of the evolution of pair-living and sexual monogamy in primates and other mammalian taxa has moved forward some important steps since Kleiman (1977) attempted the first comprehensive review, but work remains to be done. Apart from our hope that some of the issues about data quality and comparability in comparative studies that we addressed above will be dealt with more consistently in the future (see section 4.3) and that some of the hypotheses outlined in section 3 will be revisited using better datasets with clearer definitions, we suggest below several related topics that warrant and will benefit from further attention and research.

First, the likelihood of an individual encountering potential sexual partners depends on various factors, and comparative analyses looking at operational and adult sex ratios, home-range size, female dispersion, degree of home-range overlap, and species-specific life-history traits do try to take a number of those factors into account. We suggest, however, that comparative studies should strive to consider additional factors that are slowly beginning to be investigated. In particular, for pair-living species, the role of floaters in considerations of adult sex ratios has been too long neglected, and we hope that more researchers will attempt to study this elusive component of any species' population biology. We cannot emphasize enough that it took the first 6 years of our research on secretive owl monkeys in Argentina to realize the importance of a floater population; new

technologies are already contributing to carefully assessing the existence of floaters in other secretive taxa (Sabot et al., 2018).

Second, if the adult sex ratio plays such a strong role for mating systems as theory suggest (Harts and Kokko, 2013), the factors affecting the adult sex ratio require further exploration as well. For example, does a biased sex ratio start at birth or is it related to differential investment in sons and daughters that affects their survival probability? What is the influence of differential mortality among adult males and females, both residents and floaters? There have been suggestions that in polygynous primates the reduced life expectancy of males relative to females contributes to greater variance in reproductive success in males (Clutton-Brock and Isvaran, 2007; Bronikowski et al., 2011). Among pair-living sexually monogamous primates, it has been hypothesized that natural selection will favor longevity in the sex most responsible for rearing offspring (Allman et al., 1998). Owl monkeys—pair-living, sexually and genetically monogamous, and showing biparental care of offspring—provide some evidence in support of this hypothesis. Male and female owl monkeys show similar levels of intra-sexual competition and have similar life expectancies (Larson et al., 2016).

Third, more research is needed on the communication between pair-mates and between groups. van Schaik and Kappeler (2003; see also Kappeler, 2014) suggested a different ancestral state for extant dispersed vs. associated pairs, and it is clear that more work is needed to understand the various behavioral mechanisms coordinating the relationship between pair-mates. For example, in our work with three taxa (owl monkeys, titis, and sakis) that are consistently classified as pair-living and sexually monogamous, we have, over the years, documented qualitatively different patterns of male-female interaction among them (Spence-Aizenberg et al., 2016; Porter et al., 2017). Loud-calls and duetting are suggested as one important set of behaviors involved in regulating pair-bonding, group cohesion, and inter-group communication. A number of studies have explored the possible functions of loud-calls and duetting in regulating territoriality and use of space by groups of pair-living owl monkeys, titi monkeys, and gibbons (Mitani, 1985a,b; Caselli et al., 2014, 2015; Ham et al., 2016, 2017; Adret et al., 2018; García de la Chica et al., 2019), though similar studies have not yet been done on sakis.

Fourth, the need to better understand male-female relationships is also related to questions about mate-guarding and extra-pair copulations by males, and potentially also by females, as research on burying beetles has shown (Eggert and Sakaluk, 1995). In turn, more detailed knowledge on male-female interactions will allow progress in assessing the presence or not of a bond between breeding male and female (pair-bonding). This would be particularly useful, given the suggestion that these types of pairs might have evolved through different routes (van Schaik and Kappeler, 2003; Kappeler, 2014). Studies of captive individuals have provided the best data on pair-bonds in rodents and primates, including hormonal regulation, neurogenetics, neurobiology and behavioral indicators of emotional distress (Smith et al., 2010; Gobrogge and Wang, 2015; Maninger et al., 2017; Carter and Perkeybile, 2018). Unfortunately, far less is known about degree of bonding in other species and very little

physiological data on these aspects exist for wild primates, and in particular not in dispersed pairs. As humans show, a pair-bond can exist without constant proximity (Gavrillets, 2012), but pair-bonding is probably not required for keeping a pair-living social organization or even a monogamous mating system, given the occurrence of "dispersed pairs" in species like fork-marked lemurs (Schülke and Kappeler, 2003). Even if floaters were the most important source of intra-sexual competition, pair-living groups also interact with other groups, leading to opportunities for competition.

Fifth, while the relationship between a presumed father's care behavior, pair-living, and sexual and genetic monogamy have received substantial attention (Huck et al., 2014; Klug, 2018; Rogers et al., 2018), among primates (with the exception of the callitrichines) alloparental care seems to be a little explored dimension associated with sexual monogamy and pair-living. Sibling participation in infant care is virtually absent in owl monkeys, titi monkeys and siamangs (Lappan, 2008; Fernandez-Duque et al., 2009), where it is the male and the female who share parental duties. In the less strictly pair-living sakis (genus *Pithecia*), we have seen some carrying of offspring by older siblings and very rarely by an adult male (Di Fiore et al., unpublished data), and a study on an island population without dispersal possibilities found some carrying by other adult and sub-adult females in *P. pithecia* (Homburg, 1997). The variable participation of adult and sub-adult non-breeders in offspring care tentatively suggests that concession models of reproductive skew or tolerance models (see section 5.3) may sometimes be important for understanding the evolution of social and genetic mating systems in group-living primates.

Finally, we have tentatively suggested in the section on proposed terminology that, where possible, researchers should seek to abandon categorizations of potentially continuous variables. In many cases, however, it needs to be explored in more detail how this could be best approached, because unthinking use of measurable values might create new problems, and it has been suggested (though there were problems with that study as well similar to the ones discussed in the section 4.2) that using continuous data can sometimes lead to a false perception of continuity (Rubenstein et al., 2016).

7. CONCLUSIONS

Both in our work and when writing the sections above, our premise has been that evolutionary biologists attempting to understand the evolution of any aspect of an animal social system are primarily interested in two main topics. First, under the assumption that the behavioral traits that shape the social system have a genetically inheritable component, researchers are interested in understanding whether and how individual variation in those traits is associated with differences in fitness. Such consequences on fitness can be operationalized through proxies like number of copulations or genetically assigned paternity, but, unfortunately, we often lack empirical data on the fitness consequences of variation between individuals in behaviors associated with both pair-living, sexual and genetic

monogamy, such as levels of mate guarding, intolerance of same sex adults, or parental investment in offspring (but see Shuster et al., 2019 for an exciting example of what is needed). Second, as evidenced by the continued growth in the number of comparative studies, researchers are interested in understanding the evolutionary and phylogenetic history of animal social systems as emergent phenomena. These analyses aim to shed light on how, when, and why particular aspects of social systems have arisen and on inferring the social systems of extinct taxa. With respect to this second topic, we believe that at the moment no robust conclusions can yet be drawn because of the problems associated with comparative studies that we have outlined in detail above. Similar analyses based on sounder datasets with more clearly defined and comparable terms are required. Our calls for caution notwithstanding, recent analyses of the evolution of “monogamy” have provided tantalizing possible explanations and opened up further questions. If Lukas and Clutton-Brock (2013), for example, are right about a likely solitary ancestral route to a monogamous mating system in most mammalian taxa, then primatologists can look forward to decades of research trying to understand why primates seem to deviate from this pattern (van Schaik and Kappeler, 2003). There is no *a priori* reason to expect a single explanation for the evolution of pair-living, sexual or genetic monogamy either across mammals or across primates, but understanding how and why lineages differ in their evolutionary routes to these traits will help shed additional light on the ecological, social, and phylogenetic factors that influence social evolution. In this context, it is also important to incorporate all of the various elements that tend to be conflated in folk conceptions of “monogamy” (i.e., pair-living, pair-bonding, sexual monogamy, genetic monogamy, and infant care patterns) into the same comparative analyses, because, while these are partly separate phenomena, they can still clearly interact with and influence one another.

We admit to a bit of frustration at realizing that our closing recommendations for how to make progress in the comparative study of both pair-living and sexual monogamy are neither new nor theoretically ground-breaking, but rather a plea for returning to the bedrock of scientific inquiry: for sound comparative analysis, we need more high-quality natural history data on a wider range of animal taxa. Our recommendations can be summed up as follows: we must stop the deluge of lots of data of doubtful quality; we must strive for high quality natural history data; we must incorporate perspectives of all participants in a social system, not only breeding males and females, but also non-reproductive adult group members as well as floaters living outside of established groups; and we must, when

reaching conclusions, distinguish between the actual data and the statistical and evolutionary inferences (with their associated uncertainties) made from them (Schradin, 2017). Comparative studies have laudable goals, but their potential can only be realized if suitable, comparable data are available to analyze. As others have stated previously, comparative studies can be no more reliable than the data on which they are based (Smith and Jungers, 1997).

AUTHOR CONTRIBUTIONS

MH wrote the first draft of the manuscript. AD, EF-D, and MH wrote different sections of the manuscript. AD and EF-D implemented and funded the studies that resulted in the data reported. All authors contributed to manuscript revision, read and approved the submitted version.

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Monogamy: Cause, Consequence, or Corollary of Success in Wild Canids?

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The Canidae are successful, being a widespread, abundant, speciose, and adaptable family. Several canids in particular have recently experienced rapid expansions in range and abundance, with similar situations mirrored on several continents by different species. Despite extreme behavioral diversity between and within species, monogamy is a common denominator in canid societies. In this review, we ask why canids are monogamous and how monogamy is related to their success. We begin with an overview of canid social monogamy, describing the pair bonding, paternal care, and often alloparental care that is characteristic of the family, and discuss theories on the evolution of mammalian social monogamy. We discuss why and how monogamy is maintained in canids, either voluntarily or enforced, and how ecological conditions influence either the functional advantages of monogamy or ability for enforcement and thus whether social monogamy is maintained. Social monogamy does not necessitate exclusive mating and many canids exhibit extra-pair paternity. We consider the costs and benefits of extra-pair mating for male and female canids and how ecological conditions can shift this cost/benefit balance and thus affect its prevalence. Monogamy may be responsible for many of the unusual canid reproductive characteristics through facilitating alloparental care and monogamy enforcement, and the domestic dogs' departure from monogamy supports our interpretation that it is an adaptation to resource availability. In asking whether monogamy is responsible, at least in part, for their success, we propose the *monogamy as pro-cooperative hypothesis*, suggesting four characteristics have contributed to canid success: (1) ecological flexibility, (2) high mobility, (3) high reproductive rates, and (4) sociality/cooperation, with the latter two being consequences of monogamy. These four interconnected traits enhance one another and it is their combination, with monogamy at its foundation enabling cooperative sociality and thereby enhanced reproduction and survival, that together comprise the formula of canid success.

Keywords: paternal care, alloparental care, extra-pair mating, sociality, cooperation, canidae, carnivores, pair bond

INTRODUCTION

Of their many notable attributes, three stand out about the Canidae: first, they are remarkably similar; second, they are remarkably different; and third, they are remarkably successful.

First, the similarity lies in the anatomical and behavioral traits that makes all 37 species of the family—from fennec fox (*Vulpes zerda*) to gray wolf (*Canis lupus*)—immediately recognizable as dogs (for a *dramatis personae* see Macdonald and Sillero-Zubiri, 2004). Not only are the largest species essentially morphologically inflated identikits of the smaller ones, but their expressions and demeanors are similar, as are their societies, all built around monogamy (Macdonald et al., 2004). Social monogamy is unusual amongst mammals, adopted by only 3–9% of Mammalia species and 16% of Carnivora species (Kleiman, 1977; Lukas and Clutton-Brock, 2013), yet is found in all canid species studied to date. In no other mammalian family is the pair bond so ubiquitous. In an overview of carnivore societies, Macdonald (1992) emphasized the phylogenetic descent that weaves canidness and monogamy throughout the family (as it does similarly for felidness and polygyny throughout the Felidae) (Macdonald and Kays, 2005).

Second, the canid family is highly diverse. Body sizes range from the 0.8 kg fennec fox to the 60+ kg gray wolf (Nowak, 2005). Their diets range from the almost exclusively insectivorous (e.g., bat-eared fox [*Otocyon megalotis*]) to almost exclusively carnivorous (e.g., African wild dog [*Lycaon pictus*], bush dog [*Speothos venaticus*], Ethiopian wolf [*Canis simensis*], Marino et al., 2010), with a full spectrum of omnivory between (e.g., red fox [*Vulpes vulpes*], golden jackal [*C. aureus*], African golden wolf [*C. lupaster*]). Such extremes in diets are reflected in their dentition, because while most canids have 42 teeth well-suited for generalist diets (e.g., carnassials for shearing flesh and molars for omnivory), bat-eared foxes have up to 50 less-specialized teeth (the most of any land mammal) for extreme insectivory (Klare et al., 2011), whereas the dholes, bush dogs, and African wild dogs have reduced or absent molars and enhanced carnassials for hypercarnivory (Van Valkenburgh, 1991). Canids are found in nearly all terrestrial habitats, including such extremes as Arctic tundra (Arctic fox [*Vulpes lagopus*]), desert (fennec fox), tropical forest (dhole [*Cuon alpinus*]), high-altitude environments (e.g., Ethiopian wolf, Marino, 2003; Himalayan wolf [*C. [lupus] himalayensis*], Werhahn et al., 2017, 2018) and human cities (e.g., coyote [*C. latrans*]). Some even partially exploit aquatic (e.g., short-eared dog [*Atelocynus microtis*], de Oliveira, 2009; British Columbia coastal wolf, Darimont and Paquet, 2002; Stronen et al., 2012) and arboreal (e.g., gray fox [*Urocyon cinereoargenteus*], Trapp and Hallberg, 1975) habitats. Canid social systems range from generally solitary species like the maned wolf (*Chrysocyon brachyurus*), where pairs share a territory but associate only during the mating season (Dietz, 1984), through the spatial groups of red and Arctic foxes (e.g., Hersteinsson and Macdonald, 1982, 1992), to species forming large, complex packs (e.g., Ethiopian wolves, Sillero-Zubiri and Gottelli, 1995a; bush dogs, Macdonald, 1996; African wild dogs, Creel et al., 2004; gray wolves, Jedrzejewski et al., 2005). Even within species, canids exhibit substantial variation

(Macdonald and Moehlman, 1982; Moehlman, 1989; Creel and Macdonald, 1995; Geffen et al., 1996; Moehlman and Hofer, 1997) and variability within a species may be larger than that between species (Macdonald and Moehlman, 1982; Creel and Macdonald, 1995). For example, gray wolves, coyotes, black-backed jackals (*Lupulella mesomelas*) and red foxes may live solitarily, in pairs, or in large groups (Kleiman and Brady, 1978; Messier and Barrette, 1982; Mech and Boitani, 2003; Baker and Harris, 2004; Kamler et al., 2019). Red fox home ranges vary between populations by three orders of magnitude, their societies varying between ubiquitous socially monogamous pairs and spatial groups of six adults (Macdonald, 1981), while gray wolves occupy ranges varying from 75 to 2,500 km² with groups varying from pairs to packs of up to 42 (Mech and Boitani, 2003). Arctic foxes can exist as a “coastal” ecotype, feeding on temporally stable seabirds and marine resources and consequently living a moderate lifestyle with litters averaging five cubs produced yearly. Alternatively, arctic foxes can exist as a “lemming” ecotype, feeding on rodents with extreme cyclic population variations and consequently mirroring this extreme lifestyle, producing litters of up to 18 cubs during rodent peaks and rarely reproducing during years of low prey availability (Tannerfeldt and Angerbjörn, 1998). Though they often exist as a single breeding pair, they may form large social groups of up to 31 individuals, referred to as “fox towns” (Elmhagen et al., 2014). Ethiopian wolves, Afroalpine specialists, also display such plasticity: pairs with large territories dominate in low productivity environments, while packs of up to 18 adults/subadults defend small territories in optimal habitats (Sillero-Zubiri et al., 2004).

Third, canids are successful, both over evolutionary and modern times. Evolutionarily, canids usurped Hyaenidae from the dog-niche in the Pliocene (Macdonald, 1992). Nowadays, many species of canids flourish alongside humanity. A canid currently claims the title of the world’s most widely distributed non-domestic terrestrial mammal: the red fox (Macdonald and Sillero-Zubiri, 2004), who usurped this title from another canid, the gray wolf (Mech, 1995; Macdonald and Sillero-Zubiri, 2004), while free-ranging domestic dogs are found across the globe (Lord et al., 2013). Several canids have recently rapidly expanded their ranges: coyotes have become ubiquitous across North and Central America over the past two centuries (Gompper, 2002; Macdonald and Sillero-Zubiri, 2004), while golden jackals (Tóth et al., 2009; Rutkowski et al., 2015) and raccoon dogs (Helle and Kauhala, 1991; Kauhala and Saeki, 2004; Sutor, 2007; Kauhala and Kowalczyk, 2011) mirror this same rapid expansion across Europe. Following introductions of red foxes to Australia and eastern North America, they rapidly spread throughout most of continental Australia and USA (Kamler and Ballard, 2002). Despite intensive human efforts to control populations of red foxes, coyotes, golden jackals and free-ranging domestic dogs, these species continue to survive and thrive. Even gray wolves, driven to the brink of extinction in the 1800s, are now returning to their former range in North America and Europe (Mech, 1995, 2017; Breitenmoser, 1998; Wydeven et al., 1998; Phillips et al., 2004). That these expansions are mirrored across several parts of the world

raises the question of what has allowed these canids to achieve such wide distributions and high abundances, rapid expansion, colonization and biological invasion, and resilience to human population control.

Together, these canid attributes—similarity resulting from evolutionary conservatism and differences from behavioral flexibility—prompts the question of what are the limits to variation in each species, and if those limits differ between species, what evolutionary constraints have set them? And since the unusual common denominator of canid societies is monogamy, why are they monogamous and what role has this played in the family's success, both in evolutionary time and the Anthropocene?

Monogamy has long been an area of interest for evolutionary and behavioral ecologists (Orians, 1969; Emlen and Oring, 1977) and numerous early hypotheses attempted to explain its evolution and maintenance (e.g., Orians, 1969; Emlen and Oring, 1977; Wittenberger and Tilson, 1980). Decades of empirical and theoretical research suggest factors affecting monogamy's origin and maintenance can be complex, differ among taxa, and are subject of a constant evolutionary interplay between monogamy and associated traits (Klug, 2018; Lambert et al., 2018). However, most research on monogamy has focused on birds (Reichard and Boesch, 2003), unsurprisingly since ~90% of bird species exhibit social monogamy. In contrast, 95–97% of studied mammals are polygamous (i.e., polygynous, polygynandrous, and less commonly, polyandrous) (Kleiman, 1977; Lukas and Clutton-Brock, 2012)—Canidae are one of the main exceptions (Kleiman, 2011). There are variations on every theme, and some cases in wild canids of polygyny, polyandry, polygynandry, plural breeding, communal breeding, cooperative breeding, and promiscuity exist. Nonetheless, we are aware of no study of any canid species that has not revealed a mated pair at its nucleus. Sexual dimorphism generally correlates with mating system (Weckerly, 1998), and amongst canids monogamous mating and paternal care are associated with little or no sexual dimorphism (Kleiman, 1977, 2011; Bekoff et al., 1981; Johnson et al., 2017). The heavy investment by females in internal fertilization, gestation and lactation leaves females committed to much of the burden of parental care and provides considerable opportunity for males to desert their partners to seek additional mating opportunities (Orians, 1969; Trivers, 1972; Maynard Smith, 1977; Clutton-Brock, 1989). Why then would canids form prolonged, year-long pair bonds, maintained not only outside of the breeding season, but often for many years? And what variations of monogamy are exhibited among and within canid species and what causes these variations?

To begin this review, we first consider social monogamy, then reveal differences between canid social and genetic mating systems, i.e., social monogamy does not dictate exclusive mating. We consider canid-specific reproductive traits that may have developed from social and genetic monogamy and, following a detour around the anomalous case of domestic dogs, we reflect on whether monogamy, and the flexible social systems built around it, is a factor in the success of members of the canid family.

CANID SOCIAL MONOGAMY

Characteristics of Canid Social Monogamy

The fundamental canid social unit, irrespective of group size, is the socially monogamous pair. The primary defining characteristic of social monogamy is spatial congruence of a single breeding male and female. However, this basic criterion is generally exceeded in canid pairs by an affiliative social pair bond, including high rates of social interaction, cooperative territorial defense, mutual offspring care, den sharing, and intrasexual aggression directed at individuals outside the pair bond (Lord et al., 2013). **Box 1** provides an overview of variations of social monogamy in canids.

Pair Bonding

Most socially monogamous animals practice serial seasonal monogamy, short-term pairing that lasts only a single breeding season, replaced by a new monogamous bond the following year (e.g., ducks of the *Anas* genus, Mock et al., 1985). Canids, in contrast, often maintain long-term affiliative and cooperative pair bonds and typically remain with the same partner, unless mortality intervenes (e.g., Island fox [*Urocyon littoralis*], Roemer et al., 2001; swift fox [*Vulpes velox*], Kitchen et al., 2005a; kit fox [*V. macrotis*], Ralls et al., 2007; cape fox [*V. chama*], Kamler and Macdonald, 2014). For example, high mortality rates were responsible for serial monogamy in populations of red foxes (Zabel, 1986), swift foxes (Kamler et al., 2004a) and in intensely hunted gray wolves (Jedrzejewski et al., 2005). Amongst Ethiopian wolves, the dominant female's position changes only with her death, though male turn-over is more frequent (Sillero-Zubiri et al., 1996a, 2004). Pairings as long as 8 years have been reported in coyotes (Hennessy, 2007) and black-backed jackals (Moehlman, 1989) and up to 9 years in gray wolves (Doug Smith, oral communication). The degree to which a pair associates outside the breeding season differs between species. For many large canids, such as gray wolves and African wild dogs, the mated pair remain closely associated year-round, coordinating their behavior and hunting together (Creel and Creel, 1995; Mech and Boitani, 2003). For small species, such as cape foxes, swift foxes, and kit foxes, mated pairs share a territory throughout the year but hunt solitarily; they share dens and closely associate only during the breeding and cub-rearing seasons whereas other times of the year they use different dens and associate with each other less frequently (Kitchen et al., 2005a; Ralls et al., 2007; Kamler and Macdonald, 2014). The maned wolf may be an extreme example of this, as mated pairs apparently do not associate with each other at all outside the of the breeding and pup-rearing season (Dietz, 1984), although intraspecific differences among populations might occur. Medium-sized canids, such as coyotes and jackals, may exhibit variations in year-around associations of mated pairs, possibly related to group size or prey size.

Paternal Care

Although paternal care occurs in only 5–10% of mammalian species (Kleiman and Malcolm, 1981; Clutton-Brock, 1991; Woodroffe and Vincent, 1994), it is nearly ubiquitous in canids (Malcolm, 1985; Asa and Valdespino, 1998; Kleiman, 2011).

BOX 1 | Variations of social monogamy in canids.

Social monogamy: Social structure involving a single breeding male and female, which in canids typically involves an affiliative pair bond, shared territory with mutual territory defense, and biparental offspring care. Group-living canids may exhibit social monogamy, with a single breeding male and female pair and additional non-breeding group members (often their offspring).

Genetic monogamy: Exclusive reproduction between one male and one female (i.e., no extra-pair paternity).

Pair bonding: Affiliative bond between a breeding male and female, which in canids is generally maintained for several years, often until the death of one of the pair. In some canids, the mated pair maintains close associations year-round, whereas in maned wolves and many small canids, although a pair shares and defends a territory year-round, close associations and den sharing occur primarily during the breeding and pup-rearing seasons (Dietz, 1984; Kitchen et al., 2005a; Ralls et al., 2007; Kamler and Macdonald, 2014).

Canid variations of social monogamy Pairs: A single pair-bonded mating male and female share a territory year-round and young disperse. Example: swift fox (Kitchen et al., 2006).

Trios: A single pair-bonded dominant mating male and female, plus an additional subordinate non-breeding adult. The additional adult is usually the offspring of at least one of the pair from a previous year, though not always. The third adult may or may not actively help in raising young, and trios may be stable over several years. Example: kit fox (White and Ralls, 1993).

Groups: A single pair-bonded dominant male and female, plus additional subordinate non-breeding adults. Additional adults are usually offspring of at least one of the pair from previous years, though not always. In some cases, additional adults may actively help in raising pups and groups may cooperatively hunt and defend resources, in which case it can be considered **cooperative breeding** (though cooperatively breeding groups could also be polygamous). Example: gray wolves (Bekoff and Wells, 1982). In other cases, additional adults do not actively help in raising pups and group members do not coordinate behavior. Example: Blanford foxes (Geffen and Macdonald, 1992).

Double litters/Plural breeding: Multiple (usually two) non-interbreeding pairs of males and females share a den and territory and produce litters. Two litters may be born in the same den (e.g., coyote: Hennessy, 2007), or two litters may later merge (e.g., arctic fox: see Norén et al., 2012). The two females are often close relatives (e.g., mother-daughter). Note that these terms have also been used to describe polygynous/polygynandrous systems. Although double litters are commonly reported in coyotes, more genetic research is needed to distinguish cases where these are in fact multiple litters or large litters with size differences between pups, or whether this represents polygamous systems, though one study has confirmed two genetically monogamous pairs (Hennessy, 2007). If alloparental care is provided to the other litter (e.g., allo-nursing between females can be common), this represents **communal breeding** (i.e., not social monogamy).

Deviations from social monogamy: Group-living canids may instead exhibit social polygyny (e.g., bigamous red foxes: Zabel and Taggart, 1989), social polyandry (e.g., African wild dogs, Spiering et al., 2010), polygynandry/communal breeding (e.g., African wild dogs, Spiering et al., 2010).

Kleiman and Malcolm (1981) categorized mammalian parental care into indirect care, which does not require physical contact with young, and direct, which does. Indirect care includes territory acquisition, maintenance and defense, shelter or den construction, anti-predator defense, and mate care through guarding and provisioning. Direct care includes huddling, grooming, transporting, feeding, active defense against predators or conspecifics and playing and socializing. In some species,

indirect paternal care predominates (e.g., Blanford's fox [*Vulpes cana*], corsac fox [*V. corsac*], Geffen and Macdonald, 1992; Asa and Valdespino, 1998; Kleiman, 2011); in others, females spend more time with the pups while males provide food (e.g., gray fox, Nicholson et al., 1985; swift fox, Poessel and Gese, 2013); in yet others, males spend more time with pups than the mother and exhibit every care-giving behavior except lactation (e.g., bat-eared fox, Malcolm, 1986; Maas, 1993; Maas and Macdonald, 2004; Wright, 2006; African wild dog, Asa and Valdespino, 1998; raccoon dog [*Nyctereutes procyonoides*], Kauhala et al., 1998). At an extreme, Kleiman (2011) reports that captive female bush dogs call their mate while giving birth, and the male helps remove pups from the birthing canal, grooms the neonates, and may help in removing the placenta (see also Macdonald, 1996).

Provisioning both the pups and lactating mother is widely documented paternal care amongst canids (Asa and Valdespino, 1998). As Macdonald (1992) noted, regurgitation of partially digested food is widely described in the lupine canid lineage (present in all species in the genera *Canis*, *Lycan*, *Cuon*, *Chrysocyon* and *Speothos*; Biben, 1982; Johnsingh, 1982; Rasmussen and Tilson, 1984; Asa and Valdespino, 1998; Lord et al., 2013) but absent in the vulpine lineage (though see Poessel and Gese, 2013). In these more carnivorous canids, this economical means of transporting prey to the den without the risk of kleptoparasitism is clearly advantageous (e.g., van Lawick-Goodall and Lawick-Goodall, 1970). African wild dogs can carry an estimated 3 days' worth of food in their stomachs to the pups and mothers (Reich, 1981; Creel and Creel, 1995), which allows males to successfully raise pups if the mother dies (Estes and Goddard, 1967). Species feeding on medium-sized prey can carry prey to the den, allowing both parents to provision young once they are old enough to be left alone at the den (e.g., red fox, Macdonald, 1977; arctic fox, Cameron et al., 2011), but for largely insectivorous canids, this is unfeasible. In largely termitivorous bat-eared fox (Klare et al., 2011), nursing mothers must spend >85% of the night foraging (Wright, 2003), leaving males primarily responsible for guarding, huddling and grooming cubs (Lamprecht, 1979; Malcolm, 1986; Maas, 1993; Maas and Macdonald, 2004; Wright, 2006). As bat-eared fox cubs begin foraging, the male accompanies them (Wright, 2006), acting as both protector and teacher, indicating patches of food to the cubs and occasionally pre-chewing larger beetles (Maas and Macdonald, 2004). A similar division of labor is reported amongst other insectivorous canids (e.g., raccoon dog, Kauhala et al., 1998; hoary fox [*Lycalopex vetulus*], Courtenay et al., 2006), where males compensate for their inability to directly feed cubs by guarding them.

An early theory by Moehlman (1986) posited that requirements for paternal investment in canids, along with other life-history traits, relate to body size. She argued that large canids have relatively smaller infants in larger litters, requiring heavy, prolonged post-partum parental (and alloparental) investment, whereas smaller canids have relatively larger young in smaller litters, requiring less post-partum parental investment. However, other studies concluded female weight was not a strong predictor of canid litter size (Bekoff et al.,

1981; Geffen et al., 1996; but see Johnson et al., 2017) and that there was either no correlation between litter size and neonate weight (Geffen et al., 1996) or a positive correlation (Bekoff et al., 1981). Instead of body size, the need and capacity for paternal care is likely determined by diet. The greater energy requirements of large canids mean they must rely more heavily on carnivorous diets and thus larger prey, whereas smaller canids can be more omnivorous (Carbone et al., 1999; Slater, 2015). Large prey not only allow males to directly feed pups, but are also more difficult for young to learn to acquire, thus requiring a longer period of dependency and greater parental investment to ensure pups are fed; offspring even older than 1 year may be directly provisioned by adults by regurgitation in gray wolves (Mech et al., 1999) and black-backed jackals (Moehlman, 1986). With smaller omnivorous species there is less capacity and less need for males to provision young. For example, Blanford's fox males cannot economically carry insects to the cubs so they are entirely reliant on the mother's milk (Geffen and Macdonald, 1992). Diet, and more specifically prey size, therefore probably determines variations in paternal care (Kauhala et al., 1998).

Alloparental Care

Alloparental care by non-breeding adult “helpers” is widespread across canids (see Macdonald et al., 2004). Helpers are usually, but not invariably, related to the pups (e.g., Zabel, 1986; Sillero-Zubiri et al., 2004; Jedrzejewski et al., 2005). There are many examples of “helpers” benefiting pup survival. Cases of alloparenting allowing litter survival despite the mother's death have been documented in red fox (Macdonald, 1979a; von Schantz, 1984) and African wild dogs (Estes and Goddard, 1967). In black-backed jackals, the presence of one additional helper tended to result in survival of one additional pup ($R^2 = 0.89$, Moehlman, 1979). Similar but much weaker associations between pup survival and the number of helpers are found in coyotes (Bekoff and Wells, 1982) and African wild dogs (Malcolm, 1979). The presence of helpers can lead to larger litter sizes in African wild dogs (Gusset and Macdonald, 2010; Angulo et al., 2013), perhaps by increased provisioning of pregnant females. In red wolves (*Canis rufus*) and Ethiopian wolves, helpers increased female lifetime reproductive success by extending the female's reproductive lifespan (i.e., age of last reproduction), thereby increasing the number of reproductive events and thus lifetime reproductive success (Sillero-Zubiri et al., 2004; Sparkman et al., 2011a). Helpers reduce time pups are left unattended at the den in African wild dogs (Courchamp et al., 2002) and Ethiopian wolves (Sillero-Zubiri et al., 2004) and can actively defend against predators (Macdonald, 1979a; Bekoff and Wells, 1982; Malcolm and Marten, 1982; Creel and Creel, 1995; Kamler and Gipson, 2000; Kamler et al., 2013a).

Other studies, however, have not found helpers to be beneficial. In Blanford's foxes, non-breeding adults were not observed providing direct care to the young (Geffen and Macdonald, 1992), though perhaps they provide indirect care by territory defense or pup guarding. Helpers did not affect offspring production and/or survival in studies of Arctic foxes

(Kruchenkova et al., 2009), red foxes (Zabel and Taggart, 1989; Baker et al., 1998) and Ethiopian wolves (Sillero-Zubiri et al., 2004; Marino et al., 2012). It is, however, possible that helpers provided other benefits, such as acting as insurance if a parent dies by adopting the litter (as seen in red foxes: Macdonald, 1979a; von Schantz, 1984), or lightening the work load for the parents (as in Ethiopian wolves: Sillero-Zubiri et al., 2004), which may increase the breeding pair's future reproductive success (Marino et al., 2012, 2013). The benefit provided by helpers likely depends on ecological conditions. In gray wolves (Harrington et al., 1983) and African wild dogs (Malcolm and Marten, 1982), older siblings were observed feeding pups and thereby increasing pup survival only when there was a food availability surplus (Malcolm and Marten, 1982; Harrington et al., 1983). Furthermore, when food is scarce, not only do helpers not feed pups but will even steal food from them (Malcolm and Marten, 1982). Consequently, in lean years, pup survival can be negatively affected by competition with non-breeders (Harrington et al., 1983). Similarly, in red wolves, pup mass and survival positively correlated with the presence of helpers at low population densities, but negatively correlated with pup mass (though not survival) at high population densities. Furthermore, whilst the presence of helpers increases the breeding females' lifetime reproductive success, it can decrease the males' (Sparkman et al., 2011a). In African wild dogs, yearlings and pack size can increase pup survival (Malcolm and Marten, 1982) and there seems to be a minimum pack size threshold below which packs face an increasing probability of extinction due to the need of helpers for hunting, defense, and reproduction (i.e., an Allee effect) (Courchamp and Macdonald, 2001; Angulo et al., 2013). However, there also seems to be an optimal upper limit to pack size above which the increased competition can decrease pup survival (Macdonald and Carr, 1989; Creel and Creel, 1995). Theoretical research shows that if subordinates are related to the dominant pair, they do not need to have a positive effect to be accepted as group members and can even have a slight negative effect, if ecological constraints are such that they are unlikely to survive or reproduce if expelled from the group (Kokko et al., 2002). Dominants can increase their net fitness by allowing unhelpful or even damaging subordinates to remain in a group if it means they survive and can later reproduce (Kokko et al., 2002). Retaining subordinates in a group is often more for their benefit than that of the dominant pair (Kokko et al., 2002).

Evolution of Social Monogamy

Phylogenetic studies suggest that social monogamy has evolved independently perhaps as many as 61 times in mammals (Lukas and Clutton-Brock, 2013). Historically, suggestions for factors influencing its evolution include the need for biparental care, infanticide protection, and male mate guarding, each of which is discussed below.

Need for Biparental Care

The association between paternal care, social monogamy, and pair bonding led to an early emphasis amongst scholars on the need for biparental offspring care as the adaptive

significance of monogamy (e.g., Orians, 1969; Kleiman, 1977; Wittenberger and Tilson, 1980; Kleiman and Malcolm, 1981; Clutton-Brock, 1989). These early hypotheses suggested that if females cannot successfully rear young without help and males cannot successfully divide care between multiple litters, both would benefit from social monogamy with biparental care (Kleiman, 1977; Wittenberger and Tilson, 1980; Kleiman and Malcolm, 1981; Malcolm, 1985; Birkhead and Møller, 1996). Canids typically have a single, large litter each year (modal litter size: 3–6, Hayssen et al., 1993) and young are altricial with a long dependency period, relative to other mammals (Asa and Valdespino, 1998; Lord et al., 2013). For example, it takes as long as 8 months for pups to reach independence in black-backed jackals, side-striped jackals (*Lupulella adusta*), African golden wolves and gray wolves (reviewed in Lord et al., 2013). The commonness of canid paternal care and the prolonged post-partum parental investment required thus supported these early views that the need for male help favored the evolution of canid monogamy (e.g., Kleiman, 1977).

However, several more recent phylogenetic analyses suggest mammalian paternal care likely evolved after monogamy and that paternal care is a consequence of social monogamy, not the cause (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013; Opie et al., 2013). If both sexes are monogamous for other reasons, paternal care may be the best option to improve fitness (Emlen and Oring, 1977; Lukas and Clutton-Brock, 2013), particularly as in this situation there is high paternity assurance (Trivers, 1972; Queller, 1997; Kvarnemo, 2005; Fromhage and Jennions, 2016). Similarly, rather than large litter sizes requiring paternal care, litter size and paternal care likely coevolved (Stockley and Hobson, 2016). Canid litter sizes can be highly variable and dependent on food availability (Geffen et al., 1996; Marino et al., 2006, 2012), supported by field experiments in Arctic foxes showing provisioning increases litter sizes (Angerbjörn et al., 1991, 1995). Coevolution of paternal care and litter size resulted in larger litters which require paternal and even alloparental care to survive (Stockley and Hobson, 2016). If the need for bi-parental care was not what caused social monogamy to evolve, it is likely crucial to its maintenance (Klug, 2018).

Female choice likely contributed to the evolution of paternal care (Kvarnemo, 2005; Lukas and Clutton-Brock, 2013; Lambert et al., 2018). Kvarnemo (2005) suggested that if females select males that care for young, this can explain the correlation often observed between paternity and male care but in the opposite direction of causation to that often suggested (i.e., caring males are more likely to sire offspring, rather than males that sire offspring are more likely to provide care). This hypothesis has received far less attention than the reverse direction of causation and has been little investigated in mammals (but see Freeman-Gallant, 1996; Kvarnemo, 2005, and Alonzo, 2012 for support from invertebrates, fish, and birds). Nonetheless, there is evidence in at least one mammal: in a group-living monkey where males exhibit extreme degrees of care often toward unrelated young (Campbell, 2019), males that provide more care experience greater future mating success the following

breeding season through female choice (Ménard et al., 2001). A male would therefore directly benefit from providing care, regardless of whether he cares for his own offspring or not. Sexual selection can therefore better explain cases where males care for unrelated young (e.g., red foxes: Baker et al., 2004; bat-eared foxes: Wright et al., 2010; wolves: Cassidy et al., 2016) than natural selection (Kvarnemo, 2005; Alonzo, 2012). However, this process would only be possible where females are able to assess males' investment in young before mating and bias mating toward those males (Alonzo, 2012). While this may not apply to the majority of socially monogamous taxa that display seasonal serial monogamy, finding new partners each year (see section Pair Bonding), the long-term partnerships of canids could allow females to bias paternity based on male care provided to the previous year's litter. Male canids can vary in the quality of paternal care bestowed (e.g., bat-eared foxes, Wright, 2006), making this trait subject to sexual selection. Furthermore, even with large litters, a female can compensate for the male's work when he is absent or reduces investment (although at apparent cost to her health and survival, therefore compromising potential future reproductive success) (Sacks and Neale, 2001; Cameron et al., 2011) and females may adjust effort according to litter size (Mech et al., 1999), supporting that male care can be a female preference, rather than pure necessity. Lambert et al. (2018) suggested that monogamy and paternal care co-evolved when selection initially favored affiliative males, which subsequently evolved into paternal care.

Protection Against Male Infanticide

It had been hypothesized that infanticide may select for social monogamy in mammals. If females deter infanticide by mating promiscuously to confuse paternity, males may counter by guarding mates to ensure paternity and protect offspring (e.g., Wolff and Macdonald, 2004; Lukas and Huchard, 2014). However, phylogenetic analysis across mammals concluded that social monogamy did not evolve from high infanticide levels and that social monogamy and infanticide seemingly evolved independently (Lukas and Clutton-Brock, 2013; Lukas and Huchard, 2014).

Male Mate Guarding

Several studies concluded, based on phylogenetic and empirical evidence, that mammalian social monogamy evolved where males could not defend multiple females (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013), such as when females are solitary and occupy exclusive ranges at low density (Emlen and Oring, 1977, but also see Dobson et al., 2010). High-quality but scarce or patchy resources likely provided the selective pressures leading to social monogamy by increasing female feeding competition, resulting in female territoriality and intolerance. If breeding is also seasonal and synchronized, as with most canids (Asa and Valdespino, 1998), the temporal availability of oestrous females is also limited, such that males cannot effectively guard more than one (Lukas and Clutton-Brock, 2013). This combination of factors, making it more

beneficial for males to monopolize their current partner than seeking others, is a powerful explanation for the evolution of mammalian social monogamy (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013).

Maintenance of Social Monogamy

Social monogamy should be maintained only if (a) it is the optimal strategy for both the male and female, or (b) it is the optimal strategy for one sex and enforcement mechanisms are employed to prevent their mate from adopting other strategies, referred to as “voluntary” and “enforced” monogamy, respectively (Kvarnemo, 2018).

Voluntary Monogamy: Monogamy as the Optimal Strategy

If bi-parental care is highly beneficial or necessary for offspring survival, social monogamy may be the optimal strategy for both sexes. Because most canids are seasonal breeders (Asa and Valdespino, 1998; Lord et al., 2013), investment in one female limits the investment males can make in another (Kleiman and Malcolm, 1981). In bat-eared foxes, the best predictor of the number and proportion of surviving young is the amount of male den attendance (rather than parental age/size, territory quality, and maternal den attendance) (Wright, 2006). Males spend 30–57% of their time at the den, and a 10% increase in attendance corresponds with a 16% increase in cub survival, with complete litter survival when a male spends 49% of his time at the den (Wright, 2006; Wright et al., 2010). Males therefore cannot care for litters at two dens without severely sacrificing offspring survival at one or both. Similarly, male raccoon dogs may be required to keep pups warm while the female forages (Kauhala et al., 1998) and in black-backed jackals, an entire litter died following the male's death (Moehlman, 1986).

Enforced Monogamy: Reproductive Suppression of Subordinates

In group-living canids, social monogamy is commonly enforced by reproductive suppression of subordinates (Moehlman, 1989; Creel and Creel, 1991; Creel and Macdonald, 1995; Moehlman and Hofer, 1997; Asa and Valdespino, 1998). In a review of 25 canid species, Moehlman and Hofer (1997) found reproductive suppression in 44%. The mechanism often involves copulation interference and aggression toward same-sex individuals attempting to breed (e.g., gray wolf, Rabb et al., 1967; Derix et al., 1993; African wild dog: Malcolm, 1979; red fox: Macdonald, 1979a) and infanticide, either by directly killing subordinates' pups (African wild dog: van Lawick, 1973; dingo [*C. familiaris dingo*]: Corbett, 1988) or indirectly, such as interfering with provisioning of subordinates' pups (African wild dog: Frame et al., 1979) or causing subordinate mothers to become so excessively anxious that their offspring die from the mother's fretfulness (red fox: Macdonald, 1979a; bush dog: Macdonald, 1996).

Physiological mechanisms of reproductive suppression are less documented in canids, but there is evidence for them (e.g.,

African wild dog: Creel et al., 1997; coyote: Moehlman and Hofer, 1997; Spiering et al., 2010; Ethiopian wolf: van Kesteren et al., 2012, 2013). In Ethiopian wolves, typically only the dominant females breed during a short mating season (Sillero-Zubiri et al., 1998). A study of adjacent Ethiopian wolf packs demonstrated increased oestradiol concentration in feces from eleven dominant females but not in the nine subordinates sampled and no aggression from the dominant female preventing subordinate breeding was documented, indicating hormonal suppression of subordinate females (van Kesteren et al., 2013). Although female gray wolves can breed as yearlings (Medjo and Mech, 1976), they rarely do in the wild before age three, suggesting subordinate females may experience delayed maturation or suppressed oestrus. In African wild dogs, subordinate females were hormonally suppressed, preventing ovulation likely by elevated estrogen and estrogen/progestin ratios (Creel et al., 1997). However, the detailed physiological mechanisms involved in reproductive suppression remain unclear in many species; increased glucocorticoids from social stress is a mechanism of reproductive suppression in some other taxa (e.g., Hackländer et al., 2003), but no evidence of this has been found in canids (African wild dog: Creel et al., 1997; van Kesteren et al., 2013). Glucocorticoid levels in female African wild dogs did not differ according to dominance status (average fecal glucocorticoid concentration for dominant breeding females during the mating season was 207.47 ± 43.69 (SE) ng/g while for subordinate non-breeding females it was 202.5 ± 52.3 ng/g), suggesting other mechanisms were responsible for reproductive suppression (van Kesteren et al., 2013).

Reproductive suppression of subordinates may not be solely for the benefit of the dominant pair. Packard et al. (1983) suggest that deferred reproduction in gray wolves could have evolved by individual selection, as future reproductive fitness may be enhanced by remaining longer in a juvenile role in the native pack. Similarly, delayed dispersal in red wolf males lowers mortality, thereby increasing the chances of becoming reproductive (Sparkman et al., 2011b). Kokko and Johnstone (1999) showed that the delayed benefits of acquiring dominant status in the future (“social queuing”) can provide enough incentive for subordinates to remain peacefully in a group without themselves breeding. Additionally, if larger groups experience greater survival (e.g., African wild dogs, Carbone et al., 1999), individuals may experience greater benefits by remaining as a non-breeding subordinate and helping to raise new group members, rather than dispersing to breed alone (Kokko et al., 2001). Furthermore, subordinates increase their inclusive fitness by helping to raise and improve the survival of their parents' next litter, since they are on average as closely related to their siblings as they would be to their own offspring (Moehlman, 1983, 1986).

Social dominance may play a role in reproductive suppression. Macdonald (1979a, 1987) reported that, although normally only the alpha red fox female bred, when the dominance status of the previously-alpha female waned until becoming equal with another vixen in the group, both conceived the following year. Similarly, Zabel (1986) observed that although a clear dominance relationship existed between dominant breeding females and

submissive non-related helpers, social groups with two breeding females had no obvious female dominance hierarchy.

Subordinate reproduction can also be thwarted by expelling them from the group (Jungwirth and Johnstone, 2018) or not allowing subordinates to join (e.g., females “floating” on the periphery of Ethiopian wolf groups, Sillero-Zubiri et al., 1996a; male bat-eared foxes are aggressively territorial toward young males that intrude on the territory, Maas and Macdonald, 2004). Intrasexual aggression is common in canids (e.g., Rabb et al., 1967; Kleiman and Malcolm, 1981; Zabel, 1986), as is the expulsion of same-sex subordinates. The pros and cons of tolerating additional group members are explored by Macdonald and Carr (1989). In Ethiopian wolf packs with more than one subordinate female, the mother expelled the lowest-ranking female at 18–28 months old, with assistance from the dominant sister (Sillero-Zubiri et al., 1996a). Similarly, pregnancy in subordinate Ethiopian wolves can result in pack splitting, thus restoring social monogamy (Marino et al., 2013).

Interestingly, one strategy for subordinate females to avoid reproductive suppression is to raise a litter at the edge of their parent's territory, typically with a subordinate male from a neighboring group, seen in crab-eating foxes (Macdonald and Courtenay, 1996), red foxes (Baker et al., 2000), black-backed jackals (Kamler et al., 2019) and gray wolves (Mech and Boitani, 2003). In this way, subordinates may get the best of both worlds by avoiding risky dispersal into unknown areas yet allowing reproduction. However, the tolerance of alphas letting betas raise litters and use their territory edges might vary according to food abundance and dispersion and kinship.

Ecological Correlates of Social Monogamy

Social monogamy is maintained because either it is the optimal strategy for both sexes, or because polygamy (incl. polygyny, polyandry, polygynandry) is restricted due to monogamy enforcement mechanisms or ecological conditions. Ecological conditions can shift monogamy to other social systems, either by affecting the benefits (motivations) of social monogamy itself or by affecting the ability to enforce it (summarized in Table 1).

Resource Availability: Paternal Care and the Polygyny Threshold Model

One of the primary benefits of social monogamy in canids is benefits to offspring survival due to biparental care (Moehlman, 1989), though resource availability affects the degree to which male care is both necessary and feasible: when resources are plentiful, females may successfully raise pups with less male input (Maas, 1993) and males are able to provide more paternal care (Wright, 2006). The polygyny threshold model (Verner, 1964, Verner and Willson, 1966, Orians, 1969) posits that there is a threshold at which a female can raise as many young sharing a male and territory of higher quality (in a polygynous system) as she could being the sole female with an inferior male/territory (in a monogamous system). Thus, if male help is required and a male cannot share care between multiple litters without decreasing the quality and offspring survival below what could be achieved with his full attention on a single litter, monogamy would be the optimal strategy. If, however, resources are such

TABLE 1 | Correlates of social and genetic monogamy in canids.

Correlate	Summary
Social monogamy vs. alternative strategies	
Resource availability	High resource availability reduces the probability of social monogamy by either reducing reliance on male care of infants and thus the benefits of monogamy or by allowing males to provision multiple litters.
Social Structure	The costs and benefits of canid group formation are influenced by many ecological factors (e.g., resource availability/dispersion, prey size, inter- and intraspecific competition, predation pressure, population density, territory availability). Larger social groups are less likely to exhibit social monogamy.
Genetic monogamy vs. extra-pair mating	
Resource availability	High resource availability reduces reliance on male care of infants and thus the potential cost of reduced male investment from engaging in extra-pair mating.
Diet: Foraging strategy	Canids that can forage with their mate can more effectively mate guard, whereas canids that must forage solitarily to reduce food competition have more opportunity to engage in extra-pair mating.
Diet: Time budget	Canids that must allocate more time to foraging (e.g., insectivorous species) have less time available to seek extra-pair mates.
Population density	High population density increases the availability of extra-pair mates and reduces potential costs of seeking extra-pair mating (reducing distances between individuals, increasing encounter rate and the probability of finding extra-pair mate).
Social structure	More potential breeders in a group increases the probability of extra-pair mating. As with population density, the costs of embarking on extra-territorial forays are reduced if extra-pair mating is within the group.

that a female can raise as many offspring in a polygynous system, either because male help is less needed or because a male can provision multiple litters as well as he could one, the “polygyny threshold” can be crossed. Supporting this, Zabel and Taggart (1989) report that when food availability was high, 71% of the island population of red foxes they studied were bigamous, i.e., a single male cared for the litters of two females, and bigamous females had equal or greater (1.4 times) reproductive success than monogamous females when considering offspring survival in the first year (mean litter size of 4.3 ± 0.29 in bigamous vs. 4.0 ± 1.0 in monogamous females, Zabel and Taggart, 1989). However, when the food supply crashed, the population shifted entirely to monogamy. Red foxes in Sweden also displayed polygyny with multiple breeding females when prey availability was high but a single breeding female when prey availability was low (von Schantz, 1984, see also West, 2014). Similarly, food availability influenced the probability of forming larger groups across four populations of arctic fox, with variations including polygyny, plural breeding and communal breeding where food abundance differed substantially between years, whereas social monogamy

is found in areas of stable resources (Angerbjörn et al., 2004; Elmhagen et al., 2014) and in marginal habitats with low food availability (Norén et al., 2012; Elmhagen et al., 2014).

Social Structure

As described in **Box 1**, canid social monogamy is not restricted to pair-living individuals but also includes group-living variations where social groups contain a single breeding male and female, in addition to non-breeding group members. Alternatively, canid groups may exhibit polygyny, polyandry, or polygynandry with multiple breeding adults. Social monogamy is, unsurprisingly, most common in smaller social groups (Clutton-Brock and Isvaran, 2006; Spiering et al., 2010). A greater availability of potential breeders is more difficult for the dominant pair to suppress (Marino et al., 2013). Spiering et al. (2010) found that many packs of African wild dogs contain only one adult female and thus inevitably only one breeding female. However, in the 30% of groups containing subordinate females, only half were socially monogamous: beta females also bred in 54.5% of years, though theta females never bred. In contrast, subordinate males always secured some paternity, but were only present in 47% of groups. Similarly, in bat-eared foxes studied by Maas and Macdonald (2004), social monogamy depended on the number of females in the group—additional females invariably bred, and in only 1 of 65 breeding events was there a non-breeding adult male in the group. In Ethiopian wolves, packs recovering from disease outbreak can become unusually large and contain more than two subordinate females, increasing the likelihood of pregnancy in subordinate females (Marino et al., 2013).

The mechanisms shaping sociality in carnivores, and in canids specifically, have been reviewed elsewhere (e.g., Macdonald, 1983; Creel and Macdonald, 1995; Macdonald and Sillero-Zubiri, 2004; Macdonald et al., 2004). Canid groups generally form by retention of offspring that do not disperse (e.g., black-backed jackal: Moehlman, 1979, 1983; red fox: Macdonald, 1980; arctic fox: Hersteinsson and Macdonald, 1982; kit fox: Ralls et al., 2001; bat-eared fox: Maas and Macdonald, 2004; hoary fox: Courtenay et al., 2006; Kamler et al., 2013b, 2019; Cape fox: Kamler and Macdonald, 2014) and thereby avoid dispersal costs (Bekoff and Wells, 1982; Macdonald and Carr, 1989; Lucas et al., 1994; Kamler et al., 2019). This results in family groups, though unrelated individuals can sometimes join existing groups (e.g., red fox: Zabel and Taggart, 1989; gray wolf: Jedrzejewski et al., 2005). Macdonald and Carr (1989), drawing heavily on canid examples, presented a profit and loss account of tolerating additional group members. A primary cost is food competition (Schmidt and Mech, 1997; Creel and Creel, 2002), but the list also includes increased risk of infectious disease (e.g., rabies, Macdonald and Bacon, 1982; Loveridge and Macdonald, 2001) and parasite transmission (Hoogland, 1979), and mate sharing (Zabel and Taggart, 1989; Spiering et al., 2010).

The adaptive functions of canid groups include greater hunting success (e.g., African wild dogs: Fanshawe and Fitzgibbon, 1993; Creel and Creel, 1995) and capacity to tackle larger prey (Fanshawe and Fitzgibbon, 1993). Larger African wild dog groups better defend food against spotted hyenas (*Crocuta crocuta*, Fanshawe and Fitzgibbon, 1993; Carbone et al., 2005),

larger golden jackal groups can steal food from smaller groups (Macdonald, 1979b) and packs of dholes can steal prey from leopards (Venkataraman and Johnsingh, 2004). Larger groups also benefit territory defense, as victory in intergroup contests generally goes to the larger group (e.g., Ethiopian wolves: Sillero-Zubiri and Macdonald, 1998; Marino et al., 2012; gray wolves: Cassidy et al., 2017). Grouping can also increase breeding success through alloparental care (e.g., Moehlman, 1979) and decreased predation vulnerability (Kamler et al., 2013a). Sociality can also provide thermoregulatory, energetic and physiological benefits through social thermoregulation (Campbell et al., 2018). Though social thermoregulation is little studied in canids, Hennemann et al. (1983) found that crab-eating foxes reduced heat loss and oxygen consumption (a measure of basal metabolic rate) by 5–18% when huddling with a partner, suggesting huddling can significantly impact daily energy expenditure in this and other canid species (Hennemann et al., 1983).

Large prey can favor cooperative hunting and larger groups (e.g., coyotes: Bowen, 1981). Intense intraspecific and interspecific competition and predation may favor group formation for strength in numbers: recolonizing gray wolves, displaying intra-guild aggression toward coyotes, led coyotes to form larger groups (Arjo and Pletscher, 1999) and higher jackal numbers increased bat-eared fox group sizes (Kamler et al., 2013a). Similarly, arctic foxes tend to form complex groups when facing greater predation pressure from red foxes (Norén et al., 2012) and a mother-daughter pair merged their litters into one den when facing red fox predation, despite low food availability at the time (B. Elmhagen, unpublished data, from Norén et al., 2012).

The costs of dispersal increase when the journey is hazardous and/or the availability of vacancies is low (Ballard et al., 1987; Norén et al., 2012). Therefore, population density, likely linked to food availability, affects the advantages of group formation such that polygamy can be associated with high population density (e.g., swift foxes, Kamler et al., 2004a; red foxes, Baker et al., 2004; Iossa et al., 2008a; gray foxes, Weston Glenn et al., 2009). Iossa et al. (2008a) found 60% of red fox groupings were socially monogamous at low population density but 23% at high population density. Similarly, in swift foxes at high population density from low predation pressure, 30% of social groups exhibited polygyny with communal denning and 40% included non-breeding females (in 10 social groups), whereas in low density/high predation pressure, only monogamy was observed, with no non-breeding helpers (16 groups, Kamler et al., 2004a).

Finally, group formation may occur not only when groups are beneficial or dispersal is costly, but rather when grouping carries little cost (Macdonald and Carr, 1989; Macdonald and Johnson, 2015). The resource dispersion hypothesis (RDH, Macdonald, 1981, 1983; Carr and Macdonald, 1986) posits that when resources are dispersed heterogeneously, the minimum territory needed to meet a breeding pair's resource requirements can often support additional group members with little or no cost to the dominant pair. Greater heterogeneity leads to larger group sizes. Macdonald (1980, 1987) reviewed the early literature to show that monogamous red fox pairs are associated with spatio-temporally homogeneous resources (e.g., farmlands

of USA Midwestern states, Storm et al., 1976), often at low population density, whereas groups more commonly form where food availability is more spatio-temporally heterogeneous and foxes that exploit cyclic rodent populations may accommodate additional group members in peak rodent years (Macdonald, 1984; von Schantz, 1984; Elmhagen et al., 2014; see also Macdonald et al., 2016). Similarly, if the cost of tolerance is low, its benefits may be minimal: Geffen and Macdonald (1992) report dominant Blanford's fox pairs tolerating non-breeding subordinate vixens, but found no evidence that they act as helpers.

The balance of these costs and benefits of group formation, determined by local ecological conditions, will therefore influence the social structure of canids and thus whether they exist as a socially monogamous pair, one of the variations on social monogamy described above, or depart from monogamy altogether.

CONTRASTING CANID SOCIAL AND GENETIC MATING SYSTEMS: POTENTIAL FUNCTIONS AND ECOLOGICAL CORRELATES OF EXTRA-PAIR MATING IN CANIDS

Social monogamy is no guarantee of genetic monogamy, i.e., exclusive mating (Klug, 2018; Lambert et al., 2018), and, indeed, almost every genetically studied canid species has revealed extra-pair paternities (EPP) (see Hennessy, 2007 for an exception). For example, extra-pair males sired 25% of 16 offspring in Island foxes (Roemer et al., 2001), 52% of 19 offspring from 15 litters in swift foxes (Kitchen et al., 2006), 31% of 176 offspring in arctic foxes (Cameron et al., 2011) and in red foxes from 38% of 38 offspring (Iossa et al., 2008b) to as much as 80% of 30 offspring (Baker et al., 2004). Many of these examples are drawn from pairs, rather than larger social groups.

In group-living canids, extra-pair mating can occur both within-pack and with extra-pack individuals. In Ethiopian wolves, despite the dominant pair's apparent social monogamy, extra-pair copulations (EPC) happen both within (rarely) and outside (more commonly) the pack (Gottelli et al., 1994): Sillero-Zubiri et al. (1996a) observed that 70% of copulations were between a female and male in adjoining packs and Randall et al. (2007) found that 50% of litters had offspring sired by an extra-pack male, with 28% of offspring with resolved paternities sired by extra-pack males. Though red wolves were found to be highly genetically monogamous, with only 4 of 174 litters (2%) showing EPP, these rare cases included extra-pair mating within and outside of the pack (Sparkman et al., 2012). In contrast, two studies in African wild dogs found that, although extra-pair mating was common, extra-pack males never sired offspring (of 226 offspring, Spiering et al., 2010, and 39 offspring, Moueix, 2006); when subordinate males existed in a pack, levels of mixed paternity in litters were 53% (of 15 litters, Spiering et al., 2010) and 100% (of 5 litters, Moueix, 2006).

Benefits and Costs of Genetic Polygyny

For males, whose reproductive success is generally limited by access to females, the benefit of extra-pair mating is obvious: mating with additional females can directly increase reproductive success by producing more offspring, and especially when these are cared for by another male. For example, male red foxes studied by Baker et al. (2004) sired more offspring with extra-pair females than with their social mate and traveled as far as 2.7 territories away during extra-territorial forays; consequently, they could have sired offspring in as many as 32 neighboring groups (Baker et al., 2004). Such males benefit doubly, genetically and from the parental investment of cuckolded males, thus extra-territorial forays are widely recorded amongst canids during the courtship and mating periods (e.g., Macdonald, 1981; Zoellick and Smith, 1992; Baker et al., 2004; Deuel et al., 2017; Kamler et al., 2017, 2019). However, the costs of male philandering include leaving their mate unguarded and therefore increasing their own risk of being cuckolded, increased exposure to sexually transmitted disease and parasites (Poiani and Wilks, 2000; McLeod and Day, 2014), and risks of mortality, predation, intraspecific conflict and stress when traveling in unfamiliar areas (Harris and Smith, 1987; Young and Monfort, 2009).

Benefits of Genetic Polyandry

For females, whose reproductive output is limited, the benefits of extra-pair mating are less obvious. Various hypotheses have been proposed to explain why females engage in extra-pair mating (summarized in Table 2).

Increase Genetic Quality

A favored explanation for extra-pair mating in birds is increased genetic fitness of offspring by mating with the highest quality

TABLE 2 | Potential functional explanations for extra-pair mating by female canids.

Functional hypothesis	Support in canids
Increase genetic quality	Some support. Extra-pair mating is biased toward more dominant or larger males in some canids; may depend on circumstances/species.
Increase genetic diversity	Could be a common motivation. Extra-pair mating is generally associated with multiple paternity in canids.
Inbreeding avoidance	Little support. Social pairs are generally unrelated so other mechanisms may be responsible for inbreeding avoidance, and breeding with close relatives can occur both with social mates and extra-pair mates in canids.
Infanticide protection by paternity confusion	Little support, unlikely. Infanticide does not increase males' breeding opportunities because canids breed seasonally and annually; little evidence that male canids engage in infanticide.
Fertilization assurance	Could be a common motivation due to canid monoestrus, but has not been studied.
Increased alloparental care by paternity confusion/dilution	Unlikely to apply to most cases where extra-pair mating with individuals outside the social group, but may be relevant when extra-pair mating is within the group.

males (Birkhead and Møller, 1996; Jennions and Petrie, 2000; Westneat and Stewart, 2003). In monogamous social systems where most individuals are paired, mate choice is constrained and thus most females would be partnered with suboptimal males. The majority of females would therefore benefit from seeking EPC with superior males. This may be the motivation for extra-pair mating by female red foxes studied by Iossa et al. (2008a,b). Red fox females typically engaged in EPC with dominant males from adjoining territories (Iossa et al., 2008a) and extra-pair males that sired offspring were always larger than the female's cuckolded social partner (Iossa et al., 2008b). By mating with males of higher quality than their partner, females can increase the genetic quality of their offspring. Similarly, three of four cases of EPP observed in Island foxes were by the two largest males in the study (Roemer, 1999, 2004), suggesting females engaged in extra-pair mating with high-quality males. Furthermore, multiple mating may also increase genetic quality of offspring by inciting sperm competition and allowing cryptic female choice (e.g., Kvarnemo and Simmons, 2013; Annavi et al., 2014).

Genetic quality, however, is not the only factor, as illustrated by female Ethiopian wolves that mate outside their pack being notably unselective about the dominance status of these mates (Sillero-Zubiri et al., 1996a; Randall et al., 2007) and similar observations of other red foxes being unselective outside, but selective within, the group in regards to male dominance status (Baker et al., 2004). While it is possible that females select for genetic quality using indicators other than dominance status (which is often influenced by size, health, strength), these studies suggest that, at times, other explanations are involved besides quality of the extra-pair mates (especially considering females are likely well-informed of their neighbours' social status). The case of Bristol's urban red foxes is revealing in showing how motivations for extra-pair mating can change: in 1992–1994, females appeared to be unselective in the quality of extra-group males, mating with both dominant and subordinate males (Baker et al., 2004). In 1994–1996, the population declined by 80% due to mange (Baker et al., 2000; Iossa et al., 2008a). Subsequently, in 2002–2004, females became highly selective, reducing the frequency of extra-pair mating and mating only with males that appeared to be of higher quality than their social mate (Iossa et al., 2008b). Furthermore, rates of mixed paternity dropped from 38–69% pre-outbreak to 0% post-outbreak (Baker et al., 2004; Iossa et al., 2008b). Thus, it seems that following substantial pressure from disease, females changed their reproductive strategy to emphasize genetic quality, which may increase the probability of their offspring surviving disease.

Increase Genetic Diversity

Canid litters can be sired by multiple males. Thus, polyandry might function to increase within-litter genetic diversity (Yasui, 1998; Jennions and Petrie, 2000; Slatyer et al., 2012). This was proposed to explain polyandry in arctic foxes, where 26% of litters were sired by multiple males (Cameron et al., 2011). In fluctuating environments, such as the harsh arctic, the fittest genes may be unpredictable and thus increased within-litter genetic diversity may increase the probability that at least some offspring survive (Yasui, 1998; Jennions and Petrie, 2000). The

majority of cases where female canids engage in EPC result in mixed paternity litters (e.g., Baker et al., 2004; Moueix, 2006; Randall et al., 2007; Spiering et al., 2010; Cameron et al., 2011; Converse, 2013, but see Iossa et al., 2008a,b and Cameron et al., 2011 for exceptions). Increased within-litter genetic diversity may therefore be a common motivation for extra-pair mating in canids.

Inbreeding Avoidance

Extra-pair mating may function to prevent inbreeding (Stockley et al., 1993; Jennions and Petrie, 2000; Tregenza and Wedell, 2002; Annavi et al., 2014; Arct et al., 2015). This may be particularly important where territories are inherited by successive generations or there is a lack of dispersal (e.g., Ethiopian wolf, Sillero-Zubiri et al., 1996a; bat-eared fox, Maas and Macdonald, 2004), leading to highly related groups. However, in most canids that have been genetically investigated, mated pairs are generally unrelated (e.g., African wild dog: McNutt, 1996; Girman et al., 1997 [average relatedness of social pairs: 0.05 ± 0.11 , $N = 5$]; gray wolf: Smith et al., 1997 [0.01 ± 0.14 , $N = 16$]; arctic fox: Cameron et al., 2011 [0.01 ± 0.14 , $N = 13$]; kit fox: Ralls et al., 2001 [-0.07 ± 0.07 , $N = 10$]; coyote: Hennessy, 2007 [0.00 ± 0.14 , $N = 7$]; swift fox: Kitchen et al., 2006 [-0.01 ± 0.23 , $N = 48$]; red wolf: Sparkman et al., 2012, $R < 0.50$ for 95% of 174 mating events). Although there are occasional instances where social pairs are closely related (e.g., Hennessy, 2007: 1/7 coyote pairs, $R = 0.26$; Kitchen et al., 2006: 1/48 swift fox pairs, $R = 0.48$; Weston Glenn et al., 2009: one gray fox pair, $R = 0.36$; Roemer, 1999: 4/15 Island fox pairs, $R = 0.19$, 0.35 , 0.35 , 0.52 ; Jedrzejewski et al., 2005: one gray wolf half-sibling pair), there are also cases where extra-pair mating occurs between relatives. For example, Baker et al. (2004) found four incestuous EPPs between close relatives with experiential histories (mother-son for 2 years, father-daughter, and half-brother-half-sister) and three additional pairings between more distantly related individuals (e.g., $R = 0.13$) in red foxes, Cameron et al. (2011) found one incestuous mother-son case of EPP (of 13 mated pairs, 7.6%) between arctic foxes that were socially paired with non-relatives, and Sparkman et al. (2012) found 4 parent-offspring and 4 full-sibling matings (of 174 mated pairs, 9%). There may be greater risk of this where there is neighborhood settlement by dispersers, as in crab-eating foxes (Macdonald and Courtenay, 1996), bat-eared foxes (Kamler et al., 2013b), swift foxes (Kitchen et al., 2005b) and black-backed jackals (Kamler et al., 2019). When it has been investigated, relatedness between social mates and extra-pair mates did not differ (e.g., Cameron et al., 2011: mean \pm SD relatedness between social mates: 0.05 ± 0.12 , $N = 9$; between extra-pair mates: -0.09 ± 0.11 , $N = 4$). It therefore seems that canids achieve inbreeding avoidance by other mechanisms, such as avoiding mating within ones' natal pack, sex-biased dispersal and adult dispersal (Kamler et al., 2004c, 2013b; Geffen et al., 2011; Sparkman et al., 2012; Kamler and Macdonald, 2014).

One exception, however, could be in Ethiopian wolves. A lack of dispersal opportunities from shrinking habitat, coupled with male philopatry, results in highly related packs (Sillero-Zubiri et al., 1996a; Randall et al., 2007). Sillero-Zubiri et al. (1996a)

observed that the majority (70%) of copulations by female Ethiopian wolves were with males from adjoining packs, rather than her own pack, and thus extra-pack mating was suggested to be an inbreeding avoidance strategy. Females rejected advances from all males within their packs except those from the alpha male, yet were unselective concerning the status of extra-pack males with which they mated, suggesting outbreeding was of importance rather than mate quality (Sillero-Zubiri et al., 1996a). However, subsequent research found that, although packs are indeed highly related (mean pairwise relatedness within packs was 0.39) and there is a high prevalence of incestuous pairing (22% of mating pairs within packs were closely related [$R = 0.18-0.44$]), members of neighboring packs were also closely related so incestuous pairing occurred with both within-pack and extra-pack mating (33% of extra-pack mating pairs were closely related [$R = 0.42-0.44$]). In this case, female dispersal appears to contribute more than extra-pack mating to reduce inbreeding (Randall et al., 2007). Was this an artifact of the unusual, modern, circumstances of these wolves? Perhaps extra-pack mating evolved as an inbreeding avoidance strategy, but modern conditions, exacerbated by recurrent rabies outbreaks (Mebatsion et al., 1992; Sillero-Zubiri et al., 1996b; Whitby et al., 1997; Randall et al., 2004, 2006; Marino et al., 2006), changes in dispersal and demographic events led to neighboring packs and breeding pairs being more closely related than during evolutionary time (Randall et al., 2007).

Infanticide Protection by Paternity Confusion

Based on evidence across 33 mammal families, Wolff and Macdonald (2004) concluded that the most convincing explanation for polyandry across mammals is paternity confusion to deter infanticide. This hypothesis, originally proposed by Hrdy (1974, 1979), relies on female promiscuity being an effective counterstrategy against male infanticide (Lukas and Huchard, 2014) and predicts that females mate with many males. However, a complication is that, in contrast to some taxa (notably felids, see Macdonald et al., 2010), male infanticide in canids would not hasten female oestrus because most canids are seasonal breeders (Asa and Valdespino, 1998; Valdespino et al., 2002; Lord et al., 2013), notwithstanding some possible exceptions in African wild dogs (Frame et al., 1979), bat-eared foxes (Rosenberg, 1971), and bush dogs (Porton et al., 1987). This raises the question of what male canids could gain by infanticide. Indeed, amongst canids infanticide appears most commonly practiced by females (e.g., African wild dog: van Lawick, 1973; coyote: Camenzind, 1978; dingo: Corbett, 1988; gray wolf: McLeod, 1990; Ethiopian wolf: Sillero-Zubiri et al., 1996a; Girman et al., 1997), either as suppression of subordinate breeding attempts by the dominant female (Corbett, 1988; McLeod, 1990; Sillero-Zubiri et al., 1996a; Girman et al., 1997) or perhaps to increase availability of breeding territories or dens (see Zabel, 1986). Although examples of male infanticide are numerous amongst ursids and felids (e.g., Loveridge et al., 2007), we know of none in canids. The closest reports seem to be a description of a lone female red fox being harassed by males who intruded on her den and eventually the entire litter died (Zabel, 1986; Zabel and Taggart, 1989) and Latham and Boutin

(2011) suggested that the death of a gray wolf pup may have been infanticide by a male, though the evidence was inconclusive and might best be explained by intergroup resource competition. Furthermore, in contrast to infanticidal male takeovers in other taxa (e.g., Loveridge et al., 2007), quite the opposite has been reported in gray wolves: when a new and unrelated alpha wolf takes over a pre-existing pack, he provisions and cares for pups that are not his own, which may increase his acceptance by the pack (Cassidy et al., 2016). Thus, paternity confusion to prevent infanticide is an unconvincing explanation for extra-pair mating in canids.

Fertilization Assurance

Females may engage in EPC for fertilization assurance to guard against male infertility (Wetton and Parkin, 1991; Hoogland, 1998; Hasson and Stone, 2009). Canids are unusual among Carnivora in that they are monoestrous, having only one ovulation event each season (Asa and Valdespino, 1998; see section Monoestrus), making the stakes high if a female's mate is infertile. Multiple mating may guard against this possibility.

Alloparental Care From Paternity Confusion/Dilution

In communal or cooperative breeding situations, selective female promiscuity with group members could be beneficial by confusing or diluting paternity and thus potentially increasing offspring care, particularly when paternal care is indivisible. This would not apply to most cases of EPC in canids where mating occurs outside of the social group (e.g., Sillero-Zubiri et al., 1996a; Baker et al., 2004). However, in African wild dogs, despite previous beliefs that only the alpha pair breeds, research found females frequently mate with subordinate males and documented high levels of paternity sharing, though none of the offspring analyzed (39 pups, Moueix, 2006; 226 pups, Spiering et al., 2010) were sired by extra-pack males. Spiering et al. (2010) found that the three top-ranking males always sired pups, or, if there were only two males in a pack, they shared the litter's paternity equally (similarly see Moueix, 2006). Male African wild dogs invest heavily in offspring care (Creel et al., 2004) so by mating with multiple males in a group, females may dilute paternity and increase the amount of care for her offspring while also increasing within-litter genetic diversity.

Costs of Genetic Polyandry

Like males, females engaging in extra-pair mating risk increased exposure to sexually transmitted disease and parasites (Poiani and Wilks, 2000; McLeod and Day, 2014) and increased stress (Young and Monfort, 2009) and mortality (Harris and Smith, 1987). Additionally, females may lose investment in her offspring by her mate or other group members.

Loss of Paternal Care

If males adjust investment according to confidence in paternity (Trivers, 1972; Møller and Birkhead, 1993; Sheldon, 2002), females should be less likely to seek EPCs when paternal care is important (Mulder et al., 1994; Westneat and Stewart, 2003; Lambert et al., 2018). Such reduced paternal investment by males with unfaithful partners is observed in arctic foxes: Cameron et al.

(2011) found that, in faithful partnerships, den attendance rates were similar for males and females, whereas cuckolded males showed a 56% reduction in den attendance compared to non-cuckolded males and a non-significant 52% reduction in food provisioning. Overall rates of food provisioning did not differ between litters, meaning greater burden of care was placed on unfaithful females. The potential costs to males were substantial: 11% of litters were cared for by a male that did not sire any of the offspring. In contrast, in bat-eared foxes, cuckolded males did not invest less than other males (Wright et al., 2010). One explanation for this difference is that, because canids can have mixed paternity litters, when male care is indivisible among pups, such as vigilance against predators, females may be able to get away with some EPP without reducing male investment. Amongst bat-eared foxes, male den attendance is important and cannot be split amongst the young, whether sired by that male or not; conversely, food provisioning by male arctic foxes could be preferentially directed toward their own progeny, although this is untested (Wright et al., 2010; Cameron et al., 2011). However, this presupposes males can recognize their own offspring, which may be unlikely considering success of cross-fostering in coyotes (Kitchen and Knowlton, 2006), red wolves (Gese et al., 2015), gray wolves (Goodman, 1990; US Fish Wildlife Service, 2004) and dingoes and African wild dogs (Kitchen and Knowlton, 2006) and cases where cuckolded male foxes care for litters sired entirely by other males (Baker et al., 2004; Cameron et al., 2011). An alternative explanation for this difference between arctic and bat-eared foxes relates to the potential risk and costs. Comparative research across taxa suggests males reduce investment when cuckolded only when there is high cost and high risk of cuckoldry (Griffin et al., 2013). EPP was twice as frequent in arctic foxes as in bat-eared foxes and arctic males faced high potential costs of caring for litters sired entirely by other males (Wright et al., 2010; Cameron et al., 2011). A third explanation relates to female choice: if females preferentially mate with males that provide care, males can increase future breeding success by caring even for unrelated young (Kvarnemo, 2005; Alonzo, 2012; see section Need for Biparental Care). If females adjust the amount of extra-pair mating according to levels of male care (as in some birds: Freeman-Gallant, 1996), this can even paradoxically result in greater male investment when cuckolded to avoid losing future breeding opportunities.

Loss of Alloparental Care

A similar potential cost to engaging in extra-pair mating is the possible loss of alloparental care by philopatric young (who might otherwise be assumed to be related to new pups as full sibs). However, although there is little research on how EPP affects alloparental care, increased inclusive fitness is not the only motivation for alloparenting. Helpers are not always related to pups (Zabel, 1986) and may receive other benefits, such as inheritance of dens/territories (Lindström, 1986; Zabel, 1986; Kokko et al., 2002; Marino et al., 2012, 2013; Converse, 2013) or dominance status (Baker et al., 1998; Kokko and Johnstone, 1999), or where individuals achieve greater fitness by being in larger groups (e.g., African wild dogs: Carbone et al., 1999), thus making alloparental care beneficial even when

helpers are unrelated to the young ("group augmentation"; Kokko et al., 2001).

Ecological Correlates of Extra-Pair Mating

Ecological conditions can affect the balance of these costs and benefits of extra-pair mating and thus its prevalence (summarized in Table 1).

Resource Availability and Reliance on Paternal Care

When resources are abundant, offspring survival may be less dependent on male care and thus the potential costs of EPCs may be outweighed by potential benefits (Norén et al., 2012). Though desirable, there are cases where paternal care is not essential and females can at least sometimes raise litters without male assistance (e.g., bat-eared fox: Maas, 1993; coyote: Sacks and Neale, 2001; swift fox: Kamler et al., 2004b; cape fox: Kamler and Macdonald, 2014). This leads to the prediction that in socially monogamous species with biparental care, EPCs should increase with increased resource availability; a prediction supported for birds (Møller, 2000; Griffith et al., 2002). A comparative analysis of 15 mammal species (including three canids) found that rates of EPP correlated with levels of paternal care (Huck et al., 2014; see also Dillard and Westneat, 2016). Similarly, EPCs may be more common in mammals than in birds because paternal care is more common in birds (Isvaran and Clutton-Brock, 2006).

Within canids, among the lowest reported values of EPP thus far found is in bat-eared foxes (9.8–15.6%, Wright et al., 2010), a species wherein male care can be highly beneficial for offspring survival (Wright, 2006). The frequency of EPP in arctic foxes studied by Cameron et al. (2011) was argued to reflect variations in the need for paternal care: EPP correlated with spatial variation in food availability, being more frequent when closer to a goose colony. However, this study did not control for effects of population density, which often correlates with resource availability (e.g., Clark, 1972; White and Garrott, 1997) and thus could have been responsible for greater EPP closer to the goose colony. However, this hypothesis was not supported in a study of urban coyotes, wherein despite optimal food availability, pairs were strictly genetically monogamous (96 offspring from 18 litters, Hennessy et al., 2012).

Diet (Foraging Strategy and Time Budget)

Mate guarding is a common strategy to prevent EPCs, though the feasibility is affected by mate proximity during foraging and/or foraging time budgets. Solitary foragers (e.g., Island fox: Roemer, 1999; red fox: Baker et al., 2004; swift fox: Kitchen et al., 2006; Iossa et al., 2008a; Arctic fox: Cameron et al., 2011) may have greater opportunity to engage in clandestine EPCs, allowing relatively high levels of EPP (Island foxes: 25%, Roemer, 1999; red fox: 38–80%, Baker et al., 2004; Iossa et al., 2008b; swift fox: 52%, Kitchen et al., 2006; Arctic foxes: 31%, Cameron et al., 2011). These typically solitary foragers apparently try to reduce EPCs by spending more time closer to their partners during the breeding season (Kitchen et al., 2005a). In contrast, the relatively low levels of EPP in bat-eared foxes (9.8–15.6%, Wright et al., 2010) may reflect their insectivorous diet which enables partners to forage together (Wright, 2003). Additionally, insectivorous

species with high foraging requirements may not have time to search for extra-pair mates: bat-eared foxes spend 80% of the night feeding (Wright et al., 2010), leaving little free time to search for extra-pair mates.

Population Density

Population density and female dispersion can be key factors affecting levels of EPC (Iossa et al., 2008a). High population density decreases the potential risks of embarking on extra-territorial forays to search for mating opportunities by decreasing distances between individuals, increasing encounter rates between males and females seeking EPCs and allowing males to assess the reproductive conditions of neighboring females (Gorman and Trowbridge, 1989). High population densities are associated with high levels of EPP in red foxes (up to 80% of cubs sired by extra-pair males at a density of 19.6–27.6 adults/km²; Baker et al., 2004) and Island foxes (25% of 16 offspring sired by extra-group males with population density of 2.4–15.9 foxes/km²; Roemer et al., 2001).

Particularly compelling evidence of the effect of population density on extra-pair mating comes from a population of red fox that experienced severe population declines while food availability remained constant. In a shift from high density (19.6–27.6 adults/km²) to low (4.0–5.5 adults/km²) from mange outbreak, EPP rates decreased from 80% (30 offspring) to 38% (38 offspring) and multiple paternity rates of litters decreased from 38–69% (16 litters) to 0% (10 litters, Baker et al., 2004; Iossa et al., 2008a). Fox body mass did not differ between the high and low density periods, indicating the population was not resource-limited at high densities (Soulsbury et al., 2008), suggesting food availability was not responsible for these differences.

However, population density did not seem to affect EPP in swift foxes studied by Kitchen et al. (2006) and urban coyotes living at high density with high resource availability were entirely genetically monogamous (Hennessy et al., 2012).

Social Structure

The number of potential breeders in a group influences the probability of extra-pair mating in canids (Spiering et al., 2010) and in mammals more generally (Clutton-Brock and Isvaran, 2006; Isvaran and Clutton-Brock, 2006; Lambert et al., 2018). Thus, the factors affecting group formation (described in section Ecological Correlates of Social Monogamy: Social Structure) can influence EPC.

THE UNUSUAL CANID REPRODUCTIVE SYSTEM: ANOMALOUS CANID REPRODUCTIVE TRAITS AND THEIR POTENTIAL RELATIONSHIP WITH MONOGAMY

Canids exhibit a suite of reproductive and physiological features that are unusual or even unique among mammals (Asa and Valdespino, 1998). The ultimate cause of these unusual traits could relate to the monogamous social system of canids by facilitating alloparental care and enforcing monogamy.

Facilitation of Alloparental Care

Long-term monogamous mating results in high levels of kinship between group members, an important factor in the evolution of mammalian alloparental care and cooperative breeding (Lukas and Clutton-Brock, 2012). Phylogenetic research shows that mammalian cooperative breeding evolved from social monogamy (Lukas and Clutton-Brock, 2012; Dillard and Westneat, 2016). Canids have developed several physiological characteristics that facilitates caring of offspring by individuals other than the mother, including the ability to provide food through regurgitation, obligate pseudopregnancy with potential spontaneous lactation, and seasonal prolactin surges. The conflict between whether to help raise siblings or breed is minimized since older offspring of a monogamous pair are equally related to their full-siblings as they would be to their own offspring.

Regurgitation

An innovation in canids is the ability to directly feed both pups and mother by regurgitation of partially digested food. This ability is found in all wolf-like canids (*Canis*, *Cuon*, and *Lycaon* genera, Johnsingh, 1982; Lord et al., 2013) as well as maned wolves (Rasmussen and Tilson, 1984) and bush dogs (Biben, 1982). Regurgitation is generally absent from vulpine canids, although it was recently reported in the swift fox (Poessel and Gese, 2013). Regurgitation may be seen as an evolutionary adaptation facilitating paternal care, alloparental care and cooperative breeding, which would be advantageous in a closely-related monogamous social system.

Hormonal Priming of Alloparental Care

Canid ovulation that does not result in pregnancy is followed by a remarkably long dioestrous phase of nearly the same duration as pregnancy (2 months, Asa and Valdespino, 1998), during which time progesterone and prolactin are elevated, similar to pregnancy. This is therefore called pseudopregnancy. Spontaneous ovulation followed by obligate pseudopregnancy with hormonally-primed allomaternal care and the potential for additional lactating females has clear benefits for helping the pack and caring for the dominants' offspring.

All canid species whose reproductive physiology have thus far been studied exhibit obligate pseudopregnancy, including gray wolves, coyotes, arctic foxes, red foxes, Ethiopian wolves and culpeos (*Lycalopex culpaeus*, Asa, 1997; Asa and Valdespino, 1998; van Kesteren et al., 2013). The endocrine similarity of obligate pseudopregnancy to true pregnancy hormonally primes all females that have ovulated for maternal behavior, regardless of whether they conceived, thereby encouraging allomaternal care by non-breeding subordinate females. The hormonal similarity of pseudopregnancy and pregnancy can even cause spontaneous lactation, providing the possibility for females aside from the mother to nurse pups (Jöchle, 1997; Asa and Valdespino, 1998; van Kesteren et al., 2013). Allonursing has been reported in all *Canis* species except golden jackals (Lord et al., 2013) and can increase pup survival (Sillero-Zubiri et al., 2004). The potential for allo-suckling may be an adaptive function of pseudopregnancy (Macdonald, 1992; Jöchle, 1997). In gray wolves, all pack members experience seasonal peaks in prolactin

coinciding with pup birth. All adult wolves, even gonadectomized individuals, experience this prolactin peak, which is identical for males and females (Kreeger et al., 1991). Prolactin is associated with parental care in other species (reviewed by Angelier and Chastel, 2009) and thus this is likely related to the parental care exhibited by all pack members, including males (Kreeger et al., 1991; Jöschle, 1997).

Monogamy Enforcement Post-copulatory Lock

A post-copulatory tie has been reported for all canid species where copulation was observed, though of varying duration (Asa and Valdespino, 1998). In African wild dogs, the lock can be very brief (Asa and Valdespino, 1998), while in fennec foxes, locks can last as long as 2.75 h (average 1.8 h, Valdespino et al., 2002). The function may be to increase the probability of fertilization and enhance sperm transport. It has also been suggested to be an anatomical adaptation to encourage monogamy as a form of post-copulatory mate-guarding, since no other males can access the female during the period of sperm transport (Gomendio, 1998).

Monoestrus

The only carnivores to exhibit monoestrus, the restriction of seasonal reproduction to a single ovulatory cycle (Asa and Valdespino, 1998), are canids and their close relatives, ursids (Hayssen et al., 1993; Agnarsson et al., 2010). Polyoestrus, which is typical of most other mammals, is characterized by successive cycles of oestrus and ovulation without an intervening period of anoestrus (reproductive quiescence), which can be seasonal or year-round. Thus, if a female fails to conceive at one ovulation she has additional opportunities. Seasonal monoestrus limits females to a single conception opportunity per year—potentially a very risky reproductive strategy.

In ursids, the risk of monoestrous leading to missed mating opportunities is reduced by induced ovulation, meaning females only ovulate in the presence of appropriate stimuli (e.g., a male or copulation), similar to many other Carnivora species (e.g., felids, mustelids, Hayssen et al., 1993). Canids, however, not only have a single ovulatory cycle per season, but also exhibit spontaneous ovulation (Conaway, 1971; Asa and Valdespino, 1998), seemingly a derived trait as there is evidence of induced oestrus and ovulation in the most basal canid genus, *Urocyon* (Lindblad-Toh et al., 2005): Island foxes (*U. littoralis*) ovulate only in the presence of males (Asa et al., 2007) (whether there is induced oestrus and ovulation in the other member of the *Urocyon* genus [e.g., gray fox, *U. cinereoargenteus*] is unknown). Canids are thus unique in that they exhibit both spontaneous ovulation and monoestrus. This combination may increase the value of long-term pair bonding. Although the risks of monoestrous are reduced by the long oestrous period in canids (lasting ~1 week, contrasting with the 1-day oestrous of many mammals, Asa and Valdespino, 1998), with only a single spontaneous oestrous cycle per year, there would be considerable risk if a female does not find a partner during the limited window of reproductive opportunity or if a female unknowingly paired with an infertile or genetically

incompatible mate; long-term successful pairing may provide assurance against these possibilities.

Asa and Valdespino (1998) argue that the ultimate cause for monoestrus could be the canid social system, facilitating social monogamy and cooperative breeding through reproductive suppression. Monoestrus eliminates the opportunity for additional periods of oestrus in subordinates, which could cause social tension. They argue that if canids were polyoestrous, the dominant female would likely conceive on the first cycle but subordinates would continue cycling. However, due to canids' long oestrous period (Asa and Valdespino, 1998), the duration of time in oestrus may be equivalent between monoestrus and polyoestrus, resulting in the same amount of effort needed for reproductive suppression, regardless if over several cycles or one.

THE EXCEPTION PROVES THE RULE: SOCIAL AND MATING SYSTEM OF THE DOMESTIC DOG

The domestic dog presents an interesting case because its social and mating system differs from all other members of the *Canis* genus. Domestic dogs derived from the gray wolf an estimated 11,000–40,000 years ago (see reviews by Driscoll et al., 2009; Driscoll and Macdonald, 2010; Wang et al., 2013; Frantz et al., 2016; Botigué et al., 2017). Despite their close evolutionary history, the general *Canis* pattern of social monogamy, pair bonding, extended paternal and alloparental care and monoestrous seasonal reproduction is conspicuously absent from dogs (Lord et al., 2013).

Free-living dogs generally exhibit a promiscuous mating system with no breeding hierarchy (Lord et al., 2013), though they can exhibit a range of mating systems (Pal, 2011). All adults can have the opportunity to breed and thus dog social groups can contain multiple lactating females with litters, in addition to other male and female group members (Macdonald and Carr, 1995; Pal, 2011; Paul et al., 2014). Though free-living dogs often live in groups, they do not always form a structured pack (Macdonald and Carr, 1995; Kamler et al., 2003a; Majumder et al., 2014). A social group may defend a territory together, but groups can be dynamic in composition, influenced by mating interests, resource availability, and closeness to source populations (Macdonald and Carr, 1995; Kamler et al., 2003a; Majumder et al., 2014). Some groups hunt cooperatively (Kamler et al., 2003b; Fleming et al., 2006) while others seemingly do not (Macdonald and Carr, 1995). Care is predominantly provided by the mother (Macdonald and Carr, 1995; Lord et al., 2013), though there are some observations of paternal (Pal, 2005) and alloparental (Paul et al., 2014) care. Although regurgitation and provisioning of offspring by males and helpers is characteristic of all other *Canis* species, it is rare in domestic dogs and mainly exhibited by the mother (Malm, 1995; though see Pal, 2005; Lord et al., 2013). Dogs reach independence much earlier than other *Canis* species, at 10–13 weeks, compared to an approximate average age of 6 months for other members of the genus (Pal, 2005; Lord et al., 2013). Dog pups do not receive extended parental care. After weaning, dog pups are independent of

parenting and no longer directly fed; they instead must find their own food and compete with adults and juveniles. Wild *Canis* all exhibit reproductive seasonality, including dingoes, with births coinciding with seasonal increases in food availability; dogs are the only exception, with females coming into oestrous approximately every 7 months and males always being capable of reproducing, though there can be concentrations of breeding during certain times of the year (Lord et al., 2013). Thus, dogs exhibit approximately two oestrus per year, unlike all other monoestrous *Canis* (Asa and Valdespino, 1998; Lord et al., 2013). This vastly different social and mating behavior of domestic dogs compared to wild *Canis* is associated with different ecological conditions, providing an opportunity for understanding the ecological conditions that shape monogamy in other canids.

Are These Differences Adaptive?

Although Macdonald and Carr (1995) cautioned against interpreting the behavior of a domesticated species as adaptive, Lord et al. (2013) argue that humans have had little reproductive control over the vast majority of dogs because most are free-ranging. They argue that the differences in the reproductive systems and behavior of dogs compared to other *Canis* are adaptations to a new ecological niche created by the permanent and stationary settlement of humans and the associated food resource availability, rather than by artificial selection or reduced natural selection. The proposition that their behavior is adaptive is supported by findings that two different dog communities behaved very differently when exposed to contrasting ecological circumstances (Macdonald and Carr, 1995).

Dogs tend to cluster in areas of human waste and the diet of most free-ranging dogs originates from humans, either directly through provisioning or indirectly from scavenging (Kamler et al., 2003a; Vanak and Gompper, 2009). Dogs are therefore released from seasonal fluctuations in resource availability, avoid high costs of having to hunt and generally experience high resource abundance (Macdonald and Carr, 1995; Kamler et al., 2003a; Pal, 2008; Lord et al., 2013). The ease of finding and processing food decreases the necessity for energetically-expensive parental care behaviors, making male care less valuable for domestic dogs than for wild canids. The reliable, year-round availability of human-derived food likely favored the loss of reproductive seasonality (Lord et al., 2013). Freed from seasonality in resource availability, dogs can breed continuously throughout the year, avoiding competition with other dog litters even within the same social group. This also allows early age at first reproduction as dogs can breed as soon as they come into maturity, rather than waiting for the next breeding season (Lord et al., 2013). By avoiding energetically-costly parenting behavior, dog parents can redirect energy into breeding year-round and multiple times per year, thereby increasing fecundity (Lord et al., 2013).

Although for wild canids the optimal strategy for maximizing reproductive success is often monogamy with biparental care, for domestic dogs paternal and alloparental care is not necessary due to more stable resource availabilities and thus they benefit from adopting an entirely different strategy. The genus-atypical reproductive and parental behavior of domestic dogs supports

the hypothesis that monogamy in canids is largely an adaptation allowing wild canids to make the most of fluctuations in resource availability (Lord et al., 2013).

CANID SUCCESS: CAUSE, COROLLARY OR CONSEQUENCE OF MONOGAMY, THE PRO-COOPERATIVE HYPOTHESIS

Canid Success

This essay was prompted by the question of whether monogamy is a cause, consequence, or correlate of Canidae success, as individuals, species and family. Unlike many other carnivore families, canids have thrived in the rapidly changing conditions of the Anthropocene (Wang et al., 2007; Wang and Tedford, 2008). The world's most widely distributed wild terrestrial mammal is a canid: the red fox, found from the Arctic Circle to North Africa, North America and Eurasia and introduced and now widespread in Australia and USA (Macdonald and Sillero-Zubiri, 2004). Prior to the ascent of red foxes, this title was held by another canid, the gray wolf, originally distributed throughout the Northern Hemisphere in every habitat large ungulates were found (Mech, 1995; Macdonald and Sillero-Zubiri, 2004), until widespread human persecution caused their near-complete extirpation by the late 1800s (Mech, 1995; Phillips et al., 2004). But canids are resilient and gray wolves are now returning to their former range in both North America and Europe (Mech, 1995, 2017; Breitenmoser, 1998; Wydeven et al., 1998; Phillips et al., 2004). Coyotes have dramatically increased their range over the past two centuries. Previously found only in the prairies and deserts of western North America, they are now ubiquitous in every country and state from Alaska to Panama, found in nearly all available habitats, including forest, prairie, desert, mountain, tropical habitats, and cities (Gompper, 2002; Macdonald and Sillero-Zubiri, 2004). Coyote range expansion was likely catalyzed by the extermination of gray wolves, thus reducing intra-guild competition (Macdonald and Sillero-Zubiri, 2004), and land conversion through logging and agriculture which opened up additional habitat (Méndez-Carvajal and Moreno, 2014). The rapid expansion of coyotes in North and Central America is mirrored by that of golden jackals in Europe. Native to the Middle East and southern Asia, golden jackals arrived at the southern edge of Central and Eastern Europe around 8,000 years ago and began slowly expanding in the nineteenth century, but since the 1950's their expansion has accelerated into the north and west of Europe (Tóth et al., 2009; Rutkowski et al., 2015). They are now found as far north as Finland, four degrees below the Arctic Circle (Banea and Giannatos, 2019), and as far west as Switzerland (Arnold et al., 2012; Trouwborst et al., 2015) and their continued expansion, for reasons paralleling those for coyotes, seems likely (Arnold et al., 2012). In addition to these natural rapid expansions, introductions of canids by humans allowed several to thrive as invasive species. Raccoon dogs, originally from Siberia, East Asia and Japan, were introduced as a furbearing species in the Soviet Union from 1928 to 1955 and within 50 years had colonized 1.4 million km² of northern and eastern Europe (Helle and

Kauhala, 1991; Kauhala and Saeki, 2004; Sutor, 2007; Kauhala and Kowalczyk, 2011). The reintroduction and subsequent rapid spread of red foxes in mainland Australia and USA is another classic example of biological invasion (Kamler and Ballard, 2002; Fleming et al., 2006). The domestic dog, a few genes adrift from gray wolves, is one of the world's most successful mammal: population estimates range from 700 million (Hughes and Macdonald, 2013) to over one billion (Lord et al., 2013), roughly 80% of which are estimated to be free-ranging (Lord et al., 2013). Despite considerable efforts, humans have been unable to control the populations of these canids.

What has allowed these canids—red fox, gray wolf, coyote, golden jackal, raccoon dog, and domestic dog—to be so successful as to rapidly colonize new areas, dramatically increase in abundance, and continue to do so despite human efforts to control populations, and could their monogamous lifestyle be partially to blame? We suggest that canid success may be attributed to four main characteristics: (1) their generalist nature, adaptability, flexibility, and intelligence, allowing them to adapt to diverse habitats, diets and circumstances; (2) their high mobility and capacity for long-distance travel, facilitating fast colonization, expansive gene flow and genetic diversity, creating a selective advantage in changing environments and minimizing the risk of inbreeding from founder effects (Reed and Frankham, 2003); (3) their high reproductive rate, allowing them to quickly increase in number and recover following population declines from disease and persecution; and (4) their sociality and ability to cooperate, which can provide numerous benefits (see section Ecological Correlates of Social Monogamy: Social Structure; Macdonald and Carr, 1989; Macdonald et al., 2004). We argue that while the first and second attributes on this list are conserved traits that arose early in canids' phylogenetic history, the third and fourth are consequences of monogamy, and that it is the combination of these four characteristics that contribute to canids' success.

Canid Success Traits That Are Consequences of Monogamy

High Reproductive Rates

Co-evolution of paternal care and litter size resulted in the large litters that are characteristic of canids, thus increasing reproductive output (Stockley and Hobson, 2016). Canids can also reproduce in their first year and breed annually (Lord et al., 2013). In comparison to other omnivorous Carnivores, canids are distinguished by the platform provided by monogamy for benefiting from paternal care, cooperative breeding and allopaternal care, all of which can enhance lifetime reproductive success (Lukas and Clutton-Brock, 2013; Opie et al., 2013). Rapid reproduction allows canids to withstand high mortality rates (from human persecution and disease, itself often anthropogenic; Goltsman et al., 1996; Laurenson et al., 1998; Rhodes et al., 1998) and quickly colonize new areas. Despite widespread persecution, red foxes, coyotes, golden and black-backed jackals and raccoon dogs are able to thrive, while wolves continue to recover in North America and Europe despite ongoing illegal killings (Mech, 1995, 2017).

High reproductive rates may also allow for rapid phenotypic and genotypic adaptations to cope with new or changing environments and prevents inbreeding depression (Reed and Frankham, 2003). Furthermore, socially monogamous mating systems are predicted to produce greater reproductive output and genetic diversity compared to polygynous or polyandrous systems, leading to larger effective population sizes (Parker and Waite, 1997; Waite and Parker, 1997).

Sociality and Cooperation

The complex, cooperative social systems of canids that evolved from monogamy (Lukas and Clutton-Brock, 2013; Dillard and Westneat, 2016) provides numerous benefits discussed in section Canid Social Monogamy (e.g., cooperative hunting, food defense, reproductive success). Furthermore, the cooperation that first developed between members of the monogamous pair can spill over to other individuals, generally kin, when resource dispersion facilitates cohabitation by a spatial group (see Macdonald and Johnson, 2015). While this might originally be focused on young, it is a small step to cooperating with, and even assisting, other adult group members (e.g., adult red foxes caught in traps may be fed by other foxes [Garcelon et al., 1999]).

Canids have among the largest relative brain sizes in Carnivora (Gittleman, 1986; Swanson et al., 2012) and an enlarged pre-frontal cortex compared to felids and other carnivores (Rakinsky, 1969), associated with increased intelligence and behavioral complexity and flexibility. Across carnivore species, experiments show that greater relative brain size is associated with greater problem solving (Benson-Amram et al., 2016) and across mammals, larger brain sizes are associated with the ability to successfully adapt to, colonize, and invade novel habitats (Sol et al., 2008). The sociality and cooperation that evolved in canids from monogamy may have increased canid brain size through influence on diet. Cooperative hunting allows canids to tackle larger vertebrate prey and increases hunting success (Fanshawe and Fitzgibbon, 1993; Creel and Creel, 1995). Carnivore species that consume vertebrates have the largest brains, omnivores intermediate, and insectivores the smallest (Swanson et al., 2012). This could be because hunting vertebrate prey is more cognitively demanding than omnivory or insectivory, and particularly when synchronizing hunting behavior with pack mates, or because consuming higher-energy foods allows evolution of metabolically expensive brain tissue (Swanson et al., 2012).

Increased brain size is also argued to be a consequence of the complex social relationships that monogamy requires. Shultz and Dunbar (2007) found that larger relative brain size is correlated with socially monogamous pair bonding in Carnivora, other mammalian orders, and birds. Furthermore, bird species with long-term monogamous pair bonds (like that of most canids) have larger brains than species with short-term seasonal monogamy (Shultz and Dunbar, 2007; West, 2014). Shultz and Dunbar (2010) concluded that increased brain size evolved in birds as a result of long-term pair bonding, not that larger brains allowed long-term pair bonding. Three hypotheses have been proposed for why monogamous pair bonding may select for larger brains. Shultz and Dunbar (2007) and Dunbar (2009)

argue that the cognitive demands of behavioral coordination, synchronization, and negotiation necessary for navigating and maintaining stable pair bonded partnerships is responsible for increased brain sizes seen with monogamy. Alternatively, the potentially high costs of selecting an unreliable or infertile mate, particularly in species forming long-term monogamous pair bonds where there is reduced availability of alternative mates, may have selected for cognitively-demanding mate selection processes (Dunbar, 2009). A third hypothesis relates to the pressures of mate guarding and procuring fitness-increasing extra-pair copulations while maintaining social partnerships (West, 2014). This is supported in birds, where larger brains not only correlate with social monogamy but also with extra-pair paternity: as rates of extra-pair paternity increase, so does brain size. This suggests there is an intersexual co-evolutionary arms race with both sexes trying to outsmart each other in trying to sneak extra-pair copulations while preventing their mate from doing the same, leading to larger brains in both sexes (West, 2014).

Sociality beyond the pair bond may also contribute to increased brain sizes. Swanson et al. (2012) found that carnivoran social complexity is positively correlated with relative cerebrum volume (but not total brain volume), in line with the social brain hypothesis in primates which posits that larger brains evolved due to the cognitive demands posed by complex social systems (Dunbar, 1992; Shultz and Dunbar, 2007; but see DeCasien et al., 2017) (studies on the relationship between total relative brain volume and carnivore sociality have found conflicting results, see Gittleman, 1986; Dunbar and Bever, 1998; Pérez-Barbería et al., 2007; Shultz and Dunbar, 2007; Finarelli and Flynn, 2009; Swanson et al., 2012).

Thus, the sociality and cooperation that evolved in canids as a result of monogamy also likely made them more intelligent and adaptable compared to other carnivore families, which would have further facilitated the relative dominance of canids and allowed several canid species to prosper even during the Anthropocene.

In this sense, monogamy primed pro-cooperative, pro-social behaviors in ancestral canids that were, and largely remain, facultative rather than obligate. This facility for cooperation offers canids a selective advantage to maximize opportunities more readily than would have been the case without the pro-cooperative bonus brought by monogamy.

Conserved Traits for Success Amongst the Canidae

Intra-Specific Ecological Flexibility

Canids are highly flexible and adaptable in their ecology, able to exploit a wide range of diets, habitats, and social structures. Although the central theme of canid social and mating systems is monogamy, their extreme flexibility leads to intraspecific variation in social behavior as adaptations to varying ecological conditions, allowing them to take advantage of superior strategies when opportunity permits. Consider the finding of Robertson (2016) that in areas with low resource availability, female coyotes delay reproduction and instead bide at home as helpers, more

than half breeding only after their third year. In areas with high resource availability, almost half bred as yearlings, and almost all did so by their third birthday. This flexibility allows rapid increases in numbers, contributing to resilience to intense hunting pressure (Berger, 2006). Interspecifically, consider the domestic dog, which abandoned the *Canis* pattern of monogamy and its associated social and reproductive traits to take advantage of the abundant resources in its niche, allowing domestic dogs to become the most abundant carnivore on earth (Hughes and Macdonald, 2013; Lord et al., 2013). The remarkable intra-specific flexibility of canids means that while monogamy, and the cooperation it facilitates, is their norm, they can survive and even sometimes thrive alone when needed (much like omnivorous viverrids and musteloids) or adopt polygamy when ecological conditions present that as a superior strategy. They can be flexible as necessity or circumstance requires or permits.

High Mobility

Canids are capable of fast and wide-ranging movements. Movements of 86 km in a little over a month and 230 km in ~3 months have been recorded in the African golden wolf (Karssene et al., 2018), gray wolves disperse as far as 1,000 km in search of new territories and mates (Mech et al., 1995; Ciucci et al., 2009) and minimum dispersal distances documented for coyotes are 94 km for females and 113 km for males (Harrison, 1992). The interplay of this high mobility with their ecological flexibility allows canids to quickly move to new areas and adjust to local conditions.

Formula for Canid Success: the Monogamy as Pro-cooperative Hypothesis

The four attributes presented above may be the keys to the formula of canid success among carnivores. This hypothesis might be termed the *monogamy as pro-cooperative hypothesis* (Figure 1). In short, monogamy appears to have arisen when females are dispersed between sharable territories that arise as a result of the dispersion of available resources (Macdonald and Johnson, 2015), preventing males from defending multiple females but nonetheless allowing them to cohabit with one, such that guarding a single female is the most efficient male strategy (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013), emerging from the ancestral canids' ecological circumstances. Monogamy together with biparental and alloparental care allowed for high reproductive output and cooperative sociality and intelligence. This perspective is congruent with Lukas and Clutton-Brock (2013) conclusion, based on phylogenetic analysis, that biparental care evolved from social monogamy, and cooperative breeding systems evolved from that. Their high mobility allows canids to quickly expand to new areas, their intelligence and generalist nature allows them to adapt to new diets and habitats in these new areas, and together with their high reproductive output and cooperative sociality allows them to quickly increase in numbers and successfully colonize.

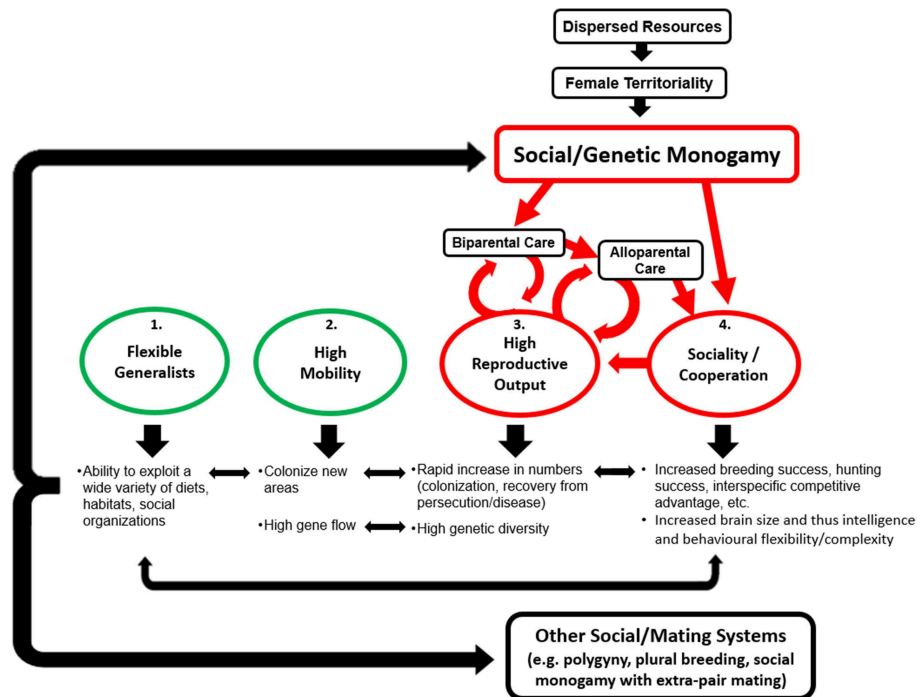


FIGURE 1 | The monogamy as pro-cooperative hypothesis: Canid success may be attributed to four characteristics: (1) their flexible, generalist, adaptable nature, (2) high mobility, (3) high reproductive rates, (4) sociality and cooperation. Traits 1 and 2 appear to be early traits of canids' phylogenetic history, while 3 and 4 arose from monogamy. Dispersed resources, insufficient to support multiple breeding females but sufficient for a female and male within a territory, seem to have led to the evolution of social monogamy, which in turn led to the evolution of biparental care and, thus, where ecological circumstances allow, alloparental care and sociality/cooperation (trait 4) and high reproductive rates (trait 3). These create feedback loops, where biparental/alloparental care, sociality and cooperation lead to higher reproductive output, which, in turn require biparental/alloparental care, sociality and cooperation. These four canid traits are interconnected and enhance one another. For example, high mobility allows canids to move to new areas, their generalist flexible nature allows them to adapt to these new areas, their ability to quickly increase in number through high reproductive rates allows them to establish in these new areas, with survival and reproduction further enhanced by their sociality and cooperation. The interplay of rapid reproduction and high mobility, allowing gene flow and enhancing genetic diversity, contributes to their adaptability and flexibility, and sociality further contributes to their flexibility through its association with enhanced intelligence, in line with the social brain hypothesis. This flexibility means that canids can adapt social and mating systems to suit local ecological conditions, which may result in social monogamy, or, if ecological conditions are such that superior strategies exist, canids can exploit alternative social/mating strategies yet retain the benefits of high reproductive rates and sociality/cooperation that monogamy afforded (see section Ecological Correlates of Social Monogamy for ecological conditions affecting maintenance of social monogamy vs. alternative strategies, such as polygyny, plural breeding, etc., and section Ecological Correlates of Extra-Pair Mating for ecological conditions affecting genetic monogamy vs. extra-pair mating). It is thus the combination of these four traits, with monogamy at its foundation, that together make up the formula of canid success, explaining the rapid expansion, colonization, and invasion of multiple canid species in recent years.

Comparison Within Canidae

To consider further the role these four traits play in canid success, we explore how some of the most successful wild canids, as outlined above—red fox, golden jackal, coyote, raccoon dog—differ from those species that are not faring so well. Of the 37 extant Canidae species, one is listed by the IUCN as Critically Endangered (red wolf) and four as Endangered (Ethiopian wolf, African wild dog, dhole and Darwin's fox); no species are listed as Vulnerable and only one canid has gone extinct in historical times (Falkland islands wolf, *Dusicyon australis*, in 1876). How do these species differ? For the Falkland islands wolf and Darwin's fox, their small and isolated ranges, was and is their main downfall. For the other species mentioned here, they lack a critical piece of the puzzle for canid success—their generalist, adaptable nature. African wild dogs and dholes are hypercarnivorous, with specialized dentition for a diet primarily of large vertebrate prey.

Their large body size coincides with high energy requirements (Carbone et al., 1999; Slater, 2015), meaning they must consume large prey for foraging to be energetically economical. This results in a greater reliance on cooperative hunting, such that, unlike other canids that can adjust social structure and thrive alone, as pairs, or in groups, these species may have a minimum pack size threshold for successful hunting and breeding (Carbone et al., 1999). The African wild dog and dhole are also among the least monogamous canids—dholes tend to exhibit communal breeding, living in large clans and more often with multiple breeding females in a group (Fox, 1984), while African wild dogs are often polyandrous or polygynandrous with multiple litters in a pack (see section Ecological Correlates of Extra-Pair Mating). African wild dogs deviate from other canid patterns—they exhibit the shortest recorded post-copulatory lock (Frame et al., 1979; Asa and Valdespino, 1998), which we

suggested could be a monogamy enforcement adaptation (section Post-copulatory Lock). The Ethiopian wolf has also increased dietary specialization, but in the opposite direction—rather than specializing on large prey, this species specializes on Afroalpine rodents, which can comprise as much as 97% of prey volume of their diet (Sillero-Zubiri and Gottelli, 1995b). Afroalpine rodent communities can therefore limit the distribution of Ethiopian wolves (Sillero-Zubiri et al., 1995a,b).

Comparison Among Carnivora

To isolate the importance of monogamy within the canid syndrome of breeding fast and cooperating as opportunity allows requires solving the algebra of alternative evolutionary pathways that led other generalist, omnivorous carnivores to life histories that do not involve monogamy. How do they fare?

Consider the feliform solution to the same evolutionary problem, the Viverridae (genets and civets). Although viverrid biology is not well-known (e.g., Ross et al., 2017) they too excel at omnivory, but exhibit classic carnivorean polygyny, produce small litters, and lack the pioneering adaptability and cooperative tendencies of canids. The same might be said of most omnivorous musteloids and ursids, themselves carrying much of the caniform phylogenetic baggage shared by canids (Koepfli et al., 2017), but with societies conspicuously lacking monogamy (Macdonald and Newman, 2017). The comparison is not flawless, but sufficiently compelling that the role of monogamy in the syndrome of canid attributes is part of their particular success. Perhaps the extinction of the tenth family of caniforme Carnivores, the Amphicyonidae (the “bear-dogs”), 2.6 million years ago, probably due to competition with true dogs, lay in the trump card of monogamy. The point might even be stretched to explain how, five million years ago, canids ousted the dog-like Hyaenidae that once outnumbered them (Macdonald, 1992). Amongst the Caniforme suborder of Carnivora, despite

their close phylogenetic relationships, Canidae are the only family to exhibit monogamy. Of the 37 extant canid species, only 5—13.5%—are listed as threatened (Critically Endangered, Endangered, or Vulnerable) on the IUCN Red List. This is the lowest proportion among all Caniforme families. An avenue worth exploring may be associations between the conservation status of species in a family and the number of the critical traits identified here that they exhibit (amongst Caniforme families we think that none other than canids display all four).

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Are We Monogamous? A Review of the Evolution of Pair-Bonding in Humans and Its Contemporary Variation Cross-Culturally

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Despite a long history of study, consensus on a human-typical mating system remains elusive. While a simple classification would be useful for cross-species comparisons, monogamous, polyandrous, and polygynous marriage systems exist across contemporary human societies. Moreover, sexual relationships occur outside of or in tandem with marriage, resulting in most societies exhibiting multiple kinds of marriage and mating relationships. Further complicating a straightforward classification of mating system are the multiple possible interpretations of biological traits typical of humans used to indicate ancestral mating patterns. While challenging to characterize, our review of the literature offers several key insights. 1) Although polygyny is socially sanctioned in most societies, monogamy is the dominant marriage-type within any one group cross-culturally. 2) Sex outside of marriage occurs across societies, yet human extra pair paternity rates are relatively low when compared to those of socially monogamous birds and mammals. 3) Though the timing of the evolution of certain anatomical characteristics is open to debate, human levels of sexual dimorphism and relative testis size point to a diverging history of sexual selection from our great ape relatives. Thus, we conclude that while there are many ethnographic examples of variation across human societies in terms of marriage patterns, extramarital affairs, the stability of relationships, and the ways in which fathers invest, the pair-bond is a ubiquitous feature of human mating relationships. This may be expressed through polygyny and/or polyandry but is most commonly observed in the form of serial monogamy.

Keywords: monogamy, mating system, sexual selection, anthropology, evolution

INTRODUCTION

How best to characterize the human mating system is a subject of intense and polarized debate. On the one hand, sex differences in reproductive investment, and resultant differing potential reproductive rates, are argued to favor elevated mating effort behavior in males (i.e., a short-term, multiple mate seeking orientation; Symons, 1979) and polygyny. However, on the other hand, an evolved sexual division of labor, with offspring dependence on paternal care, is argued to generate overlapping interests in long-term, monogamous relationships for both men and women (Washburn and Lancaster, 1968; Lancaster and Lancaster, 1987; Kaplan et al., 2000). Given the

varied sources of support for both approaches, disagreement exists on how best to describe mating patterns in humans. Particularly challenging is to generate an agreed upon definition of a species-typical strategy often used in comparative studies. This review is focused on an attempt to offer resolution regarding the current debate. After reviewing the literature on marriage and mating systems in humans, we present a cross-cultural examination as well as comparative and evolutionary evidence for and against particular lines of inquiry.

WHAT IS THE HUMAN MATING SYSTEM?

Confusion and debate describing a human-typical mating pattern are warranted given the diversity of strategies both across and within cultures. For example, data from the Standard Cross-Cultural Sample (Murdock and White, 1969), a representative global sample of primarily pre-industrial societies, indicates that polygynous marriage (one male, multiple females) is sanctioned in nearly 85% of societies (Figure 1). This figure is often used to support claims of the mating effort intensive nature of males given that most societies allow men to have multiple wives. However, upon closer inspection, within a small-scale polygynous society, the majority of marriages are monogamous (Murdock and White, 1969; Flinn and Low, 1986; Binford, 2001). For example, among the Savanna Pumé (South American hunter-gatherers) while polygyny occurs (20% of women and 11% of men are polygynously married at some point during their lives), most marriages are monogamous, consistent with other foraging groups (Marlowe and Berbesque, 2012; Kramer et al., 2017).

Although most marriages are monogamous at any one point in time, over the life course individuals may reenter the marriage market more than once. Among hunter-gatherers, industrializing societies, and many contemporary Western populations, remarriage is common after spousal death and/or divorce, resulting in serial monogamy where both men and women have multiple partners over their reproductive careers (Fisher, 1989; Hill and Hurtado, 1996; Borgerhoff Mulder, 2009; Jokela et al., 2010). Nonetheless, while individuals may have more than one partner across their life, sexual fidelity within a marriage is generally expected. Marriage is common to all human societies and publicly acknowledges who has sexual access to whom, with divorce often resulting from extramarital relationships (Irons, 1983; Marlowe, 2003; Kramer and Greaves, 2011). However, typical of the range of behavioral variation expressed by humans, many exceptions exist, and sex is found outside of marriage both cross-culturally and among individuals in any one society (Box 1: Sex outside of the pairbond across human societies). Yet, while engaging in sex outside of marriage likely occurs to some extent in all societies, because men and women typically live in long-term pairbonds within the same residential unit, they have been described as practicing social monogamy (Reichard, 2003; Strassmann, 2003). While human patterns are distinct from genetic monogamy, defined as two individuals who only reproduce with one another, levels of extra pair paternity are relatively low compared to other socially monogamous species. Estimates of non-paternity rates range

from 0–11% across societies (Simmons et al., 2004; Anderson, 2006; with median values falling between 1.7–3.3%) while among birds these rates regularly exceed 20% (Griffith et al., 2002).

In sum, a simple classification of a human-typical mating system is challenging given the variety of pairing strategies observed. Monogamous, polyandrous, polygynous, and short-term mating patterns are found across contemporary human societies, with most societies exhibiting multiple kinds of marriages and mating relationships (Marlowe, 2000; Fortunato, 2015). What can be most simply distilled from this is that humans form long-term pairbonds. However, while polygynous and polyandrous marriages are found in many societies, ethnographic evidence indicates that most individuals within a society live in monogamous marriages that are generally, but not always, sexually exclusive. It is important also to emphasize that these unions are commonly serially monogamous, and that regardless of divorce rates, this likely would have been the case in the past due to high rates of spousal mortality under premodern mortality schedules (Gurven and Kaplan, 2007).

ANCESTRAL MATING SYSTEM IN HUMANS

Although cross-cultural information may illuminate contemporary variation in mating patterns, it tells us less about their antiquity. To seek additional support to characterize the human mating system, we turn to indicators of ancestral mating patterns. Sexual selection is a widely recognized force influencing behavioral and physical traits across animal taxa (Andersson, 1994). Differences between males and females within and across species can offer insight into both historical and contemporary selection pressures. Mating systems are amazingly diverse across mammals generally, and primates in particular (Dixon, 1997; Kappeler and van Schaik, 2002). Given human placement in the primate order, here we approach human mating from a comparative perspective to better understand behavioral and physical traits that either are shared or distinguish us from our closest living relatives. We target three commonly examined traits in reference to predicting primate breeding systems: sexual dimorphism, testis size, and concealed ovulation (Dixon, 2009). We review each of these and discuss whether the evidence supports a human monogamous past that may serve to explain the mating system's current prevalence.

Sexual Dimorphism

Sexual dimorphism exists within a species when, in addition to differences between the sexual organs themselves, males and females differ in size or appearance (Andersson, 1994). Across primates, minimal levels of sexual dimorphism in body weight and canine size are generally associated with monogamy and low rates of male antagonistic competition (e.g., gibbons; Harcourt, 1981). Size differences are expected to be most pronounced within single-male/multi-female polygynous species where male competition can be intense, and stakes high, because winners have much to gain. For example, among mountain gorillas (*Gorilla beringei beringei*) dominant males monopolize sexual

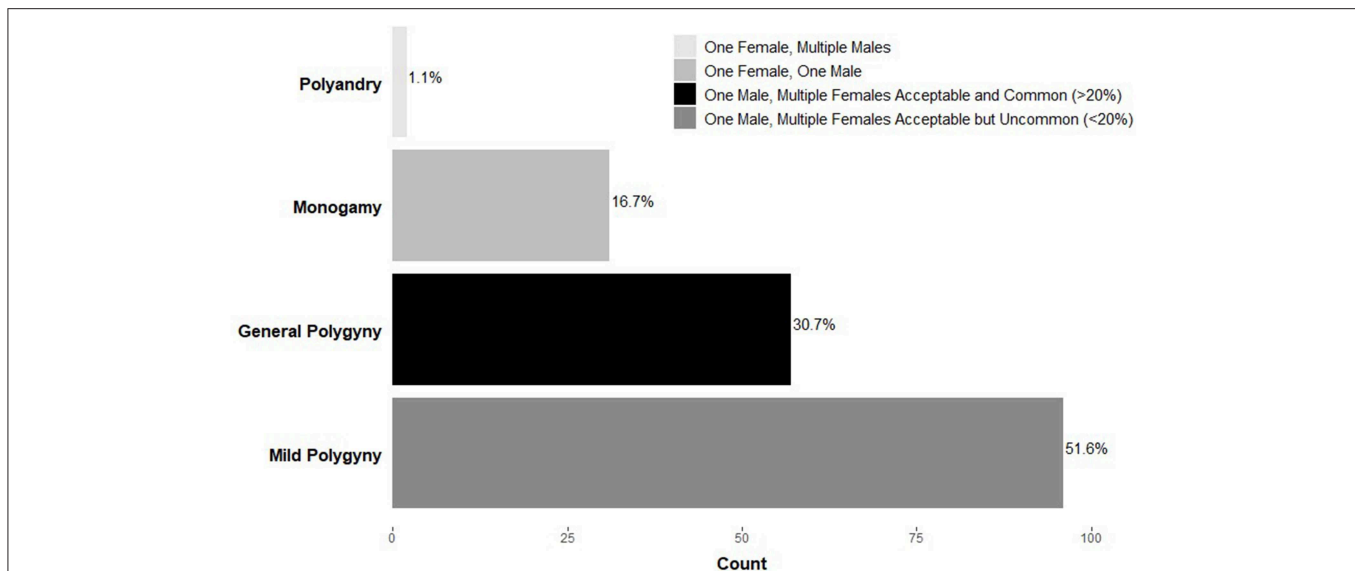


FIGURE 1 | Frequency of marriage systems across societies ($n = 186$) in the Standard Cross-Cultural Sample (Murdock and White, 1969). Adapted from Marlowe (2000).

BOX 1 | Sex outside of the pairbond across human societies.

While humans form long-term pair bonds that are recognized as marriages in all societies, sexual relations also occur outside of marriage. In some societies and incidences these relations are clandestine and considered transgressions with punishments that range in severity. But in other cases, uncommitted sexual liaisons are socially permissible, and generally fall under two well-documented ethnographic contexts. The first occurs prior to first marriage when adolescent girls are in a life stage when they have a low probability of conceiving and are given freedom to explore different premarital relationships (Mead, 1928; Irons, 1983; Parker, 1985; Gregor, 1987). For example, among the Makushi of Guyana, recently sexual mature individuals receive parental support to engage in pre-marital sex (Schacht, 2013). The stated purpose of this mating behavior is to allow for mutual mate choice and the identification of a possible long-term mate. However, once married, copulation outside of the pair-bond is expected to cease. A second socially sanctioned form of sex outside marriage occurs in the context of either partible paternity or wife sharing during prescribed situations. For example, among some lowland South American groups, women regularly have several sexual partners in addition to their husband (Beckerman and Valentine, 2002; Walker et al., 2010). This practice is common where the contribution of multiple men is thought to be required for fetal development. While women do not formalize additional relationships through marriage (i.e., polyandry is not institutionalized), these men are expected to provide protection for and investment in children as they develop – a long-term commitment (Beckerman et al., 1998). In other societies, wife sharing may occur during publicly acknowledged situations. A well-described example comes from many different ethnographic sources of the Inuit, where monogamous couples engage in “wife-swapping” (Boas, 1907; Rubel, 1961; Hennigh, 1970; although husband-swapping may be more accurate). This exchange was reportedly agreed upon by all parties, and often, though not always, resulted in long-term social (and sexual) relationships. Other extrapair relationships are more clandestine, likely because of penalties that may follow (e.g., violence in response to sexual jealousy). Nonetheless, there are many examples of men offering food and other resources in exchange for extramarital sex (Holmberg, 1969; Gregor, 1987; Hill and Hurtado, 1996; Pollock, 2002).

access to a group of females and perform up to 70% of all copulations (Stoinski et al., 2009). Unsurprisingly, gorillas exhibit high levels of reproductive skew and males are nearly twice the size of females (Leigh and Shea, 1995). However, for species that live in multi-male/multi-female groups, such as chimpanzees, body size dimorphism tends to be intermediary between monogamous and polygynous species (Dixon, 2009). Given these patterns, what evidence of sexual dimorphism do we see in our hominin line (i.e., the phylogenetic group consisting of all modern humans, extinct human species, and our immediate ancestors) and what inferences can be drawn of ancestral mating systems?

Determining size dimorphism from the fossil record is fraught with debate due to interpretations that vary across researchers (Lockwood et al., 2007; Gordon et al., 2008; Reno et al., 2010; Plavcan, 2012). However, the general consensus is that

dimorphism was greater in our past and has diminished over time. This is often interpreted to suggest that male mating competition decreased in intensity over the course of hominin evolution in conjunction with a rise in monogamy. When this transition occurred, however, is debated. Some researchers speculate that dimorphism was fairly modest around 4 million years ago among *australopithecines* and place monogamy and male provisioning deep in the hominin line (Lovejoy, 1981; Reno et al., 2003, 2010). Others contend that *australopithecines* were highly dimorphic; therefore, monogamy had yet to become established (Lockwood et al., 1996, 2007; Gordon et al., 2008). Nonetheless, because of the fragmentary nature of fossil remains, difficulties in assigning sex, and the number of different species and subspecies, the fossil record may be an unreliable indicator of mating behavior in extinct species (Plavcan, 2000, 2012; Churchill et al., 2012). For example, male competition may be

expressed in many ways besides physical aggression (e.g., sperm competition, social status, and wealth), and so size dimorphism may underestimate male competition (Puts, 2010; Marlowe and Berbesque, 2012).

Regardless of the timing of the reduction in sexual dimorphism, humans today express only slight differences in body size by sex compared to closely-related promiscuous and polygynous species. For example, human body size dimorphism by weight averages about 1.15 (i.e., males are 15% heavier), with chimpanzees at 1.3 and orangutans and gorillas near 2 or more (Willner, 1989; Plavcan and van Schaik, 1992; Dixson, 2009). Humans fit more neatly in the range of variation typical of monogamous gibbons (e.g., *Hylobates lar*) who exhibit very little difference in body size by sex (1.07; Willner, 1989; **Box 2**: Which living ape is the best model for the breeding system of our last common ancestor?).

Testis Size

Testis size is another commonly used metric of mating system as it indicates, generally, female multiple mating, such that large testis relative to body size is positively correlated with the frequency of females mating with multiple males simultaneously (Harcourt et al., 1981; Kenagy and Trombulak, 1986; Møller, 1988; Parker, 2016). Adjusting for body size, human testes are smaller than would be predicted, and, when compared to our closest living relatives, are considerably smaller than those of chimpanzees (Harcourt et al., 1981; **Figure 2**). Together this provides evidence of relatively low rates of sex outside of a pairbond. However, human testes are somewhat larger than those of other monogamous primates, leading some to argue that this hints at a measure of extrapair copulation not expected in a monogamous species. Yet studies employing genetic methods find that rates of non-paternity are low among humans (~2%) when compared to those of socially monogamous birds (~20%) and mammals (~5%; Anderson, 2006; **Box 1**), casting doubt on claims of relatively high rates of extrapair engagement in human males compared to males in other monogamous species.

While testis size is a predictor of the extent to which females multiply mate, it is often mistakenly used as an indicator of monogamy. Testis size cannot discriminate between monogamy and polygyny because, in both cases, females mate with a single male for each offspring, resulting in relatively low sperm competition (Martin and May, 1981; Dixson, 2009). Thus, testis to body size complicates a simple story of ancestral mating derived from sexual dimorphism alone because human values are encompassed within the range of variation found among gorillas and orangutans—great ape species with polygynous mating systems. Therefore, we can only say that human values are consistent with pair-bonded polygynous species, but not with species where females mate multiply.

Concealed Ovulation

Human females lack obvious visible signals of ovulation, particularly in comparison to the conspicuous sexual swellings of, for example, chimpanzees and baboons (Strassmann, 1981; Dixson, 1983; Sillén-Tullberg and Møller, 1993; Rooker and Gavrilets, 2018). As a result, human ovulation is argued

to be concealed, with several functional arguments put forward to explain this phenomenon. Commonly claimed is that concealed ovulation and constant sexual receptivity of human females facilitates social monogamy (Morris, 1967; Campbell, 1974; Lovejoy, 1981) by limiting information available to males regarding fertility, thereby promoting monogamy through mate guarding and/or paternal care (Alexander and Noonan, 1979). Specifically, given that humans live in multi male/multi female groups, concealed ovulation is argued to minimize male-male competition and allow for stable, monogamous unions (Marlowe and Berbesque, 2012). However, more recently this association has been rethought as it is increasingly apparent from comparative study that concealed ovulation is not only characteristic of humans and other monogamous primates, but species from other mating systems as well. Many polygynous primates do not have overt signs of ovulation (Sillén-Tullberg and Møller, 1993). While human ovulatory cycles are indeed particularly concealed, what appears to be more remarkable are cycles that are particularly conspicuous. For example, chimpanzee females' estrus swellings are unambiguous and concentrate attention from multiple males during a short window of fertility (Hrdy, 1988; Smuts and Smuts, 1993; Gowaty, 1997; Nunn, 1999).

The traits discussed above, when interpreted singly, allow for different perspectives on ancestral mating in humans. For example, while men are larger on average than women, weight and canine dimorphism are slight compared to that of polygynous gorillas and more comparable to monogamous gibbons (Plavcan, 2012). This relative lack of dimorphism suggests diverging histories of sexual selection among the great apes regarding male reliance on contest competition for reproductive success (Dixson, 2009; Marlowe and Berbesque, 2012). Yet, while size dimorphism suggests a more monogamous past, relative testis size implies the extent to which females mate with multiple partners is higher than would be predicted for a monogamous primate. Human testes to body size values are lower than chimpanzees, higher than that of other monogamous primates, but not significantly different from gorillas. And, while concealed ovulation was once thought to be a human adaptation to promote monogamy, it is common among anthropoid primates, highlighting that what is notable are more conspicuous displays of fertility (e.g., sexual swellings) rather than their absence.

What becomes clear when the traits above are viewed collectively is that humans fall within the range of variation typical of pairbonded species. The lack of exaggerated sexual dimorphism or testis size seems to rule out a history of elevated reproductive skew typical of *highly* promiscuous or polygynous mating systems. Instead, biological indicators suggest a mating system where both sexes form a long-term pairbond with a single partner (Møller, 2003). And while polygyny was likely present in the human past, as it is across contemporary human societies, the weight of evidence seems to support social monogamy. This does not preclude males and females from taking multiple partners through serial monogamy, or by occasionally engaging in uncommitted sexual relationships (as indicated by testis to

BOX 2 | Which living ape is the best model for the breeding system of our last common ancestor?

Which ape mating system best serves as the baseline from which directionality in the fossil record should be interpreted? Chimpanzees have long been used as the behavioral model assumed to best resemble our last common ancestor. However, this has more recently given way to debate about whether past hominins (our bipedal ancestors) lived in multimale/multifemale groups like chimps (Hrdy, 2009; van Schaik and Burkart, 2010; Gavrillets, 2012) or were instead organized in polygynous, gorilla-like harems (Dixon, 2009; Chapais, 2011; Grueter et al., 2012) or had a hamadryas baboon-like structure with multiple single-male groups living together within a larger population. While this debate is ongoing, most researchers agree that ancient hominins were a group living animal, and that these groups were organized in nested multi-level societies (e.g., biological families, extended families, bands, tribes, etc.) with multiple breeding females, who commonly lived within socially recognized long-term pairbonds (Chapais, 2008; Grueter et al., 2012). Thus, whether pairbonds developed in the context of a polygynous or polygynandrous breeding system remain ambiguous. What we can say with certainty is that if our last common ancestor were “gorilla like,” we have become less dimorphic and less polygynous. And if it were more “chimpanzee like,” we have reduced body-size dimorphism only slightly, but have become much less promiscuous.



FIGURE 2 | A chimpanzee brain in comparison to a single testis. Photo credit: Martin N. Muller.

body size values). However, while extra-pair paternity (EPP) varies across socially monogamous animals, human rates of non-paternity are comparatively low.

CAUSES AND CONSEQUENCES OF MONOGAMY

The human life history pattern (i.e., short birth intervals, relatively high child survival, and a long period of juvenile dependence) means that mothers are often in the position of supporting multiple dependents of various ages simultaneously. Because infants, juveniles, and adolescents each require different kinds of time and energy investments, mothers are posed with an allocation problem throughout much of their reproductive career: how to care for infants and small children without compromising time spent in activities that provide food and other resources for older children (Lancaster, 1991; Hurtado et al., 1992; Hrdy, 1999; Kaplan et al., 2000; Kramer, 2005b, 2010; Kramer and Veile, 2018). How mothers resolve this trade-off to support a rapid reproductive pace has long been theoretically tied

to monogamy and the cooperation of fathers, siblings, and others to help mothers raise dependents.

Cooperative Breeding

Humans are typically described as cooperative breeders (although see Bogin et al., 2014), which in addition to male parental investment, is a key defining aspect of human sociality, cognition, and demographic success (Hrdy, 2005, 2009; Kramer, 2010; van Schaik and Burkart, 2010; Kramer and Greaves, 2011). Several recent phylogenetic analyses provide compelling evidence that cooperative breeding in bird, insect, and mammalian taxa was preceded by an ancestry of monogamy (Hughes et al., 2008; Cornwallis et al., 2010; Lukas and Clutton-Brock, 2012). The logic is that in a non-monogamous mating system, a sexually mature individual is likely to be more closely related to his or her own offspring ($r = 0.5$) than to siblings who may have a different parent (r between siblings $= 0.25$). Consequently, after sexual maturity, individual fitness is generally maximized by investing in one's own offspring rather than helping to raise siblings. In a monogamous mating system, however, the value for a sexually mature sibling to stay

in his/her natal group and help full siblings is equal to that of rearing one's own offspring ($r = 0.5$ for both) (Boomsma, 2007, 2009; Lukas and Clutton-Brock, 2012, 2013). Because kin-based benefits are diluted under female multiple mating, monogamy is hypothesized to be a critical step to raise relatedness within groups and sibships and thus to favor the evolution of kin-biased cooperative breeding (Boomsma, 2007, 2009; Hughes et al., 2008; Lukas and Clutton-Brock, 2012).

To add a bit of complexity, while monogamy may motivate the evolution of cooperative breeding and explain why reproductive-aged individuals help, non-reproductive individuals are able to realize kin-based benefits regardless of mating system. In many human societies, juvenile siblings and older females constitute much of the childrearing work force, contributing not only to childcare but also to resource provisioning (Flinn, 1988; Ivey, 2000; Lee and Kramer, 2002; Lahdenpera et al., 2004; Kramer, 2005b; Leonetti et al., 2005; Hrdy, 2009; Kramer and Veile, 2018). This help is empirically associated with improved maternal fertility and offspring outcomes (Turke, 1988; Blurton Jones et al., 1994; Hawkes et al., 1995a; Bliege Bird and Bird, 2002; Ivey et al., 2005; Kramer, 2005a, 2010). Among cooperative breeding mammals and eusocial insects, juveniles and subadults make important contributions to rearing and ensuring the survival of other's offspring (Clutton-Brock, 2002, 2009; Russell, 2004; Gilchrist and Russell, 2007; Boomsma, 2013). And, while grandmothering is rare in other species (McAuliffe and Whitehead, 2005), it is well-documented in humans (Hawkes et al., 1998). As a general point, while monogamy may facilitate the cooperation of sexually mature siblings, cooperation between a mother and juvenile, and a grandmother and her daughter can be favored irrespective of breeding system because of high coefficients of relatedness and low opportunity costs (reviewed in Kramer and Russell, 2014, 2015).

Paternal Care

Established claims in the anthropological literature posit that human mothers can support a rapid reproductive pace compared to our other ape relatives because fathers provide investment to both a partner and children (e.g., calories, protection). This argument hinges on an assertion that during human evolution, the increased need for paternal investment (due to big brains and expensive children) generated selective pressure for long-term pair bonds and a sexual division of labor (Washburn and Lancaster, 1968; Lancaster and Lancaster, 1987). However, phylogenetic analyses suggest that paternal care evolves only *after* monogamy becomes established in a population (Brotherton and Komers, 2003). Because male investment likely would have resulted in male absence (e.g., through resource provisioning), caring males would have faced potential fitness costs due to freerider males who are liable to steal paternity (Hawkes et al., 1995b; Gavrillets, 2012). Specifically, males that do not care benefit directly from caring males' investments in offspring that are not theirs. As a consequence, the assumption that paternal care drives monogamy is likely overly simplistic (Mathews, 2003; Fromhage et al., 2005). For example, a recent survey found that over 40% of socially monogamous species exhibit no indication of male care (Lukas and Clutton-Brock, 2013).

While paternal care is rare across animal taxa, it is generally present across human societies. However, if the needs of offspring did not drive the evolution of male care, how did it come to be? Under certain circumstances, monogamy can increase male fitness more than deserting a partner and remating (Grafen and Sibly, 1978; Yamamura and Tsuji, 1993; Fromhage et al., 2005; Schacht and Bell, 2016). Social and ecological factors that reduce male mating opportunities, such as females being dispersed or rare, reduce opportunity costs associated with monogamy and allow for selection to act on male paternal investment. Under these conditions, selection is expected to favor paternal investment if this investment improves offspring survival or quality, particularly when payoffs to desertion are low and paternity certainty is high (Dunbar, 1976; Thornhill, 1976; Perrone and Zaret, 1979; Clutton-Brock, 1991; Westneat and Sherman, 1993). Once biparental care becomes established, specialization of care tasks by males and females may serve to stabilize the pair-bond. The modal pattern cross-culturally is a life history characterized by specialization in child care by females (i.e., direct investment) and resource provisioning by males (i.e., indirect investment; Murdock and Provost, 1973). This specialization can result from and further lead to synergistic fitness benefits tied to offspring success (Leonetti and Chabot-Hanowell, 2011; Barta et al., 2014). These payoffs both constrain the behavioral options available to a parent and decrease sex-biased asymmetries in the costs of performing a parental investment task. Thus, task specialization can serve to strengthen biparental care once it emerges against invasion by other strategies.

Human fathers regularly provide care to dependent offspring well into the second decade of their life, and often care for multiple children at the same time (e.g., Kaplan et al., 2000; Gurven and Hill, 2009; Gray and Anderson, 2010). However, men still regulate the time and energy they allocate between mating and parental effort (Kaplan and Lancaster, 2003; Ross et al., 2016). Human paternal investment, while often substantial in relation to other mammals, is facultative rather than obligatory, and the anthropological record indicates considerable cross-cultural variability in how and how much fathers invest in their children (Marlowe, 2000; Lamb, 2004; Gray and Anderson, 2010; Shwalb et al., 2013). A key variable found associated with male investment is paternity certainty. Often males invest less where extra-pair relationships are more common (Gaulin and Schlegel, 1980).

Thus, while a gender division of labor appears to be a human universal, paternal investment is sensitive to a variety of conditions and seems to be regulated, at least in part, by testosterone. Testosterone is an androgenic steroid hormone that supports many aspects of male mating effort, including the development and maintenance of sexually dimorphic musculature and bone structure as well as courtship and male-male aggression (Archer, 2006; Bribiescas et al., 2012). Accordingly, testosterone levels are argued to reflect a male's allocation to reproductive effort at a particular point in time. Levels of circulating testosterone in males are thus reasoned to reflect the evolved hormonal regulation of investment in mating vs. parenting effort (Wingfield et al., 1990). In

support of this claim, cross-sectional and longitudinal evidence indicates that married men have lower testosterone levels than unmarried men, and that married men with children have the lowest levels. These results suggest that partnered men, and in particular fathers, are hormonally primed to invest more time and energy into parenting rather than mating effort (Gettler et al., 2011; Gray, 2011).

Kin Discrimination

While mammalian mothers are certain of their maternity, fathers may be uncertain of their paternity. Monogamy ensures relatedness between fathers and their purported children, and permits for both the paternity confidence and relatedness necessary to favor investment by fathers. Because cooperation among close relatives increases the fitness benefit gained by cooperators, mechanisms for discriminating between kin and non-kin, and between close and more distant kin, are critical for its evolution (Hatchwell et al., 2001; Griffin and West, 2003; Chapais, 2008, 2009). If fathers and siblings are able to identify one another, relative payoffs to investment vs. desertion increase for fathers, as do the payoffs for cooperative breeding among siblings. For humans, language and the ability to identify a range of relations through kin classificatory systems likely amplified payoffs to kin-biased cooperation by allowing distinctions in relatedness among group members to be recognized (Kramer and Greaves, 2011; Kramer and Russell, 2014). Complex kin systems are highly developed in traditional human societies and permit distinguishing classificatory from biological kin and close kin from distant kin. This allows individuals to selectively identify and cooperate with close kin, and to make decisions about when and how much to help. In the case of fathers, kin discrimination allows for a range of paternal relationships (e.g., biological, social, and/or stepfathers), all of which have societally prescribed roles.

One interesting implication of language-based kin classificatory systems found in all human societies is that, even in the absence of monogamy, they allow children to identify their siblings and father and fathers to identify their children. Because serial monogamy was likely the norm throughout human history due to long breeding careers and high rates of spousal death and divorce, kin terms allow parents and children to identify each other and close relatives despite not cohabiting or living in proximity. Moreover, kinship classificatory systems attenuate the requirement of monogamy for the maintenance of

cooperation between mothers, fathers, and siblings by facilitating payoffs to investing in kin outside of a current household (Kramer and Russell, 2015). Thus, the range of breeding systems that we see across and within human societies may be an outcome of our ability to identify close relatives and preferentially invest in them even in the absence of monogamy.

CONCLUSION

Consensus on a human-typical mating system has remained elusive in the literature. Across human societies today, monogamous, polyandrous, polygynous, and short-term mating patterns are present, with most societies exhibiting multiple types of marriages and mating relationships. Further complicating a straightforward classification of mating system are the multiple possible interpretations of biological traits typical of humans used to indicate ancestral mating patterns. While challenging, our review of the literature offers several key insights. 1) Although polygyny is socially sanctioned in most societies, monogamy is the dominant marriage-type within any one group cross-culturally. 2) Sex outside of marriage occurs across societies, yet human extra pair paternity rates are relatively low when compared to those of socially monogamous birds and mammals. 3) While the timing of the evolution of certain anatomical characteristics is open to debate, human levels of sexual dimorphism and relative testis size point to a diverging history of sexual selection from our great ape relatives.

In sum, we conclude that while there are many ethnographic examples of variation across human societies in terms of mating patterns, the stability of relationships, and the ways in which fathers invest, the residential pair-bond is a ubiquitous feature of human mating relationships. This, at times, is expressed through polygyny and/or polyandry, but is most commonly observed in the form of monogamous marriage that is serial and characterized by low levels of extra-pair paternity and high levels of paternal care.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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The Monogamy Paradox: What Do Love and Sex Have to Do With It?

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Genetic monogamy is rare—at least at the level of a species—and monogamy can exist in the absence of sexual fidelity. Rather than focusing on mating exclusivity, it has become common to use the term “social monogamy” to describe a cluster of social features, including the capacity for selective and lasting social bonds, central to what humans call “love.” Socially monogamous mammals often exhibit selective aggression toward strangers and form extended families. These features of social monogamy in mammals are supported by patterns of hormonal function originating in the neurobiology of maternity, including oxytocin, as well as a more primitive vasopressin pathway. Another key feature of social monogamy is reduced sexual dimorphism. Processes associated with sexual differentiation offer clues to the mysteries surrounding the evolution of monogamy. Although there is consistency in the necessary ingredients, it is likely that there is no single recipe for social monogamy. As reviewed here, genes for steroids and peptides and their receptors are variable and are subject to epigenetic regulation across the lifespan permitting individual, gender and species variations and providing substrates for evolution. Reduced sensitivity to gonadal androgens, and a concurrent increased reliance on vasopressin (for selective defense) and oxytocin (for selective affiliation) may have offered pathways to the emergence of social monogamy.

“A **paradox** is a logical puzzle that seems to contradict itself. **Paradoxical** statements may seem completely self-contradictory, but they can be used to reveal deeper truths.”

<https://www.vocabulary.com/dictionary/paradox>

Keywords: monogamy, oxytocin, vasopressin, testosterone, estrogen, androgens, prairie vole

OVERVIEW

Social interactions are linked to the ability to mate, survive, and thrive within an always changing environment. For these reasons, explanations for species and individual variations in social behavior were initially discussed in terms of evolution, fitness, and reproduction (Kleiman, 1977; Dewsbury, 1987; Komers and Brotherton, 1997; Lukas and Clutton-Brock, 2013; Klug, 2018).

In attempts to create order in the description of socio-sexual behavior across species as well as among human cultures it became common to cluster patterns of presumed sexual behavior, and label these as mating systems including polygyny, polygamy, polyandry, or monogamy. Among these, monogamy seemed particularly difficult to understand. Having a single mate, especially in males, was not easily explained by theories based on reproductive fitness (Barash and Lipton, 2002). Adding to the confusion, genetic tests for paternity revealed that in species presumed to be “monogamous,” sexually monogamy was actually rare—at least when considered at the *level of a given species* (Solomon et al., 2004).

If monogamy was not primarily about sexual exclusivity, then what was it? Perhaps monogamy was better understood as a social system, and one that offered the advantages of shared parenting, protection of resources, and social support (Wilson, 1975; Gowaty, 1996). And if so, what were the features and the origins of what would come to be known as “social monogamy”? Here we offer a brief personal account of the events that led us to emphasize the importance of viewing monogamy as a social system, and a system that could be understood in terms of its neuroendocrinology.

Social systems are inherently variable. However, the specific neural substrates upon which hormones act differ between and among species, and can be compared in socially monogamous vs. non-monogamous rodents. This work began in the genus *Microtus*, but as more comparative studies have appeared variations in the effects of hormones, often due to differences in target receptors are becoming more apparent. Keeping this variation in mind, we have attempted to uncover patterns of hormone action that may help to explain the phenotype and origins of the traits of social monogamy (Table 1). From rodent data, discussed in depth throughout this review, it appears that socially monogamous traits emerge during the course of development, in part through the combined actions of steroids and peptides (Choleris et al., 2008).

Among the several unsolved mysteries associated with social monogamy is the apparently independent emergence of a set of shared traits in unrelated mammals ranging from rodents to canids to New World monkeys (Kleiman, 1977; Lukas and Clutton-Brock, 2013; French et al., 2018). The repeated appearance of the cluster of behavioral and anatomical features that have been termed social monogamy raises an important basic question. What are the mechanisms through which these traits have emerged on over 60 occasions in unrelated mammalian species? Has social monogamy emerged primarily through parallel or convergent evolutionary mechanisms, or some combination of the two? Did a shared physiology permit the evolution across species of social monogamy? Or are there several pathways to social monogamy?

Here we examine the hypothesis that the neurobiology of sexual differentiation and masculinization offers a template for understanding the origins of social monogamy. Research in prairie voles has repeatedly indicated that voles are insensitive to androgens. It is possible that a comparative lack of functional availability of androgens during development, for example, through changes in either the androgen receptor or based on inhibitory effects of other molecules, such as glucocorticoids and oxytocin, may help to explain some of the unique traits that have emerged in socially monogamous mammals. We further propose that alterations in mechanisms underlying the behavioral and anatomical traits of social monogamy, shifting from a reliance on androgens to a dependence on peptides would be adaptive, and also would permit the emergence of the prosocial traits of social monogamy. For example, the components of behavior prominent in males of non-monogamous species, including non-selective aggression, which rely in part on direct actions of androgens may be specifically downregulated in social monogamy. However, selective protective behaviors and selective aggression, such as

that seen in socially monogamous species, are supported by estrogens and vasopressin/oxytocin and may continue to be expressed.

MONOGAMY

What Is Monogamy? “What’s in a Word?”

Confusion concerning monogamy has arisen across disciplines in part because of different uses of the word. Monogamy is often defined in dictionaries as “the habit of having only one mate.” The Greek origins of the word monogamy translate to “one wedding or marriage.” This anthropomorphic perspective implies that monogamy involves some form of ceremony and/or legal contract between two individuals. Biologists later borrowed the term monogamy, and alternatives to monogamy, such as polygamy, as a means for categorizing mating systems and social relationships, usually between males and females.

In both common usage and within the field of biology the term monogamy often infers sexual exclusivity either across the life-span or at a given point in time. Definitions of monogamy were applied to a single pair of partners or sometimes even to one individual within a pair. However, over time the word “monogamy” began to be used to classify mating systems at the *level of the species* (Kleiman, 1977; Dewsbury, 1987).

“Monogamy,” loosely defined, had been described by naturalists in hundreds of mammalian species and thousands of bird species (Lack, 1968). Among the estimated 4,000 or more different species of mammals for which behavioral data are available, it was estimated that between 3 and 5 percent of species, including apparently unrelated taxa, exhibited the traits of monogamy (Kleiman, 1977). A more recent survey of ~2,500 mammalian species, estimates that about 9 percent of species show features of monogamy, defined by the authors as a single breeding male and a single breeding female that share a home range and remain together for more than one breeding season, with or without offspring (Lukas and Clutton-Brock, 2013). This is in comparison to birds in which over 90 percent of species are considered to be “monogamous” (Lack, 1968). As is discussed in depth later in this review, there is also a great deal of intraspecies variation in displays of monogamy behaviors in both mammalian and avian species.

Most early behavioral studies in mammals or birds did not differentiate between mating and social systems, assuming homogeneity between these. In fact, a given species might be simply classified either as “monogamous” or “non-monogamous.” However, early studies describing a species as “monogamous” were based on the largely untested assumption that males and females living together for extended periods of time and exhibiting joint care of offspring also were showing sexual exclusivity and raising their own young (Kleiman, 1977). Sexual preferences were assumed to be the *sine qua non* of monogamous species. This assumption has repeatedly been shown to be incorrect.

What Is Social Monogamy?

As it became clear that in both avian and mammalian species living in long-term pairs might *not* always be sexually

TABLE 1 | Hypotheses for the roles of steroids and peptides in the emergence of social monogamy.

Primary Hypothesis: The behavioral and morphological traits associated with social monogamy emerge during development due to the combined actions of steroids and peptides

- A shift from a reliance on androgens to a stronger dependence on peptides may facilitate the prosocial traits of social monogamy

Testosterone: Features of social monogamy emerge in part via a reduction in the functional effects of androgens

- Mutations in the androgen receptor gene reduce the effects of androgens, reducing morphological and behavior sex differences and masculinization
- Variations in the 5- α reductase gene reduce sexual dimorphism by reducing the conversion of testosterone to the more potent dihydrotestosterone
- High levels of glucocorticoids outcompete testosterone for the androgen receptor, reducing sexual dimorphism

Estrogens: Created as a metabolic by-product of testosterone, estrogens play a role in the regulation of the traits of social monogamy and sexual differentiation

- Testosterone is aromatized to estradiol, which in turn facilitates actions of peptides, allowing for displays of the behavioral traits of social monogamy

Peptides: Oxytocin has the capacity to prevent masculinization by acting as an anti-inflammatory agent that inhibits the actions of androgens

- Variation in the oxytocin and vasopressin systems is shaped by factors such as genetics, epigenetics, and developmental experiences; differences in these systems help to explain the variation in sociality among species and between individuals within a species

exclusive, it became increasingly common in biology to narrow definitions of monogamy to describe what is now called *social monogamy* (Carter et al., 1995; Gowaty, 1996). A concurrent set of behavioral, anatomical, and physiological characteristics—*beyond the selection of sexual partners*—emerged that was found in most, but not all, apparently monogamous species (Kleiman, 1977; Carter et al., 1995; Table 2). Of particular value to identifying the biology of social monogamy were within-genera comparisons of apparently monogamous species to closely related non-monogamous relatives.

The broader use of the term social monogamy involved descriptions of animals cohabitating in male-female pairs, remaining together after mating, and jointly defending resources. Thus, the formation of *selective* and lasting pair bonds between two opposite sex individuals is the most consistent feature of social monogamy. Paternal or alloparental care is sometimes, but not always, observed (Kleiman, 1977; Komers and Brotherton, 1997). In addition, incest avoidance and reproductive suppression of non-breeding animals are common (Carter et al., 1995; Solomon and French, 1997).

In some cases, extended families formed, usually around the original male-female pair. Under these conditions members of a group might forego the opportunity to reproduce directly, remaining as philopatric helpers or alloparents in the natal family. The capacity to experience reproductive and juvenile growth suppression is not limited to socially monogamous species, but may be especially apparent in species that carry the traits of social monogamy. Components of this pattern also are described as *cooperative breeding* in which non-parents, both related and unrelated, play a major role in the care of offspring (Carter and Roberts, 1997; Solomon and French, 1997; Hrdy, 2009). In cooperative breeding groups one or more breeding females may exist with other members of the group supporting the breeders. Under some environmental conditions, social monogamy can morph into cooperative breeding and colonies, but, at least in rodents, at the core of these it is common to find one primary breeding pair (Solomon and French, 1997).

As described in more detail below, an important clue to the origins of social monogamy is a relative absence of sex differences in anatomical traits including body size and external genitalia. The same processes that have been implicated in mammalian

TABLE 2 | Features of social monogamy.

Selective social interaction with an opposite-sex pair mate; may or may not include exclusive mating with the social partner

Selective aggression toward unfamiliar animals, perhaps to guard mating access, offspring or other resources

Biparental care and paternal provisioning for offspring

Communal living within the family group

Alloparental care of younger offspring in the family nest

Reduced sexual dimorphism

Species categorized as socially monogamous may display some or all of these traits.

sexual differentiation and masculinization (Arnold, 2017) are plausible substrates for differential expression of monogamous (vs. non-monogamous) traits. As detailed below, variations in the sensitivity of androgen receptors or the production of androgens are among several likely sources of the sexual dimorphism seen in monogamy. Other steroids, and especially estrogen, also regulate the behavioral effects of neuropeptides (Carter, 1998). Conversely, peptides, such as oxytocin and vasopressin, may affect behavior in part through interactions with steroids or their receptors, especially during development (Carter et al., 2009; Van Anders et al., 2011; Perkeybile et al., 2018).

A PERSONAL HISTORY OF THE STUDY OF MONOGAMY AND LOVE IN PRAIRIE VOLES

It was the desire to understand proximate mechanisms supporting lasting social attachments and parenting, that motivated one of us (CSC) to study monogamy from a neuroendocrine perspective (Carter et al., 1995; Carter, 1998). The history of that ongoing journey is summarized below. This journey weaves together several threads including documentation from Lowell Getz, accumulating in the 1970s, that prairie voles were living in life-long pairs, my personal experiences with birth, lactation and oxytocin, and finally being accused by the media of studying “love.” Extrapolations from pair bonding in prairie voles to human love had not been my

original intent. However, the notion that love was “hormonal” was not novel (Klopfer, 1971), especially for someone who came of age in the 1960s. Thus, this challenge also pushed me to organize two international conferences asking “Is there a neurobiology of love” (Carter et al., 1997; Carter, 1998).

Monogamous Voles

Over the last four decades the prairie vole has become a favored model for studying the neurobiology of social monogamy. However, before we began our work with this species, both voles and lemmings, were widely studied as ecological models for understanding population dynamics (Getz, 1985). In prairie voles (*Microtus ochrogaster*), there was evidence of extreme and rapid variation in population density. This led Lowell Getz, a mammologist and my colleague at the University of Illinois, to conduct field and semi-natural studies, some of which continued over a period of more than 25 years (Carter and Getz, 1993; Getz and Carter, 1996). Booms and crashes in populations were not easily explained by environmental factors such as food, water, climate or predation. Emerging from those studies was evidence that prairie voles were sharing nests in long term pairs, generally remaining together for life. Furthermore, both sexually-naïve and experienced males were reliably parental when exposed to an infant. Families built around these pairs sometimes grew into communal groups, or cooperative breeders where young prairie voles help to care for new siblings, usually (but not always) with only one breeding female. In fact, about 70 percent of young prairie voles of both sexes that remained in the nest did not reproduce (Getz and Carter, 1980). In parallel studies, meadow voles (*Microtus pennsylvanicus*), often studied in the same fields, did not show these traits (Carter and Getz, 1993).

Monogamy: What Does Sex Have to Do With It?

In the 1970s when I began to collaborate with Getz, monogamy was generally used to refer to a mating system, and discussed in terms of reproductive fitness. At that time almost no one believed that a small rodent, such as the prairie vole, was capable of any kind of monogamy. We brought prairie voles, as well as the apparently non-monogamous meadow voles, into our laboratory. Assuming that sexual preferences would be of particular relevance to pair bonds, we repeatedly attempted to study *mating preference* as an index of social bonds; those attempts were unsuccessful. Both female and male prairie voles failed to show sexual preferences for familiar partners (vs. strangers).

Methods for DNA fingerprinting were first described in the mid-1980s (Jeffreys et al., 1985). The addition of DNA fingerprints increased the body of evidence indicating that social and sexual monogamy are *not* always coherent. Using DNA fingerprints from the offspring, we observed in prairie voles that a female given a choice voluntarily mated with and could produce mixed litters sired by both a familiar and an unfamiliar male (Carter et al., 1990). These early laboratory data, and later field studies in voles done by others (Solomon and Jacquot, 2002; Solomon et al., 2004; Ophir et al., 2007, 2008), have supported the notion that within a given individual or within a species,

social and sexual preferences were not necessarily synonymous. However, despite the absence of a reliable sexual preference, careful observations of the behavior of established pairs of prairie voles revealed that even when mating preferences were not shown, prosocial contact behaviors were reliably more likely to be directed toward a familiar partner (Carter and Getz, 1993). Although sexually promiscuous, female and male prairie voles showed a high level of partner specificity for *non-sexual contact*, and after mating showed aggression toward intruders of both sexes presumably to guard the mate or other resources (Gavish et al., 1983).

At this same time, controversies were arising from many sources around the concept of monogamy. Other species, including birds, were beginning to be described as socially monogamous, but again evidence for genetic monogamy was rare (Wickler and Seibt, 1983; Gowaty, 1996). Sexual monogamy as a unitary concept, especially at the species level, was becoming increasingly less useful.

Oxytocin, Monogamy, and Love

In 1980, I gave birth to my first son. I was infused with oxytocin during the birth. This transforming experience left me obsessed by the possible behavioral effects of the hormones of motherhood, and especially oxytocin, for both parents and babies. I became convinced that the social bonds between adults, as well as parents and infants, and other experiences that humans call “love,” must depend on a shared underlying neural substrate (Carter, 1992, 1998). Although with the exception of one study of maternal behavior in rats which had just appeared (Pedersen and Prange, 1979), there was at that time virtually no experimental data available to support this notion. This fixation led me to try to understand the effects of oxytocin on both sexual behavior and pair bonding in voles. In research first conducted in our laboratory by Diane Witt, we observed that following oxytocin treatment, female prairie voles were more likely to engage in social contact, although exogenous oxytocin did not facilitate sexual behavior (Witt et al., 1990). In this context, we then began to examine the hypothesis that oxytocin played a role in pair bond development.

Working with Jessie Williams and Kenneth Catania, we developed a paradigm for measuring partner preferences in prairie voles that continues to be used (Williams et al., 1992; Young et al., 2011). When prairie voles were given ample time to make a choice, a clear *social* preference could be detected (Williams et al., 1992). Under similar test conditions meadow voles did *not* show social preferences for a familiar partner (Carter and Getz, 1993). These findings were replicated several times. Pair bonding, as measured by a selective partner preference, could be assessed even in the absence of a sexual preference. Reluctantly, we and others abandoned the notion that sexual preference could serve as an index of monogamy.

However, using this simple choice paradigm we discovered that prior sexual interactions facilitated subsequent pair bonding, although in females mating was *not* essential for partner preference formation. It was already known that sexual behavior could release oxytocin a variety of species (Carter, 1992). The experiments that followed allowed us to describe a role for both

oxytocin (Williams et al., 1994) as well as vasopressin (Winslow et al., 1993) in pair bond formation in both sexes. If access to either the oxytocin or vasopressin receptor was blocked within the brain, then selective preferences did not form, although animals remained indiscriminately and highly social. However, if *both* the oxytocin and vasopressin receptors were blocked then social preferences disappeared and both males and females showed a significant reduction in social contact (Cho et al., 1999). These experiments supported the broader notion that oxytocin was not simply a female reproductive hormone, acting on the uterus or breast or facilitating maternal behavior (Pedersen and Prange, 1979; Keverne and Kendrick, 1992). Oxytocin also was capable of increasing sociality in both sexes. If there was a hormone of “love,” then oxytocin was a prime candidate, and the study of peptide pathways in pair bonding in prairie voles was an opportunity to test this hypothesis (Carter, 1998).

Selective Aggression and Vasopressin

Although prairie voles were initially social even to unfamiliar animals, we also observed that after mating, both females (Bowler et al., 2002) and males (Gavish et al., 1983) engaged in selective aggression toward unfamiliar intruders. This aggression probably served as defense of the home range and as well as mate guarding. However, oxytocin, which in our studies usually increased measures of positive sociality, did not seem to be a likely candidate as a substrate for lethal aggression.

Contemporaneous research by Ferris et al. (1984) in golden hamsters had shown that vasopressin treatment induced territoriality and defensive aggression. Thus, vasopressin also was a likely candidate for a role in the defensive components of social monogamy. Based on behavioral studies, first conducted in our laboratory by Gavish et al. (1983) and later repeated by Nicholas Hastings, we were able to block male postmating aggression with antagonists to the vasopressin receptor (Winslow et al., 1993). During this time Geert De Vries and his colleagues also found that central vasopressin changed following mating in male prairie voles (Bamshad et al., 1994). Taken together these studies laid the foundation for the emerging hypothesis that at least two of the major traits of social monogamy (partner preferences and mate guarding) depended on interactions between oxytocin and vasopressin (Carter, 1998, 2017). Subsequent studies implicated these same peptides in male parental and alloparental behavior in prairie voles (Bales et al., 2004a,b).

THE NEUROENDOCRINOLOGY OF MONOGAMY

“What’s Love Got to Do With It?” The Peptides of Maternity as the Neuroendocrine Foundation for Mammalian Sociality

The hormones of maternity, including birth and lactation, are foundational for the emergence of mammalian social behaviors. Mammals are differentiated from non-mammals by the presence of mammary glands and lactation. Care of offspring is not unique to mammals (Maclean, 1990), but dependence of young on

a mother, or an allomother, for nutrition and maternal-infant interactions (Hrdy, 2009) are universal features of mammalian life. Even the most primitive mammals, including the egg-laying platypus, show some degree of maternal engagement with their offspring and some form of lactation. Modern mammals are believed to have evolved from non-monogamous ancestors (Lukas and Clutton-Brock, 2013), but the proximate or genetic mechanisms underlying this evolution are only now becoming apparent.

The evolution of maternity depends in part on a specific cocktail of hormones including oxytocin-like molecules; these molecules and their receptors were apparently co-opted as substrates for social monogamy (Carter, 2014; Carter and Keverne, 2017). In maternal behavior (Fleming et al., 1999), as in social monogamy, hormonal effects have been traced to effects on a network of brain regions that influence approach to others and reductions in social fear (Albers, 2015; Caldwell, 2017).

Oxytocin allows immobility without fear in the presence of offspring or partners (Porges, 1998). Oxytocin also has a central role in the formation of *selective* social bonds between mothers and offspring (Keverne and Kendrick, 1992), between adults (Carter, 1998) and also in paternal behavior (Kenkel et al., 2012; Rilling, 2013). The more ancient mammalian neuropeptide, vasopressin, in dynamic interplay with oxytocin, also regulates birth (Arrowsmith and Wray, 2014). In conjunction with oxytocin, vasopressin was critical to pair bond formation and selective sociality (Cho et al., 1999). Vasopressin also plays a major role in defensive behaviors such as mate guarding. Both males and females are affected by oxytocin and vasopressin (Carter, 2017). However, the physiological effects of vasopressin support physical mobilization and defensive aggression, which may be especially critical in male mammals. Although both males and females synthesize oxytocin and vasopressin, there are often differences in the roles these molecules play in behavioral regulation in males vs. females (Bales et al., 2007a; Albers, 2015; Caldwell, 2017).

Oxytocin and its sibling peptide, vasopressin primarily originate in the nervous system, but both have receptors throughout the body (Grinevich et al., 2016; Chini et al., 2017). Because of the structural similarity between oxytocin and vasopressin, and their receptors, these peptides have many levels of interactions. Oxytocin evolved in mammals, at least 100 million years ago, associated with the evolution of lactation, as well as the positive sociality that much later allowed the emergence of modern humans (Carter, 2014). Over the last two decades a virtual “tsunami” of evidence has revealed that oxytocin promotes social engagement, attention, and synchrony in diverse mammalian species (Feldman, 2017; Hurlemann and Grinevich, 2018; Jurek and Neumann, 2018).

Arginine vasopressin and the vasopressin receptor (AVP V1a) are closely related to the ancestral molecule, vasotocin, and are considered more primitive than oxytocin. Vasotocin plays a role in egg production and the vasotocin receptor became the primary receptor for vasopressin (Goodson and Kingsbury, 2013). The oxytocin receptor presumably evolved more recently. Vasopressin can acutely override the actions of oxytocin. However, many of the functions of oxytocin are

actually mediated via stimulation of the vasopressin receptors, possibly inhibiting at least some of the defensive and protective functions of vasopressin, and permitting the reduction of fear and emergence of prosocial behaviors (Albers, 2015; Caldwell, 2017; Carter, 2017).

The interactions of these peptides are not always antagonistic. Instead, oxytocin and vasopressin work together in a kind of dynamic dance that allows rapid changes in behavioral processes and emotional states. Of particular relevance to social monogamy is the fact that both peptides are necessary for the *selective sociality* that characterizes pair bonds and certain forms of parental behavior. Other molecules and neural pathways, including those that involve dopamine and opioids, are necessary for selective forms of sociality including pair bonds. These are described elsewhere in the context of social monogamy and maternal behavior (Aragona and Wang, 2009; Burkett and Young, 2012). In general, it appears that networks regulated by oxytocin and vasopressin function together with other molecules to facilitate pair bonding.

Steroids, Peptides, and Monogamy

When the field of behavioral neuroendocrinology emerged in the twentieth century most research in this area focused on steroid hormones, usually of gonadal or adrenal origins. It had become common to attempt to explain major features of social and sexual behavior, especially in males, based on variations in androgens. In addition, adrenal steroids, in the context of “challenges” across the life-cycle were described as central to the interpretations of within or between species variations in positive social behavior and aggression (Wingfield et al., 1990). However, early research in prairie voles had shown that the basic features of social monogamy, continued to be present following removal of the gonads and in females formation of social bonds was facilitated by removal of the adrenal glands (DeVries et al., 1996).

Attempts by our group and others to modify the traits of social monogamy with injections of gonadal hormones generally were not successful (Carter and Roberts, 1997). Gonadal hormones were not essential for the *adult expression* of either pair bonding or aggression (Williams et al., 1992). Even in early life exogenous testosterone had very little effect on either behavior or anatomy in prairie voles. For example, in adult prairie voles castration did not prevent pair bonding or male-male aggression. However, *neonatal castration did disrupt pair bonding*, a change which could be *reversed with injections of vasopressin* (Cushing et al., 2003). Findings such as these led us to focus on neuropeptides and social behavior, a journey that has continued for over three decades. **Table 3** details the behavioral traits associated with social monogamy and the influence of selected steroids and neuropeptides in expression of these traits.

Variations in the Features of Social Monogamy Are Experience and Hormone Dependent

Research categorizing species according to their patterns of social behavior focused initially on attempts to identify prototypical patterns of behavior that reliably differed between species.

The notion that monogamy, either considered as a mating system or a social system, was based on a set of fixed traits has been challenged by laboratory and field data. However, even within species that have been described as socially monogamous there are substantial individual differences in the expression of the traits of monogamy. As detailed below, there is now increasing evidence that genetic and endocrine changes, including variations in peptide and steroid sensitivity, are likely to be important in the emergence of both socially monogamous species and are permissive for within species variations in the traits of social monogamy.

Much of the early research on the neurobiology of social monogamy was conducted in voles of the genus *Microtus*, comparing closely-related species that are either non-monogamous or socially monogamous. Recent work with other rodent genera, including *Peromyscus*, *Ctenomys*, and *Phodopus*, continues to implicate these peptides in social monogamy (Beery, 2015). Neural and behavioral substrates affected by oxytocin, vasopressin, androgens and estrogens, and interactions among these, regulate social behaviors in each of these species. However, striking species and individual variations exist.

Understanding both the consistency and flexibility underlying the traits of behaviors may be useful to dissecting the mechanisms responsible for the evolution of social monogamy. Traits that are more variable, may be especially sensitive to evolutionary pressures.

Here we use comparative examples from closely related rodents that include both monogamous and non-monogamous species within the same genera. These studies implicate oxytocin and vasopressin in social monogamy, but also reveal between and within species variation. The sources of this variation remain to be fully identified, but as shown in the examples below, can be regulated by genetics, epigenetics, and experience across the life span (Carter et al., 2009; Perkeybile and Bales, 2017; Perkeybile et al., 2018).

OXYTOCIN AND VASOPRESSIN

Oxytocin plays a central role in social behaviors used to define social monogamy. Evidence for this comes from experiments especially in prairie voles. Oxytocin injected into the central nervous system facilitated partner preferences in female (Williams et al., 1994) and male (Cho et al., 1999) prairie voles. Mating facilitates pair bond formation (Williams et al., 1992), and also releases oxytocin (Carter, 1992; Ross et al., 2009b). More recently intranasal infusions have been successfully used in voles to examine the role of oxytocin in pair bonding (Bales et al., 2013). Endogenous variation in the oxytocin system also has been associated with social behavior across a number of species (Beery, 2015).

Specific Brain Regions as Targets for Oxytocin

Among many brain regions relevant to reproductive and social behaviors is the nucleus accumbens, a region implicated in reinforcement and reward. The nucleus accumbens is capable

TABLE 3 | Features of social monogamy and functional effects of associated peptide and steroid hormones (based on the prairie vole model).

Traits of social monogamy	Selective sociality	Selective aggression	Alloparental care	Paternal behavior	Reduced sexual dimorphism
Functional effects of:					
Oxytocin	↑	↓/↑?	↑	↑	↑?
Vasopressin	↑	↑	↑	↑	
Testosterone	↑	↓ or NC		↓	↓?
Estradiol	↑	↑		↑	

The peptides oxytocin and vasopressin and the steroids testosterone and estrogen are implicated in several of the common traits of social monogamy, acting in some cases to increase the expression of a trait and in others to decrease it.

of being influenced by both social and hormonal experiences. In prairie voles the density of oxytocin receptors (Insel and Shapiro, 1992) has been positively related to both the female's capacity to pair bond with a male partner and to show maternal behavior. In the case of alloparenting, females with lower levels of oxytocin receptor density in the nucleus accumbens were less likely to exhibit alloparenting and more likely to be infanticidal (Olazabal and Young, 2006a,b). Upregulating expression of the oxytocin receptor in this region using a viral vector gene transfer facilitated alloparenting behavior (Ross et al., 2009b; Keebaugh and Young, 2011), while decreasing expression of the receptor by RNA interference was associated with a decrease in alloparental behavior (Keebaugh et al., 2015).

Oxytocin activity in the nucleus accumbens also is vital in females for partner preference formation. Mating induced an increase in extracellular oxytocin concentrations within the nucleus accumbens (Ross et al., 2009a). Activating oxytocin receptors in the nucleus accumbens by administering oxytocin directly to this region induced partner preferences in virgin females, while blocking the receptors prevented partner preference formation (Young et al., 2001; Liu and Wang, 2003). Overexpression of the oxytocin receptor in the nucleus accumbens, using a viral vector gene transfer, accelerated pair bonding in adult females after a short cohabitation with a male partner (Ross et al., 2009b), providing further evidence that receptors in this region are involved in selective sociality. A similar facilitation of pair bonding was seen if the overexpression occurs developmentally (Keebaugh and Young, 2011), while a developmental knockdown (but not elimination) of the oxytocin receptor disrupted pair bonding in adulthood (Keebaugh et al., 2015).

Under natural living conditions only a subset of animals leave the natal group to form pair bonds (Getz and Carter, 1996). Individual differences in the density of oxytocin receptors in the nucleus accumbens may help to explain the variation seen in sociality across individuals in this species. Male prairie voles typically exhibit one of two mating strategies—that of a resident male, maintaining a selective social bond with a female partner, or that of a wandering male, that does not live with a single partner, but instead engages in several acute mating interactions with females, similar to the pattern observed in non-monogamous vole species (Getz et al., 1993). This flexibility in sociality in males is reflected in variation in oxytocin receptor density in the nucleus accumbens. Resident males that are selectively social with a long-term partner have higher oxytocin receptor density in this

region compared to males adopting a non-monogamous social strategy (Ophir et al., 2012). Whether this is true for females remains to be studied.

Epigenetics and the Oxytocin System

Both social behavior and oxytocin receptors in the nucleus accumbens can be regulated epigenetically in early life by different amounts of parental care. For example, exposure to higher levels of parental care was associated with an increase in oxytocin receptor gene (*Oxtr*) expression and oxytocin receptor density and reduced levels of *Oxtr* DNA methylation (Perkeybile et al., 2018). Animals that experienced higher levels of parental care in early life exhibited higher levels of alloparenting and a facilitation of pair bonding later in life (Bales et al., 2007a; Perkeybile et al., 2013; Del Razo and Bales, 2016). This variability in later behavior in response to varied early experience appears to be regulated by epigenetic mechanisms, including *Oxtr* DNA methylation, controlling expression of *Oxtr* in the nucleus accumbens. Findings such as these suggest possible pathways to individual differences in sociality within prairie voles, as well as flexibility in social behavior between species.

The individual differences seen in sociality in this species have been associated with genetic variation in the *Oxtr*, which influences variation in receptor protein expression (King et al., 2016). *Oxtr* expression is sensitive to both adult and developmental epigenetic regulation via histone acetylation, and can be affected by mating. Administration of a histone deacetylase inhibitor, which serves to increase gene expression by increasing histone acetylation, facilitated preference formation without mating in both sexes and also was associated with an upregulation of *Oxtr* and the oxytocin receptor in the nucleus accumbens (Wang et al., 2013; Duclot et al., 2016). This provides additional support for the hypothesis that mating with a partner upregulates *Oxtr* gene expression in the nucleus accumbens through an epigenetic mechanism, helping to facilitate the formation of selective social bonds.

There is an increase in oxytocin receptor binding in the nucleus accumbens of female monogamous prairie voles, compared to non-monogamous meadow voles (Insel and Shapiro, 1992). This suggests that, similar to intraspecies variation in behavior, the differences in sociality between prairie voles and their non-monogamous counterparts, including both meadow and montane voles, arise due to differences in the density of oxytocin receptors in the nucleus accumbens, among other regions. In this case, high levels of oxytocin receptor

density are associated with lasting selective sociality while low receptor density may be associated with acute sociality, but not a selective partner preference. While overexpression of these receptors in virgin female prairie voles induced a partner preference even without mating, the same was not true for meadow voles; upregulating oxytocin receptors in the nucleus accumbens using a viral vector transfer of prairie vole genes to the meadow vole did not alter the meadow vole's social preference behavior (Ross et al., 2009b). Variations in sociality appear to arise from additional factors beyond oxytocin receptor density in the nucleus accumbens.

Species-Typical Variations in the Oxytocin System Associated With Sociality

Although much of the research characterizing a role for oxytocin in sociality and monogamy was originally conducted in prairie voles, additional comparative studies using closely related species have provided a broader perspective on variations in receptor system.

There are several striking differences in the patterns of peptide receptors between socially monogamous and non-monogamous species. For example, oxytocin receptor density was lower in a number of regions in the socially monogamous, territorial California mouse (*Peromyscus californicus*), when compared to the closely related, but non-monogamous deer mouse (*Peromyscus maniculatus*), especially in regions that typically control social behaviors, including the anterior olfactory nucleus, the central amygdala, and the bed nucleus of the stria terminalis (BNST), (Insel et al., 1991). This pattern of oxytocin receptor density is nearly opposite that observed in socially monogamous vs. non-monogamous voles. These findings indicate that multiple neural pathways may regulate variations in sociality. There also are few sex differences in distribution and density of oxytocin receptors in *P. californicus*, while sex differences are seen in most oxytocin receptor-rich regions in *P. maniculatus* (Insel et al., 1991). This may be related to species differences in sociality and territoriality that extend beyond pair bonding. The behavioral phenotype of male and female *P. californicus* tend to be similar, with both sexes engaging in high levels of parental care and both sexes working to maintain the home range and defend against intruders. However, males of this species are larger than females (Klein and Nelson, 1997) possibly implicating the demands of territoriality in sexual dimorphism in this species.

The colonial tuco-tuco (*Ctenomys sociabilis*) is a highly social South American rodent that forms selective and long-lasting female-based social groups, in which several females share a burrow with a single male (Lacey et al., 1997). In contrast, closely related Patagonian tuco-tucos (*Ctenomys haigi*), which occupy a similar habitat, are strictly solitary, with both males and females each occupying their own burrow (Lacey et al., 1998). Female colonial tuco-tucos do not show a preference for a familiar male partner over an unfamiliar male. They do, however, form long-term, selective social relationships with a small number of closely related females. This difference in sociality both between tuco-tuco species and between social tuco-tucos and monogamous prairie voles is associated with oxytocin receptor organization. *C.*

sociabilis have higher levels of oxytocin receptor in the central amygdala compared to *C. haigi*. Interestingly, these two species do not have differences in oxytocin receptor density in the nucleus accumbens, such as that seen in prairie vs. meadow voles (Beery et al., 2008). Beery and colleagues argue that the upregulation of oxytocin receptors in the central amygdala of the social tuco-tuco may be the mechanism that allows this species to form long-term extended social living groups through a decrease in aggression and social anxiety. The lack of a difference in the nucleus accumbens also may suggest a unique role for this region on behaviors relevant to male-female pair bonds, as opposed to same-sex selective sociality.

In another example, in female meadow voles, a species that typically does not form social bonds, same-sex social bonds can be induced to form under short day length conditions (Parker and Lee, 2003). This is accompanied by a rise in central amygdala oxytocin receptors, to levels similar to those seen in *C. sociabilis*. Upregulation of oxytocin receptors in the nucleus accumbens of meadow vole females, however, has no detectable impact on social bonding (Ross et al., 2009b). Variations in selective sociality between closely related species then, appear to be regulated by oxytocin receptors acting in different regions of the social brain in a species-dependent and sociality-dependent manner.

Vasopressin and Selective Sociality

Arginine vasopressin receptor V1a activation in the lateral septum and ventral pallidum is critical for long-term bond formation in male prairie voles. Both of these regions demonstrate divergent patterns of AVP V1a receptor density between socially monogamous and non-monogamous vole species (Insel et al., 1994; Pitkow et al., 2001; Lim et al., 2004), and this divergence in receptors results in predictable variations in expressions of behavior (Lim and Young, 2004; Ophir et al., 2009). Mating also facilitates the formation of selective relationships. Blocking the activity of AVP V1a receptors in either the lateral septum or ventral pallidum inhibits bond formation even after mating (Liu et al., 2001; Lim and Young, 2004), while direct activation of receptors in the lateral septum with an injection of vasopressin facilitates a selective preference even in the absence of mating (Liu et al., 2001). Altering the expression of AVP V1a receptors in the ventral pallidum also results in variations in behavior in male prairie voles; overexpression of the receptors using a viral vector gene transfer facilitates selective sociality (Pitkow et al., 2001), while receptor knockdown eliminates this behavior (Barrett et al., 2013).

Related processes may promote variability in sociality in non-monogamous species. When the AVP V1a receptor was overexpressed in the lateral septum in non-monogamous rats, using viral vector gene transfer of the prairie vole AVP V1a receptor, social recognition, and social interactions were increased beyond what is typically seen in this species; thus, increasing vasopressin receptor in specific brain regions in rats induced more "prairie vole-like" behavior (Landgraf et al., 2003). Likewise, overexpressing AVP V1a receptors in the ventral pallidum of the male meadow vole by using an AVP V1a receptor viral vector gene transfer from the prairie vole led to development

of a selective preference for a familiar opposite sex partner, a behavior not usually seen in this species (Lim et al., 2004).

As described above, associated with the formation of a selective social preference are increases in selective aggression in both male (Winslow et al., 1993) and female prairie voles (Bowler et al., 2002). Animals will show aggression toward novel animals of the same sex, likely as a form of mate guarding behavior (Kleiman, 1977; Getz et al., 1981; Winslow et al., 1993; Carter et al., 1995). Postcopulatory aggression does not occur in the non-monogamous male montane vole after mating (Shapiro and Dewsbury, 1990; Insel et al., 1995). The regulation of aggression results in part from activity of vasopressin and the AVP V1a receptor in the anterior hypothalamus. Selective bond formation is associated with increased receptor density in this region, and coincides with the onset of selective aggression in male prairie voles (Winslow et al., 1993). In socially bonded males behavioral changes in response to vasopressin in this region also occur in tests with a novel male (Gobrogge et al., 2009).

A similar pattern of vasopressin regulation of selective aggression is reported in *P. californicus* and *P. maniculatus*. Blocking activation of central AVP V1a receptors in *P. californicus* delayed aggression toward an intruder, but had no impact on aggression in non-territorial *P. maniculatus* (Bester-Meredith et al., 2005).

Taken together these data from socially monogamous rodents suggest an overlap in the role of vasopressin in the promotion of both selective social bonding and selective aggression. Both behaviors rely on an increase in vasopressin release and possibly increased sensitivity in the AVP V1a receptor, likely facilitated by mating. As vasopressin increases following mating, the male not only forms a selective preference for the female but also begins to guard access to his mate. Mated males eventually also reject unfamiliar females, even when the females are sexually receptive, helping to preserve the pair bond. These behaviors highlight the dual role of vasopressin in the formation and maintenance of social bonds. Males simultaneously engage in selective and enduring affiliative behavior with their female partner, while also engaging in selective and enduring aggressive behavior toward non-partners. The synchrony and balance between these two sets of selective behaviors may be vital for maintaining a socially monogamous system.

Comparisons in the regulation of aggression by vasopressin in socially monogamous prairie voles and Siberian hamsters (*Phodopus sungorus*), a non-monogamous and territorial species, highlight the sometimes contrasting role a single factor can play in generating variation in patterns of sociality across species. As discussed above, vasopressin activity in the anterior hypothalamus plays a role in the display of selective aggression in male prairie voles (Gobrogge et al., 2007, 2009). The anterior hypothalamus also plays a role in aggression in non-monogamous Syrian hamsters (Ferris and Potegal, 1988; Potegal and Ferris, 1989; Ferris et al., 1997). These displays of aggression, however, serve very different purposes for the two species. Male prairie voles display aggression toward other males only *after mating*, as a form of mate guarding behavior. Syrian hamsters, however, use this aggression in territorial disputes and in gaining access to a mate *prior to mating*. The fact that similar

expressions of behavior, regulated by similar vasopressinergic activity can serve different purposes between species, highlights the flexibility within these social behavior systems; the same behavior regulated by the same endocrine mechanisms can often be used in two distinct ways by species depending on their social system. Vasopressin may play a role in aggression under both circumstances. However, as hypothesized below, it is possible that the regulation of aggression and vasopressin in non-monogamous species is more likely to be regulated by testosterone, while socially monogamous species may be less reliant on androgens and more dependent on peptides, possibly linked to estrogens.

In addition to regulating variations in selective long-term sociality and aggression both within and between species, vasopressin is also involved in variations in paternal behavior. For example, new prairie vole fathers experience an increase in vasopressin mRNA in the paraventricular nucleus and supraoptic nucleus after the birth of a litter compared to virgin males. This rise in vasopressin mRNA is not found in new fathers in the non-monogamous, non-paternal montane vole (Wang et al., 2000). An increase in vasopressin gene expression associated with birth of their own litter is particularly interesting given that male prairie voles are highly alloparental as virgins. This also suggests the possibility that different factors regulate alloparental compared to paternal behavior in this species.

Within *P. californicus* fathers, variation in vasopressin immunoreactivity in the BNST corresponds to variation seen in displays of paternal care; males with increased vasopressin activity spent more time in the nest with offspring, grooming, and huddling over them (Bester-Meredith and Marler, 2003). A related pattern of changes in vasopressin correlates with paternal behavior within this species. California mouse fathers have higher levels of vasopressin immunoreactivity in the BNST compared to non-monogamous and less paternal white-footed mice fathers (Bester-Meredith et al., 1999). These and other data suggest that vasopressin has a central role in paternal investment and care within socially monogamous species, but also in closely related species with divergent behavioral patterns, including social behaviors that have been termed non-monogamous.

Steroids, Peptides, and Aggression

In male prairie voles aggression is triggered within 24 h or less by mating acting via vasopressin pathways (Winslow et al., 1993). By relying on social stimuli and vasopressin to induce or support aggression (rather than acute changes in testosterone), male prairie voles also may be able to be transformed quickly—within hours—from acting as comparatively non-aggressive, non-reproductive animals to creatures capable of showing lethal aggression toward intruders.

Female prairie voles also are capable of intruder-directed aggression, especially toward other females (Firestone et al., 1991). Although the origins of female aggression have not been well studied, preliminary studies did not implicate vasopressin (Bowler et al., 2002). The role of vasopressin in female behavior deserves additional investigation, but sex differences in the effects of vasopressin are common (Albers, 2015; Caldwell, 2017; Carter, 2017).

Circulating testosterone levels are typically found to be inversely related to expression of paternal behavior in non-monogamous males (Wingfield et al., 1990; Ketterson et al., 1992; Nunes et al., 2001). Human fathers often experience a drop in testosterone immediately after the birth of their child (Storey et al., 2000). In addition, human males who have lower levels of testosterone, whether fathers or non-fathers, respond more to the sound of infant cries than do males with higher testosterone levels (Fleming et al., 2002). In rodents declines in testosterone often coincide with a decrease in infanticidal aggression, presumably preparing the male to support, or at least not attack, his offspring (Elwood, 1977; Brown, 1986; Perrigo et al., 1991). In Mongolian gerbils (*Meriones unguiculatus*) castration increased time caring for offspring, including increases in grooming and huddling over pups (Clark and Galef, 1999). In typically infanticidal rats castration during adolescence and young adulthood decreases rates of infanticide, a behavior that is reinstated with testosterone replacement (Rosenberg et al., 1971; Rosenberg and Sherman, 1975). The same effect on infanticide is seen in male mice after adult castration (Svare and Mann, 1981). In both mice and rats, high levels of testosterone in these non-monogamous, non-paternal species may increase male infanticide.

In contrast, data from several species of socially monogamous rodents revealed high levels of testosterone around the time of birth. For example, male Djungarian hamsters (*Phodopus campbelli*), a highly social and highly paternal species, maintain elevated testosterone after the birth of a litter while still engaging in paternal care. The high testosterone levels immediately following birth might facilitate mating or mate guarding during the postpartum estrus, while the higher levels maintained several days after birth could support paternal aggression toward intruders. In contrast, the closely related but less social Siberian hamster (*P. sungorus*) typically engages in little paternal care, and experiences a drop in testosterone soon after birth (Reburn and Wynne-Edwards, 1999).

Comparatively high levels of testosterone are observed in other socially monogamous species, include California mice and prairie voles. As discussed more in depth below, *P. californicus* experience a surge in testosterone just prior to the birth of their litter that coincides with the onset of paternal behavior (Gubernick et al., 1994). In prairie voles increased testosterone appears necessary for alloparental care in males, as castration in adulthood decreased paternal care of novel pups (Wang and De Vries, 1993).

Comparisons among socially monogamous, vs. non-monogamous, rodent species suggest that testosterone does play a role in paternal behavior. However, rather than acting through androgen receptors, these effects may require conversion to estradiol and action through estrogen receptors (Trainor and Marler, 2002). There is considerable evidence for variation in estrogen receptor distribution, particularly the estrogen receptor alpha (ER- α), between socially monogamous and non-monogamous species. This is discussed in depth below. The aromatization of testosterone to estradiol, then, which facilitates the effects of both oxytocin and vasopressin, might enable males to show high levels of paternal care toward young that are in

at least some cases their own, while still engaging in selective aggression toward intruders.

Estrogen and Estrogen Receptors Are Correlated With Sociality

Based on data from non-monogamous rodents, it has been proposed that ER- α activation masculinizes behavior (Scordalakes et al., 2002; Scordalakes and Rissman, 2004; Nugent et al., 2015). Data supporting a role for the ER- α as a factor inhibiting sociality comes from patterns of selective sociality in both vole and hamster species. Pine voles (*Microtus pinetorum*) are socially monogamous, with behavioral features similar to those seen in prairie voles. In comparison, the montane vole (*M. montanus*) and the meadow vole (*M. pennsylvanicus*) are both less social, non-monogamous species with typically lower levels of paternal or alloparental behavior. Pine voles have decreased levels of ER- α in the medial amygdala compared to both non-monogamous vole species and in the BNST compared to montane voles (Cushing and Wynne-Edwards, 2006). Similarly, the highly social Djungarian hamster (*P. campbelli*) also has decreased ER- α in both the medial amygdala and BNST compared to the less social Siberian hamster (*P. sungorus*; Cushing and Wynne-Edwards, 2006). When ER- α levels are low then, as is seen in both vole and hamster species, prosocial contact is more commonly directed toward a specific partner and toward infants. Activity in both the medial amygdala and the BNST are has been related to displays of aggression and parental behavior in the prairie vole (Wang and De Vries, 1993; Wang et al., 1997), possibly mediated by stimulation of the ER- α .

Within prairie voles, there is population-level variability in social behavior that correlates with variation in ER- α expression. The home range of this species is large, stretching from New Mexico north into Alberta, Canada and as far east as the Great Lakes, West Virginia, and Tennessee (Stalling, 1990). This broad geographic home range is associated with variety in habitat resource availability and also in varying degrees of monogamous behavior. Voles from Illinois display relatively high rates of social monogamy (Getz et al., 1993; Roberts et al., 1998; Solomon and Jacquot, 2002), a low degree of sexual dimorphism, and high rates of paternal care (Roberts et al., 1998; Ophir et al., 2007). Voles from Kansas appear to be more promiscuous (Danielson and Gaines, 1987; Swihart and Slade, 1989). In males, the levels of ER- α expression in both the BNST and medial amygdala are reduced in the highly social Illinois prairie vole compared to the less social Kansas prairie vole. In socially monogamous species, stimulation of the ER- α , may inhibit the features of social monogamy, while stimulation of the ER- α could facilitate aggression. Taken together these findings suggest that neural mechanisms that allow a shift toward selective sociality may be inhibited by stimulation of the ER- α , possibly as a component of the association between masculine behaviors, androgens, and non-selective aggression which is more common in non-monogamous mammals.

In the Djungarian hamster, adult males have circulating estradiol levels as high as those found in females (Schum

and Wynne-Edwards, 2005). Castration during the partner's pregnancy lowers both plasma testosterone and estradiol levels in males. This decrease in steroid hormones results in decreased aggression toward an intruder compared to intact males, but has no impact on paternal behavior toward offspring. This supports a role for these steroid hormones in facilitating aggression, but does not support the hypothesis that the high plasma levels of estradiol seen in reproductive males serves to increase paternal behavior (Hume and Wynne-Edwards, 2005). This contrast between effects of differences in ER- α expression and plasma estradiol levels provides further support for the idea that flexibility in behavior is not always due to variation in the hormone, but rather due to variation in its receptor density. In this case, *P. campbelli* rely on low levels of ER- α in order to engage in high degrees of social behavior. Thus, following a pattern that is seen for testosterone, changes in the estrogen receptor, rather than available estradiol, may be more specifically related to observable changes in behavior.

This differs from the pattern reported in male California mice. Males show a high degree of paternal care after the birth of their first litter of offspring. This change in behavior is accompanied by a surge in plasma testosterone just prior to birth (Gubernick et al., 1994). Eliminating this rise in testosterone by gonadectomy acts to drastically reduce paternal huddling and grooming of offspring (Trainor and Marler, 2002; Marler et al., 2003), while gonadectomy coupled with testosterone replacement restores behavior to typical high levels (Trainor and Marler, 2001, 2002). In *P. californicus*, paternal behavior appears to be controlled by estradiol via its aromatization from testosterone. Gonadectomy with an estradiol replacement has the same impact of restoring paternal huddling and grooming as does testosterone replacement. Co-administration of testosterone plus fadrozole, an aromatase inhibitor, reduces paternal behaviors, an effect not seen with co-administration of testosterone and saline or estradiol and fadrozole (Trainor and Marler, 2002). This work provides evidence that testosterone is not directly impacting huddling and grooming, but rather is exerting its influence via conversion to estradiol. This differs from factors regulating paternal behavior in *P. campbelli*, in which paternal care does not appear to rely on estradiol, and provides additional evidence for species differences in how variation in sociality arises.

Taken together these findings support the hypothesis that estrogens, created as a metabolic by-product of testosterone, may play a major role in the regulation of the traits of social monogamy. In many, but perhaps not all species, estrogens act via the ER- α to increase aggression, possibly in part through downstream effects on vasopressin. However, other receptors exist for estrogen, although these are at present less well understood. It is possibly that estrogen could have effects on different receptors or actions on other brain regions, for example playing a role in the regulation of the oxytocin receptor. Thus, a given hormone, such as estrogen, might promote selective socially in some cases and aggression in others.

Coordinating Social Behaviors With Demands of the Physical and Social Environment

Steroid hormones, including androgens, estrogens, and adrenal hormones coordinate the demands of reproduction with changes in the physical environment, including seasonality and photoperiod, as well as availability of resources such as food and water (Wingfield et al., 1990). The functional properties of steroid hormones allow these molecules to play a major role in both reproductive behavior and patterns of social behavior that support reproductive success. In contrast, reproduction in socially monogamous species often includes a comparative reliance on quickly changing social cues, including those transmitted by olfaction (Dluzen et al., 1981) and behavioral experiences such as mating (Winslow et al., 1993). These effects could be more directly dependent on the rapid actions of neurosteroid hormones (Balthazart and Ball, 2016), which are being studied in avian social behavior. In addition, the actions of steroids might rely on steroid-peptide interactions with steroid effects being critical for receptor organization or physiology (Witt et al., 1991). In other cases, such as the regulation by mating of male aggression, steroids might be replaced by direct effects of peptide hormones such as vasopressin (Winslow et al., 1993).

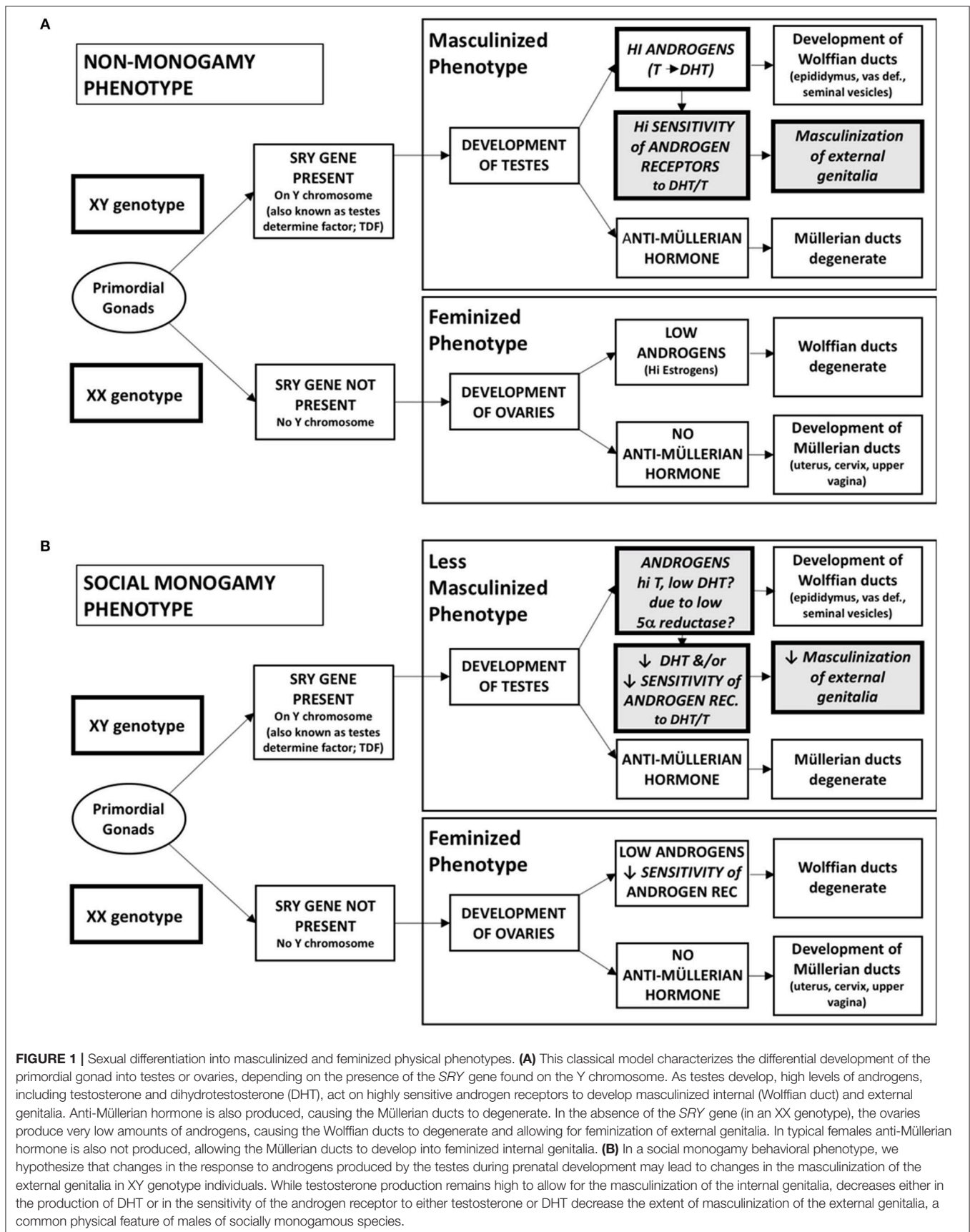
Peptides, including oxytocin and vasopressin, have many actions, including acting as neuromodulators, neurotransmitters, and hormones (Jurek and Neumann, 2018). Neuropeptides have the capacity to respond quickly to social cues, and are positioned to influence behavior by their abundant synthesis in the brain (rather than peripheral organs), with receptors in critical tissues within the nervous system, as well as the immune system and throughout the body. The production of peptide receptors also is capable of being epigenetically tuned by experience creating longer-lasting changes in the capacity to respond to social cues (Perkeybile et al., 2018).

THE DEVELOPMENTAL ORIGINS OF SOCIAL MONOGAMY

Sexual Differentiation: An Overview

Sexual differentiation is the consequence of genes including those that regulate the synthesis or action of testosterone, estrogen and their receptors (Arnold, 2017). During early development the *SRY* gene (testes determining gene), located on the Y chromosome, enables the undifferentiated gonad to become masculinized, producing primarily testosterone and sperm (Figure 1). In the absence of the *SRY* gene the gonad is feminized, primarily producing higher levels of estrogen and allowing ovulation (Arnold, 2017).

In the classical model of sexual differentiation, derived primarily from non-monogamous rodents, it has been assumed that testicular hormones are essential for masculinization (Figure 1). Steroids implicated in genital masculinization include testosterone and dihydrotestosterone (DHT). Testosterone serves as a prohormone and can be converted locally to DHT. In addition, testosterone, in the presence of the aromatase enzyme,



can be converted to an estrogen. Acting on the ER- α , it has been proposed that estrogen regulates behavioral masculinization, even in the absence of androgens (Scordalakes et al., 2002). Estrogens, possibly in conjunction with DHT, facilitate patterns of male sexual behavior including mounting and ejaculatory reflexes. Thus, at the level of the brain, testosterone *per se* may not be essential for masculine sex behavior, although a combination of DHT plus estrogen seems to be important to optimize adult male sexuality (Pfaff and Baum, 2018).

In mammals two X chromosomes lead to a feminine phenotype, vs. the XY genotype found in male mammals. However, the haploid nature of sex chromosomes has complex consequences for the vulnerability to modification of genes on the Y or X chromosome. For example, in females some (but not all) genes on one of the two X chromosomes are inactivated. This is accomplished by DNA methylation and in some cases parental genomic imprinting (Keverne, 2013). Genes on the X chromosome that escape X-inactivation or genes that are not imprinted may affect sexual differentiation (Arnold, 2017).

Sexual Differentiation as a Template for the Biology of Social Monogamy

The key behaviors that appear to differentiate monogamous from non-monogamous species are presented in **Table 2**. These are exhibited on a continuum across and within species and are sensitive to physiological changes in early life. The neuroendocrinology that regulates these behaviors also occurs on a continuum, with interspecies and intraspecies variation in these endocrine markers. Based on data primarily from rodents, it appears that the traits of social monogamy appear during the course of development as a merger of actions of steroids and peptides (Choleris et al., 2008). In this context the actions of steroids are comparatively slow, but can have long-lasting consequences, while those of neuropeptides (as well as neurotransmitters) may be more rapid, but also somewhat more transient.

In contrast to sexual behavior, social behaviors are inherently variable and must respond to a constantly changing social and physical environment. Thus, the regulation of the features of social monogamy represents a compromise between quickly adapting behavioral changes, such as those necessary for parenting and pair bonding, and more conserved traits, such as sex differences in body size or genital morphology or the distribution of receptors for both steroids and peptides.

A cardinal feature of socially monogamous species includes a relative reduction in physical sexual dimorphism, presumably as an effect of sexual selection (Emlen and Oring, 1977; Kleiman, 1977). However, with a few exceptions (Kleiman, 1977; Klein and Nelson, 1997; Roberts et al., 1998), we caution that evidence for this aspect of social monogamy seems to be primarily anecdotal, possibly based on visual observations by field biologists, rather than systematic measurements of body size or genital anatomy. Based on the hypothesis that social monogamy is associated with a shift in the male phenotype toward a less masculine pattern (**Figure 2**), we postulate here that candidate neuroendocrine processes and genes that downregulate sexual dimorphism might

also have allowed the emergence of the traits of social monogamy (**Table 3**).

Androgens and Masculinity

Several hormones have the capacity to influence testosterone's production or action. Among these are factors in the hypothalamic-pituitary-gonadal axis, including releasing hormones such as gonadotropin releasing hormone (GnRH). However, GnRH and testosterone are probably not the main source of the reductions in sexual dimorphism, at least in prairie voles. In fact, high levels of testosterone have been measured in prairie voles including during the perinatal period (Lansing et al., 2013).

In prairie voles, both during development and in adulthood, hormones originating in the gonads do not seem to be essential for pair bonding or male parental behavior (Carter et al., 1995; Carter and Roberts, 1997; Lansing et al., 2013). In addition, giving testosterone to female prairie voles has remarkably little behavioral effect and testosterone treatment in early life does not masculinize the genitalia in either sex. Taken together these findings suggest that *prairie voles may have a deficit in the capacity to respond to testosterone*.

One option through which features of social monogamy might arise more generally is via a reduction in the functional effects of androgens. This could occur through several known pathways (**Table 4**). The effects of testosterone differ according to whether they are mediated by androgen (AR) or estrogen receptors (including ER- α). In the central nervous system testosterone can be aromatized locally to estradiol (E2). As mentioned above, estrogens acting on ER- α , are considered a major factor in brain masculinization (Bodo and Rissman, 2006; Cushing, 2016).

Evidence is at present incomplete; however, studies to date suggest that although prairie voles may be comparatively insensitive to testosterone they continue to be capable of responding to estrogen. In fact estrogen, possibly by facilitating the synthesis of vasopressin (Lonstein et al., 2005), appears to play a central role in the regulation of sociality and aggression in male prairie voles (Cushing and Kramer, 2005).

Acting via the AR, testosterone and DHT also play a major role in the development of masculine physical traits including body size, anogenital distance, and phallic and scrotal development. AR is highly expressed in genitals, but also in muscle, bone, and other tissues (at least in non-monogamous mammals; **Figure 1**). This pathway was originally identified in humans by a genetic failure of the AR to bind androgens, known as *androgen-insensitivity syndrome* (AIS). In AIS, individuals with an XY chromosome pattern have an external body type that appears female, while internal organs are masculinized. Over 1,000 polymorphisms in the gene for the AR have been reported. Although the functional roles of most of these are not yet well understood (Gottlieb et al., 2012), this is a receptor already known for variation.

As mentioned above, the gene for the androgen receptor resides on the X chromosome. The X chromosome is haploid in males and may be inactivated in females. Thus, mutations in the gene for the androgen receptor or other processes that indirectly reduce the effects of androgens could be a route

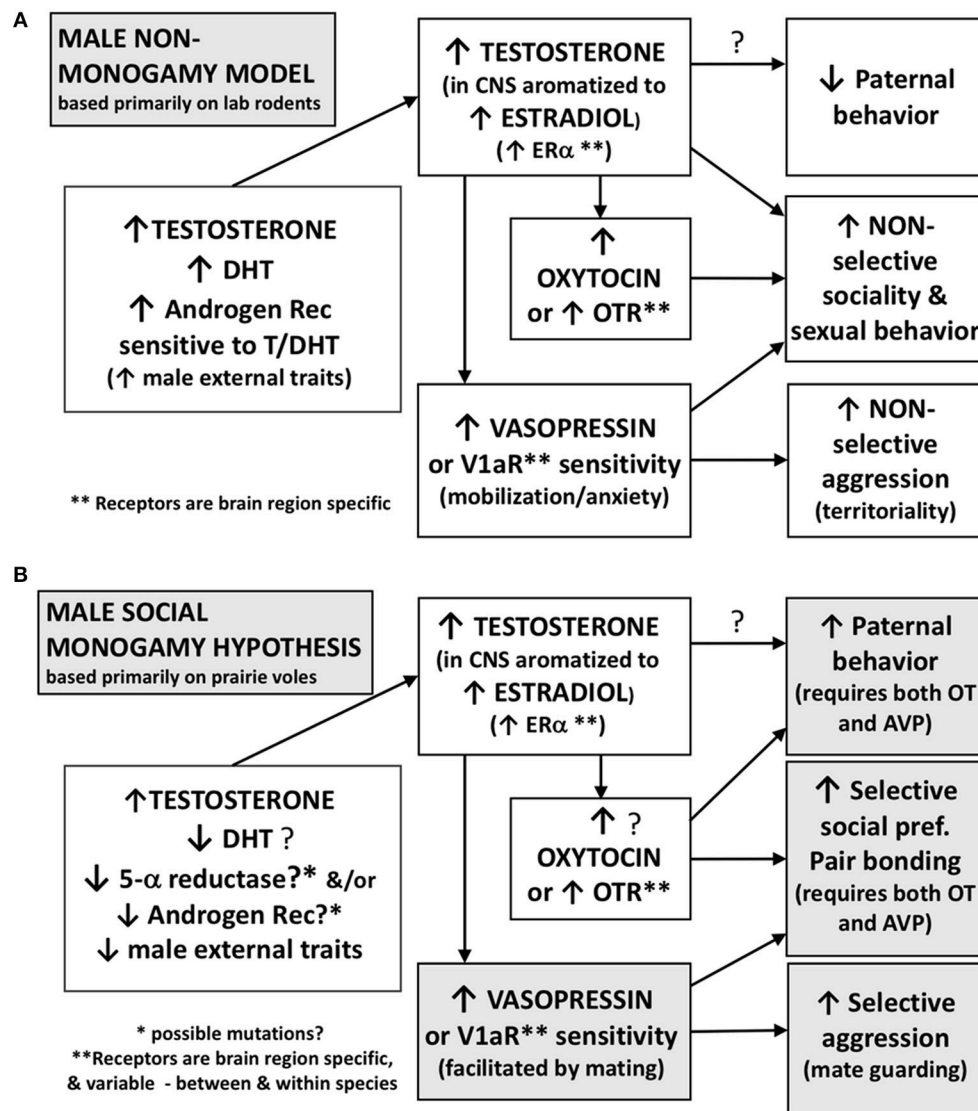


FIGURE 2 | Functional differences in the effects of steroids and peptides may contribute to non-monogamous vs. socially monogamous behavioral phenotypes in males. This hypothesis is based primarily on data from laboratory rodents including prairie voles. **(A)** Males of non-monogamous species often display a suite of behaviors that include low levels of paternal investment, non-selective social and sexual behavior, and non-selective aggression that typically occurs when competing for a mate or territory. These behaviors are facilitated by high levels of androgens and a high sensitivity of the androgen receptor. High levels of testosterone, some of which is aromatized locally to an estrogen, may contribute to low levels of paternal behavior and lead to non-selective social behavior and mating. In addition, vasopressin, facilitated by androgens, is involved in mating- and territory-related aggression in these males. **(B)** In socially monogamous males, we hypothesize that decreased sensitivity of the androgen receptor, or possibly lower levels of DHT, with a concurrent increase in vasopressin, could contribute to high levels of paternal investment, selective social preferences, and selective mate guarding aggression. Testosterone can be aromatized locally to estrogen and also facilitate the release of oxytocin and vasopressin.

to reducing sex differences and masculinization. The AR gene may be subject to particularly intense evolutionary pressure (Mokkonen and Crespi, 2015). Thus, if mutations or epigenetic silencing occurs in the X chromosome in areas relevant to the expression of the AR gene, this could reduce AR production. AR expression, especially in genital tissue is a major candidate for the regulation of masculine physical traits and thus the reduced sexual dimorphism seen in some socially monogamous mammals (Figure 1).

The metabolism of testosterone to DHT is another process that could influence peripheral anatomy. The 5-α reductase enzyme, type 2 (SRD5A2) is critical for the conversion of testosterone to DHT. In the absence of DHT, masculinization of the genitalia is disrupted (Okeigwe and Kuohung, 2014). The gene for this enzyme is also variable and subject to mutation. Variation in SRD5A2 is another putative candidate for reducing sexual dimorphism.

TABLE 4 | Putative pathways to reductions in physical sexual dimorphism and reduced "Masculine" traits.

Hypothesized pathways	Evidence in the prairie vole
1. Reduced levels of testosterone or DHT	High levels of T (Lansing et al., 2013) DHT levels have not been reported
2. Failure to convert testosterone to DHT, possibly due to variation in the 5 α -reductase enzyme	??
3. Genetic or epigenetic variation in the androgen receptor (AR)	??
4. Genes on sex chromosomes vulnerable to epigenetic modification?	??
5. Presence of inhibitory factors such as stress or high levels of glucocorticoids	Very high corticosterone, likely across the life cycle (DeVries et al., 1995, 1996) Glucocorticoid receptor insensitivity (Taymans et al., 1997)
6. Exposure to oxytocin in the perinatal period	Reduced sex difference in the brain (Yee et al., in preparation) Decreased AVP V1a receptors (both sexes; Bales et al., 2007b) May act to demasculinize via anti-inflammatory pathways (Nugent et al., 2015)

Do High Levels of Glucocorticoids Contribute to the Social Monogamy Phenotype?

Based on research in laboratory rodents, it has been assumed that the creation of a typical male phenotype (especially external masculinization) requires the relative absence of high levels of stress and associated glucocorticoids, which can inhibit masculinization (Ward and Ward, 1985). Thus, stressful experiences during early development are another possible mechanism for suppressing masculine traits, including genital masculinization (Ward and Ward, 1985). Support for this hypothesis comes from research in rats; early life stress or increases in glucocorticoids also increase male sociality and parental behavior in late life (Kinsley and Bridges, 1988).

Prairie voles have exceptionally high levels of glucocorticoids (Figure 3), 10 times those seen in non-monogamous montane voles (Taymans et al., 1997), as well as mice and rats. Prairie voles also are insensitive to drugs that mimic the effects of glucocorticoids, indicative of glucocorticoid receptor resistance (Taymans et al., 1997). A remarkably similar pattern, including high endogenous levels of glucocorticoids and glucocorticoid resistance, has been reported in New World primates, including marmosets (Chrousos et al., 1982), which show several parallel features of social monogamy (French et al., 2018). Thus, reductions in sensitivity of the glucocorticoid receptor, with a concurrent elevation in glucocorticoids, could create a hormonal environment in which glucocorticoids compete with testosterone for the AR. This is another plausible pathway through which reductions in masculine traits might occur.

Could Oxytocin Play a Developmental Role in Physical Demasculinization, While Increasing the Behavioral Traits of Social Monogamy?

We hypothesize here that oxytocin may have the capacity to prevent masculinization. For example, Nugent et al. (2015) have added compelling evidence for a role for changes in inflammation as a necessary mechanism through which testosterone creates a masculine behavioral phenotype. Oxytocin is anti-inflammatory (Yuan et al., 2016), and thus might indirectly inhibit the actions of androgens on the masculine phenotype.

Socially monogamous species, including prairie voles, often have high levels of oxytocin (Kramer et al., 2004), and might be less responsive to both the masculinizing and inflammatory effects of testosterone. In addition, a brain imaging study from our group indicates, at least in prairie voles, that a brief perinatal exposure to oxytocin can demasculinize the nervous system (Yee, Ferris et al., ms in preparation). Other studies have revealed that early life manipulations of the oxytocin system alter several traits of monogamy, facilitating pair bonding and alloparental behavior in males, with little effect in females (Carter et al., 2009).

At least one source of variation in oxytocin in early life is exposure to differential parenting. The neural systems that regulate social experiences in adulthood, also are epigenetically tuned by social experience and peptides in early life (Perkeybile et al., 2018). As one other example, in prairie voles a single exposure to oxytocin on the first day of life altered the expression of the vasopressin receptor in adulthood (Bales et al., 2007b). In contrast blocking the oxytocin receptor interferes with the behavioral traits of social monogamy, again with effects that thus far have been most apparent in males (Bales et al., 2004a; Carter et al., 2009).

CONCLUSIONS

Individual differences in social behavior are regulated by genetics, epigenetics, and patterns of short-term change in peptides and steroids. While many factors contribute to the expression of social behaviors across species, at present the best studied are variations in steroids and more recently in oxytocin and vasopressin pathways. Comparative analyses, especially in closely related yet behavioral distinct species, have been useful in identifying mechanisms through which evolutionary and proximate pressures could shape the features of social monogamy. Each of the social behaviors reviewed here, as well as several others related to social monogamy, such as the social regulation of reproduction, are adaptive and exist along a continuum. Where an individual or a species falls on that behavioral continuum is controlled at least in part by peptide and steroid systems and the interactions among these. Further adding to these variations, experiences across the life cycle serve to change and refine these systems. The same hormones necessary for the expression of the features of social monogamy, also are implicated in the development of a nervous system capable of being epigenetically tuned to high levels of sociality.

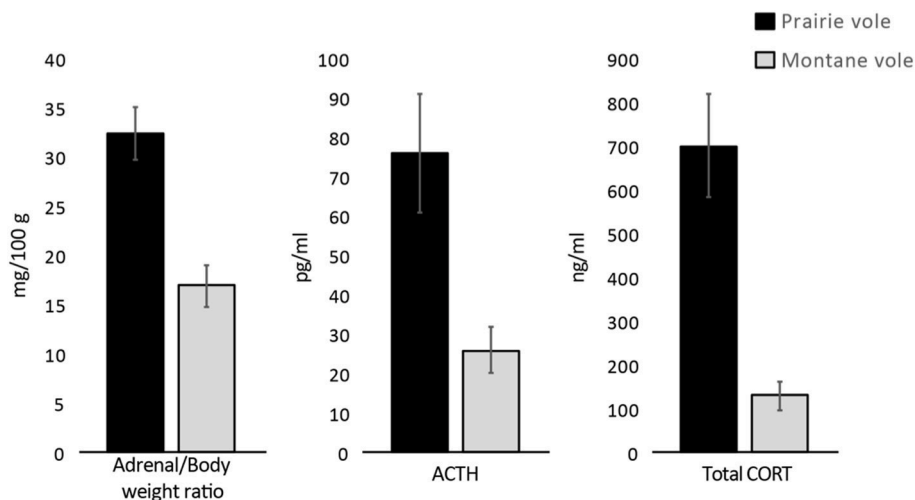


FIGURE 3 | In comparison to non-monogamous montane voles, the socially monogamous prairie vole shows higher unstimulated levels of hormones of the hypothalamic-pituitary-adrenal axis. Adapted from Taymans et al. (1997).

The full array of unique features seen in social monogamy is observed in only a small fraction of mammalian species. However, understanding these prosocial traits, such as social attachment and parenting, has translational implications for human behavior. A topic as apparently esoteric as social monogamy in voles has uncovered neural systems relevant to the biology of love (Carter, 1998, 2017), and the role of relationships in coping with stress or trauma (Smith and Wang, 2014; Sun et al., 2014; Perkeybile and Carter, 2018). Understanding natural variations, within and across species, provides knowledge that has energized multidisciplinary sciences ranging from ethology and evolution (Ophir et al., 2008, 2012) to molecular biology (Bendesky et al., 2017), to psychology (Feldman, 2017) and emerging fields such as “precision” medicine. Findings arising from the study of socially monogamous mammals have even helped to generate interest in the broad therapeutic usefulness of peptide hormones, such as oxytocin agonists or vasopressin antagonists in the treatment of developmental disorders or other illnesses, such as autism, schizophrenia, and substance abuse (Carter, 2007; Buisman-Pijlman et al., 2014; Pedersen, 2017).

It has been suggested by French et al. (2018) that social monogamy should be treated as a “menu.” However, items on a menu can occur independently. We suggest here that social

monogamy is more analogous to a biological “syndrome,” built around a recurrent set of ingredients. The features used to define social monogamy include both behavioral and anatomical traits typically, but not always, occur together. As with other syndromes, the consistent appearance of a pattern of traits suggests common underlying causes which are now being identified.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Alternative Mating Tactics in Socially Monogamous Prairie Voles, *Microtus ochrogaster*

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Alternative mating tactics appear to evolve when sexual selection is strong. Because such conditions are usually observed in species with polygynous or polyandrous mating systems, alternative mating tactics in monogamous mating systems are seldom documented and are poorly understood. In prairie voles, *Microtus ochrogaster*, a species widely known for forming monogamous pair-bonds, the expression of territoriality within each sex is dimorphic, and includes non-territorial “wanderers” as well as territorial “residents.” To explore the variance in fitness, measured in offspring numbers, among breeding individuals expressing these alternative mating tactics, we compiled parentage data over 3 years for male and female prairie voles from natural populations in Indiana and Kansas, USA. We found that: (1) the average fitnesses of males and females within each population were identical when adjusted by the sex ratio; (2) the variance in fitness in male and female prairie voles was comparable to that of highly polygynous species; (3) The average fitnesses of male tactics, and of female tactics, were equivalent within and among years within each location; (4) consistent with negative frequency-dependent selection acting on mating phenotypes, the between-tactic variance in fitness for male and female mating tactics decreased with increasing study duration; (5) consistent with negative assortative mating, resident males, and wanderer females produced offspring primarily in monogamous partnerships, whereas wanderer males and resident females produced offspring primarily in polygamous partnerships. Our results show that the conditions necessary for the persistence of alternative mating tactics are indistinguishable from those for phenotypically less flexible alternative mating strategies, and that alternative mating tactics can evolve in both sexes in monogamous species when fitness variance within each sex is large.

Keywords: behavioral polymorphism, fitness variance, opportunity for selection, reproductive strategies, best of a bad job

INTRODUCTION

Alternative Mating Tactics: Definitions and Patterns of Expression

Alternative mating tactics (AMTs) describe the discontinuous distribution of behavioral or developmental traits expressed in the context of intrasexual competition. Because variation in these mate-seeking traits is expressed more often in males than in females, most sources agree that polymorphic mating tactics allow individuals to take advantage of temporally available

opportunities to reproduce (Taborsky et al., 2008). Males expressing AMTs have been referred to as resident, territorial, parental, or bourgeois males when they express conventional mating phenotypes, or as satellite, wanderer, roamer, sneaker, or parasitic males when they express alternative mating phenotypes (Getz et al., 1993; Gross, 1996; Solomon and Jacquot, 2002; Taborsky et al., 2008). Alternative mating tactics also appear to exist in females (indigo buntings, Westneat, 1997; marine isopods, sex role-reversed birds, and arthropods, Shuster and Wade, 1991a, 2003; fish, Henson and Warner, 1997; song sparrows, Lebigre et al., 2012; fish and insects, Neff and Svensson, 2013) and where it has been investigated, genetic differences appear to underlie these examples (reviews in Shuster, 2010; Neff and Svensson, 2013). If genetic differences underlie distinct phenotypes within species, the different morphs are expected to achieve equal fitness over time (Haldane and Jayakar, 1963; Slatkin, 1978, 1979; Shuster and Wade, 2003). However, few studies have investigated the fitness outcomes of polymorphic mating phenotypes in females (lizards, Vercken et al., 2007; pea crabs, Prather and Shuster, 2015).

Alternative mating tactics and strategies are usually expressed in species in which the variance in fitness within one or both sexes is large; that is, within species in which sexual selection is strong (review in Shuster and Wade, 2003). One explanation for the covariance between alternative mating phenotypes and sexual selection begins with the observation that disproportionate mating success within one sex causes other members of the same sex to be excluded from mating (Wade, 1979; Shuster and Wade, 2003); or as Darwin (1874, p. 212), noted, "...if each male secures two or more females, many males cannot pair." This condition causes the average number of mates per mating individual, as well as the overall variance in fitness between mating and non-mating individuals to become disproportionately large (Shuster and Wade, 2003; Shuster, 2009). Alternative mating phenotypes usually succeed by appropriating some fraction of fertilizations from among the mates secured by successfully breeding individuals (Gross, 1996; Taborsky et al., 2008). Thus, as the average number of mates obtained by successful individuals increases, the fraction of fertilizations that alternative phenotypes need to obtain to achieve fitness equal to that of the average conventional individual, decreases (Shuster and Wade, 2003, p. 407). Stated differently, the greater the variance in fitness within one sex, the easier it is for alternative mating phenotypes to invade that population (Shuster, 2010). The variance in fitness within each sex is likely to be small in most monogamously mating species (Shuster and Wade, 2003, p. 23–26; Kokko and Rankin, 2006). Consistent with this observation, mating polymorphisms in monogamous species, are seldom documented and are poorly understood.

Tactics and Strategies: Theoretical Predictions

Although the evolutionary conditions required for the invasion and persistence of novel phenotypes are well-accepted and widely known (Maynard Smith, 1982), the fitnesses of individuals expressing different alternative mating tactics (AMTs) seldom

appear to be equivalent in nature (Gross, 1996; Tomkins and Hazel, 2007; Taborsky et al., 2008; Schradin and Lindholm, 2011). For this reason, AMTs are often considered distinct from alternative mating strategies (AMSs), which are less flexible in expression, often exhibit Mendelian inheritance, and appear to persist in populations because the fitnesses of the distinct phenotypes are equivalent (Slatkin, 1978, 1979; Maynard Smith, 1982; reviews in Shuster and Wade, 1991b, 2003).

Two contrasting theoretical frameworks claim to explain these differences. One framework suggests that AMTs represent behaviorally plastic, genetic "monomorphisms," in which adult behavioral phenotype depends on social status. According to this view, high status adults experience greater average fitness than lower status adults. Lower status adults appear to persist in populations, despite their inferior average fitness, because of genetic monomorphism underlying plasticity, and because they are more successful than if they had not reproduced at all; i.e., they make the "best of a bad job" (Dawkins, 1980; Gross, 1982, 1996; Tomkins and Hazel, 2007; Ophir et al., 2008a,b; Neff and Svensson, 2013).

The other theoretical framework suggests that AMTs, like AMSs, represent genetic polymorphisms, whose morphs achieve equal average fitness over time. According to this view, most AMTs are inherited as threshold traits rather than as Mendelian traits, thus their phenotypic expression is flexible rather than canalized. This view also suggests that the lower average fitnesses of adults adopting AMTs represent measurement errors rather than actual fitness differences. Measurement errors are presumed to occur because field estimates of average adult fitness either ignore individuals that fail to produce offspring, or are measured over intervals too short to capture the total variation in fitness. Such omissions tend to overestimate the average fitness, and underestimate the variance in fitness, among high status adults (Ryan et al., 1992; Shuster and Wade, 2003; Rios-Cardenas and Webster, 2008; Shuster, 2009, 2010, 2018).

A specific prediction of this latter framework is that, compared to fitness estimates that include only successful breeders, the inclusion of successfully-breeding, as well as non-breeding individuals in estimates of relative fitness, will yield a decrease in the average, as well as an increase in the variance in fitness for the focal adult population. Because most of the unsuccessful breeders in polymorphic populations express the conventional mating tactic, this prediction provides an explanation for why, compared to the inflated success of conventional breeding adults, individuals expressing alternative tactics appear to "make the best of a bad job" (Shuster, 2009, 2010).

Alternative Mating Tactics in Prairie Voles

Prairie voles (*Microtus ochrogaster*) are an excellent species for studying AMTs because, despite assertions that males in this species are monogamous, *M. ochrogaster* males commonly display two, flexible behavioral phenotypes in natural populations, as well as in semi-natural enclosures (Getz and Hofmann, 1986; Getz et al., 1993; Solomon and Jacquot, 2002; Streatfeild et al., 2011). Each resident or territorial male typically forms a pair bond with one adult female; the pair then defends a common territory and displays social monogamy (Getz

et al., 1993). However, resident males may also live in groups composed of more than two adults that defend a group territory, whereas wanderer males typically occupy larger home ranges that overlap with the ranges of multiple females and appear to lack a strong pair bond with one female (Getz et al., 1993; Solomon and Jacquot, 2002). Unlike residents, male wanderers make no investment in territorial defense or in rearing offspring to our knowledge, and likely spend more time and energy searching for mates than do resident males (Emlen and Oring, 1977; Davies, 1991; Getz et al., 1993; Solomon and Jacquot, 2002; McGuire and Getz, 2010). Male prairie vole AMTs do not appear to represent fixed patterns of behavior (c.f., Gross, 1996) because males have been shown to switch between resident and wandering tactics during their lifetime. Prairie vole females are also known to express behavioral variation characteristic of resident and wandering individuals, and although they exhibit patterns of nest fidelity and overall activity similar to males, less is known about the mating preferences and pair-bonding behavior of females expressing these mating phenotypes (reviews in Solomon and Jacquot, 2002; Ophir et al., 2008a,b; McGuire and Getz, 2010).

Although the territorial behavior and life histories of wanderers and residents are well-documented in natural and semi-natural populations of prairie voles (Getz et al., 1993; McGuire and Getz, 1998; Solomon and Jacquot, 2002; Ophir et al., 2008b), the relative reproductive success of residents and wanderers among males and among females remains uncertain (McGuire and Getz, 2010). Past studies of natural populations, as well as populations of voles maintained within outdoor enclosures, have shown that wandering and resident males do not necessarily differ in body size (Ophir et al., 2008a; McGuire and Getz, 2010; but see Solomon and Jacquot, 2002). However, wanderers are reported to survive longer than residents in natural and semi-natural environments, suggesting that wanderers may have a longer reproductive lifetime compared to residents (Solomon and Jacquot, 2002; Ophir et al., 2008a; McGuire and Getz, 2010). The lifetime reproductive success of male residents and wanderers can be readily determined because few individuals survive to reproduce in their second year (Getz et al., 1997). Although each of these studies collected detailed information on mating success, none of these studies have included unsuccessful individuals expressing resident or wanderer tactics within their estimates of fitness. Accumulating evidence now suggests that successful, as well as unsuccessful individuals, must be included in when estimating fitness in polymorphic populations (Gerhard et al., 1987; Waltz and Wolf, 1988; Ryan et al., 1992; Shuster and Wade, 2003; DuVal and Kempnaers, 2008; Shuster, 2010, 2011; Krakauer et al., 2011; Prather and Shuster, 2015).

Five Hypotheses

Here we present the first genetic paternity analysis of the reproductive success of resident and wanderer prairie voles in natural populations in which the number of reproducing and non-reproducing males expressing each tactic are known. We present similar results for females, and we examine the possibility that females may exhibit alternative mating tactics related to their mating behavior and persistence in pair bonds. Using 3 years of

data from two natural populations of prairie voles, we tested five specific hypotheses described below.

Our first hypothesis was, the average fitnesses of male and female prairie voles are equivalent. This hypothesis also concerned the general question, “which individuals are appropriate to include in parentage analyses of natural populations?” Although most parentage analyses strive to include every genotyped individual, such scrupulousness can enhance rather than reduce uncertainty about parentage for mating system analysis (Shuster, 2018). Our analysis included only three groups of genotyped individuals: (1) those progeny who were unambiguously assigned to both parents (with confidence $\geq 95\%$), (2) the parents of each of these unambiguously assigned progeny, and (3) the male and female adults to whom no progeny could be assigned.

We included only these three groups of individuals in our analysis to test a fundamental evolutionary hypothesis, in addition to our own. Fisher (1930) argued that in sexual populations, the contribution of males to the ancestry of all future generations is exactly equivalent to that of females, or more succinctly, all individuals have a mother and a father. This principle predicts that when the parentage of all individuals within a population is known, and therefore when the fitness of each individual, measured using offspring numbers is known, the average fitnesses of male and female parents will be identical when adjusted by the population sex ratio (see Methods; Wade, 1979; Wade and Shuster, 2005). If this explicit result is not found, it indicates either that some breeding adults and/or some progeny, were incorrectly excluded from the focal sample, or that some parents or offspring belonging to other breeding populations were incorrectly included within the focal sample. We tested this hypothesis, to determine if our samples accurately captured the breeding populations in our study, and to determine if Fisher’s (1930) famous statement was verifiable using this experimental approach.

Our second hypothesis was, alternative mating tactics will evolve when the within-sex variance in fitness is large (Shuster and Wade, 2003). This hypothesis predicts that alternative mating phenotypes will appear within those species, and within the sex, in which only a fraction of the sexually mature individuals produce offspring, as is commonly observed among males in highly polygynous animals (Wade and Shuster, 2004). Extreme skews in mating success cause the component of the variance in fitness that exists between mating and non-mating individuals to become large, and may favor unconventional mating phenotypes (Shuster, 2010; Shuster et al., 2013). In contrast, if there is little skew in the distribution of offspring numbers among members of each sex, the total variance in fitness is likely to be small, and an alternative explanation for the observed existence of polymorphic mating phenotypes in prairie voles is necessary.

Our third hypothesis was, male prairie voles adopting a wanderer tactic will experience average fitness that is less than that of resident males (c.f., Ophir et al., 2008a,b; McGuire and Getz, 2010). This hypothesis addressed the predominant explanation for the persistence of alternative mating tactics in prairie vole populations, as well as for other species expressing alternative mating tactics because this explanation suggests that

male wanderers “make the best of a bad job” (c.f., Dawkins, 1980; Gross, 1996; Tomkins and Hazel, 2007). Rejection of this hypothesis, specifically, that there was no difference in the average fitnesses of wanderers and residents, would suggest that the conditions necessary for the maintenance of these alternative mating tactics (AMTs) under natural conditions, are the same as those established for alternative mating strategies (AMSs; Shuster and Wade, 2003). That is, that the average fitnesses of individuals expressing resident and wanderer tactics are equal. Our test of this hypothesis also allowed comparison of the mean and variance in adult fitness when successful breeders, as well as non-breeding individuals are included within these calculations. In our study, we considered this hypothesis for males as well as for females.

Our fourth hypothesis was, as temporal and spatial scales of fitness estimates increase, the fraction of the total variance in fitness that exists between the alternative mating tactics, will decrease. This hypothesis addressed the assumption that AMTs represent behavioral responses to rapidly changing circumstances influencing mating success (Taborsky et al., 2008). When such conditions exist, the average fitnesses of males expressing each mating tactic could appear distinct over short durations, as is suggested in many studies of AMTs (reviewed in Oliveira et al., 2008; Shuster, 2010, 2011). However, if the success of an invading alternative mating tactic depends on the magnitude of the variance in fitness experienced by the conventional mating tactic (c.f., Hypothesis 2, also Shuster and Wade, 2003, p. 402–409), and if, after invasion, the rapid expansion of the invader population, at the expense of conventional individuals, increases the variance in mating success among these now common invaders, then the former invaders will become vulnerable to re-invasion by the now rare, conventional mating tactic. Over time, the fitness of each tactic will become negatively frequency-dependent (Shuster, 2010).

This hypothesis predicts that oscillations in fitness will arise within each mating tactic as rapidly changing mating opportunities appear. The oscillating fitnesses of each tactic will contribute to the within-tactic component of the total fitness variance, and because each mating tactic experiences highs and lows in fitness, the average fitness of each tactic will converge, thereby decreasing the between-tactic component of total fitness variance. The longer the duration of measurement, the greater the number of oscillations that will be recorded and the more the average fitnesses of each tactic will converge, further enhancing the within-tactic component, and further decreasing the between-tactic component of total fitness variance. Increasing the spatial scale of measurement is likely to accentuate this pattern if local populations experience similar frequency-dependent processes. Thus, this approach does not track the dampening of fitness oscillations themselves but rather, reveals the fitness outcome of negative frequency-dependent selection at increasing temporal and spatial scales. Patterns of within- and between-tactic variance in fitness not matching this description in prairie voles requires an explanation other than negative frequency-dependent selection.

Our fifth hypothesis was, male and female prairie voles mate at random with respect to their mating tactics. This hypothesis

concerned the kinds of breeding partnerships that male and female residents and wanderers form. Our explicit assignment of every offspring to every breeding adult in our experimental populations allowed us to determine the type of partnerships formed by all males and all females expressing each alternative mating phenotype. Goodness of fit tests provided a means for determining whether mating preferences among male and female phenotypes involves positive assortative, negative assortative, or random mating, as well as for determining whether mating preferences alone may contribute to or erode the persistence of multiple tactics within this population. Of these three possibilities, negative assortative mating is likely to contribute most effectively to the persistence of mating polymorphism (Shuster and Wade, 2003; Hedrick et al., 2016; Grunst et al., 2018).

MATERIALS AND METHODS

Study Sites and Animals

Our study was based on data collected from two natural populations. These populations, inhabiting old fields dominated by grasses and forbs with scattered tree seedlings, were located at the University of Kansas Nelson Environmental Study Area (~12 km northeast of Lawrence, Kansas; 39°03'07"N, 95°11'27"W) and the Indiana University Bales Road Preserve (~5 km north of Bloomington, Indiana; 39°13'00"N, 86°32'27"W). The fields were mowed annually to prevent changes in vegetation due to ecological succession. The size of the area live-trapped varied between sites and years (range: 1 ha Kansas 2005–2.2 ha Indiana 2007). Three field seasons were conducted at each site with fieldwork in Kansas during May–June 2005, 2006, and 2008 and during July–August 2006–2008 in Indiana (see Streatfeild et al., 2011; Chesh et al., 2012 for details). Each field season lasted for 4 weeks. We conducted fieldwork earlier in the year in Kansas because voles in the Kansas population experience a lull in reproduction during midsummer (Rose and Gaines, 1978) and also because the breeding season begins ~1 month earlier in Kansas than in Indiana (Myers and Krebs, 1971; Rose and Gaines, 1978).

Field Methods

We began each field season with grid trapping for the first week (2005–2007) or first 2 weeks (2008) using a grid with grid stakes spaced 10 m apart. Grid trapping allowed us to identify adult females, to track their nests, and provided data for estimating population density. During grid trapping, we placed a single Ugglan multiple-capture trap (Grahnb, Hillerstorp, Sweden) within 1 m of the grid stake, in a vole runway if possible. Traps were set late in the afternoon and checked in the evening and the next morning. We followed this schedule for 5 days/week from 2005 to 2007 (10 trap checks per week; see Streatfeild et al., 2011 for details) and 4 days/week during 2008 (8 trap checks per week; see Chesh et al., 2012 for details). When we were not trapping, traps were left in place but were not set. Traps were baited with cracked corn, a low-quality food (Desy and Batzli, 1989) and each trap was covered with an aluminum shield or wooden board to protect the trapped animals from heat and precipitation.

Cotton batting was placed in traps to protect animals from cold temperatures on nights when the temperature was predicted to be $\leq 10^{\circ}\text{C}$.

We used radio telemetry or fluorescent-powder tracking to locate the nest sites of adult females trapped during the initial week(s) of grid trapping (see Lucia et al., 2008 for a complete description of methods for nest location). After locating a female's nest, we placed four live-traps within 30 cm of the entrances of each nest. We conducted live trapping at these nests for either three (2005–2007) or two (2008) consecutive weeks immediately following the initial grid trapping. During nest-trapping weeks, we checked traps in the mornings and evenings from Sunday evening until Tuesday evening, and again from Wednesday evening until Friday evening, for a total of 10 trap checks per week.

At each capture, we recorded the identification number of the individual, the capture location, sex, age class, reproductive condition (males: scrotal or non-scrotal; females: non-pregnant, pregnant and/or lactating), and body mass (to the nearest 1.0 g). We determined the age of the individual based on their body mass: juvenile (<21 g), sub adult (21–30 g), or adult (>30 g, Gaines et al., 1979; Getz et al., 1993). When captured for the first time, each individual was permanently marked using a unique toe-clip combination, and the tissue was preserved at -20°C for genetic parentage analysis. All research procedures involving live animals followed the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes et al., 2011) and were approved by the Miami University Institutional Animal Care and Use Committee (IACUC), the University of Kansas IACUC and the Indiana University IACUC.

Residency Status

We determined prairie vole residency status during a 2-week nest trapping period during each 4-week field season. An adult vole was considered a resident of a nest if he or she was captured at least once per week during each of the first two nest trapping weeks, and if $\geq 75\%$ of all captures were at a single nest site (Cochran and Solomon, 2000). Seventy-five percent was a conservative cutoff because, for most residents, there was an order of magnitude difference in captures at one nest compared with elsewhere (e.g., 10 captures at one nest per 1 capture elsewhere; G.R. Cochran and N.G. Solomon, unpublished data). If an adult vole was trapped either $<75\%$ of the time at one nest ($N = 77$) or during only one of the first two nest trapping weeks ($N = 182$), it was classified as a wanderer. These criteria were similar to those used in previous studies (Solomon and Jacquot, 2002; McGuire and Getz, 2010). Our intensive trapping over a 2-week interval allowed us to classify the mating phenotype of adult prairie voles as well as collect information for parentage assignment. Although prairie voles are known to switch between tactics during their adult lives (Solomon and Jacquot, 2002; McGuire and Getz, 2010), the method we used to determine residency status, while sufficiently intense to accurately classify tactics, was unlikely to detect evidence of tactic switching because it only lasted 2 weeks. However, our collection window was designed to make accurate assignment of collectable offspring to adults whose phenotypes could be verified. For our analyses,

we assumed that all individuals retained the residency status we identified for the remainder of each 4-week breeding season.

Although voles that were captured less than once per week were classified as wanderers, some of these individuals may have been residents with their home range located mostly off the study grid. Therefore, we also analyzed the data when we assigned adult voles to one of three categories: residents, wanderers (adults that were trapped at least once per week during each of the first two nest trapping weeks but $<75\%$ of the time at one nest i.e., trapped as frequently as males classified as residents), and visitors (adults captured during only one of the first two nest trapping weeks). The results of analyses considering three instead of two tactics yielded the same general conclusions as when the males and females were classified as either just residents or wanderers. For this reason, we only present the former classification, i.e., the analyses with adult voles categorized as residents or as wanderers. To determine whether male voles expressing resident or wanderer tactics differed in age, we compared the numbers of subadult and adult males identified as residents and wanderers using a 2×2 G-test.

Population Density

We estimated prairie vole abundance using the minimum number known alive method (MNKA = number of animals captured at time t plus those individuals not captured at time t but captured before and after time t). The correlation between the MNKA and other methods of population size estimation for prairie voles is positive and strong (Slade and Blair, 2000). We considered the effective sampling area to be the size of the trapping grid for each population plus a surrounding boundary strip with a width equal to 5 m, which is half the distance between adjacent grid points. We estimated the mean adult density for each population each year as the average of the MNKA of adults during each of the four trapping weeks, divided by the effective grid area (see Streatfeild et al., 2011 for details).

Genetic Parentage Analysis

To determine the parentage of juveniles trapped in our study populations, we genotyped all voles at six microsatellite loci known to be polymorphic in prairie voles (Keane et al., 2007). We used either standard phenol/chloroform extraction techniques (Sambrook et al., 1989) or DNeasy extraction kits (Qiagen, Valencia, CA, USA) to extract genomic DNA from tissue samples and conducted polymerase chain reactions (PCR) to amplify microsatellite alleles (for details on PCR conditions see Keane et al., 2007; Solomon et al., 2009). Polymerase chain reaction products were diluted, combined with an internal size standard (Liz 500, Applied Biosystems, Foster City, CA, USA), and detected using an ABI 3130xl or 3730 DNA analyzer (Applied Biosystems). Base pair (bp) lengths of the fluorescent-labeled DNA fragments were determined with GeneMapper 3.7 software (Applied Biosystems, Foster City, CA) and alleles were binned into discreet size classes using FlexiBin (Amos et al., 2006).

We used Cervus 3.0 (Kalinowski et al., 2007) to assign parentage to juvenile prairie voles trapped in the field based on the microsatellite genotype data (see Solomon et al., 2009; Mabry et al., 2011 for details). Cervus 3.0 uses a simulation

that takes into account population allele frequencies, an estimate of genotyping error, proportion of missing genotypes, total number of candidate parents sampled, and the proportion of candidate parents sampled to calculate the statistical confidence of parentage assignments. We conducted a separate parentage simulation and analysis for each site for each year. All simulations were performed for 10,000 cycles with a genotyping error rate of 0.02. This error rate was based on empirical estimates of two potential sources of error: mutation and mis-scoring of alleles (Solomon et al., 2004). The remaining input parameters for the simulations were based on the actual data from the study populations each year.

We conducted a multistage parentage analysis, wherein we initially considered all adults trapped within 20 m of the juvenile's site of first capture as possible parents. A distance of 20 m was used in the analysis because it is the approximate average home range diameter of adult prairie voles in these populations (Streatfeild et al., 2011). We accepted a parentage assignment when the confidence level among a male-female-juvenile trio was 95%. If parentage could not be assigned to a trio at the 95% level after the initial analysis, we expanded the set of candidate parents to include all adults trapped within 40 m of the juvenile's site of first capture and reran the parentage analysis. Finally, if we could only assign a female parent at the 95% confidence level, we ran the parentage analysis using the "known mother" option and considered all males captured within 40 m of the juvenile's site of first capture as candidate fathers. In all cases where an adult female was assigned as the mother of a juvenile at the 95% confidence level the female also was captured with the juvenile in the same trap at least once, providing an independent corroboration of maternity.

Adults and Juveniles Included in the Study

We genotyped 370 juveniles (any vole <21 g when first captured). We also genotyped 381 males and 320 females (=701 adults) in our sample of adults. We used as our guide, Fisher's 1930 assertion that all individuals have one mother and one father, and therefore that the average fitness of the sexes will be equivalent when adjusted by the sex ratio; this means that if the average fitnesses of males and females are O_{σ} and O_{ϕ} , respectively, where $O_{\sigma} = N_{\text{offspring}}/N_{\sigma}$ and $O_{\phi} = N_{\text{offspring}}/N_{\phi}$, and the sex ratio, $R = N_{\phi}/N_{\sigma}$, then $O_{\sigma} = RO_{\phi}$. Note that when $R = 1$, $O_{\sigma} = O_{\phi}$ (Wade and Shuster, 2005).

We used only those adults in our estimates of fitness parameters whose progeny were identifiable with $\geq 95\%$ confidence through both parents (Shuster, 2018). For these adults, we were able to explicitly assign numbers of progeny, and therefore we were able to estimate the mean and variance in their offspring numbers relative the average of this population of breeding adults. We considered adults for whom no progeny could be assigned with $\geq 95\%$ confidence to be the non-breeding adults within this population (Shuster, 2018). These latter individuals may have produced progeny outside of our sampling area, but we could not enumerate them and therefore could not include these progeny in our estimates of relative fitness for our focal populations.

All other individuals were excluded from our fitness estimates because we could not explicitly assign relative fitness to these individuals in the same way we were able to for adults whose assigned offspring were known. These excluded individuals included progeny for whom no parents could be assigned with $\geq 95\%$ confidence. We did not include these individuals because they could not be assigned with the same confidence to the genotyped adults in our sample and so they could not be included in estimates of relative fitness for the genotyped adults.

We also excluded from our fitness estimates, progeny for whom only one parent could be assigned with $\geq 95\%$ confidence; such individuals, if included in fitness estimates, would add to the number of progeny for one sex (the sex of the known parent) but not to the number of progeny for the other sex. This procedure could not be allowed if all offspring have one mother and one father because it would cause the average fitness of the sexes to become artificially biased.

Correspondingly, we excluded from our fitness estimates, adults who were the one identifiable parent of a juvenile. Such individuals, if included in fitness estimates would add to the number of adults of one sex as well as the number of progeny for that sex, without changing the number of adults or progeny for the other sex. This procedure also could not be allowed if all offspring have one mother and one father, and it too would cause fitness estimates to become artificially biased.

We were unable to determine if missing adults produced only one or many progeny, and because we did not know, their relative fitness could not be assigned. Missing adults might have died before samples were collected, but this was not clear; we considered these adults indistinguishable from adults from other populations who could not be identified. They were not included in our estimates of relative fitness, and neither were their offspring. See **Appendix A** for the numbers of juveniles and adults used and eliminated in our study. **Appendix D** contains parentage data.

Testing Hypothesis 1

To test the hypothesis that the average fitnesses of male and female prairie voles were equivalent, we estimated the mean and variance in fitness for all adult females and all adult males included in the analysis, and we estimated the sex ratio for each sample as well as overall. If our parentage estimates accurately represented reproduction by IN and KS populations over the duration of the study, and if, as Fisher (1930) observed, all individuals had a mother and a father, we expected the average fitnesses of males and females, O_{σ} and O_{ϕ} , respectively, to be equivalent when adjusted by the sex ratio, R . We summarized our results in **Table 1**.

Testing Hypothesis 2

To test our second hypothesis, that alternative mating strategies and tactics evolve when the variance in fitness within one sex is large (Shuster and Wade, 2003), we used the method of Shuster and Wade (1991b; 2003; see also Wade and Shuster, 2004; DuVal and Kempenaers, 2008; Shuster, 2008) to partition the variance in offspring numbers within and between adult voles expressing resident and wanderer mating tactics, as well as within and among the years, and within and between the locations in which

TABLE 1 | Adult prairie vole density and the numbers of adult male, female and juvenile individuals collected in Indiana in 2005, 2007, and 2008 and in Kansas in 2005, 2006, and 2008; note that in all samples $O\sigma = R(O\varphi)$.

1	2		3	4	5	6	7	8	9
Location	Year	Density*	N Males	N females	N Offspring	Avg offspring per male	Avg offspring per female	Sex ratio	Adjusted female fitness
			N_{σ^a}	N_{φ}	$N_{\text{offspring}}$	O_{σ^a}	O_{φ}	R	$R(O_{\varphi})$
Indiana	2006	40	72	40	33	0.46	0.83	0.56	0.46
	2007	84	108	119	59	0.55	0.50	1.10	0.55
	2008	90	79	72	69	0.87	0.96	0.91	0.87
Kansas	2005	44	41	20	19	0.46	0.95	0.49	0.46
	2006	27	12	7	7	0.58	1.00	0.58	0.58
	2008	58	52	31	44	0.85	1.42	0.60	0.85
Total			364	289	231	0.63	0.80	0.79	0.63

*Density estimate based on the average of the weekly measures of the minimum number of adults known alive during four weeks of grid and nest trapping. N = total number of males.

the study was conducted. We measured fitness in terms of the number of offspring (pups) produced by individual adults, and avoided fitness proxies such as mating success, adult traits, or juvenile survivorship. We measured fitness using genetically-determined number of offspring because this metric is not made ambiguous by multiple mating, it is not confounded by genetic correlations between maternal and offspring traits, it need not be adjusted by relatedness or by the conditional expression of parental traits within offspring, and importantly, it assigned fitness directly to parents (Wolf and Wade, 2001; Shuster and Wade, 2003; Jones, 2009).

The proportion of total fitness variance that exists between mating and non-mating individuals provides a measure of the strength of selection arising from differential reproduction among members of the same sex (Wade, 1979; Shuster and Wade, 2003). We began by identifying the successfully reproducing males and females expressing each mating tactic. Next we calculated, within each year (Indiana: 2006, 2007, 2008; Kansas: 2005, 2006, 2008), and within each location (Indiana, Kansas), the average, variance and 95% confidence limits for the number of offspring produced by these individuals. We then calculated the proportion of each study population that was comprised of breeding individuals [$p_{ijkl(s)}$; **Appendix B**], as well as the proportion of each study population that consisted of non-breeding adults expressing each tactic [$p_{ijkl(0)}$; **Appendix B**]. We estimated the within- and between-individual fitness as explained in **Appendix B**, and we calculated the proportion of the total variance in fitness for each mating tactic, within each year of each study population, that was due to the proportions of individuals within each population that were successful or unsuccessful at mating.

We compared these proportions among sample years within sites, among sites, among tactics, and between the two sexes using U -tests, and because these comparisons were not distinct at $P < 0.05$, we compared the weighted average of the proportion of the total variance in fitness that existed between the mating and non-mating individuals for our entire sample of male and female prairie voles ($N = 364$ males + 289 females = 653 adults), with the weighted average of the proportion of the total variance in fitness that existed between mating and non-mating males in 26

highly polygynous species ($N = 826$ males). Many if not all of these latter species exhibit alternative mating strategies and/or tactics (Wade and Shuster, 2004).

Testing Hypothesis 3

To test our third hypothesis, whether adult voles expressing the wanderer tactic experienced average fitness that was less than that of resident adults, and therefore that wanderer adults “make the best of a bad job” (c.f., Dawkins, 1980; Tomkins and Hazel, 2007), we compared the average and variance in offspring numbers and 95% confidence limits for these parameters for male and female voles expressing each mating tactic (resident, wanderer), within each year and within each location. Rather than use the standard statistical approximation for the sample variance typical of general linear model (GLM) analyses [e.g., $V_X = (X - x_i)^2 / (N - 1)$], where V_X is the sample variance, X is the sample average, and N is the total sample size; (Sokal and Rohlf, 1995)], in this and in the following analyses, we estimated the variance in fitness in terms of offspring numbers explicitly for each sex and for each population sample (c.f., Shuster and Wade, 2003, see **Appendix A** and below).

Our use of an explicit variance-partitioning approach addressed three issues. First, it accommodated the fact that when offspring are sired, success by one adult means failure by all other adults within that sex. Such non-independence is not considered in GLM analyses of fitness, which assume that data are sampled randomly and independently of one another and therefore by extension, assume that individuals produce offspring randomly and independently of one another (Sokal and Rohlf, 1995). Second, although conservative approximations of population variance like that shown above can be appropriate for analyses that meet GLM assumptions, their use can also cause approximation errors to compound when multiple estimates of fitness variance are part of the analysis; our explicit estimates of population variance prevented these errors from affecting our result (Shuster and Wade, 2003). Third, our inclusion of the offspring numbers of successful and unsuccessful males and females introduced many zeros into our data set, causing population distributions to deviate from normality and violate the assumptions of GLM analyses (Sokal and Rohlf, 1995).

To allow comparisons of fitness variance among years and between locations, we next calculated the grand average fitness for all male and for all female voles, estimated across both mating tactics, within each year, within each location, as well as the proportion of individuals expressing each mating tactic, again, within each year, within each location (**Appendix B** in Supplementary Material). We repeated these measurements for adult voles expressing each mating tactic, among years, within each location, and across all years between the two locations. We also partitioned the total variance in male and female fitness into within and among year, as well as within and between location components. With our estimates of the mean and variance in fitness for each tactic at each temporal and spatial scale (3 years, 2 locations), we then calculated the opportunity for selection acting between tactics as well as the total opportunity for selection on males and on females. As explained elsewhere (Wade, 1979; Shuster and Wade, 2003; Shuster et al., 2013), the opportunity for selection identifies the maximum possible intensity of selection acting within a single episode of selection, or as Crow (1958) defined it, “total selection intensity.”

These calculations allowed us to again address our third hypothesis (whether adult voles expressing different tactics achieved equal fitness), but with three additional analyses. The first additional analysis provided a means for comparing the average fitnesses of each mating tactic, similar to (but not identical to) a nested (GLM) analysis of variance. By partitioning the total variance in male and female fitness into within- and between-tactic components of fitness variance, and comparing these components of fitness within- and among-years, as well as within- and between-the study locations, we determined the spatial and temporal scales at which the majority of the variance in male and female tactic fitness was found. A majority of the variance in fitness occurring *between* tactics would indicate that the fitnesses of adults of each sex employing each mating tactic were distinct. In contrast, a majority of the variance in fitness and the opportunity for selection occurring *within* tactics, would indicate that the fitnesses of adults employing each mating tactic were equivalent.

In the second additional test of hypothesis three, we used the variance components identified in the first additional analysis to identify the temporal and spatial scales at which the majority of the total opportunity for selection on mating tactics was found. A majority of the total opportunity for selection on mating tactics occurring *between* tactics would indicate that selection primarily acted to change the frequencies of each mating tactic, such that the population frequency of one tactic increased at the expense of the other tactic. In contrast, a majority of the total opportunity for selection on mating tactics occurring *within* tactics would indicate that selection primarily acted to change the average phenotype of males or females expressing a particular mating tactic. Specifically, less successful variants within each mating tactic would be eliminated in favor of more successful variants.

We obtained a third additional test of this hypothesis by comparing, using Wilcoxon signed rank tests, the mean and variance in adult fitness when only successful breeders were included in estimates, as well as when breeders and non-breeding individuals were included within these calculations. We

predicted that breeders-only estimates would overestimate the mean fitness, and underestimate the variance in fitness, compared to estimates that included all adults within each sex.

Testing Hypothesis 4

Explicit comparison of variance components in our data allowed us to test our fourth hypothesis, that the fraction of the total variance in fitness that existed between alternative mating tactics, would decrease, as the temporal and spatial scales of fitness estimates increased. We predicted that if mating tactic fitnesses oscillated widely over short durations, but showed decreasing oscillation amplitude over longer durations, as is expected under negative frequency dependent selection (Slatkin, 1978, 1979), the signature of this process would be a progressive decrease in the between-tactic variance in adult fitness as longer durations and larger spatial scales were included in the analysis.

Our explicit calculations are summarized in **Appendix B** with results summarized for males in **Tables 2A, 3A** and **Supplementary Tables 4–7A** in **Appendix C** and for females in **Tables 2B, 3B** and **Supplementary Tables 4–7B** in **Appendix C**. We report **Tables 2, 3** in the text and **Supplementary Tables 4–7** in **Appendix C**. Although we emphasized explicit partitioning of male and female fitness variation, for comparison, we also analyzed our data using a nested GLM procedure on data for adult voles of each sex to examine the effects of location (SITE), year, nested within location (YEAR[SITE]), and male and female mating tactic nested within year and location (TACTIC[YEAR, SITE]) on the number of offspring produced by males and by females.

Testing Hypothesis 5

To test our fifth hypothesis, that male and female prairie voles mate at random with respect to their mating tactics, we used 2×2 G-tests to examine the number of offspring produced in monogamous and in polygamous partnerships by resident and wanderer males and by resident and wanderer females. Significant deviations from random mating would indicate either positive associative or negative associative mating.

RESULTS

Hypothesis 1

As predicted by our first hypothesis, the average number of offspring produced by males was identical to the average number of offspring produced by females when adjusted by the sex ratio, in every year as well as over both locations (**Table 1**, column 9). The population density of adult voles varied among years and between locations, with densities somewhat, but not significantly greater overall in Indiana than in Kansas (**Table 1**). During each year, the adult sex ratio, $R (=N_{\text{females}}/N_{\text{males}})$ was male-biased in the Kansas population (0.49–0.60, **Table 1**, column 8) but varied among years from male biased (0.56) to female biased (1.10) in the Indiana population (**Table 1**, column 8).

Consistent with previous studies, our samples confirmed that both male and female prairie voles exhibited resident and wanderer tactics (Emlen and Oring, 1977; Davies, 1991; Getz et al., 1993; Solomon and Jacquot, 2002; Ophir et al., 2008a,b;

TABLE 2A | Male prairie vole fitness partitioned within and between tactics across all years (2005–08) and both (IN and KS) locations; average fitnesses between tactics were compared within years using 95% CI and *F*-tests; there were no significant differences in average fitness in any year; opportunities for selection indicated that selection occurred primarily within rather than between the mating tactics; details for calculations and variable definitions are in **Appendix B**.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																								
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																									Year	Avg	Var	N	95%CI	Prop.	Avg	Var	N	95%CI	Prop.	N _{males}	Prop.	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	V _{within(i,j)}	V _{between(i,j)}	V _{total(i,j)}	F	df1	df2	P < 0.05	Between	Total	Between/ Total																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									
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_{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}	V _{Oij}	Σ I _{ij}	P _{ij}	O _{ij}

TABLE 2B | Female prairie vole fitness partitioned within and between tactics across all years (2005–08) and both (IN and KS) locations; average fitnesses between tactics were compared within years using 95% CI and *F*-tests; there were no significant differences in average fitness in any year; opportunities for selection indicated that selection occurred primarily within rather than between the mating tactics; details for calculations and variable definitions are in **Appendix B**.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Location	Year	Residents			Wanderers			Grand	Variance in tactic fitness					Selection on mating tactics											
		Avg	Var	N	95%CI	Prop.	Avg		Var	N	95%CI	Prop.	N _{females}	Prop.	Avg	Within	Between	Total	F	df1	df2	P < 0.05	Between	Total	Between/Total
		O _{1 1•}	V _{O1 1•}	Σ I _{1 1}	P _{1 1•}	O _{1 2•}	V _{O1 2•}		Σ I _{1 2}	P _{1 2•}	Σ I _{1•}	P _{1 ••}	O _{1 ••}	V _{O1 1 1 ••}	V _{O1 1 1 2••}	V _{O1 1 1 •••}	I _{between(1 ••)}	I _{total(1 ••)}							
Indiana	2006	0.58	1.08	24	0.42	0.60	1.19	1.53	16	0.61	0.40	40	0.17	0.83	1.26	1.33	2.59	1.06	1	39	ns	1.96	3.81	0.51	
	2007	0.62	1.15	55	0.28	0.46	0.39	0.80	64	0.22	0.54	119	0.52	0.50	0.96	0.62	1.58	0.65	1	118	ns	2.53	6.43	0.39	
	2008	1.47	3.41	19	0.83	0.26	0.77	2.44	53	0.42	0.74	72	0.31	0.96	2.69	0.99	3.68	0.37	1	71	ns	1.08	4.01	0.27	
Sum				98					133			231													
Weighted avg.						0.42					0.58														
Kansas	2005	0.92	2.08	12	0.82	0.60	1.00	0.50	8	0.49	0.40	20	0.34	0.95	1.45	1.00	2.45	0.69	1	19	ns	1.11	2.71	0.41	
	2006	1.17	1.47	6	0.97	0.86	0.00	0.00	1	na	0.14	7	0.12	1.00	1.26	0.31	1.57	0.25	1	6	ns	0.31	1.57	0.20	
	2008	1.50	2.11	14	0.76	0.45	1.35	1.88	17	0.65	0.55	31	0.53	1.42	1.98	1.38	3.36	0.70	1	30	ns	0.69	1.67	0.41	
Sum				32					26			58													
Weighted avg.						0.55					0.45							0.63						0.38	

McGuire and Getz, 2010; Streatfeild et al., 2011). In all years and at both study sites, the number of male residents was less than the number of male wanderers during each year, although the proportions of residents to wanderers were similar between sites and were consistent among years (Indiana: 0.29:0.71, $N = 259$; Kansas: 0.34:0.66, $N = 105$; **Table 2A**, columns 7, 12, 13). The proportions of female residents and wanderers were more variable among years in both locations, with more wanderers in Indiana (0.42:0.58, $N = 231$) and more residents in Kansas (0.55:0.45, $N = 58$; **Table 2B**, columns 7, 12, 13).

Hypothesis 2

Consistent with our second hypothesis, the proportion of the total variance in fitness that existed between mating and non-mating individuals in each of our six sample years and two sample locations was routinely high (weighted averages for resident males: Indiana: 0.69, Kansas: 0.93; wanderer males: Indiana: 0.65, Kansas: 0.61; resident females: Indiana: 0.65, Kansas: 0.65; wanderer females: Indiana: 0.67, Kansas: 0.55; **Tables 3A, B**, columns 16, 30). Male and female residents and wanderers produced offspring within both populations and within all years of the study (**Tables 3A, B**). The proportions of male and female residents and wanderers that failed to produce offspring, ($p_{ijkl(0)}$) exceeded 0.63 for males (**Table 3A**, columns 9, 23) and exceeded 0.35 for females (**Table 3B**, columns 9, 23), with higher proportions of males excluded from mating than females (weighted average: 0.67–0.83 vs. 0.39–0.73; **Tables 3A, B**, columns 9, 23). Moreover, the average value for the proportion of the total variance in fitness that existed between mating and non-mating adult prairie voles (mean \pm 95% CI = 0.67 ± 0.28 , $N = 23$; **Tables 3A, B** column 30) was not significantly different from the proportion of the total variance in fitness between mating and non-mating males observed in 26 populations of highly polygynous species (mean \pm 95% CI: 0.56 ± 0.22 , $N = 26$; Wade and Shuster, 2004). Members of this latter group included African lions (*Panthera leo*; 0.72), red deer (*Cervus elaphus*; 0.76), Indian peafowl (*Pavo cristatus*; 0.60), strawberry poison dart frogs (*Dendrobates pumilio*; 0.53), and sponge-dwelling isopods (*Paracerceis sculpta*; 0.54).

Hypothesis 3

Each of the five different tests of our third hypothesis, that the average fitnesses of male and female prairie voles expressing resident and wanderer mating tactics were unequal, rejected this hypothesis. The specific results were as follows:

First, our explicit calculation of the mean, variance and 95% CI of offspring numbers showed no significant differences (i.e., all overlapping 95% CI) in numbers of offspring sired between males expressing resident and wanderer mating tactics, (a) within each year of the study, within each study location (**Table 2A**, columns 3–6 and 8–11), (b) among years of the study, when the numbers of offspring sired by males expressing each mating tactic were pooled across all years, within each study location (**Supplementary Table 4A**, columns 3–6 and 8–11, **Appendix C**) or (c) between study locations, when the numbers of offspring sired by males expressing each mating tactic were pooled across all years and across both locations (**Supplementary Table 5A**,

columns 3–6 and 8–11, **Appendix C**). We obtained similar results for females expressing resident and wanderer mating tactics (**Table 2B**, and **Supplementary Tables 4B, 5B**, columns 3–6 and 8–11, **Appendix C**), although a small sample in Kansas 2006 containing no wandering females prevented comparison for this year.

Second, using our explicit partitioning approach, we confirmed the above results using F-ratios, which specifically compared the within-tactic variance in numbers of offspring sired to the between-tactic variance in numbers of offspring sired ($F_{\text{between-tactics}}$; Equation 9a in **Appendix B**). We examined this ratio for resident and wandering males and females, (a) within each year of the study, within each location (**Tables 2A, B**, columns 19–22, weighted average $F = 0.62, 0.63$ for males and females in both locations respectively), (b) with the numbers of offspring sired by males expressing each mating tactic pooled across all years, within each study location (**Supplementary Tables 4A,B**, columns 19–22, **Appendix C**; weighted average $F = 0.01, 0.002$, for males and females, respectively), and (c) with the numbers of offspring sired by males expressing each mating tactic pooled across all years and across both study locations (**Supplementary Tables 5A,B**, columns 19–22, **Appendix C**; $F = 0.0028, 0.004$, for males and females, respectively).

Third, F-ratios also available using the explicit partitioning approach allowed us to compare (a) the variance in male and female fitness within and among years in each study location (**Supplementary Tables 6A,B**, columns 9–12, **Appendix C**; weighted average $F = 0.06, 0.12$ for males and females respectively) as well as (b) the variance in male fitness within and between the two study locations (**Supplementary Tables 7A,B**, columns 9–12, **Appendix C**; $F = 0.0002, 0.015$, for males and females respectively). In each of these comparisons, the among-year and the between-location components of the variance in male fitness were small fractions of the total variance in male fitness.

Fourth, consistent with our explicit partitioning results, our nested GLM analysis of the number of offspring sired by males expressing resident and wanderer tactics was non-significant overall ($F_{[11, 363]} = 1.30, P = 0.22$), and none of the effects considered within this analysis were statistically significant. Specifically, this analysis showed (a) no significant effects of study location ($F_{[\text{SITE}]} = 0.03, P = 0.86$), indicating that there were no differences in the average number of offspring sired in each study location, (b) no significant effect of the study year, nested within study location ($F_{[\text{YEAR}|\text{SITE}]} = 0.86, P = 0.49$), indicating that there were no differences in the average number of offspring sired within each study year, within each study location, and (c) no significant effect of male mating tactic nested within study year and study location ($F_{[\text{TACTIC}|\text{YEAR}, \text{SITE}]} = 1.29, P = 0.26$), indicating that there were no differences in the average number offspring sired by males expressing different mating tactics, within each study year and study location.

Our nested GLM of the number of offspring produced by females expressing resident and wanderer tactics was significant overall ($F_{[11, 319]} = 1.65, P = 0.02$), with a significant effect of

TABLE 3A | Male prairie vole fitness partitioned between breeding (p_S) and non-breeding (p_D) males, within mating tactics (R, W), within years (2005–08) and within locations (IN and KS); the fraction of the total variance in fitness that existed between breeding and non-breeding males exceeded 68% (weighted average, columns 16, 30); calculations and variable definitions are in **Appendix B**.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Residents															
Location	Year	Avg	Var	SD	$N(p_S)$	95%CI	Prop.	Prop.	$N(p_D)$	N	Avg _(adj)	V_{within}	$V_{between}$	V_{total}	%
		$O_{ij1\bullet}(S)$	$V_{Oij1\bullet}(S)$			$\Sigma I_{ij1}(S)$	$p_{ij1\bullet}(S)$	$p_{ij1\bullet}(0)$	$\Sigma I_{ij1}(0)$	$\Sigma I_{ij1\bullet}$	$[O_{ij1\bullet}(S)] [p_{ij1\bullet}(S)]$	$[p_{ij1\bullet}(S)] [V_{Oij1\bullet}(S)]$	$[O_{ij1\bullet}(S)]^2 [p_{ij1\bullet}(S)]$	$[p_{ij1\bullet}(S)] [p_{ij1\bullet}(0)]$	
Indiana	2006	1.33	0.56	0.75	6	0.60	0.26	0.74	17	23	0.35	0.14	0.34	0.49	0.70
	2007	2.00	1.47	1.21	15	0.61	0.42	0.58	21	36	0.83	0.61	0.97	1.58	0.61
	2008	1.50	0.25	0.50	6	0.40	0.38	0.63	10	16	0.56	0.09	0.53	0.62	0.85
Sum					27				48	75					
Weighted avg.							0.36	0.64							0.69
Kansas	2005	1.00	0.00	0.00	2	na	0.13	0.87	13	15	0.13	0.00	0.12	0.12	1.00
	2006	2.00	0.00	0.00	1	na	0.25	0.75	3	4	0.50	0.00	0.75	0.75	1.00
	2008	2.00	0.50	0.71	4	0.69	0.24	0.76	13	17	0.47	0.12	0.72	0.84	0.86
Sum					7				29	36					
Weighted avg.		17	18	19	20	21	22	23	24	25	26	27	28	29	30
0.93															
Wanderers															
Location	Year	Avg	Var	SD	$N(p_S)$	95%ci	Prop.	Prop.	$N(p_D)$	N	Avg _(adj)	V_{within}	$V_{between}$	V_{total}	%
		$O_{ij2\bullet}(S)$	$V_{Oij2\bullet}(S)$			$\Sigma I_{ij2}(S)$	$p_{ij2\bullet}(S)$	$p_{ij2\bullet}(0)$	$\Sigma I_{ij2}(0)$	$\Sigma I_{ij2\bullet}$	$[O_{ij2\bullet}(S)] [p_{ij2\bullet}(S)]$	$[p_{ij2\bullet}(S)] [V_{Oij2\bullet}(S)]$	$[O_{ij2\bullet}(S)]^2 [p_{ij2\bullet}(S)]$	$[p_{ij2\bullet}(S)] [p_{ij2\bullet}(0)]$	
Indiana	2006	2.08	1.58	1.26	12	0.71	0.24	0.76	37	49	0.51	0.39	0.80	1.19	0.68
	2007	1.81	1.28	1.13	16	0.55	0.22	0.78	56	72	0.40	0.28	0.57	0.85	0.67
	2008	3.00	3.70	1.92	20	0.84	0.32	0.68	43	63	0.95	1.17	1.95	3.12	0.62
sum					48				136	184					
Weighted avg.							0.26	0.74							0.65
Kansas	2005	2.43	1.39	1.18	7	0.87	0.27	0.73	19	26	0.65	0.37	1.16	1.53	0.76
	2006	2.50	0.25	0.50	2	0.69	0.25	0.75	6	8	0.63	0.06	1.17	1.23	0.95
	2008	2.57	5.24	2.29	14	1.20	0.40	0.60	21	35	1.03	2.10	1.59	3.68	0.43
Sum					23				46	69					
Weighted avg.							0.33	0.67							0.61
Total										364					

TABLE 3B | Female prairie vole fitness partitioned between breeding (p_S) and non-breeding (p_O) females, within mating tactics (R,W), within years (2005-08) and within locations (IN and KS); the fraction of the total variance in fitness that existed between breeding and non-breeding females exceeded 65% (weighted average, columns 16, 30); calculations and variable definitions are in **Appendix B**.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Residents															
Location	Year	Avg	Var	SD	N(p_S)	95%CI	Prop.	Prop.	N(p_O)	N	Avg _(adj)	V _{within}	V _{between}	V _{total}	%
		$O_{ij1\bullet}(S)$	$V_{Oij1\bullet}(S)$			$\Sigma I_{ij1}(S)$	$P_{ij1\bullet}(S)$	$P_{ij1\bullet}(O)$	$\Sigma I_{ij1}(O)$	$\Sigma I_{ij1\bullet}$	$[O_{ij1\bullet}(S)]^2 [p_{ij1\bullet}(S)]$	$[p_{ij1\bullet}(S)] [V_{Oij1\bullet}(S)]$	$[O_{ij1\bullet}(S)]^2 [p_{ij1\bullet}(S)] [p_{ij1\bullet}(O)]$		
Indiana	2006	1.75	1.19	1.09	8	0.76	0.33	0.67	16	24	0.58	0.40	0.68	1.08	0.63
	2007	1.89	1.10	1.05	18	0.48	0.33	0.67	37	55	0.62	0.36	0.79	1.15	0.69
	2008	2.80	2.76	1.66	10	1.03	0.53	0.47	9	19	1.47	1.45	1.95	3.41	0.57
Sum					36				62	98					
Weighted avg.							0.37	0.63							0.65
Kansas	2005	2.20	2.16	1.47	5	1.29	0.42	0.58	7	12	0.92	0.90	1.18	2.08	0.57
	2006	2.33	0.22	0.47	3	0.53	0.50	0.50	3	6	1.17	0.11	1.36	1.47	0.92
	2008	2.33	1.33	1.15	9	0.75	0.64	0.36	5	14	1.50	0.86	1.25	2.11	0.59
Sum					17				15	32					
Weighted avg.							0.53	0.47							0.65
17	18	19	20	21	22	23	24	25	26	27	28	29	30		
Wanderers															
Location	Year	Avg	Var	SD	N(p_S)	95%ci	Prop.	Prop.	N(p_O)	N	Avg _(adj)	V _{within}	V _{between}	V _{total}	%
		$O_{ij2\bullet}(S)$	$V_{Oij2\bullet}(S)$			$\Sigma I_{ij2}(S)$	$P_{ij2\bullet}(S)$	$P_{ij2\bullet}(O)$	$\Sigma I_{ij2}(O)$	$\Sigma I_{ij2\bullet}$	$[O_{ij2\bullet}(S)]^2 [p_{ij2\bullet}(S)]$	$[p_{ij2\bullet}(S)] [V_{Oij2\bullet}(S)]$	$[O_{ij2\bullet}(S)]^2 [p_{ij2\bullet}(S)] [p_{ij2\bullet}(O)]$		
Indiana	2006	1.90	1.09	1.04	10	0.65	0.63	0.38	6	16	1.19	0.68	0.85	1.53	0.55
	2007	1.92	0.99	1.00	13	0.54	0.20	0.80	51	64	0.39	0.20	0.60	0.80	0.75
	2008	2.73	3.26	1.81	15	0.91	0.28	0.72	38	53	0.77	0.92	1.52	2.44	0.62
Sum					38				95	133					
Weighted avg.							0.29	0.71							0.67
Kansas	2005	1.33	0.22	0.47	6	0.38	0.75	0.25	2	8	1.00	0.17	0.33	0.50	0.67
	2006	0.00	0.00	0.00	0	na	0.00	1.00	1	1	0.00	0.00	0.00	0.00	na
	2008	2.09	1.36	1.16	11	0.69	0.65	0.35	6	17	1.35	0.88	1.00	1.88	0.53
Sum					17				9	26					
Weighted avg.							0.65	0.35							0.55
Total										289					

study year, nested within study location ($F_{\text{YEAR}[\text{SITE}]} = 3.59$, $P = 0.014$), indicating that there was a significant difference in the average number of offspring produced among study years, within study locations. This result was likely due to the small sample collected for Kansas 2006 ($N = 7$) which included six resident and one wandering female; the latter individual did not successfully breed. Despite this outcome, there was no significant effect of study location ($F_{\text{SITE}} = 0.16$, $P = 0.85$), indicating that there were no differences in the average number of offspring produced by females in each study location, and importantly for the test of this hypothesis, there was no significant effect of female mating tactic nested within study year and study location ($F_{\text{TACTIC}[\text{YEAR},\text{SITE}]} = 1.34$, $P = 0.24$), indicating that there were no differences in the average number offspring sired by females expressing resident and wanderer mating tactics, within each study year and study location.

Fifth, as expected if breeders-only estimates of adult fitness tend to overestimate the mean and underestimate the variance in fitness compared to fitness estimates that include all adults within each sex (Shuster and Wade, 2003; Shuster, 2009, 2010), the average number of offspring produced by successfully mating males and females expressing resident and wanderer tactics [$O_{ij1\bullet(S)}$; **Tables 3A, B**, columns 3, 17] was consistently *larger* than the average number of offspring estimated for all males and females expressing resident and wanderer tactics ($[O_{ij1\bullet(S)}][p_{ijt\bullet(S)}]$; **Tables 3A, B** columns 3, 17, 12, 26; Wilcoxon signed rank test, $P < 0.001$, $N = 23$). Moreover, the variance in the number of offspring produced by successfully mating male and female expressing resident and wanderer tactics [$V_{Oij1\bullet(S)}$; **Tables 3A, B**, columns 4, 18] was consistently *smaller* than the variance in the number of offspring produced by all males and females expressing mating and wandering tactics (V_{total} ; **Tables 3A, B**, columns 4, 18, 15, 29; Wilcoxon signed rank test, $P < 0.05$, $N = 23$).

Hypothesis 4

Our results provided four different tests of the fourth hypothesis, that the signature of negative frequency-dependent selection between male and female mating tactics in prairie voles would be a progressive decrease in the between-tactic variance in fitness over time and space. First, as we predicted, our analysis of the variance in fitness between the two male mating tactics, in which we compared the within-tactic variance in offspring numbers to the between-tactic variance in offspring numbers (**Appendix A**; $F_{\text{between-tactics}}$, Equation 9a), showed a pattern of decreasing magnitude of the between-tactic variance in fitness: (a) within each year of the study, within each location (**Tables 2A, B**, columns 19–22, weighted average $F = 0.62$, $F = 0.63$ for males and females, respectively), (b) with the offspring numbers of voles expressing each mating tactic pooled across all years, within each study location (**Supplementary Tables 4A,B**, columns 19–22, **Appendix C**; weighted average $F = 0.01$, 0.002 for males and females, respectively), and (c) with offspring numbers of individuals expressing each mating tactic pooled across all years and across both study locations (**Supplementary Tables 5A,B**, columns 19–22, **Appendix C**; $F = 0.003$ and 0.004 for males and females, respectively).

Second, as we predicted, we observed a pattern of decreasing magnitude in the fraction of the total opportunity for selection occurring between the two mating tactics for males and for females ($I_{\text{between-tactics}}/I_{\text{total}}$), (a) within each year of the study, in each location (**Tables 2A, B**, column 25, weighted average $I_{\text{between-tactics}}/I_{\text{total}} = 0.38$, for males and females, respectively), (b) with offspring numbers of individuals expressing each mating tactic pooled across all years, within each study location (**Supplementary Tables 4A,B**, column 25, **Appendix C**; weighted average $I_{\text{between-tactics}}/I_{\text{total}} = 0.01$ and 0.002 for males and females, respectively) and (c) with offspring numbers of individuals expressing each mating tactic pooled across all years and across both study locations (**Supplementary Tables 5A,B**, columns 25, **Appendix C**; $I_{\text{between-tactics}}/I_{\text{total}} = 0.003$ for males and females, respectively).

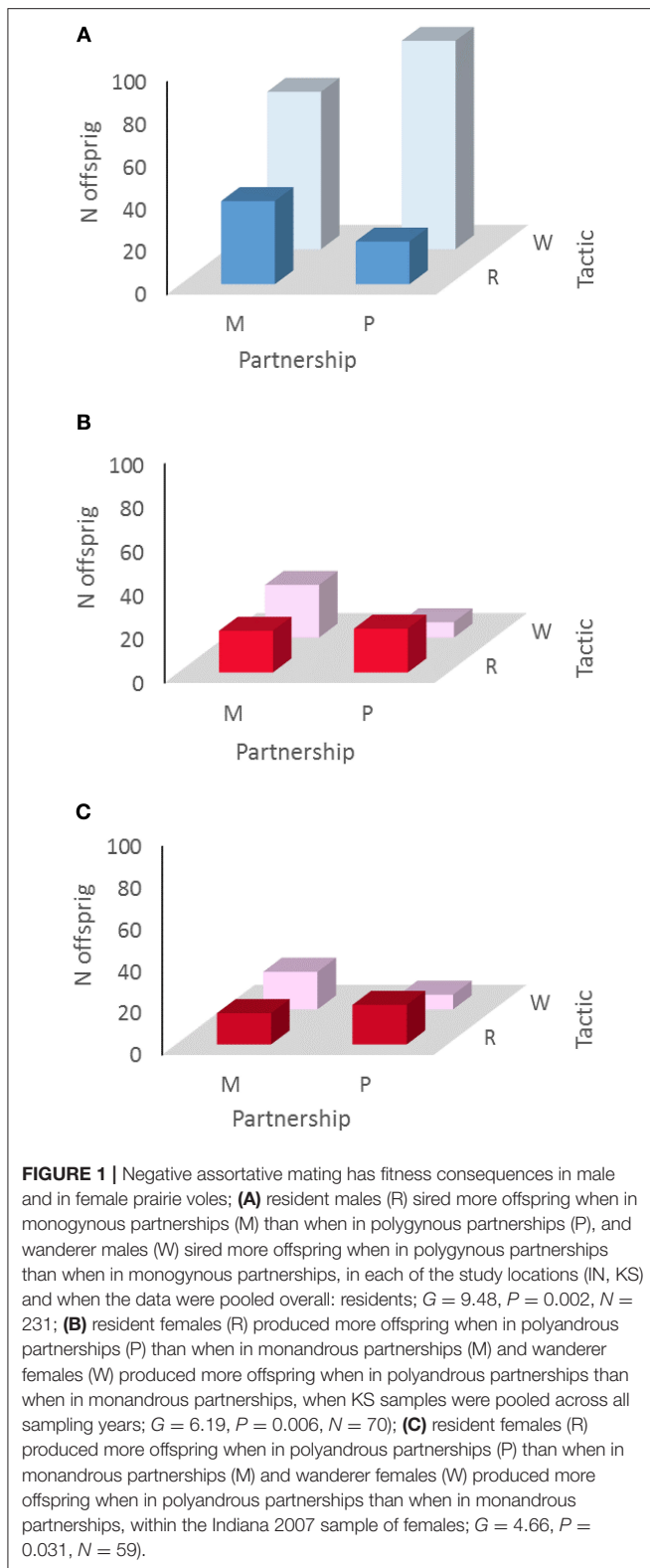
Third, as we predicted, we observed a pattern of decreasing magnitude of fitness variance yet again by examining the fraction of the total opportunity for selection acting on males and females (a) between the two mating tactics (**Tables 2A, B**, column 25, weighted average $I_{\text{between-tactics}}/I_{\text{total}} = 0.38$ for males and females, respectively) indicating that the opportunity for selection acted primarily within rather than between the male mating tactics, and (b) within rather than among years in each study location (**Supplementary Tables 6A,B**, column 15, **Appendix C**; weighted average $I_{\text{among}}/I_{\text{total}} = 0.05$ and 0.08 for males and females, respectively) indicating that the opportunity for selection acted similarly among years, and primarily within each study location.

Fourth, in our nested GLM analysis for males, the magnitude of the F-values associated with each of the effects included in the model followed the predicted decreasing pattern ($F_{\text{TACTIC}[\text{YEAR},\text{SITE}]} = 1.29 > F_{\text{YEAR}[\text{SITE}]} = 0.86 > F_{\text{SITE}} = 0.03$). This pattern was not observed for females ($F_{\text{TACTIC}[\text{YEAR},\text{SITE}]} = 1.34, < F_{\text{YEAR}[\text{SITE}]} = 3.52 > F_{\text{SITE}} = 0.85$) but again this is evidently because the small sample sizes for Kansas 2006 indicated a difference in female fitness among study years within locations.

Hypothesis 5

Our goodness of fit tests produced three main results. First, we found no significant tendency for subadult and adult males to express resident or wanderer phenotypes (residents: 94 adults, 28 subadults; wanderers: 198 adults, 61 subadults; $G = 0.02$, $P > 0.90$, $N = 381$).

Second, we found that resident males sired more offspring when in monogynous partnerships than when in polygynous partnerships and that wanderer males sired more offspring in polygynous partnerships than in monogynous partnerships. This relationship existed in each of the study locations (Indiana: residents: 29 monogynous progeny, 18 polygynous progeny; wanderers: 50 monogynous progeny, 64 polygynous progeny, $G = 4.27$, $P = 0.039$, $N = 161$; Kansas: residents: 20 monogynous progeny, 2 polygynous progeny; wanderers: 24 monogynous progeny, 34 polygynous progeny, $G = 7.50$, $P = 0.006$, $N = 70$), as well as when the data were pooled (overall: residents: 39 monogynous progeny, 20 polygynous progeny; wanderers: 74 monogynous progeny, 98 polygynous progeny, $G = 9.48$, $P = 0.002$, $N = 231$; **Figure 1A**).



Third, we found a tendency for resident females to produce more offspring in polyandrous partnerships than in monandrous partnerships and for wanderer females to produce more offspring in polyandrous partnerships than in monandrous partnerships,

although this relationship was not as consistent across all samples as was the converse relationship in males. Tendencies by female residents toward polyandry and female wanderers toward monandry was apparent in KS 2008 (residents: 6 monandrous progeny, 15 polyandrous progeny; wanderers: 16 monandrous progeny, 7 polyandrous progeny, $G = 7.60$, $P = 0.013$, $N = 44$), and when KS samples were pooled across all years (residents: 19 monandrous progeny, 20 polyandrous progeny; wanderers: 24 monandrous progeny, 7 polyandrous progeny, $G = 6.19$, $P = 0.006$, $N = 70$; **Figure 1B**). We also observed this relationship in the Indiana 2007 sample of females (residents: 15 monandrous progeny, 19 polyandrous progeny; wanderers: 18 monandrous progeny, 7 polyandrous progeny, $G = 4.66$, $P = 0.031$, $N = 59$; **Figure 1C**). However, Indiana years 2006 and 2008 showed no such pattern individually as well as when pooled (residents: 14 monandrous progeny, 28 polyandrous progeny; wanderers: 23 monandrous progeny, 37 polyandrous progeny, $G = 0.27$, $P = 0.60$, $N = 102$).

DISCUSSION

Hypothesis 1

Our first hypothesis provided support for a fundamental principle in evolutionary biology, as well as an experimental approach to verify its existence in natural populations. Fisher's (1930) statement [p. 142], that "the total reproductive value of the males...is exactly equal to the total value of all of the females, because each sex must supply half the ancestry of all future generations of the species," provides the basis for a biological fact—that the average fitness of males and females in such populations must be equivalent (Wade, 1979; Queller, 1997; Shuster and Wade, 2003; Krakauer et al., 2011). Our results confirmed this principle and the experimental approach used to obtain it. Moreover, our result confirmed that our approach for assigning parentage provided accurate estimates of the mean and variance in fitness due to differences in offspring numbers, for resident and wanderer mating tactics in both sexes (Shuster and Wade, 2003; Prather and Shuster, 2015; Shuster, 2018). Such precision is essential for any mating system analysis.

Fisher's principle is also important because it sets limits on certain widely held notions in behavioral ecology regarding male and female interactions. Central to these dynamics is the assertion that intersexual exploitation, beginning with the evolution of anisogamy, leads to escalating evolutionary arms races between the sexes (Parker et al., 1972). If the average fitness of males and females must be equivalent, then all forms of sexual exploitation are inherently self-limiting (Shuster and Wade, 2003).

On a more practical level, the literal implementation of Fisher's principle provides a means for eliminating noise in parentage analysis of natural populations. By including only progeny whose identity can be verified through both parents, as well as the parents of these offspring, it is possible to determine the actual fertilization success of each adult within the population. Moreover, by also including those adults that have no verified progeny among the genotyped young, it is possible to identify individuals that have failed to reproduce

within the population in addition to those that have succeeded. Including both of these classes of adults within parentage analyses is crucial because the largest fraction of the total variance in fitness, which is proportional to the strongest source of selection, is that which exists between the successfully and unsuccessfully breeding adults (Wade, 1979; Shuster and Wade, 2003; Shuster et al., 2013). When these three groups of individuals are included within parentage analysis, Fisher's principle is confirmed, the fitness in terms of offspring numbers for each adult in the population is known, and the total variance in fitness can be explicitly determined as we have shown (Table 1).

Hypothesis 2

Our second hypothesis postulated that alternative mating tactics are most likely to evolve when the variance in fitness is large. Over 71% of all adult males and over 45% of all adult females in our study were unsuccessful in producing offspring (weighted averages, Tables 3A, B). The magnitude of the variance in fitness generated by the large fraction of non-breeding individuals within each sex is comparable to that observed among males in many highly polygynous species (Wade and Shuster, 2004). Invasion by alternative mating tactics appears to occur most easily when the variance in fitness among individuals expressing the invaded mating tactic is high (Shuster and Wade, 2003). Under such conditions, the average fitness of the invading tactic can most readily exceed that of the invaded tactic (Shuster and Wade, 2003; Shuster, 2010). Both population genetic and game theory models require that invading phenotypes possess average fitness exceeding that of the invaded phenotype (Slatkin, 1978, 1979; Maynard Smith, 1982), a condition likely to lead to repeated oscillations in fitness characteristic of alternative mating tactics (Shuster, 2011). Studies conducted during one of these invasions, but not over a duration sufficient to capture fitness oscillations, are likely to conclude that the fitnesses of each mating phenotype are unequal.

Hypothesis 3

Our third hypothesis tested whether the fitnesses of individuals expressing resident and wandering tactics were indeed, unequal. Our results provide the most convincing evidence to date, that alternative mating tactics coexist among males, as well as among females, in the socially monogamous prairie vole, *Microtus ochrogaster*, because the average fitnesses of the different tactic phenotypes were equivalent.

In this 3-year study, involving 653 adults and 231 progeny with genetic identities confirmed through both parents, we found no significant differences in the number of offspring produced by males or by females expressing resident and wanderer tactics. Moreover, the distributions of male and female fitnesses within and between tactics were not different among study years, or between two study locations separated by over 1,600 km. We found comparable results using GLM analyses for adult voles of each sex. However, our explicit variance-partitioning approach allowed more detailed comparisons within the data than the GLM approach, and were not constrained by the parametric assumptions of GLM tests. When we explicitly partitioned variance in male and female fitnesses, all the F-ratios examined

were non-significant, indicating that the majority of the variance in male and female fitness in these analyses occurred within years, within each study location, rather than between the resident and wanderer mating tactics.

Our results are consistent with the hypothesis that the fitnesses of males and of females expressing each mating tactic were equivalent at all temporal and spatial scales of the study. Together, the results of our detailed analyses allowed us to convincingly reject the hypothesis that the average fitnesses of males expressing different mating tactics were unequal, contrary to several existing studies on prairie voles (Solomon et al., 2004; Ophir et al., 2008a,b; McGuire and Getz, 2010; Mabry et al., 2011). We found no significant differences in the average fitnesses of males, within years, among years within each study location, or between the locations for the entire study. Thus, there was no indication in any of our analyses that males expressing wanderer mating tactics "make the best of a bad job" (Dawkins, 1980; Gross, 1982, 1996; Tomkins and Hazel, 2007) at any of the temporal or spatial scales examined in this study. We also confirmed that fitness estimates focusing only on successfully breeding adults tend to overestimate the average and underestimate the variance in relative fitness of the entire adult population. We know of no more comprehensive study of this relationship than the one we present here.

Hypothesis 4

Our results also supported a fourth hypothesis, that the signature of negative frequency-dependent selection between male mating tactics in prairie voles would be a progressive decrease in the between-tactic variance in male fitness over time. Our results showed that the magnitude of the *F*-values associated with each of the effects included in the model followed the predicted decreasing pattern using explicit partitioning of variance and GLMs. However, we found a more conspicuous pattern in the former analysis, that could be substantiated using comparisons of the mean and variance in tactic fitness as well as of the mean and variance in male fitness overall.

The explicit partitioning approach also allowed analysis of the opportunity for selection on males, in which the opportunity for selection operating within the male mating tactics exceeded the opportunity for selection operating between tactics, regardless of the spatial scale at which this parameter was measured. We emphasize that this result, i.e., that selection operates primarily *within*, rather than *between* the male mating tactics, provides yet another reason to reject the hypothesis that wanderer males are making the "best of a bad job." Moreover, consistent with the second hypothesis, that negative frequency-dependent selection operated on resident and wanderer male mating tactics, the between-tactic fraction of the total opportunity for selection variance in male fitness consistently decreased over time, as did the among-male, among-year and between-location fractions of the total opportunity for selection on males. All of these conditions are necessary and sufficient to maintain genetic polymorphism within a population (Slatkin, 1978, 1979).

Our results also address the possibility that our estimates of fitness in this study were collected over too brief an interval, and therefore failed to adequately represent the lifetime fitnesses

of individuals we considered. If individual fitness was highly variable over time in a way that biased our conclusions about average fitnesses, then the variation in fitness among years, estimated for residents and wanderers of each sex, should have been high relative to the total. Instead, our results showed that variation in fitness, estimated for residents and wanderers of each sex, among-years and among-sites (**Supplementary Tables 6, 7 in Appendix C**), made up only a small fraction of the total variance in fitness. This implies that although our fitness measures were collected during a short time within each year, these intervals were similar in character in each of the 3 years they were measured. In the absence of lifetime fitness estimates, such results provide additional support for our conclusions.

Hypothesis 5

Our fifth hypothesis concerned whether mating among the male and female prairie voles displaying the different mating tactics was non-random. Although the results are more convincing for males than for females, our data suggest that a form of negative assortative mating occurs in this population wherein, resident males and wanderer females tend to produce more offspring in monogamous partnerships, and wanderer males and resident females tend to produce more offspring in polygamous partnerships. Such negative assortative mating is sufficient by itself in other species to maintain polymorphism in mating phenotype (Hedrick et al., 2016; Grunst et al., 2018). Whether this is indeed the case in prairie voles remains unclear, but the equivalency of fitnesses that we have shown between males and females expressing resident and wandering tactics provide the conditions necessary for the maintenance of genetic polymorphism. Thus, if there is a genetic basis for these alternative mating tactics, these two processes could act in concert to maintain it.

Comparisons With Other Studies

Recent molecular genetic analyses of brain function in male prairie voles (Okhovat et al., 2015) have shown that different gene products are transcribed depending on the mating tactic the individual expresses. This result is consistent with the expression of mating tactics as a behaviorally flexible, yet still genetically-mediated threshold trait (review in Shuster and Wade, 2003). According to this hypothesis, while most males are capable of expressing either form of a behaviorally flexible phenotype, the probability that a given male expresses a particular tactic depends on his genotype and the environment he experiences, which in turn determine which set of gene products are transcribed and thus which set of mating behaviors are expressed. Our data provide detailed, multiyear results from natural populations showing that males and females express alternative mating tactics, which experience equal fitness within and among breeding season. Our results corroborate the results of Okhovat et al. (2015) and provide a likely context in which such traits have evolved.

Previous studies have shown that the relative reproductive success of particular AMTs can vary depending on environmental conditions (Mills and Reynolds, 2003; Neff and Clare, 2008; Schradin and Lindholm, 2011). We detected no evidence that

population sex ratio affected the reproductive success of residents and wanderers. In our study, we found slightly male-biased populations each year in Kansas and in Indiana except during 2007, which was slightly female biased (1.13); yet wanderers and residents did not differ in the variance in reproductive success in either population in any year. Moreover, while densities differed among years in our study, density did not appear to influence the proportion of residents and wanderers in Kansas or Indiana, nor did it appear to affect the relative reproductive success of the males engaging in AMTs.

The majority of variance in male and tactic fitness occurred within rather than among the study years, suggesting that there was little oscillation among years in the relative fitness of males adopting the different tactics; instead, most oscillations in tactic fitness evidently occurred within years. This result was supported by our finding that the fraction of the total opportunity for selection acting between tactics decreased over increasing temporal and spatial scales. At the largest spatial scale, between study locations, the fraction of the total opportunity for selection operating among the Indiana and Kansas populations was <0.01%. This result indicated that, despite the possible influences of environmental factors e.g., density, temperature, and distribution of essential vegetation (Streatfeild et al., 2011) affecting the distribution of nests and residents, selection operated on male mating tactics in the similar ways over a geographic scale exceeding 1,600 km.

CONCLUSIONS

Our results show that alternative mating tactics can and do evolve in socially monogamous species. A possible explanation for this finding is that breeding success in male and female prairie voles is variable on a scale similar to that of males in highly polygynous species. We rejected the hypothesis that wandering male prairie voles “make the best of a bad job (Dawkins, 1980; Gross, 1982; Tomkins and Hazel, 2007).” Instead, we found that the average fitnesses of males expressing resident and wanderer mating tactics were equivalent, a result that is clear when adults that were successful, as well as unsuccessful in producing offspring, are included in fitness estimates (Shuster and Wade, 2003; Shuster, 2009, 2010, 2011). We showed that selection is stronger within reproductive tactics than between them, allowing both tactics to remain in the population. We found the same pattern in the opportunity for selection in both of our study populations, despite differences in environmental conditions among the years within each location, as well as between the two study locations, which were geographically separated. We further showed that variation in fitness within and among males and females expressing these mating tactics is consistent with negative frequency-dependent selection acting on behavioral phenotypes at each of the temporal and spatial scales examined in this study. We assert that similar results are likely to be found in other populations expressing alternative reproductive tactics, provided that successful and unsuccessful individuals are both included in the study, and that studies are conducted long enough to fully capture variation in individual fitness. Lastly, our results provide

the clearest indication to date that the conditions necessary for the maintenance of behaviorally flexible phenotypes are the same as those needed for maintenance of the less flexible alternative mating strategies.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00007/full#supplementary-material>

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How to Study Socially Monogamous Behavior in Secretive Animals? Using Social Network Analyses and Automated Tracking Systems to Study the Social Behavior of Prairie Voles

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Accurately recording the social and mating behavior of wild animals is necessary to test hypotheses regarding the evolution of monogamous behavior but documenting the behavior of most wild animals is challenging. Social network analyses can use patterns of spatial and temporal co-occurrence to describe the social associations of individuals within a population, such as which opposite-sex individuals are found together more frequently than others as an indicator of their degree of social monogamy. Social networks generated using automated radio frequency identification (RFID) tracking systems may provide insights into the social behavior of secretive animals because they enable the automated and continuous tracking of the social associations among individuals, which can address many of the limitations with studying these kinds of species. We assessed the potential for social networks generated using an automated RFID tracking system to describe the social behavior of prairie voles (*Microtus ochrogaster*) in semi-natural enclosures. Our aim was to assess whether social networks generated using the RFID system provided meaningful insights into the social behavior of voles by comparing this method to other methods that have been traditionally used in laboratory (partner preference tests) or field (degree of home range overlap) studies to study social monogamy in prairie voles. In partner preference tests conducted in the field, females spent more time with males with which they had stronger social network associations. Voles that had stronger social network associations also had home ranges that overlapped considerably more than dyads with lower social network associations. In addition, social networks generated from live-trapping and RFID data were comparable but social networks generated using data from our RFID system recorded almost twice as many social associations overall. Our results show that social association metrics derived

from social networks generated using the RFID tracking system reflect other commonly used measures of social monogamy in prairie voles. Overall, this suggests that patterns of spatial and temporal co-occurrence are meaningful measures of social monogamy in wild animals.

Keywords: association index, social monogamy, social network analyses, RFID system, social behavior, vole

INTRODUCTION

Understanding the evolution of social monogamy is a central aim in animal behavior research (Wittenberger and Tilson, 1980; Komers and Brotherton, 1997; Dobson et al., 2010; Lukas and Clutton-Brock, 2013; Opie et al., 2013; Klug, 2018). Definitions of social monogamy typically focus on how two opposite-sex individuals share a living space and interact with one another (Kleiman, 1977; Reichard, 2003; Tecot et al., 2016; Klug, 2018). Studying social monogamy therefore requires quantifying which opposite-sex individuals are more likely to be found together over time and the interactions between these individuals. This is possible in some species that are directly observable and able to be habituated to humans, but most species are secretive, nocturnal, or not readily habituated to human presence.

To date, many studies that characterize the socially monogamous behavior of secretive species do so indirectly such as by estimating nest sharing (Ribble and Salvioni, 1990), assessing patterns of home range overlap using telemetry (Böhm et al., 2008), or by bringing animals into the laboratory to conduct behavioral assays to quantify their socially monogamous or pair-bonding behavior (Williams et al., 1992; Salo and Dewsbury, 1995; Leese, 2012; Carp et al., 2016). However, there are potential complications with each of these methods. Estimates of home range overlap between two opposite-sex individuals are often based on methods that record an individual's location for a brief moment and may only reflect whether individuals generally use the same portions of their habitat. Although behavioral assays conducted in the laboratory may provide some insight into what can occur in a simplified environment, they may not reflect the natural behavior of wild animals.

Automated tracking systems are one way to deal with these limitations. In these systems, each individual has a passive integrated transponder (PIT) tag that corresponds to a unique number sequence for identification. Radio frequency identification (RFID) antennae then record the unique identification of any PIT tag within a given radius of the antenna for the time that the tag is within range. This information is then recorded and saved by a central reader. These systems have been used to address a number of questions (see Bonter and Bridge, 2011) such as habitat use (Harper and Batzli, 1996; Godsall et al., 2014; Soanes et al., 2015) or quantifying foraging behavior (Newey et al., 2009) and burrow use (Rehmeier et al., 2006; Smith et al., 2018). Because these systems record data continuously, they offer a larger, uninterrupted data set from throughout the day, which is useful for nocturnal species. Further, after initial setup and tagging, human presence is limited so animals do not have to be habituated.

Social network analyses, using data from RFID systems, may also be useful for quantifying socially monogamous behavior, but this has rarely been done (but see Leu et al., 2010; Streatfeild et al., 2011). These data can quantify the number and strength of social connections between opposite-sex conspecifics (Wasserman and Faust, 1994; Wey et al., 2008; Whitehead, 2008). Specifically, social network analyses allow estimation of the strength of the social interaction or association for each dyad (the association index) as well as the overall level of sociality and the total number of social connections per individual (weighted degree and unweighted degree, respectively: Wey et al., 2008; Whitehead, 2008; Farine and Whitehead, 2015).

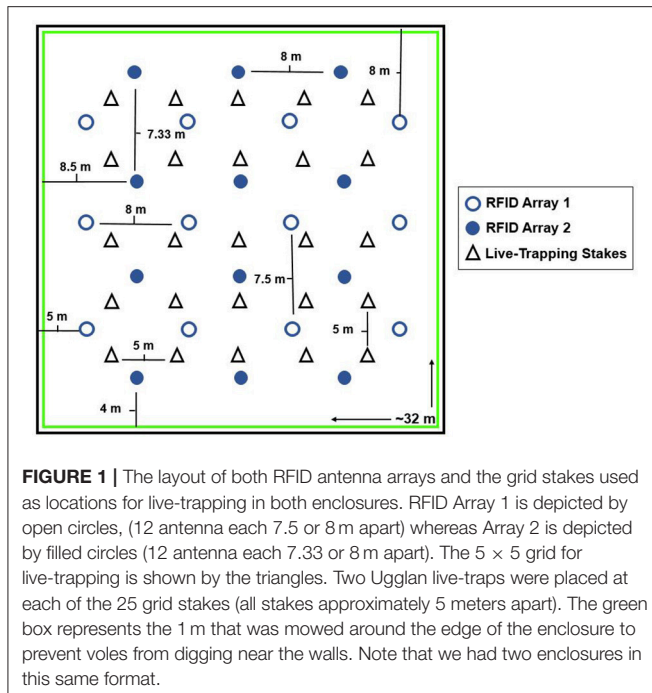
We investigated whether social network metrics derived from an automated tracking system could describe the social behavior of free-living prairie voles (*Microtus ochrogaster*) in semi-natural enclosures. Prairie voles are a model system to document the causes of individual differences in social and mating behavior (Getz et al., 1987; Hammock and Young, 2002; Solomon and Jacquot, 2002; Ophir et al., 2008b) and to understand the evolution of social monogamy (Ophir et al., 2008a; Solomon et al., 2009; Streatfeild et al., 2011). Despite being a model system to study social monogamy, the methods used to measure monogamous behavior differ between studies conducted in the laboratory and those in the field. For example, partner preference tests are commonly used to measure pair-bonding of voles in laboratory studies (Williams et al., 1992; Donaldson et al., 2010), whereas field studies employ other methods such as live-trapping males and females together at nests (Solomon et al., 2009) or radio telemetry to document the space use of males and females (Solomon and Jacquot, 2002; Ophir et al., 2008b; Lambert, 2018).

We collected spatial and temporal co-occurrence data to develop social networks using an automated tracking system that monitored voles implanted with PIT tags living within enclosures that contained an array of RFID antennas (**Figure 1**). We then used social network metrics derived from this automated RFID tracking system to quantify the social relationships in our two enclosures. Our main goal was to assess if the social associations estimated from social network analyses using data recorded from the RFID system were also found using traditional methods of quantifying social connections, including behavioral assays (partner preference test: Williams et al., 1992), home range overlap, and social network analyses using live-trapping data.

METHODS

Study Site

Field work was conducted at the Ecology Research Center at Miami University in Oxford, Ohio (39° 53'N, 84° 73'W) between



May and August 2017. We used two 0.1 ha (approximately 32 × 32 m) enclosures surrounded by a 20-gauge galvanized steel fence, 75 cm above and 45 cm below ground to prevent voles from moving between enclosures (Cochran and Solomon, 2000). Approximately 1 m was mowed around the edge of the enclosures to discourage voles from digging near the enclosure walls. Fences were regularly checked for any holes, gaps, or burrows near the edges to ensure that voles could not escape. Both enclosures contained a mix of goldenrod (*Solidago* spp.), bluegrass (*Poa pratensis*), clover (*Trifolium* spp.), fescue (*Festuca* spp.), timothy (*Phleum* spp.), and ryegrass (*Elymus* spp.; Solomon et al., 2009) that provided food and cover for voles. An electric wire was run across the top of the fence and turned on whenever researchers were not in the enclosures to prevent mammals such as raccoons from entering the enclosures and disturbing traps (although we did not encounter this during our study). Other predators, including predatory birds and snakes, could potentially enter the enclosures and we observed snakes within the enclosures (ACS and BD personal observations) and also observed predation due to avian predators (likely owls). Prior to releasing the voles inside the enclosures, we live-trapped for 3 days without catching any other small mammal species to ensure that none were in the enclosures at the start of the field season. We occasionally caught mice ($n = 5$ *Peromyscus* spp.) and shrews ($n = 2$) within the enclosures throughout the field season and released them outside the enclosures.

Study Animals

We used 7–8th generation laboratory-bred prairie voles descended from voles that were originally captured in Illinois. We released voles from this laboratory population into both enclosures in late May 2017. One enclosure started out at twice

the density of the other (48 voles vs. 24 voles, both with equal sex ratios) but reached a similar density by the end of the field season. Populations were started with different densities due to another project conducted simultaneously. Densities in both enclosures were within the natural range found in wild prairie vole populations (Getz et al., 1993, 2001). No opposite-sex siblings or opposite-sex parents and offspring were released into the same enclosure to prevent inbreeding and provide the same number of non-sibling mating partners for all individuals. If any voles were found dead within the first week of the study, we replaced them with another same-sex vole from the laboratory colony ($n = 2$ females, 1 male).

Adult voles were identified by unique passive integrated transponder (PIT) tags (Biomark: Boise, Idaho, 12 mm HPT tags) implanted before release. In two cases where we trapped voles with PIT tags that were not working, we implanted new PIT tags. For one of these voles, we were able to determine which individual it was, while the other could not be identified as any individual from the initial population. All offspring produced were left in the enclosures but were not included in any of our analyses. Voles in the enclosures were not provided with any supplemental food besides small amounts of cracked corn used to bait traps.

Live Trapping

We used live trapping to collect social interaction data, assess reproductive condition of voles, and capture offspring produced in the enclosures (as we have done previously, see Solomon et al., 2009). We placed two live-traps at each stake in a 5 × 5 grid system (stakes approximately 5 m apart, see Figure 1) for a total of 50 live traps in each enclosure. We used Ugglan multiple capture traps (Granhall, Sweden) covered with sheet metal (to protect from sun or rain), which allow for multiple individuals to be captured per trap. To locate nests, we used both powder-tracking by dipping female voles in UV fluorescent powder, releasing them, and then following their powder trail with a black light back to their burrows or surface nests (Lemen and Freeman, 1985) and VHF radio telemetry (see below). Once we identified the location of a nest, we also set two traps at each burrow or nest entrance every time we set the trapping grid to increase our chances of catching adult voles and any offspring produced. We identified 15 surface and underground nests (burrows) that were actively used, 9 in enclosure 1 and 6 in enclosure 2, resulting in a maximum of 26 or 18 additional live traps for enclosures 1 and 2, respectively.

At the beginning of the experiment, we live-trapped nearly every day but after the first 2 weeks, we reduced live-trapping to allow the RFID system to collect more data overnight and to provide more time for locating voles using VHF radio telemetry. From weeks 3 to 14, we set traps three times per week (Monday, Wednesday, and Friday) alternating between the two enclosures so that voles in each enclosure were trapped three different days during each 2-week period. Live traps were set and checked on three different schedules depending on what data were needed: set in the late evening (between 22:30 and 23:00) and checked in the morning (starting at 7:00), set in the early evening traps (between 18:00 and 19:00) and checked 2 h later, and set in

the morning (starting at 5:00) and checked 2 h later. Originally, we set traps in the evening and overnight, but stopped setting them overnight once it was likely that offspring had been born (Richmond and Conaway, 1969) and were moving independently outside the nest (N. Solomon, B. Keane, unpublished data) to prevent them from being separated from their parents for the entire night. Finally, we did not trap when there were thunderstorms but set live-traps on a different day during the week if possible. See **Table S1** for full details on trapping schedule. Each time an individual was trapped we recorded its body mass (g), reproductive condition, other individuals in the same live trap, and the trap location.

Radio Frequency Identification (RFID) Data

We placed 12 radio frequency identification (RFID) antennas in two different 3×4 arrays throughout the enclosure (see **Figure 1** for layout of both arrays), all connected to a central PIT tag reader system (Biomark, RM310/SM303 system). This system records the unique PIT tag numbers of any vole traveling within approximately 6 inches of the antenna (ACS personal observation), once per second. When multiple tags are present at the antenna, it alternates between recording the two (ACS personal observation), therefore to miss individuals present at an antenna at the same time both individuals would need to be within range of the antenna at the same time for >2 s. The antenna system was rotated every 3 days from enclosure 1 array 1, enclosure 1 array 2, enclosure 2 array 1, enclosure 2 array 2, so that the RFID system was in each enclosure for six continuous days.

VHF Radio Telemetry

To locate vole nests and record spatial movements, we tracked voles with VHF radio telemetry. We placed VHF collars (Holohil model PD-2C, approximately 3 g) on as many adult voles as possible, locating individuals four times per week between 11:00 and 16:00 h with at least an hour between each relocation. We recorded each location with a handheld GPS unit (Trimble Navigation Limited, Trimble Geo 7x) and searched around the location to identify burrows or surface nests that were actively in use (Lucia et al., 2008). Overall, each vole was located between 5 and 71 times with VHF telemetry depending on the duration they were wearing the collar, with an average of 22.36 ± 12.70 locations per vole.

Partner Preference Tests

To test how male-female associations generated from the social network analyses using the RFID system compared to measures of pair bond formation, we conducted partner preference tests in the field. Partner preference tests are an established laboratory method used to assess pair bonding in prairie voles (Williams et al., 1992). We modified a laboratory protocol to conduct partner preference tests in the field to determine if females preferred individuals they were associated with based on the social networks generated using the RFID system. These tests were conducted in a three chambered, clear plastic arena where the female was placed in the middle of the arena, with a male partner (or potential partner) on one side and a novel (or

potentially less-familiar) male called a stranger) on the other side. The three different parts of the arena ($76 \times 21 \times 30$ cm) were separated by 5 cm clear plastic dividers with a 6 cm opening for movement of focal females.

Once initial data from the RFID system were available after the first few weeks of the study, we tested females when a male and a female vole were recorded at the same antenna within ≤ 1.5 min of each other. Because this pair was recorded at least once at the same place close in time and pairs often spatially co-occur (Hofmann et al., 1984), it is likely that they would have a high association index for the entire season. Therefore, these male-female dyads became our potential pairs for the partner preference tests. Following morning live-trapping, we conducted partner preference tests (from approximately 08:30 to 12:00 h) on any potential pairs that were both caught that morning. The female from this pair would be the focal female in the trial and the male would be the potential partner. We chose the potential stranger based on the available males caught that day that were closest to the male partner in age and body mass and not caught at an adjacent live-trapping location. We note that although we chose the potential pairs after only a small portion of the field season, the average association index from social network analyses generated using the RFID system from the entire field season supported our choices. Specifically, the average association index (the strength of their social association, see below for details on calculation) for focal females with their potential partners for the entire field season was 0.04, whereas the focal female's average association index with the potential stranger for the entire field season was 0.0042.

Each female was only tested once ($n = 10$). The arena was placed in an opaque plastic bin in the shade next to the enclosures. We observed trials from a distance of approximately 1 m to ensure that trials were not disturbed. For half of the trials the partner was on the left side of the arena and for half the partner was on the right side of the arena. Which side the partner was on for each given trial was randomized. Both males were placed on their respective sides of the arena, loosely secured with a tether made from a cable-tie and monofilament line (Castelli et al., 2011) and given *ad libitum* access to water. The males were given 20 min to habituate to the tethers and the arena before the focal female was placed in the arena. The first 4 trials lasted 3 h after habituation (Curtis et al., 2001), but to conduct more trials and reduce the time that voles were kept out of the enclosures, the trial length was reduced to 1 h after a 20 min habituation period for males. The trial was recorded from above in real time by a video camera. Videos were scored by 4 observers using JWatcher (Blumstein and Daniel, 2007) to quantify the amount of time females spent on the partner's side of the arena, the stranger's side of the arena, or the neutral middle part. We defined "time spent" based on when the female's head crossed the border into a new area. For the few trials that lasted 3 h, we only used data from the first hour in order to make it more comparable to the 1-h trials. Observers could not be blind to which male vole was the potential partner and which male vole was the potential stranger because they assigned the males to each trial. However, our response variable for these trials (time spent in each part of the enclosure) should be unaffected by any observer biases.

Patterns of Vole Activity

We also investigated when voles were most active based on what time of day the RFID system recorded the most PIT tags. The circadian activity cycle of prairie voles has been suggested to be diurnal, crepuscular, nocturnal, or ultradian (Madison, 1985), although there seems to be more support for a crepuscular rhythm (Calhoun, 1945). To investigate prairie vole activity, we identified how many hits the RFID system recorded per hour. We omitted days in which live traps were set in the same enclosure as the RFID system to control for reduced activity if voles were in live traps.

Construction of Social Networks

Although social networks provide measures of the associations among conspecifics and of an individual's level of sociality, we were specifically interested in the following two measures:

1. Association index, or the strength of the association of each dyad (female-male, female-female, male-male) of voles in each enclosure;
2. Unweighted degree, or the number of unique voles each individual was connected to.

We constructed social networks and conducted social network analyses using the R package *asnipe* (version 1.1.4, Farine, 2017). To construct the social networks from the RFID system data, we ran the raw RFID system data through a Gaussian mixture model in R, which creates groups based on the distribution of voles at each antenna through time (Psorakis et al., 2012). These groups were then used to form a network where voles placed in the same group have a connection. The number of these connections (the unweighted degree) represents the number of unique individuals with which voles had associations. Each individual connection is weighted by a simple ratio index, a type of association index, which is the number of times that dyad was observed together divided by the sum of the number of the times they were observed together or separately, representing the association rate of that dyad (Cairns and Schwager, 1987). We used a simple ratio index instead of a half-weight index because we did not break key assumptions, like individuals being more likely to be recorded when associated or not recording all associations at a given time (Whitehead, 2008). Further, Krackhardt (1988) suggest that using the half-weight index may over-correct for any biases in the data. Live-trapping networks were made by creating a group-by-individual matrix, where individuals caught at the same location (the same grid stake or nest) when traps were checked were placed in the same group (Solomon et al., 2009; Streatfeild et al., 2011). The social network was then created from the group by individual matrix in *asnipe* and association indices were weighted using a simple ratio index as well. Network figures were created using the R package *igraph* (version 1.1.2, Csardi and Nepusz, 2006).

Statistical Analyses

All analyses were conducted in R version 3.4.1 (R Core Team, 2017). We visually examined the distributions of the response variables to check for normality and visually examined the

residuals to check for normality and homoscedasticity when appropriate (Zuur et al., 2010).

The full live-trapping and RFID system social networks were compared using a multiple regression quantitative assignment procedure (MRQAP: Krackhardt, 1988) in the R package *asnipe*. Specifically, we used an ordinary least squared (OLS) network regression with the live-trapping network as the predictor and the RFID network as the response variable. We used random social networks generated through network permutations on the group by individual matrix (produced from the Gaussian mixture model conducted using the RFID data) as the random networks used in the MRQAP. We also used a Spearman's rank correlation to compare how individuals were ranked based on their unweighted degree in both networks. Because the RFID system generated substantially more spatial and temporal co-occurrence data for the social networks compared to those generated using the live-trapping data (see Results), our assessments of how the social network metrics compared to the results from the partner preference tests and home range overlap were conducted using only the social network metrics generated from the RFID system and not the live-trapping data.

Using spatial coordinates from the locations generated by the RFID system, live-trapping, and VHF radio telemetry we calculated minimum convex polygon (mcp) home range area estimates in the R package *adehabitatHR* (version 0.4.15; Calenge, 2006). As required by this package, we removed any individuals that had fewer than 5 locations with each method and all individuals that were only ever located at one location (see the sample size for each method in Table 1). We compared home range estimates generated by the three methods using a linear mixed-effects model with method (live-trapping, telemetry, or RFID system), sex, and enclosure as fixed effects and vole ID as a random effect (R package *lme4* version 1.1-1; Bates et al., 2015, *P*-values calculated by *lmerTest*, version 2.0.36, Kuznetsova et al., 2017). Home range estimates were transformed by taking the square root before running the model to improve normality of the residuals.

We also compared the degree of home range overlap and social network association index between the dyads for all voles for which we could estimate home range size with VHF telemetry. To do so, we calculated home range overlap (based on the mcp home range estimates) for all dyads in the same enclosure using

TABLE 1 | The mean and standard deviation for the minimum convex polygon home range area estimates in hectares calculated from each of the three methods from adult prairie voles in two enclosures at the Miami University Ecology Research Center.

Group	RFID system (ha)	Trapping data (ha)	Telemetry data (ha)
Sample Size	<i>n</i> = 33 males <i>n</i> = 31 females	<i>n</i> = 32 males <i>n</i> = 29 females	<i>n</i> = 14 males <i>n</i> = 18 females
Enclosure 1 Males	0.01 ± 0.0093	0.0051 ± 0.0058	0.013 ± 0.0093
Enclosure 1 Females	0.0065 ± 0.0077	0.003 ± 0.0033	0.0082 ± 0.0064
Enclosure 2 Males	0.013 ± 0.010	0.0077 ± 0.0062	0.0077 ± 0.0029
Enclosure 2 Females	0.005 ± 0.0039	0.005 ± 0.0042	0.0084 ± 0.0055

the VHF radio telemetry data using the `gIntersection` function of the package `rgeos` (version 0.3–28; Bivand and Rundel, 2018). We used these estimates to calculate the proportion of home range overlap for each dyad in our two enclosures. We then used a multiple regression quantitative assignment procedure (MRQAP: Krackhardt, 1988) in the R package `asnipe` to compare the matrix of the proportion of home range overlap to the social network matrix (only including voles for which we had home range overlap estimates) based on data from the RFID system in each enclosure separately. Specifically, we used an OLS network regression with the matrix of proportion of home range overlap as the predictor and the matrix of association indices based on social network analyses of data from the RFID system as the response variable. We used random social networks generated through network permutations on the group by individual matrix of the individuals included in this analysis (produced from the Gaussian mixture model run on the RFID data) as the random networks used in the MRQAP.

For our partner preference tests, we compared how much time the female spent in each part of the arena using a binomial generalized linear model with the proportion of time the female spent in each third of arena as the response variable (stranger, partner, or middle) and the corresponding chamber (stranger, partner, or middle) as the predictor variable. We included female ID as a fixed effect since the model would not converge with female ID as a random effect. We used a generalized linear model to compare the time that the female spent on the side with each male (as the response variable) to the association index of the focal female and that specific male from the social network generated from RFID data (as the predictor variable). We included trial number as a fixed effect (to control for repeated observations in each of the three sections of the arena, from the same trial) rather than a random effect because the model would not converge when trial number was included as a random effect. We standardized the predictor variable (scaled with a mean of 0 and variance of 1) to allow for easier comparison and interpretation of effect sizes (Schielzeth, 2010). Data are shown as mean \pm 1 SD unless stated otherwise.

Ethical Note

All methods were approved by the Institutional Animal Care and Use Committee of Miami University (protocol number 979) because this was where data collection with live animals occurred.

RESULTS

Partner Preference Test Compared to Social Network Metrics

The outcome of the partner pair preference tests supported the results from the social networks generated with the RFID tracking system. Overall female voles spent significantly more time in the area of the test arena with their potential partner (Figure 2), than their potential stranger (effect of the stranger side of the arena compared to the partner side, $b = -3.46$, $z = -2.72$, $P = 0.0066$) or the empty middle chamber (effect of middle compared to the partner side, $b = -3.89$, $z = -2.73$, $P = 0.0063$). Females did not spend more time

with the potential stranger than the empty middle of the arena (effect of the stranger side of the arena compared to the middle, $b = 0.44$, $z = 0.28$, $P = 0.78$). Further, the amount of time the focal females spent with each male during the trial was related to the association index estimated from the social network using the RFID system data (effect of RFID association index, $b = 899.56$, $t_{(17)} = 3.68$, $P = 0.0019$, Figure 3).

Degree of Home Range Overlap vs. Social Network Association Index

The proportion of home-range overlap between each dyad based on VHF radio telemetry data was a significant predictor of the strength of their association index in both enclosures (enclosure 1 OLS network regression: $b = 0.017$, $P = 0.026$, model adjusted $R^2 = 0.055$, model residual standard error = 0.016, Figure 4; enclosure 2 OLS network regression: $b = 0.035$, $P = 0.0056$, model adjusted $R^2 = 0.42$, model residual standard error = 0.0088, Figure 4). Overall, home range size estimates generated by the RFID system were significantly larger than estimates produced by live-trapping (effect of live-trapping method, $b = -0.024$, $t = -3.43$, $P < 0.001$, Figure 5) but not VHF telemetry (effect of telemetry method, $b = 0.0049$, $t = 0.58$, $P = 0.56$, Figure 5). Males had significantly larger home range sizes than females overall (effect of sex, $b = 0.020$, $t = 2.54$, $P = 0.014$, Figure 5) and there were no differences between enclosures (effect of enclosure, $b = 0.012$, $t = 1.40$, $P = 0.17$).

Comparing Social Networks Generated by Live-Trapping and the RFID System

Overall, social networks generated from RFID and live-trapping data were similar, although the number of social connections varied between the two methods. On average, voles were recorded 12.78 times through live-trapping and 68.95 times through the Gaussian mixture model for the RFID system. The Gaussian mixture model produced 4,564 events from the raw RFID data. These events ranged from 0 s (i.e., voles recorded simultaneously) to 66,161 s with $655.2 \pm 3,352.84$ s being the average (or about 10 min). The strength of association indices between voles generated by live-trapping was positively related to the strength of association indices between voles from the social network generated by RFID data (OLS network regression: $b = 0.13$, $P = 0.0007$, model adjusted $R^2 = 0.105$, model residual standard error = 0.0093, Figure 6). Therefore, the network of social interactions collected through live-trapping was a significant and positive predictor of the network of social interactions collected by the RFID system. The average unweighted degree (the number of unique conspecifics each individual is connected to in the network) was 8.88 when generated from RFID data while it was 4.52 when generated from live-trapping data. Individuals were similarly ranked in terms of unweighted degree in both types of networks (Spearman's rank correlation: $P < 0.001$, $\rho = 0.64$, Figure 7), suggesting that individuals were recorded as highly social (i.e., more connections with different individuals) or less social by both

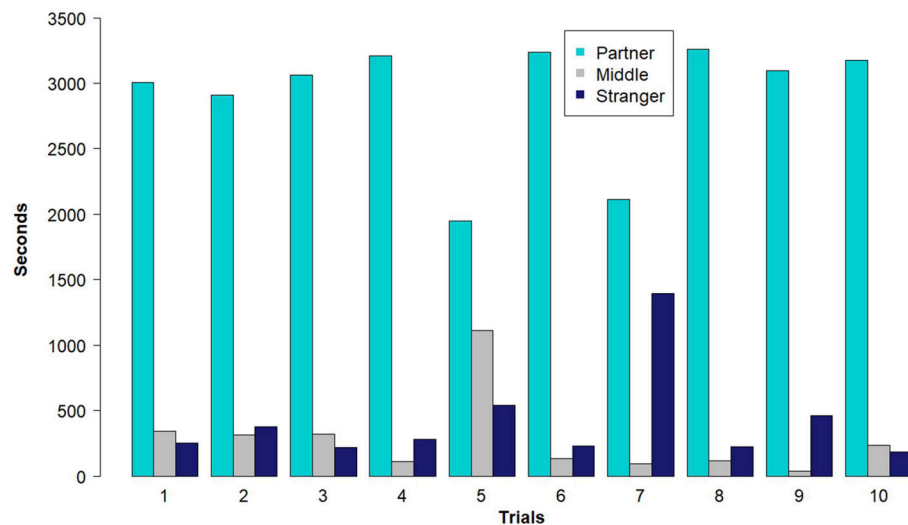


FIGURE 2 | The number of seconds that female prairie voles ($n = 10$) in each trial spent on the three sides of the partner preference arena: middle of the arena, potential partner, and potential stranger (with a possible maximum of 3,600 s). Note that trial number refers to the order trials were conducted during the field season.

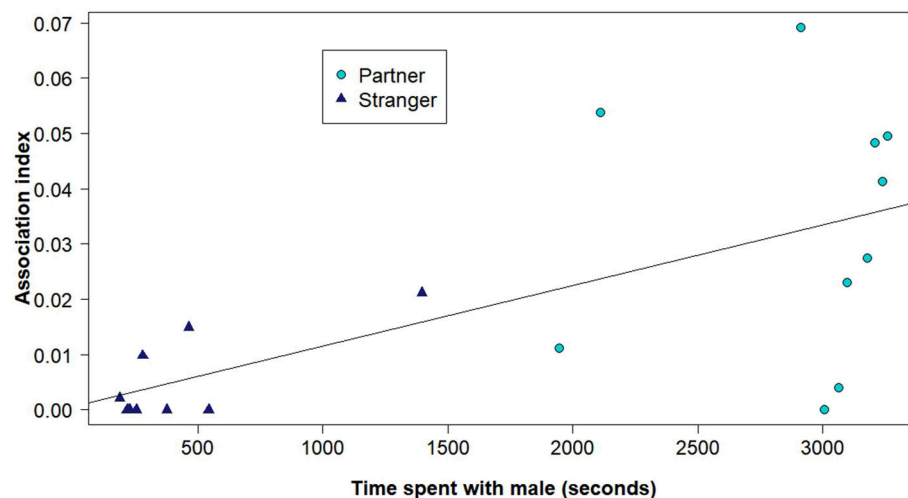


FIGURE 3 | The time that the focal female spent with each male during the partner preference test (with a possible maximum of 3,600 s) and the corresponding association index of that pair based on the social network analyses using the RFID system. The points representing either the potential partners or the potential strangers from the partner preference trials are represented as different shapes and colors.

the social networks generated from live-trapping and our RFID system.

Patterns of Vole Activity

The highest peak of activity (29.75% of all times voles were recorded) was around dusk (from 18:00 to 20:00), which supports the hypothesis that prairie voles are crepuscular and not nocturnal or diurnal, at least in this habitat during this time of year (Figure 8). However, there was not a similarly-high peak around dawn, as we would expect in a crepuscular species.

DISCUSSION

Can Social Network Metrics Describe the Socially Monogamous Behavior of Secretive Animals?

Our results provide some support that the male-female social network metrics calculated from spatial or temporal co-occurrence data provide insight into the social mating system of prairie voles. Male-female associations derived from the social network analyses using the automated RFID system were consistent with results from the partner preference tests. Specifically, female voles showed a preference for their potential

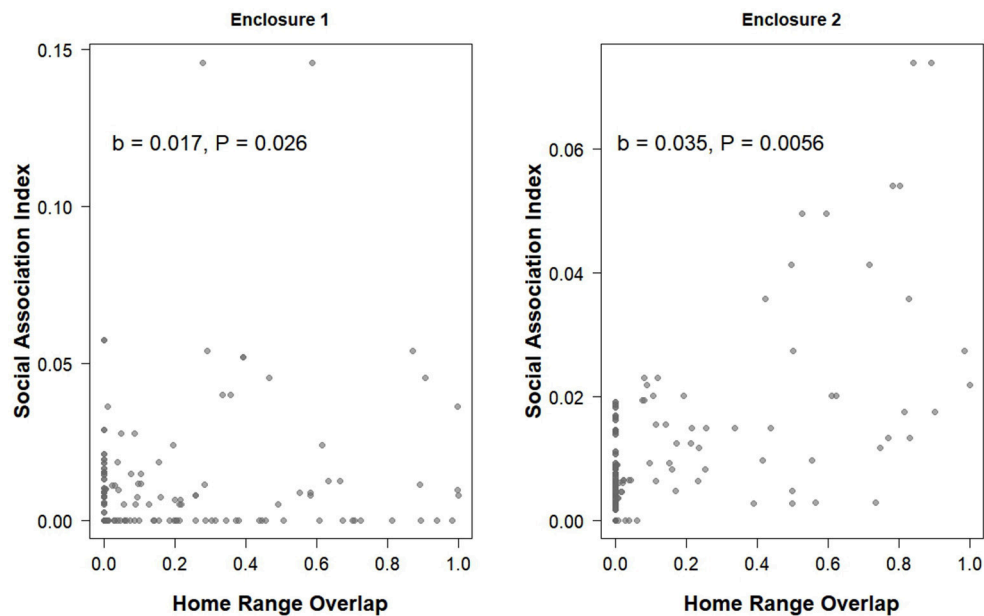


FIGURE 4 | The home range overlap between each pair of prairie voles based on the minimum convex polygon from VHF radio telemetry data and the social association index for that pair (the strength of the association) from social network analyses generated using data from the RFID system. Note that the x-axes are the same on both panels but the y-axes are different.

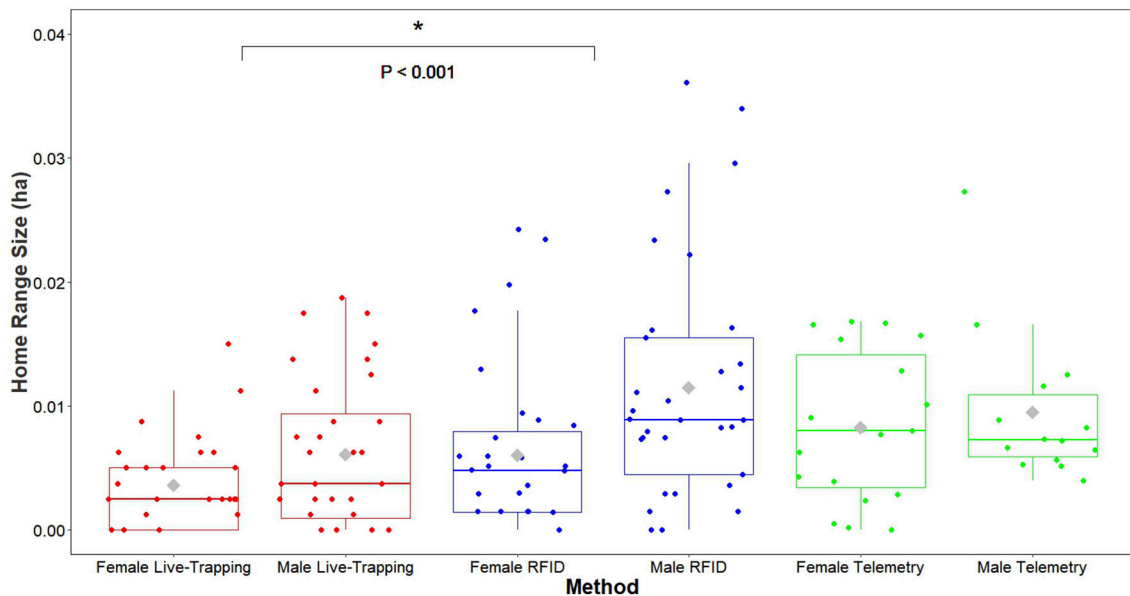


FIGURE 5 | Home range size estimates (minimum convex polygons) of adult prairie voles estimated using our automated RFID system were significantly larger than those estimated with live-trapping. Females and males were combined in these models, so P -values refer to the difference in home range estimates between methods for all adult male and female voles. * $P < 0.05$.

partner and the time spent with each male within the trial was related to the strength of the dyad's association index estimated from the social networks using the RFID system. The degree of home range overlap for each dyad was also related to the strength of their association index derived from the social networks in

both populations. Additionally, we found that social networks generated by live-trapping and the RFID system were statistically similar but that social networks generated by the RFID system provided more data per individual and thus allowed us to detect more associations.

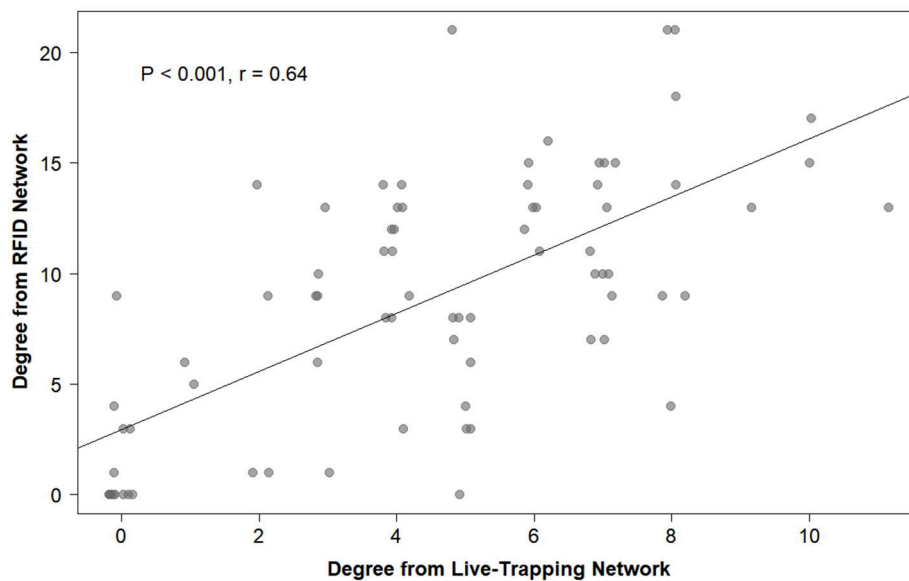


FIGURE 6 | The relationship between each individual prairie vole's unweighted degree (the number of unique conspecifics each individual is connected to in either social network) generated from the social network using the live-trapping data and the unweighted degree generated from the social network using the automated RFID tracking system.

Our results show that a small amount of spatiotemporal data generated from a RFID system can predict the behavioral preference of females in partner preference tests. This indicates that this method can be used in future studies to provide investigators with information about a female's social partner under natural conditions. This is an important result because few studies where social networks have been constructed using data from wild animals have attempted to use other methods to test the hypothesis that the spatial-temporal co-occurrence data are consistent with our knowledge of the social behavior of their study species.

Although the proportion of home range overlap was related to the strength of the association index in both populations (**Figure 4**), the R^2 -value was quite low in one of the enclosures. This could be due to the fact that this enclosure has more individuals with some level of home range overlap but an association index of zero (**Figure 4**). This was the enclosure with the higher population density at the start of the study, so voles in this enclosure may have been more space-limited resulting in home range overlap, but that they were preferentially choosing to associate with certain social partners over others, although we did not directly test this. Conversely, several dyads in both enclosures had non-zero association indices from the RFID data (suggesting some level of association) yet had no home range overlap based on telemetry data (**Figure 4**). Although the overall pattern we found in both enclosures suggests that association index and home range overlap are related, the presence of these particular data points suggests that home range overlap alone does not fully represent all social relationships or that VHF telemetry misses some relationships due to limitations on the amount of data that can be collected per individual and the fact that home ranges are calculated by constructing polygons, which

may leave out some areas where associations may occur. As we have illustrated, RFID systems provide useful information about the spatial behavior of individuals by taking into account space use and movement during all hours of the day and night instead of many traditional methods that are only point samples during one part of the day or night. Thus, social network analyses can provide additional insight into inter-individual interactions in studies of social monogamy, in addition to traditional methods like spatial overlap. Further, after individuals have initially been PIT tagged, RFID systems eliminate most human disturbance when collecting these data.

Home Range Estimates

Automated tracking systems can also provide information about individual differences in social monogamy. Studying the spatial behavior of prairie voles in particular may show us which alternative mating tactic an individual is displaying (Ophir et al., 2008b; Blondel et al., 2016), either a "resident" (a paired individual that has established a territory) or a "wanderer" (an un-paired individual that does not have only one particular nest and tends to have a larger home range, Getz et al., 1987, 1990; Solomon and Jacquot, 2002). In fact, in a previous study, reproductive success of wandering males varied with the individual's space use (Ophir et al., 2008b). Home range overlap can also tell us whether or not there are multiple potential mates and potential rivals with overlapping territories (Ophir et al., 2008b).

Comparing Social Networks Generated by Live-Trapping and the RFID System

Social networks generated from two different methods of data collection detected similar social associations among individuals

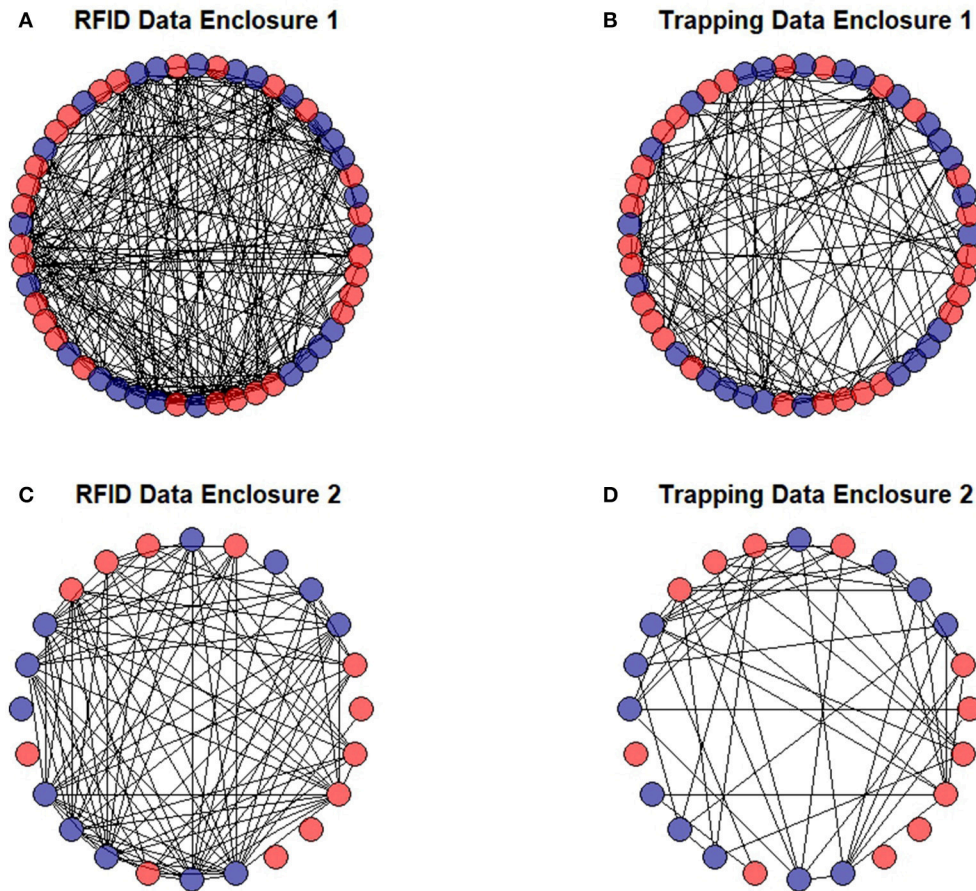


FIGURE 7 | Social networks of prairie voles in two separate enclosures generated by our RFID system (A,C) and multiple capture live-trapping (B,D). Males are shown in blue and females are shown in red. Individuals with no connections to other individuals likely died soon after they were released into the enclosures.

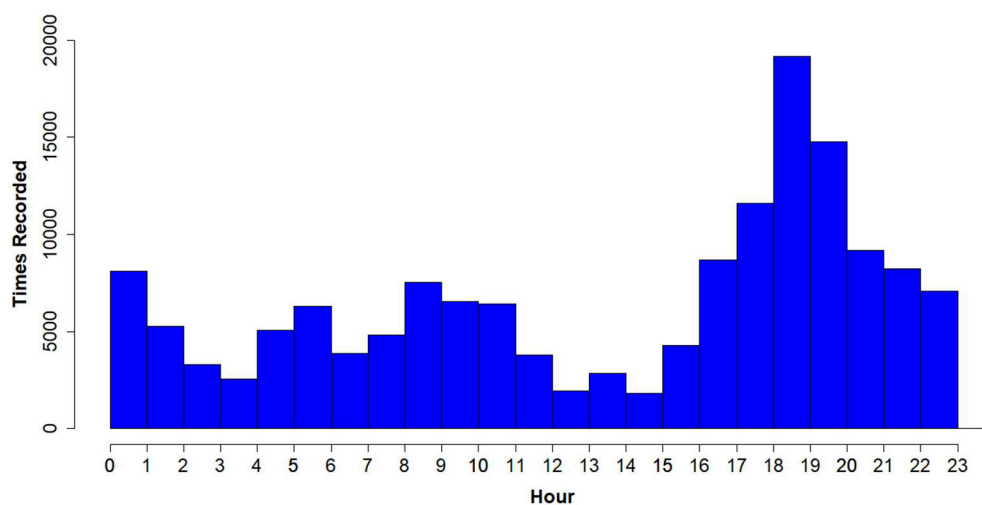


FIGURE 8 | Total number of times PIT tagged prairie voles were recorded (hits) from all RFID antennas per hour of the day (days where live-trapping took place, which may bias activity results, were removed). Note the peak in readings in the evening, from hours 18:00 to 20:00 h.

and similar levels of sociality, although our automated RFID system generated much larger data sets and detected more social associations than live-trapping. Although the maximum duration of an event for our Gaussian mixture model is quite long (66,161 s), the mean value ($655.2 \pm 3,352.84$ s) is much lower than live-trapping (which lasts several hours to overnight), suggesting that the RFID data is recording associations at a much finer scale than live-trapping. As Krause et al. (2013) indicated, data collected by repeated live-captures or focal observations at set intervals may miss weaker associations or transitions in social associations due to the much longer intervals over which focal observations, live-trapping, or VHF telemetry are spread. Because we expect socially monogamous individuals to have one main, stronger relationship, missing these weaker associations may not detract from our general understanding of their social behavior. However, because non-socially monogamous individuals may have several weaker or more transient social associations, we may miss important social connections for these individuals without the continuous finer-scale data provided by RFID systems, making comparisons between individuals incomplete. Passive animal-tracking systems, like the RFID system used here, are more likely to detect these thanks to the generally much shorter interval between recordings and less restricted time over which data are recorded.

Our results comparing the social networks generated using live-trapping and the RFID system are similar to those of Farine (2015), who showed that social networks based on proximity data and interaction data may have some structural differences (like the number of social connections) but still detect a similar pattern of sociality when comparing between individuals (e.g., whether individuals had a high or low unweighted degree). Nomano et al. (2014) also found that social networks based on passive recording data were comparable to social networks generated from direct and video observations, suggesting that this system is also beneficial in species where direct observations are possible. Overall, the automated RFID tracking system we used provide a magnitude more data per individual. This is important because it has been suggested that at least 20 observations per individual are needed to increase reliability and stability in social network metrics (Farine and Strandburg-Peshkin, 2015; Hoppitt and Farine, 2018). Despite our intensive live-trapping sessions, only 19 of 77 (24.68%) voles crossed this threshold for live-trapping data, while 48 of 77 (62.34%) voles crossed this threshold when RFID data was used. This indicates that RFID systems provide more powerful assessments of social networks for animals that are difficult to observe.

Patterns of Vole Activity

The ability of the RFID system to record when animals are active may allow researchers to tailor their field methods to specific times for optimal data collection. For example, our results (Figure 8) indicate that the optimal time to set live traps is from 18:00 to 20:00, when voles are at peak activity. Alternatively, if the aim is to find burrows where voles sleep or interact with their offspring, 12:00–15:00 would be the optimal time because this is when voles were least active (Figure 8). Therefore, reviewing data from an RFID system early

in a study can provide useful information for refining field methods.

Potential Limitations of Automated Tracking Systems

Automated tracking systems and social networks derived from such data may not be ideal for every species and question. Generating meaningful social network data requires recording a sufficient amount of social associations. This method will likely not provide a good representation of the social system if a sufficient amount of the population cannot be tagged. Further, the type of automated tracking system we used in this study will likely be less effective on larger animals with large home ranges given that the range at which an RFID antennae can detect a PIT tag is quite low. Although these types of systems can run on 12 V batteries that can be recharged using solar panels, applications to animals that live in “off grid” or in remote areas may also be limited. Therefore, researchers should consider if automated tracking systems will collect sufficient, representative data for each species and question.

CONCLUSIONS

Recording socially monogamous behavior is difficult in most wild animals. Social network analyses based on passive spatial and temporal co-occurrence data, like the data recorded by our automated RFID system, offers a useful way to record and quantify the degree of socially monogamous behavior individuals exhibit. We show that data recorded by RFID systems provide more data across all hours of the day with less human disturbance than traditional methods like live-trapping and VHF telemetry. We also show social network metrics describing indicators of social monogamy generated by this method are consistent with other methods of assessing social monogamy in prairie voles such as partner preference tests or the degree of home range overlap. Therefore, generating social networks with an automated RFID system can be useful to describe the social mating system of species that are difficult to observe.

DATA AVAILABILITY

Raw data for this manuscript is available from the senior author on FigShare at https://figshare.com/projects/Prairie_vole_social_network_data_for_Frontiers_in_Ecology_and_Evolution/56114

AUTHOR CONTRIBUTIONS

BD designed the study and experiments, AS collected data under the guidance of BD, AS conducted statistical analyses, AS and BD wrote the manuscript with contributions from NS. All authors approved of the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2018.00178/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The Bold, Silent Type: Predictors of Ultrasonic Vocalizations in the Genus *Peromyscus*

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An ongoing question related to the evolution of monogamy is how behavioral traits that characterize individuals in monogamous species evolve, and whether monogamy influences the evolution of these traits. One of the most important models for the study of monogamy in mammals is the California mouse (*Peromyscus californicus*) that uses ultrasonic vocalizations (USVs) in multiple behavioral contexts, including pair-bonding and courtship. Because the genus *Peromyscus* has many species that both use USVs and express a variety of mating systems, we were able to examine the relationship among USVs, and other ecological (e.g., xeric habitat), physiological (testosterone), and behavioral (e.g., boldness) traits across species. We measured USVs from seven species at the *Peromyscus* Genetic Stock Center and derived character traits associated with the species' ecology, physiology, and behavior from published studies, including those that had used stocks from the *Peromyscus* Genetic Stock Center. We determined whether there were USV traits that were particular to monogamous species or whether traits other than mating system best predicted USVs. The trait that best predicted USVs was not related to mating system, but rather, species boldness. Bold species produced few aggressive barks (likely a defensive agonistic USV type) at a higher mean fundamental frequency than less bold species. In relation to mating system, the barks in monogamous species were shorter in duration than the barks in non-monogamous species. Our results suggest that boldness of a species has a higher selection on USVs than the species mating system, ecology, or physiology and that selection has acted on agonistic acoustic signals. Because another type of USV, the sustained vocalization or SV type, did not differ among species in spite of mating system differences, and because all species produced bark types, we suggest that the USVs in rodents evolved as general signals that have generally been co-opted for particular functions within the mating system context that differs across species, as opposed to signals that have been shaped by mating system type.

Keywords: communication, ultrasound, USV, mating system, personality, mouse, boldness

INTRODUCTION

Monogamy is a population or species level characteristic that defines a general trait expressed by individuals within the population. There have been many hypotheses for the evolution of monogamy (review by Klug, 2018). Significant ongoing questions related to the evolution of monogamy are how behavioral and/or physiological traits that characterize individuals in monogamous species evolve, and whether the mating system influences the evolution of these traits (Klug, 2018).

One of the most important models for the study of multiple traits in monogamous mammals is the California mouse (*Peromyscus californicus*). This species has been used as a model for understanding the ecology of monogamy such as territory and space use (e.g., Ribble and Salvioni, 1990; Ribble, 1991) and habitat selection (e.g., Kalcounis-Rueppell and Millar, 2002; Reid et al., 2013). Research has extended to studies of the behaviors associated with monogamy (e.g., Ribble, 1991; Gubernick and Nordby, 1993; Becker et al., 2012; Gleason et al., 2012; Pultorak et al., 2017, 2018) and associated paternal care (e.g., Gubernick and Teferi, 2000; Kingsbury et al., 2012; Jašarević et al., 2013; Bales and Saltzman, 2016; Stockley and Hobson, 2016; West and Capellini, 2016). Finally, the monogamous behavior of California mice has been explored from the perspective of the physiology, including endocrinology, and neurobiology of monogamy (e.g., Gubernick and Nelson, 1989; Insel et al., 1991; Bester-Meredith et al., 1999; Glasper and DeVries, 2005; Oyegbile and Marler, 2005, 2006; Fuxjager et al., 2010; Gleason and Marler, 2010, 2012; Pultorak et al., 2015; Cushing, 2016).

There are many studies searching for correlations between mating systems and multiple and varied traits. One trait that appears relevant to the monogamous mating system of the California mouse that has not been investigated in this context, is its use of acoustic communication. In the California mouse, ultrasonic vocalizations (USVs) are used for both courtship and pair bonding (Pultorak et al., 2015, 2017, 2018), and USVs are related to transient testosterone increases (T pulses) both through rapid mechanisms (Pultorak et al., 2015) and long-term effects (Timonin et al., 2018). In the presence of an unknown female, a single T pulse increases the proportion of sweeps (defined below; reviewed in Kalcounis-Rueppell et al., 2018a) produced by unpaired males and decreases the proportion of sweeps produced by pair-bonded males (Pultorak et al., 2015). Thus, the behavioral trait of USV production is correlated with both hormonal and mating status of the male producing the USVs, and USV production provides a potential mechanism for pair bond maintenance. The role of pair bond maintenance may be facilitated by the potential for individual recognition of sustained vocalization (SV) calls (defined below; reviewed in Kalcounis-Rueppell et al., 2018a). There is also evidence that females may prefer longer SVs (Pultorak et al., 2017) because shorter SVs are associated with physical aggression (Pultorak et al., 2018; Rieger and Marler, 2018).

USVs in California mice may therefore represent a trait associated with monogamous mating and offer a model for testing the influence of the trait on the mating system and

the selective pressures of the mating system on the trait. The North American genus *Peromyscus* contains over 50 nominal mouse species (Bedford and Hoekstra, 2015) with considerable variation in mating systems and all species tested produce USVs. There are three main types of USVs; sweeps, sustained vocalizations (SVs), and barks also known as “squeaks” (reviewed in Kalcounis-Rueppell et al., 2018a,b). Simple sweeps are one-syllable, typically downward frequency-modulated, short calls with a peak frequency of 40 kHz. Complex sweeps are also frequency-modulated with multiple peaks but exhibit a higher peak frequency, a longer duration, and typically contain multiple inflection points. In *Peromyscus*, as well as in *Rattus* and *Mus*, sweeps are used during courtship interactions (Chabout et al., 2015; Musolf et al., 2015; Neunuebel et al., 2015; Pultorak et al., 2015; Kalcounis-Rueppell et al., 2018a). In *Peromyscus*, as well as in *Rattus* and *Mus*, barks are used during agonistic situations (Grimsley et al., 2013; Hurley and Kalcounis-Rueppell, 2018; Kalcounis-Rueppell et al., 2018a) and were specifically identified as defensive aggressive behaviors in *P. californicus* by Rieger and Marler (2018). SVs are relatively long in duration and relatively flat with little frequency modulation, have a peak frequency of ~20 kHz, and often occur in bouts that vary in the number of calls (1SV, 2SV, SSV, etc.; Kalcounis-Rueppell et al., 2018a) in a given bout (Briggs and Kalcounis-Rueppell, 2011; Pultorak et al., 2017, 2018). Barks start and end in the audible range (~12 kHz) with a peak around 20 kHz, and are broadband, noisy calls. In *Peromyscus*, SVs have been implicated in both long range (on the order of meters; Briggs and Kalcounis-Rueppell, 2011; Petric and Kalcounis-Rueppell, 2013; Timonin et al., 2018) and short range (order of centimeters) communication (Pultorak et al., 2015, 2017, 2018; Rieger and Marler, 2018). In two species that regularly use SVs in variable behavioral contexts in the field and differ in mating system (the monogamous California mouse and the polygynous brush mouse, *P. boylii*), an argument has been made that SVs are general contact calls aimed at conspecifics (Briggs and Kalcounis-Rueppell, 2011, reviewed in Petric and Kalcounis-Rueppell, 2013; Kalcounis-Rueppell et al., 2018a). Rodents other than *Peromyscus* also produce USVs (see Brudzynski, 2018; Dent et al., 2018). It is interesting to note that rats (*Rattus norvegicus*) produce long low-modulation USVs between 18 and 24 kHz that are typically used in aversive situations considered to represent negative affect, but that can also be produced by males as appetitive contact calls after copulation (review by Wöhr, 2018), suggesting a diversity of functions for SV-type calls.

The diversity of mating systems within the genus *Peromyscus* allows us to examine how traits define mating systems and whether mating systems appear to have driven the evolution of traits. As described above, there is evidence that links USV traits with monogamy [e.g., T and mate status; (Pultorak et al., 2015)]. There is also evidence that links USV traits in non-monogamous systems, such as female-female interactions (Petric and Kalcounis-Rueppell, 2013). In the case of USVs, there may be general signals that are co-opted for different uses under different contexts that manifest as part of a species mating system. For example, in a monogamous species such as *P. californicus*, SVs may function for pair bond maintenance (Briggs and

Kalcounis-Rueppell, 2011; Pultorak et al., 2017, 2018) whereas in a non-monogamous species SVs might facilitate communication between territorial neighbors (Petric and Kalcounis-Rueppell, 2013). Barks, on the other hand, may be general agonistic signals in multiple contexts and evidence suggests that these are universal signals in muroid rodents that signal aggression [reviewed across rodents in Hurley and Kalcounis-Rueppell, 2018; specifically, as defensive aggression in *P. californicus* Rieger and Marler (2018)]. If USV traits have evolved with the mating system, we would expect that particular USV parameters would correlate with mating system. On the other hand, if USV signals are general signals that are coopted for different uses under different contexts associated with mating system, we would expect that USV parameters would not correlate with mating system. We can test this hypothesis using recordings of USVs from multiple species of *Peromyscus* and published data on mating systems from those same species of *Peromyscus*. *Peromyscus* is an ideal genus for this hypothesis because it is one of the only rodent lineages for which we have information on mating system and USVs across multiple species.

The objective of our study was to examine whether spectral and temporal characters of SVs and barks (two common USV types; reviewed in Kalcounis-Rueppell et al., 2018a) produced by *Peromyscus* mice could be predicted by mating system. We also examined whether USV traits were correlated with other aspects of social behavior, reproductive physiology, and ecology. We took advantage of existing characterizations of mating system and personality measures published from mice in the genus *Peromyscus* (summarized in Wey et al., 2017). Our main reason for examining the influence of mating system on USVs is because of the growing body of literature that the monogamous California mouse (*P. californicus*) uses USVs, in particular sweeps and SVs, to facilitate pair bond formation (reviewed in Pultorak et al., 2015, 2017, 2018; Kalcounis-Rueppell et al., 2018a). This suggests that, at least in monogamous *Peromyscus*, USVs function in pair bonding and it remains to be tested whether these USVs have similar functions in other species of monogamous *Peromyscus*. Our reasoning for examining personality was that we might observe differences in the expression of USVs based on boldness and the potential for encountering individuals in nature. For example, there could be a species whose individuals, on average, are bolder than individuals of another species (independent of mating system or level of sociality). For physiological measurements, we obtained measurements of T from published literature using two variables, baseline T and social responsiveness of males to females via testes measurements (Marler et al., 2003; Trainor et al., 2006). Both variables are likely to be important in social behavior (review by Marler et al., 2003; Trainor et al., 2006; Gleason et al., 2012). The measurements of social responsiveness are restricted to testes measurements in the current study that reflect the long-term impact of male exposure to females but that could be related to different reproductive strategies. If USVs mediate reproduction and territoriality, then we expect selection on USVs in relation to baseline T and social responsiveness. Data on ecology were characterized by whether the species was primarily found in tropical or subtropical

latitudes or in biomes characterized by hot dry seasons (e.g., xeric). Our reasoning was that in xeric habitat there would be less attenuation of signals due to relative low humidity and vegetation, whereas, in mesic habitats signals would attenuate with increased vegetation and humidity. In general, we did not have specific predictions about how each predictor variable would influence the type and spectral/temporal characteristics of USVs. We were instead interested in whether there was evidence of an association among *Peromyscus* USVs and the behavioral, physiological, and ecological data available from the literature.

METHODS

We collected USVs at the *Peromyscus* Genetic Stock Center (PGSC) as described in Kalcounis-Rueppell et al. (2010) for *P. californicus*. During the sampling for Kalcounis-Rueppell et al. (2010) we also recorded USVs from six other species, *P. melanophrys*, *P. aztecus*, *P. eremicus*, *P. maniculatus bairdii*, *P. polionotus*, and *P. leucopus*.

For our dependent variables, we were interested in the USV production and spectral and temporal characteristics of vocalizations. Our independent variables were behavioral, physiological, and ecological characteristics from each species. The seven species of *Peromyscus* are not phylogenetically independent of one another; therefore, we examined USVs in relation to our behavioral, physiological, and ecological variables while accounting for phylogenetic relationships. The evolutionary relationships of these species are well-resolved, and our tree topology reflects this resolution, with estimated branch lengths, as presented in Bedford and Hoekstra (2015; **Figure 1**). We used this topology to test for phylogenetic signal and if we did not have data for a particular species, such as no baseline T (as was the case for *P. melanophrys*), that branch was pruned from the tree for the phylogenetic signal analysis. For all USV characteristics, we tested for phylogenetic signal using Blomberg's K and Pagel's λ (Pagel, 1999; Blomberg et al., 2003).

We recorded USVs at the *Peromyscus* Genetic Stock Center from racks of stock species with a directional microphone (described below) facing the rack of the particular stock. We did not otherwise disturb the cages, beyond limited movement of racks within and between rooms. We recorded USVs opportunistically during a trip to PGSC on March 2nd and 3rd, 2006. As this was opportunistic, we were not able to standardize the length of recording and therefore, we did not calculate rates of USVs and we take averages of all the USVs we were able to record from each species. Our recording schedule was primarily driven by our ability to record from isolated racks as opposed to equalizing sampling. In some cases, racks contained adults only in cages and in other cases racks contained adults and their neonate offspring; however, neonate offspring were not isolated from their parents, therefore, recorded calls were more likely produced by adults (reviewed Kalcounis-Rueppell et al., 2018b). Adults were housed following standard protocols for breeding colonies with some species-specific conditions (e.g., adult male female pair of *P. californicus* were housed together).

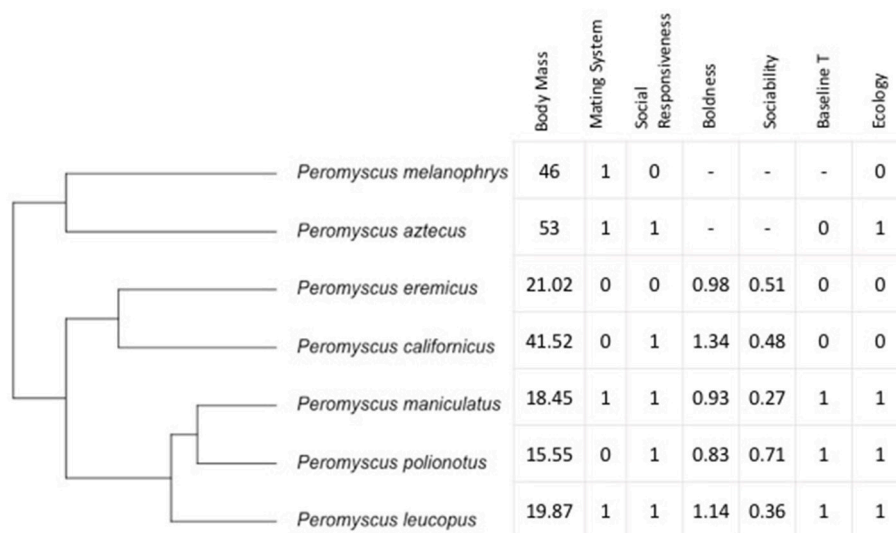


FIGURE 1 | Topology used for phylogenetic analyses (derived from Bedford and Hoekstra, 2015) with predictor variables shown for each species for which there was data available. Body Mass (g); Mating System: 0, predicted monogamous, 1, predicted non-monogamous; Social Responsiveness: 0, testes do not respond to presence of a female, 1, testes do respond to presence of a female; Boldness: unitless measure of latency to exit; Sociability: unitless measure of time spent with same sex stimulus; Baseline T: 0, low, 1, high; Ecology: 0, xeric, 1, mesic. Refer to text for sources of data.

USVs from *Peromyscus* were recorded using a remote bat detector and digital recorder. We recorded with Pettersson D240x ultrasound detectors capable of recording broadband (10–120 kHz) ultrasound (Pettersson Elektronik AB, Uppsala, Sweden). The detector sampled at 307 kHz with 8 bit resolution and was set to continuously record a 1.7 s loop of sound coming through the microphone. Upon detecting any sound in the range of 10–120 kHz the system was triggered and the previous 1.7 s of the sound were slowed down, with time expanded by a factor of ten, and recorded by iRiver digital recorders (iRiver ifp, Reigncom Ltd. Korea) or directly to a laptop. Digital files were downloaded to a computer, converted and saved as WAV files. Spectrograms of all sound files were played back and visually examined (SonoBat, DNDesign, Arcata, CA) to confirm the file contained *Peromyscus* USV. We extracted time, amplitude, and frequency characteristics from all spectrograms that contained USVs. The spectrogram rendered by SonoBat used 1,024-point fast Fourier transforms, 192 point windows, and varied window overlap to render the spectrogram with resolution greater than the screen pixel resolution. Our recording system had a frequency response up to 12 kHz and captured ultrasound up to 120 kHz (with the time expansion factor of 10). Maximum frequency resolution of the spectrographic analysis was 154 kHz.

We examined all of the recorded calls. From each unique bout of calls (a series of sounds made from one individual), we analyzed all calls (for a definition of terms see Kalcounis-Rueppell et al., 2018a). For each call analyzed, we manually placed cursors at the start, end, and at the highest and lowest frequency in the call (four cursors total) in SonoBat to determine duration, bandwidth, starting frequency, ending frequency. SonoBat also extracted the frequency at maximum amplitude (frequency at the loudest part of the call). For each species we calculated

the average frequency at maximum amplitude (kHz; hereafter frequency) and the duration of two call types, SVs and barks. We further calculated average frequency and duration of only the first SV call in a bout (1SV) and the first call in any bark bout, including bouts with only one call. In addition to calculating the average across all first calls of barks and SVs, we also calculated averages of all bark calls and all SV calls recorded from each species, regardless of where it occurred in a bout. Thus, from our recordings we calculated the following averages for each species: SVDur (duration of 1SV call), SVFmax (frequency at maximum amplitude of 1SV call), barkDur (duration of first call in a bark bout), barkFmax (frequency at maximum amplitude of first call in a bark bout), ALLSVDur (duration of all calls in SV bouts), ALLSVFmax (frequency at maximum amplitude of all calls in SV bouts), ALLbarkdur (duration of all calls in bark bouts), and ALLbarkFmax (frequency at maximum amplitude of all calls in barkbouts). We also calculated the percentage of all recorded bouts that were of the bark type.

To examine whether social behavior, physiology, and ecology could predict USVs characteristics, we examined available data from the literature as independent variables that characterized each species with determinations as in **Figure 1**. Note that many measures were obtained from animals housed and bred at PGSC. Specifically, we characterized social behavior based on descriptions of mating system, and measures of social responsiveness, sociality, and boldness. The mating system of these species is described in other comparative studies (Trainor et al., 2006; Wey et al., 2017). Briefly, of the seven species we examined, there is evidence or a prediction of monogamy for *P. californicus* (Ribble, 1991), *P. eremicus* (Eisenberg, 1963; Glasper and DeVries, 2005), and *P. polionotus* (Foltz, 1981). All other species were labeled as not monogamous based on lack of

evidence for monogamy, or evidence/prediction of promiscuity or polygyny (e.g., Millar and Xia, 1991; Ribble and Millar, 1996). Measures of social responsiveness were from Trainor et al. (2006) who determined whether males of each species would respond to the presence of a female with changes in reproductive tissue weights and plasma testosterone (T) levels. Specifically, Trainor et al. (2006) determined changes in testes mass (a T sensitive tissue) when housed with an opposite sex conspecific (Trainor et al., 2006). Measures of boldness and sociability were determined from Wey et al. (2017) and include latency to emerge and time spent with a conspecific, same sex stimulus mouse. Notably, measures from Trainor et al. (2006) and Wey et al. (2017) were conducted on mice from the same stocks used in our current study for measuring USVs at the PGSC. We obtained baseline T (no staged social interactions with unfamiliar animals) from Marler et al. (2003). Samples for the baseline T levels were originally obtained from animals from PGSC and Marler laboratory colonies using previously established methods (Trainor and Marler, 2001). *P. aztecus*, *P. californicus* and *P. leucopus* had T levels similar to those found in previous studies (e.g., Klein and Nelson, 1997; Demas and Nelson, 1998; Bester-Meredith and Marler, 2003). Data on ecology were generally characterized as in Trainor et al. (2006) based on whether the distribution of the species was primarily in tropical or subtropical latitudes or in biomes that were characterized by hot dry seasons (e.g., xeric). For a map of the distributions of all seven species see Bedford and Hoekstra (2015). We altered the characterization from Trainor et al. (2006) into a binary categorization by considering the “intermediate” type as mesic such that only “xeric” and “mesic” habitats were used.

We were also interested in whether body size could explain USV characteristics. We therefore used male body mass data as presented in Trainor et al. (2006; **Table 1** averaged between “single” and “pair”) and Wey et al. (2017; as presented) as an independent variable. Male body mass was available for all seven species whereas female body mass was only available for five species. For consistency, we used male body mass as the proxy for species body mass. Our results did not change if we used the average between male and female body mass (instead of only male body mass) for the five species where these data were available.

We used R (R Core Team, 2017) with the packages APE (Paradis et al., 2004) and phytools (Revell, 2012) for all of our phylogenetic analyses. We used JMP 13.1.0 (SAS Institute Inc., Cary, NC) for all other analyses. Our calculations of mean values to assign to each species were performed within Microsoft Excel. We used linear models for our continuous predictor variables (boldness, sociability) and non-parametric Wilcoxon signed-rank tests for our categorical, binary variables (mating system, social responsiveness, baseline T, and ecology). Our rejection criterion was set at $p < 0.05$.

RESULTS

We recorded 1,882 calls of vocalizations from the seven *Peromyscus* species of interest. Calls were not recorded evenly among species. The majority of calls were from *P. melanophrys*

TABLE 1 | Mean (\pm) SD values for USV calls recorded from seven species at the Peromyscus Genetic Stock Center in 2006.

Species	USV type	# of Calls	Mean Fmax	SD Fmax	Mean dur	SD dur
A						
<i>P. melanophrys</i>	1SV	36	20.30	5.98	104.09	102.93
	1st Bark Call	68	16.61	1.98	50.02	76.96
<i>P. aztecus</i>	1SV	25	16.94	2.06	104.51	94.95
	1st Bark Call	18	14.64	2.49	33.78	23.93
<i>P. eremicus</i>	1SV	67	19.70	5.90	60.75	62.56
	1st Bark Call	74	16.25	3.70	18.33	20.73
<i>P. californicus</i>	1SV	40	17.78	1.98	203.80	117.74
	1st Bark Call	4	18.86	2.47	25.22	18.42
<i>P. maniculatus</i>	1SV	21	19.48	4.93	94.32	87.96
	1st Bark Call	22	16.42	1.37	46.81	28.59
<i>P. polionotus</i>	1SV	4	16.38	1.27	52.42	7.55
	1st Bark Call	1	16.82	n/a	14.54	n/a
<i>P. leucopus</i>	1SV	8	19.83	4.14	64.81	16.48
	1st Bark Call	1	13.37	n/a	55.29	n/a
B						
<i>P. melanophrys</i>	All SV calls	557	27.52	13.58	81.22	58.12
	All Bark calls	191	16.51	2.49	42.81	53.62
<i>P. aztecus</i>	All SV calls	126	18.97	5.09	125.73	98.71
	All Bark calls	60	14.93	1.99	56.73	35.69
<i>P. eremicus</i>	All SV calls	302	25.47	10.39	75.63	70.41
	All Bark calls	133	16.38	3.66	17.57	19.18
<i>P. californicus</i>	All SV calls	368	18.60	2.85	208.94	84.33
	All Bark calls	4	18.86	2.47	25.22	18.42
<i>P. maniculatus</i>	All SV calls	65	21.35	4.35	111.52	70.85
	All Bark calls	32	16.76	2.14	44.37	25.77
<i>P. polionotus</i>	All SV calls	8	17.35	3.17	50.52	13.46
	All Bark calls	10	16.08	1.39	39.74	19.13
<i>P. leucopus</i>	All SV calls	10	18.89	4.24	64.34	17.17
	All Bark calls	3	17.82	4.14	51.25	9.79

Unit for frequency at maximum amplitude (Fmax) is kHz. Unit for duration is milliseconds (ms). (A) The first call and only call of 1SV type USVs and the first call of bark type USV bouts. (B) All calls of the SV type USVs and all calls of bark type USVs.

($N = 748$), *P. californicus* ($N = 385$), and *P. eremicus* ($N = 435$), a moderate number of sequences of vocalizations were recorded from *P. aztecus* ($N = 186$) and *P. maniculatus* ($N = 97$), and only a few calls were recorded from *P. leucopus* ($N = 13$) and *P. polionotus* ($N = 18$). We could not assign calling rates to species because we were recording (1) from racks of different numbers of mice per species, (2) for different time periods based on opportunity, and (3) using a ten times expansion recording system that recorded for 1.7 s on a loop and played back for 17 s once a call was recorded. Of the 1,882 calls, 188 were from bark bouts and 201 were from 1SV bouts. Thus, our sample size for first call of bark bouts was 188 and our sample size of 1SV calls was 201. The sample size for individual SVs from all SV bouts (such as 1SV, 2SV, 3SV, etc.) from the seven species was 1,436. Our sample size for all individual barks from all bark bouts, was 433. There were additionally 13 frequency modulated (FM)

calls recorded from *P. californicus* that were not included in this analysis because we did not record them from all species, and these very quiet calls are difficult to record without placing the microphone inside the cage (e.g., Pultorak et al., 2015). These are also calls that occur between members of a pair at close proximity (Pultorak et al., 2018) and were more likely produced because *P. californicus* were housed as pairs. These calls are also produced by other species (reviewed in Kalcounis-Rueppell et al., 2018a) and may occur during courtship (Pultorak et al., 2015). The mean and standard deviation values with sample sizes for all species are presented in **Table 1**. There was a correlation between the duration of 1SVs and the duration of all SV calls ($r = 0.96$, $P < 0.001$) and therefore we only included duration of 1SVs in further analyses.

There was no significant phylogenetic signal in any of our USV characteristics using either Blomberg's K (all values of $P > 0.08$; **Table 2**) or Pagel's λ (all values of $P > 0.09$; **Table 2**), therefore, for all predictive analyses we did not use phylogenetic corrections or approaches. There was also no effect of body mass on any of the USV characteristics (all values of $P > 0.05$) and this result was the same whether considering only male body mass or both male and female body mass.

Mating system was a predictor of bark USV duration (Chi Square = 4.5, $df = 1$, $P = 0.03$; see below), however, it was not the strongest predictor of USV characteristics. The strongest predictor of USV characteristics was species boldness [$F_{(1,3)} = 53.54$, $P = 0.005$]. When considering all barks recorded, species that tend to be bolder produced barks at higher mean fundamental frequencies (frequency at maximum amplitude) than species with low levels of boldness [$F_{(1,3)} = 53.54$, $P = 0.005$; **Table 3**, **Figure 2A**]. In addition, species with high levels of

boldness produced proportionally fewer barks compared to species with low levels of boldness [$F_{(1,3)} = 36.68$, $P = 0.009$; **Table 3**], when considering all barks recorded (**Figure 2B**). Thus, bold species produced fewer barks in proportion to SVs, but produced barks at higher frequencies than species that are less bold. Species predicted to be monogamous produced bark calls that were shorter in duration than species that were not predicted to be monogamous and this was true for both the first call in a bark bout and all individual barks (Chi Square = 4.5, $df = 1$, $P = 0.03$ for both variables; **Figure 3**). There was no effect of measures of sociality, social responsiveness, baseline T, or ecology on USV characteristics (**Table 3**). In addition, none of the variables predicted SV characteristics (**Table 3**).

DISCUSSION

Our analysis was a broad phylogenetic approach to examining whether monogamy was important for shaping the spectral and temporal characteristics of USVs across species of *Peromyscus* mice. Such a phylogenetic approach across species of *Peromyscus* has been successful for identifying other traits such as paternal investment as a predictor of monogamy (Jašarević et al., 2013; Wey et al., 2017), but this is the first study examining USVs. As we only calculated a single value for each species, we may not have captured within species variation. It would be very interesting to examine our predictor and response variables within specific *Peromyscus* species. Regardless, our study serves as a starting point to ask questions about the evolution of ultrasonic vocalizations across rodent species, and the selective pressures that maintain them.

TABLE 2 | Tests for phylogenetic signals in USV characters using both Blomberg's K and Pagel's λ .

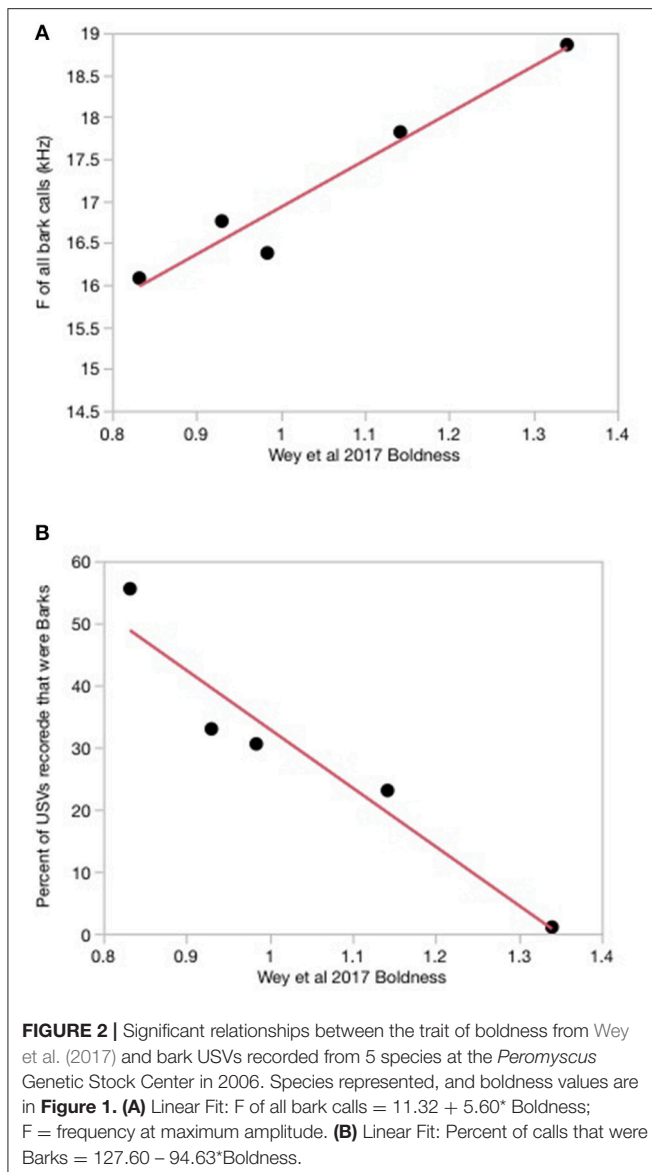
	1SV duration	1SV Fmax	1st Bark duration	1st Bark Fmax	All SV duration	All SV Fmax	All Bark duration	All Bark Fmax	Proportion barks
Blomberg's K	0.78	0.54	0.55	0.70	0.75	0.86	1.16	0.85	0.68
p-value	0.46	0.88	0.86	0.60	0.52	0.25	0.08	0.35	0.70
Pagel's λ	5.37e-05	5.37e-05	5.37e-05	5.37e-05	5.37e-05	5.37e-05	1.35	5.37e-05	5.37e-05
p-value	1	1	1	1	1	1	0.12	1	1

Test statistics and p-values for all characteristics are shown and none had a significant phylogenetic signal.

TABLE 3 | Test statistics and p-values for all comparisons of predictors and USV characteristics.

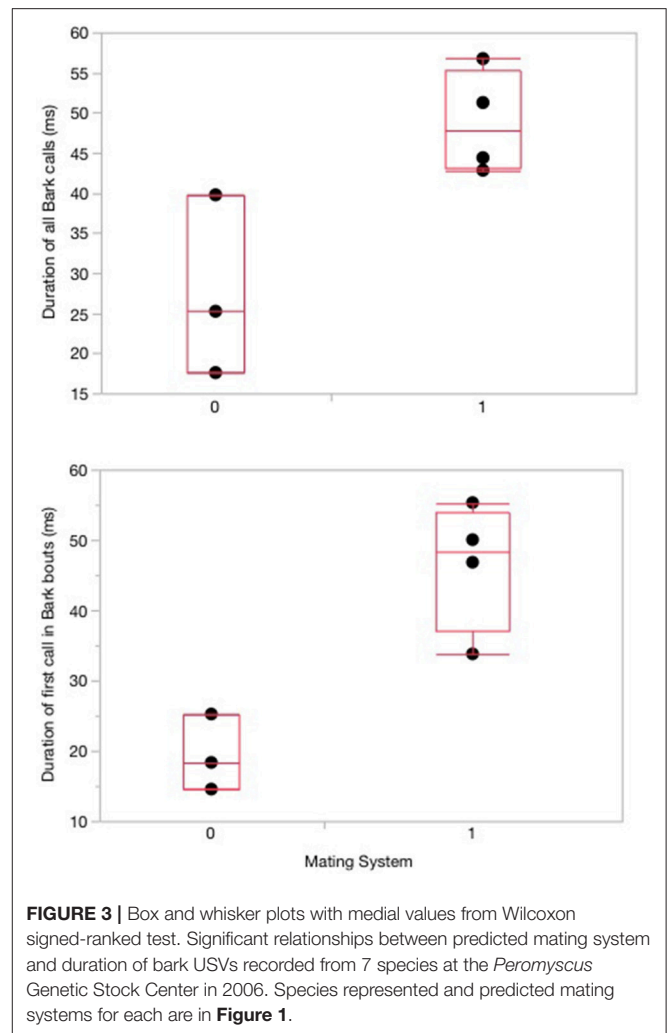
	1SV duration	1SV Fmax	1st Bark duration	1st Bark Fmax	All SV duration	All SV Fmax	All Bark duration	All Bark Fmax	Proportion barks
Social Responsiveness	0.15, .70	2.40, 0.12	0.00, 1.00	0.00, 1.00	0.15, 0.70	3.75, 0.05	1.35, 0.25	0.15, 0.70	0.15, 0.70
Baseline T	1.19, .23	0.05, 0.83	0.43, 0.51	0.05, 0.83	2.33, 0.13	0.43, 0.51	0.43, 0.51	0.05, 0.83	1.19, 0.28
Ecology	0.50, .48	1.13, 0.29	0.13, 0.72	1.13, 0.29	0.50, 0.48	1.13, 0.29	3.13, 0.08	0.50, 0.48	2.00, 0.16
Mating System	0.50, .48	1.13, 0.29	4.50, 0.03	2.00, 0.16	0.13, 0.72	1.13, 0.29	4.50, 0.03	0.00, 1.00	0.00, 1.00
Sociability	0.09, .79	5.51, 0.10	8.65, 0.06	0.41, 0.57	0.18, 0.70	0.23, 0.67	0.44, 0.55	0.42, 0.56	0.82, 0.43
Boldness	5.66, .10	0.07, 0.81	0.15, 0.73	0.16, 0.72	4.49, 0.12	0.09, 0.78	0.14, 0.73	53.54, 0.005	36.68, 0.009

For Social Responsiveness, Baseline T, Ecology, and Mating system, the test was a non-parametric Wilcoxon rank sum test with a ChiSquare test statistic and a df of 1. For Sociability and Boldness, the test was a bivariate linear fit with the F Ratio as a test statistic and a df of 1 (model) and 3 (error). In each cell, the test statistic precedes the p-value. The significant tests are in bold.



In spite of our broad approach, we found a very compelling result suggesting that personality is more important in defining USV types and parameters than other physiological, behavioral, and ecological species level traits. Specifically, boldness has an impact on the spectral frequency and number of barks produced. Species that are bold produce fewer barks at a higher mean fundamental frequency. Barks are agonistic calls within rodents. Thus, bold species produce agonistic calls at higher frequencies, but produce these calls less often, at least under the conditions under which these calls were collected.

This finding initially is counter intuitive as bold species are typically expected to produce agonistic calls more often. However, our results suggest that at least within *Peromyscus* mice, the bold species infrequently relies on defensive agonistic calls, and when they do, the effective distance of the calls is lower because higher frequencies attenuate more quickly. The



simplest explanation for our result is that bold species are more likely to encounter con- and/or hetero-specifics than non-bold species, and when in close proximity, the calls are not generally broadcasted but instead directed at local individuals. This is a testable hypothesis. Another way of explaining this result is that barks may serve different antagonistic functions depending on the species that is producing them. Bold species may produce high frequency barks because they are more effective for short distance and more directed communications. High frequency barks of bold species would be directed toward a specific individual or group and more likely to occur if individuals are closer together. On the other hand, non-bold species may produce lower frequency barks that travel further and are broadcast as very general signals, that may help with avoidance of close encounters. This also explains the result we observed showing that bold species produce proportionally fewer barks than non-bold species because in this scenario bold species would only produce barks during close encounters, whereas non-bold species would produce barks regularly as advertisement with the function of decreasing interactions. Lastly, if barks represent defensive aggression as suggested by Rieger and Marler (2018),

then one could speculate that more bold species would display less appeasement behavior, hence the reduction in number of barks.

We can again only speculate, but it is interesting that in one of the species that is characterized as non-monogamous and bold there appears to be significant variation in how bold individuals are, as defined by how frequently they scent marked an open arena (Fuxjager et al., 2010). Males that were “bolder” and scent marked more were more likely to win a male-male encounter in resource supplemented environments. *Peromyscus leucopus* expresses significant variation in territorial tendencies in both the laboratory and field (Wolff, 1985; Oyegbile and Marler, 2006). The bolder individuals may be more likely to adopt territorial behavior in which individuals maintain exclusive territories. If the goal is not to establish a dominant-subordinate interaction but rather maintain exclusion, then a call that moderates aggression would be less likely to be used. It might however be a very useful call for moderating aggression between members of a pair bond.

Our results might suggest that agonistic acoustic signaling is used more frequently as a communication modality for less-bold species, however this would need to be tested. This hypothesis could be tested both inter- and intra-specifically. For example, rodent species that are bold would be predicted to use barks less in a natural or experimental context than other species that are not as bold. Similarly, within species, those individuals that were bold should not use as many barks as those individuals that are not bold.

While boldness was most closely associated with the number of barks produced, it is intriguing to note that the duration of barks was of shorter duration in monogamous species. Signal duration increases the effective distance of this signal, and our results suggest that monogamous species use barks with a lower effective distance. The most parsimonious explanation for this result is that for our monogamous species, the barks we recorded were between pairs that were housed together (e.g., they were close together) whereas the barks that we recorded from non-monogamous species were from mice between cages (e.g., they were farther apart) or mice that were not pair-bonded. It is interesting that pair-bonded mice would produce barks with one another but there are behavioral contexts for barks within pairs that are regularly recorded in the wild (Kalcounis-Rueppell, unpublished data). Moreover, while barks decrease over time between an introduced male and female *P. californicus* as they bond, intersexual barks do occur (Pultorak et al., 2018). Thus, this result suggests that barks are shorter between mates. This hypothesis could be tested intraspecifically because we predict that barks produced in the presence of a mate (for example near or in a nest site) would be shorter than barks produced alone or in the presence of a non-mate (for example at a territorial boundary). We will be able to test this hypothesis with our ongoing field study.

The two variables that related to T were not associated with mating systems. The first is baseline levels of T. Male California mice have surprisingly low levels of baseline T that originally seemed consistent with a framework proposed by Wingfield et al. (1990) suggesting that low baseline levels of testosterone occur

because of less male-male-competition (see also Hau, 2007). A previous, non-phylogenetic comparison was made between baseline levels of a smaller subset of monogamous and non-monogamous *Peromyscus* species (Marler et al., 2003) that did not reveal a pattern related to mating system (Marler et al., 2003). A later comparison was made to investigate whether social stimulation or day length activates testes growth (Trainor et al., 2006) among monogamous and non-monogamous *Peromyscus*. We used plasticity in size of testes (a testosterone sensitive tissue) as a proxy for T level changes in response to social conditions that could be related to monogamous vs. polygynous mating systems. Testosterone responsiveness to social stimuli as measured in the plasma (review by Gleason et al., 2012) was not tested in the current phylogenetic analysis. Overall there was no evidence that testosterone levels were related to mating systems either in the form of baseline or socially responsive levels.

Whether considering boldness or mating system as a predictor of the USV trait, it is interesting that effects were only seen in bark calls as opposed to SV calls. *Peromyscus* produce three main calls types, SVs, barks, and sweeps (Kalcounis-Rueppell et al., 2018a). As in other species of mice, including lab mice, barks are normally associated with distress or agonistic interactions (Grimsley et al., 2013; Kalcounis-Rueppell et al., 2018a). In contrast, although there is much to learn about SV calls, they are much more likely to be used as non-aggressive contact calls, especially those with a small number of calls in a bout (e.g., 1SV, 2SV, 3SV; Kalcounis-Rueppell et al., 2018a). Our results suggest that it is the agonistic or distress calls that have more selective pressure to be species specific; in other words, selection might be stronger on the agonistic components of calling as opposed to the affiliative. We cannot draw any conclusions here about sweep calls because they were not recorded as part of this study, likely because sweeps were present but high frequency calls attenuate quickly. Overall, sweeps are difficult to detect unless the microphone is very close to the mouse producing the call (Kalcounis-Rueppell et al., 2018a). We also may have obtained different results if we had considered bouts instead of calls. In our analysis we combined all SV call types independent of whether they were part of a 2SV, 3SV, 4SV etc. Species specific responses may have been found had we examined our USVs in this way, however this was not feasible because we would not have had a balanced data set across species for all the SV types due to sample size. This is something to consider because selection may not be acting on the SV call itself but instead on the way the SV is arranged in bouts.

Our recording paradigm was one of complete eavesdropping. We did not measure age, sex, reproductive condition and we did not stage agonistic or affiliative contexts for any of the mice we were recording. Thus, there was no experimental reason for the mice to be agonistic or affiliative in their cages. Any effects that we observed in barks in this study would likely be enhanced if we had experimentally examined aggression. Similarly, any effects that we observed are most likely muted because we know there is less variation in the spectral and temporal characteristics of USVs recorded in the lab when compared to those in nature (Kalcounis-Rueppell et al., 2010). In addition, we only examined five to seven out of over 50 species of *Peromyscus* and it could be

that our results are unique to this set of species we analyzed. For these reasons, future studies could examine barks in the context of personality in the field under naturally aggressive contexts and include more species of *Peromyscus*. Another advantage to including more species, would be that the binary scales used herein could be more refined (e.g., distinguishing between obligate and facultative mating patterns and specific ecological associations).

In conclusion, our results suggest that boldness of a species has a higher selection on USVs than the species mating system. Moreover, the effects of boldness and mating system are seen only in defensive barks, as opposed to SV call types. It appears that USVs in rodents evolved as general signals that have been co-opted for particular functions within the mating system context that differs across species.

ETHICS STATEMENT

Animals in the *Peromyscus* Genetic Stock Center are housed and bred under an approved institutional animal care protocol of the University of South Carolina. The *Peromyscus* Genetic Stock Center is a facility accredited by the Association for the Assessment and Accreditation of Laboratory Animal Care, International, and in accordance with the Guide for the Care and

Use of Laboratory Animals. For our recordings we did not handle animals nor cause any disturbance beyond what they would normally experience under the approved animal care protocol (USC Animal Use Protocol # 1321) that covers their welfare.

AUTHOR CONTRIBUTIONS

MK-R conceived of the study through discussions with CM and RP. MK-R collected the USV data at the *Peromyscus* Genetic Stock Center, performed all statistical analyses presented in the study, and wrote the initial draft of the manuscript. RP analyzed all of the *Peromyscus* USV data that were used as the dependent variables in the study and contributed to the writing of the manuscript. CM contributed to the writing of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Genetic Monogamy in Socially Monogamous Mammals Is Primarily Predicted by Multiple Life History Factors: A Meta-Analysis

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Background: We still do not understand the key drivers or prevalence of genetic monogamy in mammals despite the amount of attention that the evolution of mammalian monogamy has received. There have been numerous reviews of the hypotheses proposed to explain monogamy, some of which focused on animals in general, while others focused on particular classes like birds or mammals, or on specific orders within a class. Because monogamy is rare in mammals overall but relatively common in some of the orders in which it has been observed (e.g., Primates, Macroscelidea, and Carnivora), mammals provide a unique taxon in which to study the evolution and maintenance of monogamy. However, the term “monogamy” encompasses related but separate phenomena; i.e., social monogamy (pair-living by opposite-sex conspecifics) and genetic monogamy or reproductive monogamy (mating exclusivity). A recent review of mammalian monogamy reported that 226 species (9%) in 9 orders (35%) were socially monogamous, although socially monogamous mammals are not necessarily genetically monogamous.

Methods: Since factors that predispose socially monogamous mammals to be genetically monogamous are still subject to debate, we conducted meta-analyses using model selection to determine the relative importance of several life history, demographic, and environmental factors in predicting genetic monogamy.

Results: We found sufficient data to include 41 species in our analysis, about 2x more than have been included in previous analyses of mammalian genetic monogamy. We found that living as part of a socially monogamous pair vs. in a group was the best predictor of genetic monogamy, either by itself or in combination with high levels of paternal care. A male-biased sex ratio and low population density were inversely related to the number of pairs that were genetically monogamous, but not to the production of intra-pair young or litters.

Conclusion: Our results agree with the results of some previous analyses but suggest that more than one factor may be important in driving genetic monogamy in mammals.

Keywords: genetic monogamy, social monogamy, extra-pair paternity, mammals, paternal care, social structure

INTRODUCTION

The evolution of monogamy has long drawn attention from many scientists studying animal behavior, partially due to its rarity in some taxa and especially because monogamous behavior by males is puzzling because their reproductive success is typically driven by the number of females with which they are able to reproduce (Trivers, 1972). Although monogamy typically had been considered to encompass living with an opposite-sex conspecific, formation, and maintenance of a pair-bond, mating exclusivity, and biparental care (Kleiman, 1977; Wittenberger and Tilson, 1980; Mock and Fujioka, 1990), we now understand that “monogamous” species are quite variable in their social and reproductive behaviors (Westneat et al., 1990; Gowaty, 1996; Griffith et al., 2002) and that these social and reproductive aspects of monogamy may be under selection from different evolutionary pressures. This has resulted in the use of the terms social monogamy (who is living with whom) and reproductive or genetic monogamy (who is mating with whom; Wickler and Seibt, 1983; Fuentes, 1998, 2002; Reichard, 2003; Tecot et al., 2016). Although much research has been devoted to the evolution of social monogamy, genetic monogamy has received much less attention even though it may be more important from an evolutionary standpoint because it is linked directly to reproduction.

Current evidence suggests that female dispersion is the primary driver of social monogamy in mammals (Dobson et al., 2010; Lukas and Clutton-Brock, 2013). This conclusion is supported by phylogenetic analyses that show many independent transitions to social monogamy in mammals (Komers and Brotherton, 1997; Lukas and Clutton-Brock, 2013). In nearly all of these cases, social monogamy evolved where females lived solitarily in discrete home ranges and selection favored males that shared a home range with only one female (Brotherton et al., 1997; Lukas and Clutton-Brock, 2013). Other hypotheses argue that social monogamy provides protection from conspecific infanticide (Wolff and MacDonald, 2004; Opie et al., 2013), although this does not seem to be supported in mammals other than primates (Lukas and Clutton-Brock, 2013). Other traits associated with social monogamy such as paternal care, pair-bonding, group-living and cooperative breeding likely all evolved after the evolution of social monogamy (Komers and Brotherton, 1997; Lukas and Clutton-Brock, 2012, 2013; Opie et al., 2013). It is unclear, however, if genetic monogamy occurs as a consequence of the life history traits of socially monogamous species or is mainly driven by demographic or environmental factors.

Both males and females face trade-offs between seeking extra-pair mates or remaining genetically monogamous. Males face a trade-off between seeking extra-pair copulations (EPCs) and investing in their direct reproductive success by preventing cuckoldry of their mate, protecting their mate/offspring from predation/infanticide, or providing paternal care (Magrath and Komdeur, 2003; Shuster and Wade, 2003; Westneat and Stewart, 2003). Females might seek EPCs for benefits such as genetic variability in their offspring (Petrie and Kempenaers, 1998), mate confusion to prevent infanticide (Harcourt and Greenberg, 2001;

Wolff and MacDonald, 2004) or seeking a higher quality mate (Kempenaers et al., 1992; Spencer et al., 1998; Griffith et al., 2002), but this may come at the loss of direct parental care or indirect parental care e.g., territory defense from their male social partner (Ihara, 2002; Westneat and Stewart, 2003).

Rationale

These trade-offs may be influenced by life history traits, demographic or environmental factors. Much of the previous research on genetic monogamy has focused on life history hypotheses, i.e., hypotheses that suggest that genetic monogamy is driven by traits such as group living or coloniality (Møller and Birkhead, 1993; Cohas and Allaine, 2009), breeding seasonality and synchrony (Stutchbury and Morton, 1995), or paternal care (Wade and Shuster, 2002; Magrath and Komdeur, 2003; Westneat and Stewart, 2003; Huck et al., 2014). Such evolved characteristics may determine the availability of EPCs and how likely an individual is to seek extra-pair mates. However, genetic monogamy may be driven more by demographic or environmental factors such as population density (Westneat and Sherman, 1997), a strongly male biased adult sex ratio (Fromhage et al., 2005), or environmental variability (Botero and Rubenstein, 2012). Despite previous attention from investigators, we still do not understand the most important drivers of mammalian genetic monogamy.

Objectives

Prior analyses investigating the relative importance of different drivers of genetic monogamy have not reached consistent conclusions for several reasons. One reason is the difference in species included in the analyses. The first comparative studies examined mammals from various mating systems (Clutton-Brock and Isvaran, 2006; Isvaran and Clutton-Brock, 2007), while the more recent studies included only socially monogamous mammals (Cohas and Allaine, 2009; Huck et al., 2014). Even these latter studies defined social monogamy differently. In addition to including species from multiple mating systems vs. only socially monogamous mammals, each of these analyses assessed only a small subset of hypotheses proposed to explain genetic monogamy. In these various studies one or two of the following were found to be good predictors of genetic monogamy: the pattern of association between males and females (intermittent vs. continuous), the number of breeding females per social unit or group, the length of the mating season, social structure (single female, male-female pair, or group), and occurrence of paternal care. Although these studies found different explanations for genetic monogamy, the relative importance of these various hypotheses has not been directly compared. Therefore, our objective was to determine the relative importance of hypotheses proposed to explain genetic monogamy in socially monogamous mammals. We examined all hypotheses for which we could find sufficient data: four life-history, two demographic, and one environmental hypothesis (Table 1).

The life history traits that we examined were paternal care, pair association, social structure, and breeding seasonality. The paternal care hypothesis predicts that care by the male parent,

TABLE 1 | Hypotheses* proposed to explain genetic monogamy in mammals.

Hypothesis	Trait	Categories or metric used
(A) LIFE HISTORY HYPOTHESES		
Higher male investment	Paternal care	4 levels from no care to intense care
Close male-female association	Level of association between male and female	Intermittent or more frequently associated
Pair-living	Social structure	Male-female pair, group, or intrapopulation flexibility between pair and group
Breeding seasonality	Reproductive seasonality	Aseasonal (no), seasonal (breed during 2–6 months/year) or highly seasonal (breed <1 month/year i.e., high synchrony)
(B) DEMOGRAPHIC HYPOTHESES		
Low population density	Population density	# adults or individuals per square km * mean adult mass
Male-biased sex ratio	Sex ratio	# males/# females
(C) ENVIRONMENTAL HYPOTHESIS		
Environmental variability	Climatic variability	Koppen-Geiger's climate classification of study area, ranked from least (tropical) to most variable (polar)

*We were able to find sufficient data in the literature to test these hypotheses using model selection procedures.

in addition to that provided by the mother, is critical for optimal offspring growth and survival. Due to this benefit, males seek paternity assurance to avoid caring for extra-pair offspring and females limit extra-pair matings to secure paternal care, both of which promote genetic monogamy (Birkhead and Møller, 1996; Gowaty, 1996). The pair association hypothesis predicts that the trade-off between mate guarding and pursuing EPCs determine levels of genetic monogamy (Clutton-Brock and Isvaran, 2006). Close association between a male and female makes it easier to guard ones' partner but harder for both individuals to obtain EPCs. The social structure hypothesis predicts that individuals living in groups would not be expected to be as genetically monogamous as those that live in male-female pairs (Møller and Birkhead, 1993) because there are more opportunities for EPCs in groups with multiple adults of one or both sexes. Finally, the breeding seasonality hypothesis makes two contrasting predictions. The first prediction is that when females are receptive at about the same time, males will benefit by seeking as many mating opportunities as possible. Thus, breeding synchrony provides more opportunities for mating and thus increases the opportunity for EPCs by males (Stutchbury and Morton, 1995; Stutchbury, 1998a,b). Consequently, there will also be more males nearby providing opportunities for females to engage in EPCs similar to what is observed in lek mating systems (Wagner, 1992). When reproduction occurs within a limited time, it may be too difficult to guard a mate and attempt to gain EPCs; therefore, those engaging in genetic monogamy may be making the best of the bad situation. But, if mate guarding occurs, then genetic monogamy would be favored; this is referred to as the "asynchrony hypotheses" by Neodorf (2004).

Alternatively, the breeding seasonality hypothesis predicts that a long breeding season would constrain individuals to be genetically monogamous because females would be receptive asynchronously, thus opportunities for EPCs would be limited (Stutchbury and Morton, 1995; Westneat and Sherman, 1997) and competition for these matings would be high.

The demographic and environmental factors that we examined included population density, adult sex ratio, and climatic variability. These demographic and environmental factors could affect the occurrence of genetic monogamy by influencing the costs and benefits to males of pursuing EPCs or the potential costs of EPCs to females (Westneat and Stewart, 2003). For example, population density may be important because low densities would constrain individuals to be genetically monogamous because there would be limited opportunities to mate with other opposite-sex conspecifics, while genetic monogamy would be much less common at high population densities due to numerous opportunities to mate with multiple individuals (Westneat and Sherman, 1997). The adult sex ratio in the population may also influence genetic monogamy because male-biased sex ratios may result in a large number of extra-pair males seeking matings, resulting in increased opportunities for female extra-pair matings and increased costs associated with mate guarding (Fromhage et al., 2005). Alternatively, female-biased sex ratios could provide opportunities for males to mate with multiple females. Finally, climatic variability may be important because environments with low variation might reduce the genetic benefits of EPCs while highly variable climates favor EPCs that would increase genetic diversity in offspring (Botero and Rubenstein, 2012).

METHODS

Search Strategy

To test functional hypotheses proposed to explain genetic monogamy in socially monogamous mammals, we first obtained a comprehensive list of mammals considered to be socially monogamous (229 species) from Lukas and Clutton-Brock (2013). For the purposes of our study, we define socially monogamous mammals as all pair-living mammals as well as group-living mammals that have a dominant breeding pair (*sensu* Cohas and Allaine, 2009; Lukas and Clutton-Brock, 2013). During our literature search and review of previous work on genetic monogamy, we also came across data from nine socially monogamous species not included in Lukas and Clutton-Brock (2013). We included them in our data set, bringing the total number of socially monogamous species to 238.

We then searched the primary literature for genetic parentage data on all these species using the ISI Web of Science database with combinations of the species' common or scientific name, along with the phrases "paternity" or "parentage analysis," similar to Cohas and Allaine (2009). We first searched the species' common/scientific names and if this resulted in 20 or fewer results, we examined the titles of all these publications. In contrast, if there were more than 20 results, we combined additional search terms with the common/scientific names. So,

for each species we performed 2 or 4 different database searches. We only included data from wild populations.

For each species with genetic parentage data, we calculated up to three different indices of genetic monogamy because genetic parentage data is not always presented in the same way in the literature. These three indices were: the proportion of a female's young sired by her social partner (referred to as intra-pair young, hereafter IPY); the proportion of all litters that were sired exclusively by a social pair (referred to as intra-pair litters, hereafter IPL), i.e., all offspring of a particular litter are assigned to one mother and one father (her social partner); and the proportion of pairs that had only within-pair offspring or litters (referred to as genetically monogamous pairs, hereafter GM pairs). Although we used three different indices, it is important to note that these are not three different outcomes but rather different attempts to quantify genetic monogamy. Furthermore, although many papers also included information which allowed us to determine which males were paired with which females, this was not always the case (e.g., Weston Glenn et al., 2009). For papers without this information, we calculated lower-end and upper-end estimates of our three indices of genetic monogamy based on the assumption that at least one of the sires of a litter was the male social partner when multiple-paternity was detected (although we understand it is possible that none of the sires were the male social partner). We then calculated one mean for each species from these lower and upper-end estimates and used these means in our models. We found two published papers with parentage data for three species and used the paper with the largest sample size and/or the paper from which we could calculate the specific index of genetic monogamy for our analyses.

For our list of socially monogamous mammalian species with genetic parentage data, we performed another set of literature searches to find information on variables that would allow us to examine functional hypotheses for genetic monogamy. For each variable of interest, we first searched the paper in which we had found the genetic parentage data for that species and the *Mammalian Species* account for that species when available. If we could not locate the information in these sources, we searched the ISI Web of Science database following procedures similar to those used in our initial literature search. We found enough data to test 7 hypotheses: 4 life history hypotheses, 2 demographic hypotheses, and 1 environmental hypothesis (Table 1; Supplementary Data Sheet 1). The variables we examined based on these hypotheses were: the type/amount of paternal care provided to young, frequency with which the male and female were closely associated, the type of social unit most common in the species, the seasonality of the species' breeding, population density (square root of the density multiplied by average mass of an adult individual), the population sex ratio, and climatic variability (as assessed by the Koppen-Geiger's climate classification, Peel et al., 2007) for the study site.

Data Analysis

In our analyses, we controlled for the phylogenetic relatedness across all of our species to account for the lack of independence among closely-related species (Garland et al., 1999; Freckleton et al., 2002). This type of phylogenetic regression is similar

to analyses in previous comparative studies on genetic monogamy (Isvaran and Clutton-Brock, 2007; Huck et al., 2014). To accomplish this, we used a subset of a Mammalian supertree downloaded from TimeTree (on Dec 14, 2017), a publicly available phylogenetic tree synthesized from published phylogenies (Hedges et al., 2006, 2015; Kumar et al., 2017), that included our species of interest (Supplementary Image 1).

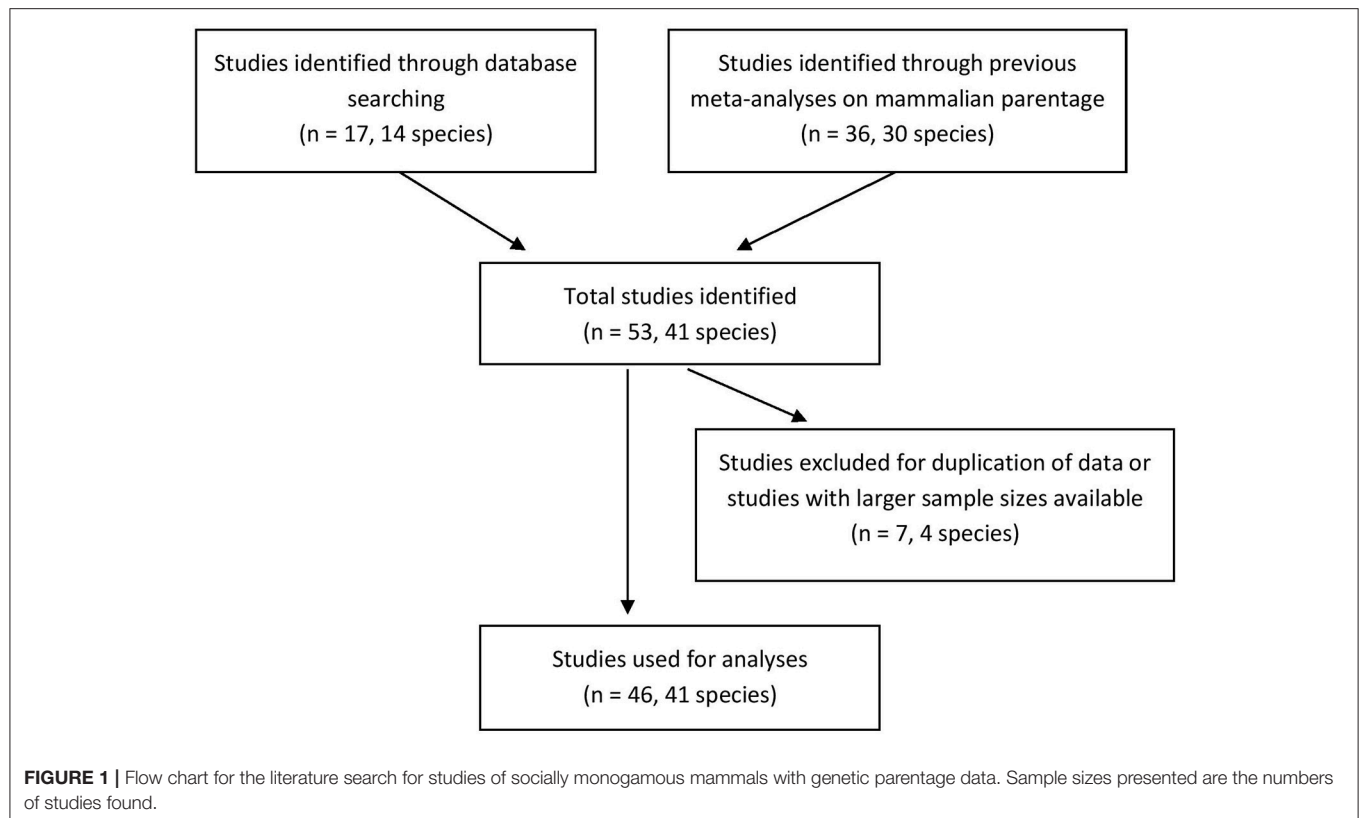
We analyzed our dataset using AICc model selection of phylogenetic least squares regression models that included different combinations of our predictor variables (Martins and Hansen, 1997; Freckleton et al., 2002). We created 12 *a priori* models that consisted of different combinations of the life history, demographic, and environmental hypotheses for which we had data from a sufficient number of species (Table 1), including models based on the results of previous comparative studies on mammalian extra-group paternity (see Supplementary Table 1; Clutton-Brock and Isvaran, 2006; Isvaran and Clutton-Brock, 2007; Cohas and Allaine, 2009; Lukas and Clutton-Brock, 2013). We ran 3 rounds of AICc model selection, one for each dependent variable, with the 12 *a priori* models using the means of IPY, IPL, and GM pairs. All of these variables were proportional data, therefore they were arcsine square-root transformed for the analyses. All presented coefficients are back-transformed. These models included a phylogenetic correction following the Brownian model of character evolution (Garland et al., 1999; Huck et al., 2014) and were weighted using $1 \div \sqrt{n}$ to control for the wide range in sample sizes among studies (Gurevitch and Hedges, 1999; Griffith et al., 2002; Perry et al., 2002; Zaykin, 2011). For each model selection process, models were ranked from lowest- to highest-AICc and the Δ AICc and model Akaike weights were calculated. The weights are the probability that the model is the best model, given the data and other models in the candidate set (Wagenmakers and Farrell, 2004). All analyses were performed in R (R Core Team, 2018) using the *ape* (Paradis et al., 2004) and *nlme* packages (Pinheiro et al., 2018). All of our procedures followed the applicable meta-analysis standards set forward by the PRISMA statement (Moher et al., 2009).

RESULTS

Study Selection and Characteristics

We found genetic data for 41 mammalian species (17% of the socially monogamous mammals on our list) in 53 different studies and used 46 of these studies for our analyses (Figure 1; Supplementary Data Sheet 1). We found the most species for the order Carnivora (14/41 = 34%), Primates (11/41 = 27%), and Rodentia (13/41 = 32%). Four other orders were represented by 1–3 species.

In seven of our 41 species (17%), all pairs were genetically monogamous i.e., had no extra-pair young detected, although the sample size for the Bornean gibbon (*Hylobates muelleri*) was only 5 offspring. The mean \pm SE proportion of IPY was 0.76 ± 0.03 ($N = 39$ species; range 0.17–1.00; median number of offspring/species = 40). The mean \pm SE proportion of IPL was 0.73 ± 0.04 ($N = 28$ species; range: 0.34–1.00; median number of litters/species = 18). The mean \pm SE proportion of GM pairs was



0.70 ± 0.04 ($N = 34$ species; range: 0.40–1.00; median number of pairs/species = 16).

Synthesized Findings

Each model competition procedure resulted in 1 to 3 models that were within 2 ΔAICc of the top model; these are shown in **Table 2** (For all models, see **Supplementary Table 1**). The variable we refer to as social structure of the species was present in 4 of the 6 (66.7%) top models. Species that are group-living had lower levels of IPY, IPL, and GM pairs compared to species in which individuals lived in pairs or displayed intermediate social structure (**Figure 2, Table 3**). The level of paternal care appeared in all 3 of the top models for IPY and IPL, with an increasing level of paternal care always positively associated with more IPY/IPL (**Figure 3, Table 3**). The level of male-female association appeared in 1 of the top models for GM pairs; species where pairs were more closely associated had lower proportions of IPY than species with intermittent levels of association between the male and female. However, this outcome is likely to have been caused by multi-collinearity between pair association and social structure in the model, since this was the only model where pair association had this effect. Sex ratio appeared in two of the top models for GM pairs and population density appeared in one of them. Each of these variables had a negative effect on the measure of genetic monogamy. None of the other variables or combinations of variables appeared in a top model.

TABLE 2 | Top models from AICc model selection of different indices of genetic monogamy (GM).

Response	Model parameters	K	AICc	ΔAICc	AICc wt
IPY	Social structure (–) + Care (+)	5	31.28	0	0.82
IPL	Social structure (–) + Care (+)	5	33.20	0	0.48
	Care (+)	3	34.54	1.34	0.25
GM Pairs	Social structure (–) + M-F Association (–)	5	38.00	0	0.40
	Social structure (–) + Sex ratio (–)	5	39.15	1.15	0.22
	Sex ratio (–) + Density (–)	4	39.52	1.52	0.19

Only models with a $\Delta\text{AICc} < 2$ are shown here. The sign (–/+) indicates the direction of the relationship (further explained in the footnotes).

IPY = proportion of intra-pair young.

IPL = proportion of litters that were exclusively intra-pair.

GM Pairs = proportion of male-female pairs that produced only intra-pair litters.

Social structure = how living in a group vs. a male-female pair or variable social structure affected the measure of GM.

M-F association = how more “closely” associated pairs influenced the measure of GM.

Care = how increasing levels of paternal care influenced GM.

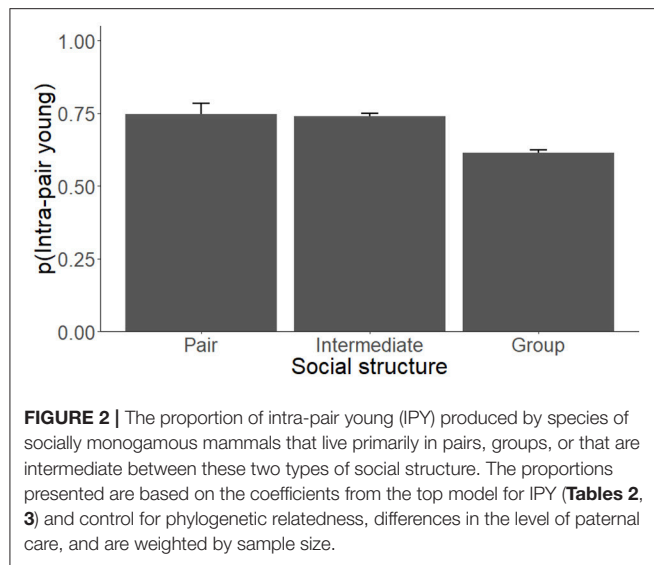
Density = how $p(\text{individuals}/\text{km}^2 \times \text{mass in kg})$ influenced GM.

Sex ratio = how increasing numbers of males:females influenced GM.

DISCUSSION

Summary of Main Findings

Our results show that no one model was consistently the best for all our indices of genetic monogamy. Life history variables, specifically social structure and paternal care, were the only type



of predictor variables for IPY and IPL and the life history variable referred to as social structure was in two of the top models for GM pairs. Demographic variables, specifically sex ratio and population density, only appeared in two of the top models for GM pairs.

The only predictive variable found for all three indices of genetic monogamy was social structure (Table 2), specifically living in a socially monogamous pair or intermediately (i.e., sometimes as a monogamous pair and sometimes in a group) as opposed to living primarily in a group. Individuals that lived as a member of a socially monogamous pair showed higher levels of genetic monogamy compared to individuals found primarily in a group with other sexually mature conspecifics. Living as a member of a pair was an important predictor of genetic monogamy either by itself or in combination with other life history variables such as paternal care, the amount of male-female association or sex ratio. Paternal care was important in explaining IPY and IPL, especially in combination with pair living (Table 2). Sex ratio and population density were the only demographic variables in any top model. They were found in the top models for GM pairs but not in models for any other index of genetic monogamy. No other demographic or environmental variables were in any of our top models. These results suggest that the levels of genetic monogamy across socially monogamous mammals are likely not driven by merely one variable but a combination of variables, and different variables may be more important for different species (see also Klug, 2018).

Our study, including twice as many species as prior studies, is consistent with results from the largest previous comparative study of socially monogamous mammals (Cohas and Allaine, 2009) that showed that group-living species had higher levels of EPY than pair-living species. Although there are numerous possible benefits to group-living, including increased group vigilance resulting in increased protection from predation, foraging benefits, increased production, or survival of offspring due to helping by other group members (Krause and Ruxton,

TABLE 3 | Model coefficients and standard errors from the top phylogenetic regression models explaining three indices of genetic monogamy (GM).

Model	Variable	Estimate	SE
IPY- 1st model	Intercept	0.746	0.038
	Paternal care	0.022	0.003
	Intermediate	−0.006	0.010
	Group	−0.131	0.008
IPL- 1st model	Intercept	0.706	0.033
	Paternal care	0.034	0.006
	Intermediate	−0.003	0.017
	Group	−0.095	0.015
IPL- 2nd model	Intercept	0.584	0.022
	Paternal care	0.051	0.006
GM pairs- 1st model	Intercept	0.975	0.071
	Intermediate	−0.033	0.015
	Group	−0.367	0.023
	Close association	−0.217	0.041
GM pairs- 2nd model	Intercept	1.000	0.051
	Intermediate	−0.021	0.014
	Group	−0.097	0.017
	Sex ratio	−0.090	0.020
GM pairs- 3rd model	Intercept	0.996	0.023
	Sex ratio	−0.206	0.017
	Density	−0.0003	0.0001

The estimated coefficients presented here have been back-transformed from the arcsine square-root transformation performed for each model. See Table 2 for the list of these models.

IPY = proportion of intra-pair young.

IPL = proportion of litters that were exclusively intra-pair.

GM Pairs = proportion of male-female pairs that produced only intra-pair litters.

Group/intermediate = how living in a group or a variable social structure affected the measure of GM.

Close association = how more “closely” associated pairs influenced the measure of GM.

Paternal care = how increasing levels of paternal care influenced GM.

Density = how $\sqrt{(\text{individuals}/\text{km}^2 \cdot \text{mass in kg})}$ influenced GM.

Sex ratio = how increasing numbers of males:females influenced GM.

2002; Ward and Webster, 2016), it appears that a major cost to group living is being unable to prevent one's mate from engaging in EPCs (Suter et al., 2009; Nichols et al., 2015).

A high level of paternal care was also associated with increased levels of genetic monogamy for all models in which it was present (Table 3). The positive relationship between levels of paternal care and IPY is consistent with the results of Huck et al. (2014), even when we include group-living species in the data set (see also Kvarnemo, 2006). Previous studies show that paternal care likely evolved after transitions to social monogamy (Komers and Brotherton, 1997; Lukas and Clutton-Brock, 2013). For this reason, we suggest that genetic monogamy may have co-evolved with paternal behavior when selection initially favored males that were more affiliative toward females and offspring and, subsequently these affiliative behaviors became modified into paternal care (Komers and Brotherton, 1997; Dillard and

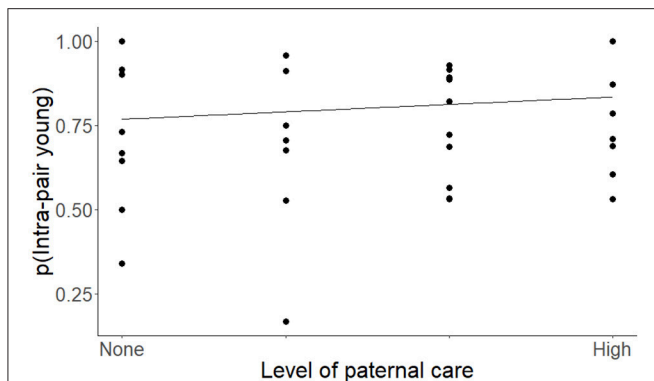


FIGURE 3 | The proportion of intra-pair young (IPY) produced by species of socially monogamous mammals with differing levels of paternal care, ranked from species that provide no paternal care to those that provide intensive paternal care. The regression is based on the coefficients from the top model for IPY (Tables 2, 3) and controls for phylogenetic relatedness, differences in social structure, and is weighted by sample size.

Westneat, 2016). Selection might then have favored males that provided parental care only when paternity was certain to allow males to limit investing in offspring sired by other males. If females engaged in EPCs and males were able to detect this, then these females could face high costs from losing male investment and may then have decreased or refrained from engaging in extra-pair mating to ensure male care. Over evolutionary time, females might have produced offspring that were increasingly reliant on male care or male care might have resulted in greater fitness benefits through the quality or number of offspring. Either of these scenarios could result in stabilizing selection for male care and genetic monogamy (Smith, 1977; Dunbar, 1995; Wade and Shuster, 2002; Stockley and Hobson, 2016). This may be the explanation for the high level of genetic monogamy in the California mouse (*Peromyscus californicus*), for example, where providing paternal care and remaining genetically monogamous results in greater reproductive success for a male than the alternative (Gubernick and Teferi, 2000; Ribble, 2003).

Demographic variables were not good predictors of IPY or IPL but the combination of sex ratio and either social structure or population density were two of the top models for GM pairs, with increases in population density or the proportion of adult males in the population having a negative effect on GM pairs. This was consistent with our predictions and also has been found in previous avian studies (Westneat and Sherman, 1997). Higher population densities may provide greater opportunities for EPCs since there would be a greater likelihood of encountering opposite-sex conspecifics, thus lower costs of pursuing EPCs while resulting in increased difficulty in guarding one's own mate to prevent EPCs. A male-biased sex ratio likely has similar effects because unpaired or subdominant males may pursue matings with paired females.

There are a number of possible reasons that we found different top models depending on the index of genetic monogamy that

we examined. Variation in the number of offspring produced per reproductive bout could influence the outcome of model selection. Approximately 24% of species in our data set give birth to singletons, e.g., many primates, while others such as canids have larger litters. The difference in the number of offspring per reproductive bout could result in different associations between IPY, IPL, and GM pairs. For example, EPCs may result in a small proportion of EPY for species with litter sizes much greater than one. If 5 pairs each have 5 offspring with 1 EPY each, 100% of the pairs would be considered non-GM but only 20% of the total number of offspring would be by IPY. Additionally, the length of the studies and of the pair-bonds differ greatly among species in the data set. Although some studies provided data from multiple breeding seasons or years (e.g., Alpine marmots, Ferrandiz-Rovira et al., 2016), others either did not follow pairs across multiple seasons or only sampled within one breeding season (e.g., Bornean gibbon, Oka and Takenaka, 2001). Finally, although our three indices of genetic monogamy are each different ways to quantify genetic monogamy, they are not necessarily of equal biological importance. Previous studies have focused on EPY (or IPY for our study), and this may be the best index from an evolutionary perspective because it is the closest to reproductive success, which is often used to index fitness (Gimenez and Gaillard, 2018).

Limitations

We had to exclude several potentially biologically important variables from our analyses due to the lack of field data from a sufficient number of species. These variables include the role of female spacing, sexually transmitted disease, relatedness between members of a pair, potential genetic benefits of EPC, and other environmental variables that may influence the interactions between unpaired individuals e.g., habitat structure (Biagolini et al., 2017). Female spacing has been proposed to be a very important driver of social monogamy (Komers and Brotherton, 1997; but see Dobson et al., 2010) and may also influence genetic monogamy due to the inability of males to control access to more than one female (see also Isvaran and Clutton-Brock, 2007). Furthermore, under certain circumstances the presence of sexually transmitted diseases may selectively favor genetic monogamy because mating with one only one opposite-sex conspecific allows individuals to decrease the probability of being infected (Loehle, 1995; Thrall et al., 1997; Kokko et al., 2002; McLeod and Day, 2014). Additionally, relatedness between members of a pair and the genetic benefits of EPY can influence the levels of EPCs in a variety of socially monogamous species (Blomqvist et al., 2002; Varian-Ramos and Webster, 2012; Leclaire et al., 2013; Arct et al., 2015). If we were able to include additional variables in our analysis, we might have found different variables in our top models. Future studies focusing on these potentially important variables may increase our understanding of mammalian genetic monogamy or increase our confidence that the variables in our top models are the most important drivers of genetic monogamy.

Furthermore, some of these variables might interact, be highly related to each other, or be bidirectional, making it challenging to unravel the most important predictors of genetic monogamy. For example, estrous synchrony and spatial distribution of females could interact to affect the probability of males obtaining EPCs. If all females are fertile or in estrus at the same time but are dispersed as opposed to being clustered, the prospects for a male seeking EPCs would differ. Additionally, variables such as population density and seasonality may be highly related, as seen in vole populations where population density typically is lower in winter and spring than in the fall (Getz et al., 1993). Finally, some variables may be bidirectional i.e., they may influence genetic monogamy as well as being influenced by the level of genetic monogamy (Andersson, 1994; Alonzo, 2010). For example, if females engage in EPCs we would predict the level of paternal care to decrease. Conversely, the level of paternal care could also influence the likelihood of females seeking EPCs (Westneat et al., 1990; Birkhead and Møller, 1992; Andersson, 1994; Alonzo, 2010). These examples highlight some of the challenges in trying to encapsulate relevant factors into a model that predicts genetic monogamy across numerous species.

Although a comparative approach can allow us to determine predictors of genetic monogamy across mammals, we realize that all mammalian species do not fit the patterns found. For example, some group-living species in our study had high levels of genetic monogamy despite the overall finding that group-living species had lower levels (Patzenhauerová et al., 2013; Ferrandiz-Rovira et al., 2016). Tight synchronous breeding (Platner, 2005; Hilgartner et al., 2012) and male territory defense (Sommer and Tichy, 1999; Sommer, 2003) are hypothesized to drive high levels of genetic monogamy in two of our species despite low degrees of pair association and no paternal care in both species. Although comparative studies may detect overall evolutionary or environmental trends, the results are not expected to adequately explain the complex processes that result in genetic monogamy in every species.

Another important consideration is how genetic monogamy might differentially benefit conspecifics within or between populations. Differential benefits among individuals may complicate the interpretation of data analyzed at the species-level. Some hypotheses proposed to explain genetic monogamy (e.g., the paternal care hypothesis) predict that individuals will display uniform mating behaviors within a population, other hypotheses predict a lack of uniformity in genetic monogamy. For example, selection for genetic compatibility between members of a pair may result in pairs with low genetic compatibility being less likely to be genetically monogamous than more genetically compatible pairs within the same population (Griffith et al., 2002). Furthermore, populations living in highly variable environments may face different selection pressures and evolutionary trade-offs resulting in intraspecific differences in levels of genetic monogamy (Bishop et al., 2004; Streatfeild et al., 2011). We did not attempt to account for this intraspecific variation in our models because we only found a few species with genetic parentage data from more than one population.

CONCLUSIONS

Our study provides the most comprehensive comparative examination of genetic monogamy in mammals to date. Previous studies have primarily focused on life history traits that have been proposed to explain levels of genetic monogamy, and our integration of demographic and environmental variables with these life history variables allowed us to better test additional hypotheses. Although we found no single model that best explained all our indices of genetic monogamy, our results strongly demonstrate that social structure and paternal care are important in explaining variation in genetic monogamy of mammalian species, with some evidence for a couple demographic variables. Data from more species would allow us to determine if any additional variables are important drivers of genetic monogamy. Furthermore, data on variables not yet examined in many socially monogamous species e.g., relatedness between members of the breeding pair, would allow us to test additional hypotheses proposed to explain genetic monogamy. Based on the available data, our results suggest that genetic monogamy is likely to be a consequence of multiple factors in mammals, but that social structure and paternal care appear to be especially important.

AUTHOR CONTRIBUTIONS

CL, AS, and NS all participated in the literature search and in compiling data. CL organized the dataset, conducted the data analyses, and wrote most of the first draft of the manuscript. AS and NS contributed to and revised the manuscript. All authors read and revised numerous versions of the manuscript. All authors approved of the final version of the submitted manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2018.00139/full#supplementary-material>

Supplementary Table 1 | Model selection for the level of intra-pair young across 39 mammalian species. See **Table 1** for more information on the variables included in model selection.

Supplementary Table 2 | Model selection for the level of intra-pair litters across 28 mammalian species. See **Table 1** for more information on the variables used in model selection.

Supplementary Table 3 | Model selection for the level of genetically monogamous pairs across 34 mammalian species. See **Table 1** for more information on the variables included in model selection.

Supplementary Data Sheet 1 | This data sheet contains a list of all the species used in our analysis, the indices of genetic monogamy calculated from parentage data for each species, and the seven variables used in our analyses for each species, along with all the references for these.

Supplementary Image 1 | The phylogeny of the 41 Mammalian species used for the phylogenetic regressions. Phylogeny was created by sub-setting the Mammalian supertree accessed from TimeTree (<http://www.timetree.org/>) on Dec 14, 2017 to the species used in each analysis.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Patterning of Paternal Investment in Response to Socioecological Change

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Human paternal investment, and that of many other species, is facultatively expressed and dependent on a diverse array of individual, social, and ecological conditions. Well-documented are the various ways in which men invest in offspring and the household. Specifically, local ecology structures pay-offs to male investment and has been shown to be an important predictor of the sexual division of labor. However, while variability in paternal investment has been well-characterized cross-culturally, plasticity within a group in response to changing socioecological conditions remains largely unstudied. To address this, we use recent economic development and market access to explore how changes in socioecology alter behavioral options for men and their resultant investment decisions. Among the monogamous Maya, we find that, associated with the introduction of novel subsistence opportunities and incentives for intensified paternal investment, fathers spend more time in the household, more time in domestic activities and more time interacting with their children. The changes in paternal investment documented here are largely contingent on four conditions: increased efficiency in subsistence brought about by mechanized farming, limited opportunities to engage in wage labor, increased opportunities to invest in offspring quality, and a monogamous mating system. Thus, Maya fathers appear to repurpose found time by furthering investment in their families.

Keywords: paternal investment, mating effort, division of labor, Maya, life history theory

INTRODUCTION

Across human societies, men and women typically engage in different yet complementary patterns of parental investment (Murdock and Provost, 1973). This type of role specialization, where males and females engage in sex-specific activities within a pairbond, is observed across many animal taxa (Barta et al., 2014). What is distinctive to humans, however, are the variable ways in which this investment occurs. For example, in some societies males provide nearly all of the calories for subsistence and little childcare (Rasmussen, 1931), in others mothers and fathers contribute relatively equally to household provisioning and men engage considerably in childcare (Griffin and Griffin, 1992; Hewlett, 1993; Kramer, 2009), and still in others men invest little beyond gametes (reviewed in Hewlett and Macfarlan, 2010).

Local ecology, paternity certainty, and opportunities for mating effort have all been shown to be important determinants of paternal involvement because they generally structure pay-offs to male investment across environments (e.g., Marlowe, 2007). However, while variability has been well-described cross-culturally, within-group plasticity in response to changing socioecological

conditions remains largely unstudied. Here we target recent economic development and market access in a small-scale Yucatec Maya society to examine the role that changing subsistence options for men play in their parental investment decisions. Below, we briefly review the literature on paternal investment across animal taxa to more broadly situate our research question.

Social Monogamy and Biparental Care

Social monogamy is relatively uncommon across mammals (3–9% of species; Kleiman, 1977; Lukas and Clutton-Brock, 2013), with paternal investment occurring even less frequently (Wright, 1990; Pleck, 1997). This rarity may be driven by sexual conflict, which challenges the emergence of a simple cooperative system of biparental care (Borgerhoff Mulder and Rauch, 2009; Székely, 2014; McNamara and Wolf, 2015). Both parents share the benefits of effort put into raising young, but investing parents may pay an individual opportunity cost or experience lowered survival and/or fertility (Kokko and Jennions, 2008). This raises possible conflict between parents over who pays the costs of care because each is incentivized to minimize their own reproductive costs (e.g., through desertion) at the expense of their partner (Trivers, 1972; Clutton-Brock, 1991; Lessells, 1999; Houston et al., 2005).

Obligate and elevated reproductive costs among females (e.g., gestation, lactation) are commonly referenced to explain the preponderance of maternal care across mammalian taxa (Trivers, 1972). Payoffs to mating multiply are argued to select against paternal care and for males to invest in mating effort (Bateman, 1948). Nonetheless, social monogamy and biparental care are observed across animal taxa and, while rare among mammals (Kleiman, 1977; Wright, 1990), are typical among ~90% of bird species (Cockburn, 2006). So why do males invest among some animals and not others? Life history theory offers an evolutionary framework from which to understand variable patterning in paternal investment (Stearns, 1992; Charnov, 1993; Hill, 1993). If resources allocated to reproduction can be directed toward offspring quantity or quality, natural selection is expected to shape investment decisions based on fitness payoffs to time and energy allocated to mating vs. parenting effort.

Under certain circumstances, monogamy can increase male fitness more than deserting a partner and remating (Grafen and Sibly, 1978; Yamamura and Tsuji, 1993; Fromhage et al., 2005; Kokko and Jennions, 2008; Schacht and Bell, 2016). Parental investment theory (Trivers, 1972) outlines several conditions under which male provisioning might evolve: (1) low opportunity costs associated with paternal investment due to, for example, social and ecological factors that reduce male mating opportunities; (2) investment improves offspring survival and/or quality, particularly when payoffs to desertion are low (Dunbar, 1976; Thornhill, 1976; Perrone and Zaret, 1979; Clutton-Brock, 1991; Westneat and Sherman, 1993) and (3) paternity certainty is high, which is necessary for males to avoid squandering investment. Once paternal investment becomes established, specialization of care tasks by males and females may serve to stabilize the pair-bond. Specifically, specialization can lead to synergistic fitness benefits tied to offspring success (Leonetti and Chabot-Hanowell, 2011; Barta et al., 2014). These payoffs

both constrain the behavioral options available to a parent and decrease sex-biased asymmetries in the costs of performing a parental investment task. Thus, task specialization strengthens biparental care against invasion by other strategies (Barta et al., 2014).

Role of Fathers

Fathers contribute to their offspring's well-being in a variety of ways. While typically characterized as focused on forms of indirect investment (e.g., resources, calories, protection, monetary investments; Kleiman and Malcolm, 1981), fathers variably engage in the direct care of offspring (e.g., carrying, holding, tending, feeding, and grooming offspring). Among humans, local ecology has been shown to play an important role in mediating payoffs to indirect vs. direct investment (Marlowe, 2007). For example, among the Ache hunter-gatherers of Paraguay, high hunting returns cause food provisioning to earn men higher fitness payoffs (measured as reproductive success) than time spent in other activities, such as childcare (Hill and Kaplan, 1988). Other studies emphasize that variation in male provisioning reflects differences in paternal quality within a population. Aka fathers (Ituri forest hunter-gatherers), for example, hold or are within arm's reach of their infants nearly 50% of the day. But the investments of individual fathers are highly variable and depend on their attractiveness as partners. Poorer, lower status Aka fathers spend more time with their children and provide more childcare than do wealthier, higher status fathers (Hewlett, 1988). Cross-cultural variation in paternal investment can additionally be understood as a response to helper availability (Griffin and Griffin, 1992; Fouts, 2008). For example, among the Agta, foragers native to the Philippines, fathers spend more time in childcare early in a marriage when a mother does not have a daughter old enough to assist (Griffin and Griffin, 1992). Among the Hadza (sub-Saharan hunter-gatherers), husbands spend more time hunting when their wives have diminished foraging efficiency due to a dependent infant (Marlowe, 2003). Maya fathers too respond in this manner and perform all of the agricultural labor when mothers have a nursing infant and also increase their time allocation to food production as family size increases and their children mature (Kramer, 2009).

Male Investment in Response to Socioecological Change Among the Maya

While human fathers participate in indirect and direct investment to varying degrees across human societies, how best to characterize male motivations for investment remains a point of contention (e.g., Gurven and Hill, 2009; Hawkes et al., 2010). However, whether male paternal investment is motivated by mating or parenting benefits is not the focus of the research here. Instead we target a largely unaddressed question: how do patterns of paternal investment alter within a population in response to socioecological change and the introduction of novel provisioning and caring opportunities? This is a relevant and timely question given the rapid rate of market entry and integration experienced by many small-scale societies today. Because human paternal investment is facultative and not obligate, as it is for women (Geary, 2000), men have behavioral

options in the face of changing conditions. Specifically, among the Maya, the recent introduction of mechanized farming, which allows fathers to refocus their time and energy saved from food production (once reliant on hand-farming techniques) to, for example, childcare, leisure, or pursuing new mating opportunities. Here, we focus on the understudied question of how males allocate time and energy in a changing economic landscape when opportunities for and payoffs to direct and/or indirect investment opportunities are altered.

While males can choose how to allocate their time, payoffs to a particular behavioral strategy depend on marginal returns to offspring investment (e.g., Hurtado and Hill, 1992). As child success becomes more care-dependent and resource intensive, fathers are expected to adjust their investments accordingly (Pennington and Harpending, 1988). Economic development and a market-based economy are associated with intensified male investment in children. In the US, for example, paternal investment, including income and childcare, is associated with better academic performance in childhood and higher socioeconomic status in adulthood (Pleck, 1997; Kaplan et al., 1998; Gray and Anderson, 2010). As economically independent children become more expensive in terms of resources (e.g., school expenses) and childcare, we expect fathers to invest less in other activities tangential to child success (e.g., leisure).

Leveraging data that were collected in a Maya community across two distinct time periods and spanning 20 years (1992 and 2011), we analyze changes in male investment before and after economic development. Traditionally, Maya men spent much of the time outside of the home, away from the village and attending agricultural fields. This limited opportunities for men to engage in childcare and other household activities. An agrarian economy also limits payoffs to concentrated investment in a few children because large families provide agricultural help for food production and foster relational and labor-based wealth (Kramer and Boone, 2002; Kramer, 2005). However, recent infrastructure development (e.g., a paved road connecting the community to a regional highway) has reduced travel time to once distant urban markets and permitted the adoption of mechanized farming. Both of these changes decrease the time fathers need to spend in travel and farming and, consequently, allow them to reallocate this found time in other ways. Thus, here, we center on socioecological changes as important drivers of variation paternal time allocation. Following a life history approach, and potential payoffs to more intensive child investment in response to economic development, we predict that fathers will invest more in the nuclear family unit in the later time period by spending more time with their immediate family and in childcare activities.

METHODS

The Population

To examine questions about shifts in paternal investment, we use time allocation data that were collected across two distinct time periods in a remote rural Maya community in the interior of the Yucatan Peninsula, Campeche, Mexico. Economic, demographic, subsistence, and social trends have been studied

in this community since 1992. The first sample of behavioral data used in the following analyses was collected during a year-long time allocation study (Kramer, 2005, 2009). At that time, all families made their living as swidden maize farmers. While the household was the unit of production and consumption, labor and food were exchanged across households. The community's isolation and the lack of roads and vehicles limited opportunities to monetize surplus crop production or engage in the market economy through wage labor. Most agricultural field locations were within several kilometers (about a half hour walk) of the village. By the age of eight, children often accompanied their fathers to the family's farmed fields, where they spent up to 20% of their day (Kramer, 2005). All maize processing (shelling, hauling, soaking, grinding, and cooking) occurred within the household.

However, in the mid-2000s, rapid economic development began when a paved road was built linking the community to the regional economy. The road facilitated access to new farming methods, the transportation of crops to market, and people to wage labor jobs. The introduction of tractors and mechanized farming minimized agricultural labor inputs and time spent farming. These changes too expanded the potential for men to pursue different and new subsistence options in and out of the community, which allowed them to generate cash. However, wage labor opportunities were low-paying and temporary and did not allow households to completely transition to a dependency on market jobs. While wage-labor opportunities outside of the village are generally low-skill, parents recognize that education is an important contributing factor for their children to be competitive on this new economic landscape and to secure a well-paying and permanent position in the future. Thus, formal education also has become a priority for most families. To this point, time spent in school among children 6–15 years of age increased by 50% between 1992 and 2011.

While the subsistence economy changed over the 20-year interval, many aspects of reproduction remained the same. During both time periods (1992 and 2011), Maya marriages can be described as life-long and monogamous (Cashdan et al., 2016). Some women (~25% in the 2011 sample) currently use birth control, although mean completed fertility has only slightly declined over the past 20 years (1992 mean = 7.5 ± 1.74 , $n = 24$; 2011 mean = 6.1 ± 3.01 , $n = 40$). Infant survival is estimated to be 96% (IMR = 37/1000) and has not significantly changed between the two time periods (Veile and Kramer, 2018). From ethnographic observations, fathers are generally engaged with their families and enjoy spending time with their children. Moreover, household relationships are largely egalitarian and husbands and wives jointly make decisions about their children's lives and economic futures.

Data Collection

To evaluate how much time Maya fathers invest in their children and how childcare versus provisioning behaviors change before and after economic development, we compare time allocation data from 1992 to 2011. Time budget information is combined with economic and household composition data for the two time periods from databases collected and maintained by KKK. Birth records are used to determine father's and children's ages and

are available for both samples. The ages of participants without birth records have been cross checked during multiple annual censuses.

Time allocation data were collected using instantaneous scan sampling techniques. Instantaneous scan sampling is a behavioral observation technique widely used in both non-human animal and human studies to measure the frequency of activities (Washburn and Lancaster, 1968; Altmann, 1974; Borgerhoff Mulder and Caro, 1985; Hames, 1992). Over repeated observations, instantaneous scan sampling is a reliable method to estimate the proportion of time that an individual spends in various activities (Altmann, 1974; Dunbar, 1976; Simpson and

Simpson, 1977) and is more accurate than interview or survey methods to estimate time budgets (Reynolds, 1991).

For both the 1992 and 2011 observation periods, each participant was drawn from the community census and then observed on at least four separate occasions. During those periods, scan samples were recorded, with each observation period lasting ~4 h. An individual's activity and location were recorded at 15 min intervals. The Maya scan data were collected on a subset of the community (112 individuals or 30% of total population in 1992 and 91 individuals or 18% of total population in 2011), which included 15 fathers in each time period whose average ages were not significantly different (mean

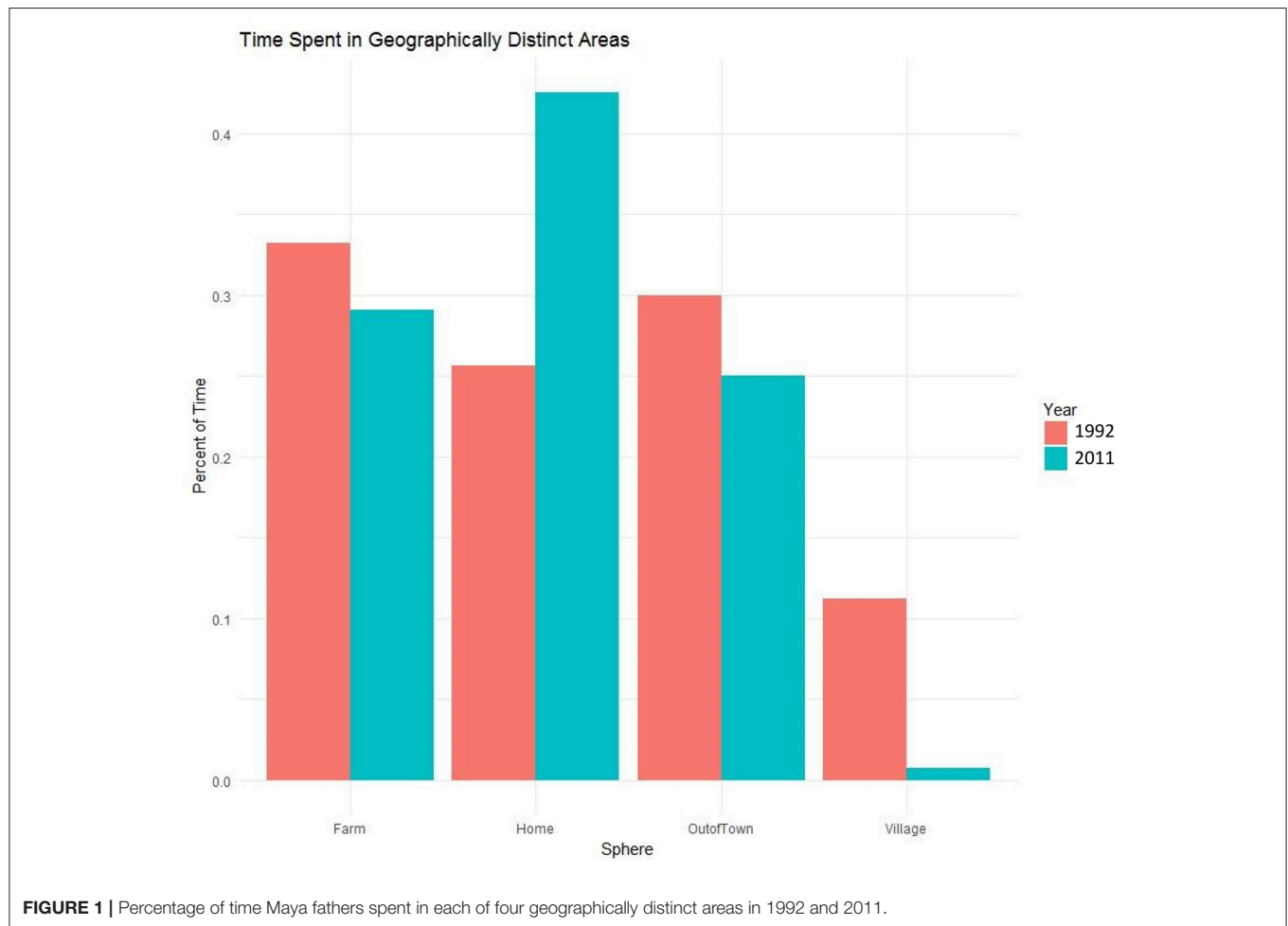


TABLE 1 | Logistic regression with Year as the predictor and geographic areas as outcomes.

	Home		Village		Farm		Out of town	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
(Intercept)	0.34***	0.31–0.38	0.13***	0.11–0.14	0.50***	0.46–0.54	0.43***	0.39–0.47
Year	2.32***	1.98–2.71	0.07***	0.03–0.13	0.84*	0.71–0.99	0.79**	0.67–0.94
Observations	3189		3189		3189		3189	

Odds-ratios and confidence intervals presented. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

age is 36.7 years in 1992 and 34 years in 2011). During a scan sample, individuals were located at specific time intervals, with the researcher recording where they were and what they were doing. Over 400 types of activities were coded, which in addition to childcare, included subsistence (foraging, fishing, hunting, fieldwork), domestic (collecting firewood, water, processing food, cooking, sewing, washing), children's play, social, leisure, and hygiene activities. Scan observations primarily occurred in the household. If a person could not be located during a sampling interval, family members were asked about where the individual was and what he or she was doing. Since several hours were spent with a family during each bout, in many cases a person would be observed leaving and then returning with, for example, a load of firewood or a basket of maize, and location and activity information could be confirmed with the participant. The same methods and suite of hierarchical codes were used to record behaviors in 1992 and 2011. Across the two time periods over 25,000 scan samples were recorded, which were

culled to paternal observations ($n = 2194$ in 1992, $n = 1021$ in 2011). Observations were aggregated by the location in which they occurred, which was recorded at the time of each scan, to determine the proportion of time fathers spent in each of the four geographic spheres (Figure 1): at home, in the village at large, in their agricultural fields (1–15 km distant from the village), or out of town (in distant, larger communities where men travel > 20 km for wage labor, to buy and sell goods, as well as manage children's school registration and education needs).

Within the home a father's time was further categorized into one of three activities: interacting with a child (i.e., direct and indirect childcare), domestic work, or leisure. Direct care (e.g., holding, grooming, carrying, feeding), and indirect care (e.g., helping with homework, disciplining, talking to) were merged into a single childcare category. Domestic work includes food processing and preparation, cleaning, washing, repairing, building, or gardening within the household compound. Leisure

TABLE 2 | Generalized linear multilevel logistic regression with traits of fathers as predictors and geographic areas as outcomes for 1992.

	Home		Village		Farm		Out of town	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
FIXED PARTS								
(Intercept)	0.03***	0.01–0.16	0.16	0.01–3.10	0.04***	0.01–0.26	3.96	0.40–39.54
Children (#)	0.77	0.58–1.02	0.71	0.42–1.19	0.95	0.70–1.29	1.24	0.82–1.88
Age	1.06**	1.02–1.10	1.00	0.93–1.07	1.03	0.98–1.07	0.97	0.92–1.03
Infant present	4.27**	1.55–11.82	2.78	0.42–18.29	1.09	0.35–3.36	0.46	0.10–2.01
Cultivated Land	1.02	0.78–1.33	1.05	0.65–1.68	1.86***	1.38–2.49	0.53**	0.36–0.78
RANDOM PARTS								
N_{ID}	15		15		15		15	
ICC_{ID}	0.087		0.251		0.105		0.182	
Observations	2194		2194		2194		2194	

N_{ID} is a count of the number of fathers included as random effects and ICC_{ID} is a measure of how strongly observations within a father resemble each other (0: not at all, 1: identical). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, # = number.

TABLE 3 | Generalized linear multilevel logistic regression with traits of fathers as predictors and geographic areas as outcomes for 2011.

	Home		Village		Farm		Out of town	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
FIXED PARTS								
(Intercept)	0.86	0.13–5.82	472.70	0.02–12338856.50	1.90	0.11–33.42	0.11	0.00–4.79
Children (#)	0.78	0.60–1.02	0.42	0.16–1.08	0.83	0.58–1.18	1.75*	1.04–2.94
Age	1.00	0.96–1.04	0.80*	0.65–0.98	0.98	0.92–1.04	1.00	0.92–1.08
Infant present	1.28	0.53–3.07	0.01*	0.00–0.67	0.26*	0.07–0.95	1.78	0.33–9.50
Cultivated Land	1.15	0.97–1.37	1.09	0.68–1.74	1.05	0.83–1.32	0.73	0.52–1.03
RANDOM PARTS								
N_{ID}	15		15		15		15	
ICC_{ID}	0.091		0.000		0.164		0.301	
Observations	995		995		995		995	

N_{ID} is a count of the number of fathers included as random effects and ICC_{ID} is a measure of how strongly observations within a father resemble each other (0: not at all, 1: identical). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, # = number.

was defined as time spent in self-maintenance, bathing, napping, or engaging in social activities with anyone other than a father's children. These suites of activities were then used to calculate the percentage of time fathers engaged in a particular set of behaviors at both time points.

Research protocols and consent procedures were approved by the University of New Mexico's Institutional Review Board (Maya 1992 data) and Harvard University's Institutional Review Board (Maya 2011 data).

Statistical Approach

To evaluate the role of economic development on paternal involvement in the household and investment in children, we first conduct logistic regression to assess whether fathers time

allocation budget were different across the two time periods. The year the data were collected is the predictor variable and paternal presence in a particular geographic sphere is the outcome variable. We then use generalized linear mixed models (GLMM) to explore individual predictors of fathers for their presence/absence in a geographic sphere. Fixed effects include: (1) infant in household (<1 year old), (2) number of children in the household (between 1 and 16 years old), (3) the amount of land under cultivation (in hectares) as a measure of wealth, and 4) father's age. Because each father has multiple observations, random effects for "father" are included to account for the nested structure of the data and associated clustering. Random effects allow for heterogeneity in the outcome by individual and for unbalanced observations per person.

TABLE 4 | Logistic regression with Year as the predictor and activities within home sphere as outcomes.

	Domestic		Leisure		Interactions	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
(Intercept)	0.24***	0.20–0.30	0.50***	0.42–0.59	0.69***	0.59–0.82
Year	1.45*	1.08–1.94	0.59***	0.45–0.78	1.35*	1.06–1.74
Observations	1021		1021		1021	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

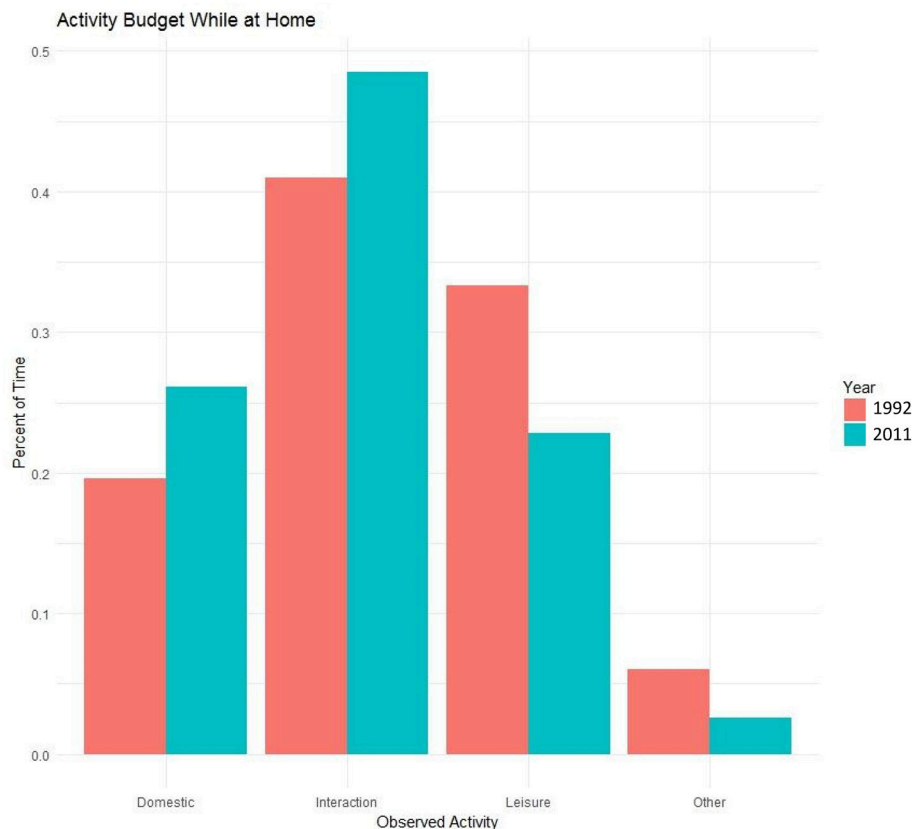


FIGURE 2 | Percentage of time Maya fathers spend in different activities while in the home.

To then evaluate how fathers spend their time at home and whether changes occur in childcare activities, we use logistic regression to assess whether activities within the home differ across the two time periods. The year data were collected is the predictor variable and whether a father was observed interacting with his children, engaged in domestic work, or in leisure are the outcome variables. To explain variation among fathers in how they spend time at home, we apply GLMM, with individual predictors of fathers as fixed effects, individuals as random effects, and paternal presence in a particular activity while at home as the outcome.

Analyses were performed in R [35] using lme4 [36]. Multilevel models, where employed, were selected as the best analytic approach because (1) they are appropriate for nested data; (2) intercepts are allowed to vary by the group-level variable (random effect; father); and (3) fixed effects are shared across all groups. All multilevel models include fixed effects for infant in household, number of children in the household, the amount of land under cultivation, and father's age and random effects for individual.

RESULTS

Following economic development, fathers appear to spend more time at home at the expense of time spent in other areas (Figure 1). We find that year is a significant predictor for the probability of spending time in each geographic sphere. For ease of interpretability, we transform the model parameter estimates into odds ratios (OR; Table 1). An OR greater than 1 indicates increased odds that an outcome will occur as the predictor increases. An odds ratio < 1 indicates decreased odds of an outcome as the predictor increases. We find that fathers in 2011 are at increased odds to be observed at home (OR = 2.32) and at decreased odds to be spending time in the village (OR = 0.07), at their farm fields (OR = 0.84), or out of town (OR = 0.79; Table 1).

Within each period, we then fit generalized linear mixed models to evaluate which paternal characteristics are associated

with the probability of a father being observed in a particular geographic sphere. In 1992, and focusing on our significant results, we find that older fathers and those who have an infant in the home are at increased odds to be observed at home (OR = 1.06 and 4.27 respectively; Table 2). Moreover, fathers with more land under cultivation are at increased odds to be found in their agricultural fields (OR = 1.86) and at decreased odds to be out of town (OR = 0.53). Twenty years later, following economic development, these associations are no longer significant. Instead, older fathers and those with an infant are at decreased odds to be found socializing in the village (OR = 0.80 and 0.01 respectively; Table 3). Additionally, fathers with infants are at decreased odds to be observed in their farm fields (OR = 0.26) and those with more children at increased odds to be observed out of town (OR = 1.74; Table 3).

We then ask, when fathers are at home, what are they doing (Figure 2)? A significant shift occurs over the 20-years in whether a father was observed in domestic work, leisure, or child care. In 2011, fathers were at increased odds to be observed in domestic work (OR = 1.45) and interacting with their children (OR = 1.35) and at decreased odds to be observed at leisure (OR = 0.59; Table 4).

We then assess the role of fathers' individual traits in predicting how a father spends his time while at home. In 1992, fathers with more children under the age of 16 are at increased odds to be observed in domestic work (OR = 1.35) and at decreased odds to be observed in leisure (OR = 0.64). Odds to be observed at leisure, however, increases with age (OR = 1.04) and if the father has an infant in the home (OR = 4.50; Table 5). In 2011, however, fathers with more land under cultivation are at increased odds to be observed in domestic work (OR = 1.99) and decreased odds to be observed in leisure activities (OR = 0.71), or in childcare (OR = 0.79). Fathers with infants are over five times as likely as those without to be observed in domestic work (OR = 5.57; Table 6).

In summary, we report seven key findings of relevance to male paternal investment behaviors. After the introduction of

TABLE 5 | Generalized linear multilevel logistic regression with traits of fathers as predictors and activities at home as outcomes for 1992.

	Domestic		Leisure		Interactions	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
FIXED PARTS						
(Intercept)	0.43	0.13–1.47	0.18*	0.04–0.87	1.24	0.35–4.39
Children (#)	1.35**	1.11–1.65	0.64***	0.51–0.81	0.51–0.81	0.89–1.33
Age	0.97	0.95–1.00	1.04*	1.00–1.07	0.99	0.96–1.02
Infant present	0.37*	0.17–0.85	4.50**	1.70–11.97	0.74	0.33–1.68
Cultivated Land	0.98	0.77–1.25	1.06	0.80–1.41	0.84	0.66–1.06
RANDOM PARTS						
N _{ID}	15		15		15	
ICC _{ID}	0.000		0.028		0.018	
Observations	561		561		561	

N_{ID} is a count of the number of fathers included as random effects and ICC_{ID} is a measure of how strongly observations within a father resemble each other (0: not at all, 1: identical).

*p < 0.05, **p < 0.01, ***p < 0.001, # = number.

economic development, which facilitated access to urban markets and alternative ways to allocate time, fathers spend: (1) more time at home; (2) less time in their agricultural fields and out of town; (3) less time in social activities with other men in the village, particularly when they have an infant in the home; (4) more time interacting with their children (5) more time in domestic work; (6) less time in leisure; and (7) an increasing amount of time out of town in response to more children in the home.

DISCUSSION

Paternal investment can range from genetic inheritance (Savalli and Fox, 1998; Hunt and Simmons, 2000), to pre- or postnatal provisioning (Clutton-Brock, 1991; Kaplan and Lancaster, 2003), to assisting in social development and direct care (Alberts and Altmann, 1995; Kaplan et al., 2000; Marlowe, 2000; Shenk and Scelza, 2012). Among the Maya recent economic development has introduced new subsistence opportunities that subsequently altered the payoff structure for paternal investment. Traditionally, Maya fathers spent much of their day either farming or outside of the community selling agricultural goods. However, the introduction of a paved road, vehicles, and mechanized farming allow the same amount of resources (either food, or cash produced by the sale of agricultural goods) to be generated in less time. These developments have also ushered in rapid social change and a transition from an agrarian economy with few opportunities for formal education to one that is recognized, community-wide, as increasingly skills-based, with children now spending much more of their day in school as a consequence (Kramer, 2005; Veile and Kramer, 2017; Kramer and Veile, 2018; Urlacher and Kramer, 2018).

For this project, we leveraged insight from life history theory as well as research on paternal investment in industrialized populations. Now that Maya fathers have their time open to other pursuits, what do they do with this found time? We predicted that in response to economic development and a transition to a skills-based and education dependent economy, fathers would devote a greater proportion of their time budget to the needs

of their children. Economic development and a market-based economy have been shown to incentivize intense investment in children, both in terms of indirect and direct investment (Pleck, 1997; Kaplan et al., 1998). As child success becomes more care dependent and resource intensive, fathers are expected to adjust their investments accordingly. Consistent with this expectation we found that fathers indeed began investing more in the nuclear family unit by spending more time at home, more time interacting with their children, and less time in leisure. Thus, children today are getting a larger share of their father's time budget than they did in the past.

The complementary nature of the division of labor as well as normatively enforced monogamy among the Maya results in few investment options outside of the pair-bond for men. Marriage to a single partner is the avenue toward adulthood, household formation, and the production of children. Over the 20-year period considered here, divorce and out of wedlock birth have never been reported. Thus, generalizing from this case study, we would predict that, in a monogamous population with few opportunities for males to earn fitness benefits through other means, when opportunities arise to augment offspring quality, fathers will respond by intensifying investment in their children.

Monogamy describes the Maya mating pattern, however, sexual exclusivity within marriage is not a human universal, neither for men nor women (Neel, 1972; Beckerman and Valentine, 2002; Anderson, 2006; Scelza, 2013). In societies where monogamy is either not the norm or not enforced, economic development may lead men to invest less in their children. This is likely in societies where lifelong monogamy is atypical and where payoffs to direct and/or indirect care by men are outweighed by benefits to mating effort. Among Caribbean households, for example, both paternity uncertainty and limited male economic opportunities have been offered to explain why men are typically peripheral to family structure (and why offspring success appears to be more dependent on female kinship networks; reviewed in Gray and Brown, 2015). Moreover, within polygynous pastoral societies, fathers may focus turning new found wealth into additional partners, as

TABLE 6 | Generalized linear multilevel logistic regression with traits of fathers as predictors and activities at home as outcomes for 2011.

	Domestic		Leisure		Interactions	
	Odds ratio	CI	Odds ratio	CI	Odds ratio	CI
FIXED PARTS						
(Intercept)	0.01**	0.00–0.24	0.43	0.09–2.01	2.16	0.18–25.84
Children (#)	1.00	0.68–1.48	1.08	0.87–1.34	0.92	0.65–1.30
Age	0.99	0.93–1.05	1.02	0.99–1.06	1.02	0.97–1.07
Infant present	5.57*	1.47–21.12	0.75	0.37–1.54	0.38	0.12–1.20
Cultivated Land	1.99***	1.50–2.65	0.71***	0.62–0.82	0.79*	0.64–0.99
RANDOM PARTS						
N _{ID}	15		15		15	
ICC _{ID}	0.118		0.009		0.126	

N_{ID} is a count of the number of fathers included as random effects and ICC_{ID} is a measure of how strongly observations within a father resemble each other (0: not at all, 1: identical).

*p < 0.05, **p < 0.01, ***p < 0.001, # = number.

opposed to intensified investments in children (Hedges et al., 2016). Here, again, life history theory offers an evolutionary framework from which to understand variable patterning in paternal investment (Stearns, 1992; Charnov, 1993; Hill, 1993). Because male investment is facultative, when fitness payoffs toward time and energy allocated to mating effort outweigh parenting effort, we expect men to invest less in direct and indirect care.

While the nuclear family (i.e., mother, father, and dependent children as a self-contained economic entity) is often thought to be the fundamental human unit, this family structure is typical of industrialized rather than small-scale societies. It is well documented that the human family exhibits remarkable flexibility within and across populations and social organization typical of cooperative breeders (Hrady, 2009; Russell and Lummaa, 2009; Kramer, 2010; van Schaik and Burkart, 2010; Kramer and Russell, 2015). While some form of pair-bonding is observed cross-culturally, with mothers as the primary infant caregiver, extended kin, and alloparental support are also necessary for offspring success. However, economic development may lead to the economic nuclearization of the household (Keilman, 1987). Among the Maya, as fathers spend less time in other activities unrelated to indirect and direct provisioning (e.g., leisure) and less time out of the household socializing, male relational wealth is likely to decrease. Large networks are

indeed important for managing resource needs of large families, particularly under conditions of resources scarcity. However they can also limit the ability of households to accumulate wealth necessary for child success where education is costly, yet necessary in a skills-based economy (Stack, 1974). Thus we may see the emergence of the nuclear family as an independent economic unit among the Maya as fathers intensify their investment in fewer children and spend less time and resources on both extended-kin and non-kin. Possibly of concern in the current Maya context, particularly given that fertility has remained high, is that nuclear households may not yet be self-sufficient, and so child outcomes may suffer in response to smaller sharing networks until fertility declines.

Economic development across a broad swath of small-scale societies is currently occurring very rapidly. However, we do not expect outcomes to be uniform across place. Optimal levels of paternal investment are expected to vary by socioecological factors, including subsistence type, social organization, and mating system. The changes in paternal investment documented here are largely contingent on four conditions: increased efficiency in subsistence brought about by mechanized farming, limited opportunities to engage in wage labor, increased opportunities to invest in offspring quality, and a monogamous mating system. Because males can choose how to allocate their time, payoffs to a particular strategy are expected

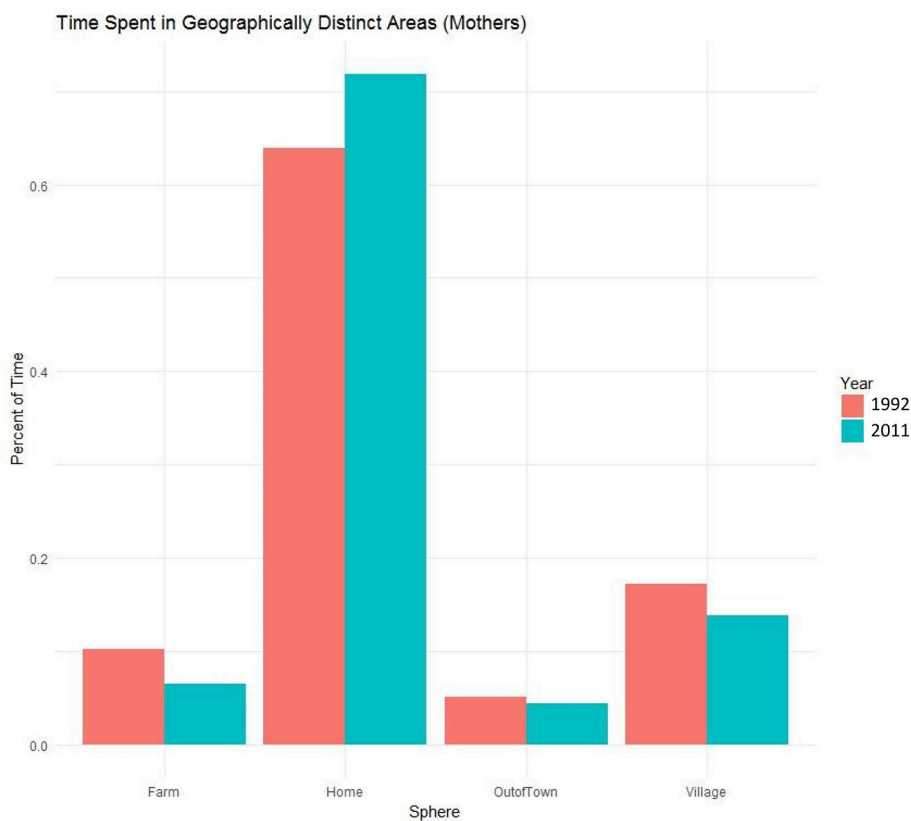


FIGURE 3 | Percentage of time Maya mothers spent in each of four geographically distinct areas in 1992 and 2011.

to be sensitive to marginal returns to offspring investment. Fathers with additional time on their hands as a consequence of mechanized farming are not universally expected to invest more in their children. This time could be reallocated to mating effort, leisure, socializing, or in a number of other ways. However, among the Maya, as a consequence of monogamous marriage and a transition to a skills-based economy, fathers are directing “found time” to their children. In other small-scale societies, economic development in contrast has opened up opportunities for fathers to work outside of the community, which has led to fathers to adopt market jobs as opportunities to provision the family, and thus spend more time away from their children (Mattison et al., 2014). However, in rural Mexico, these positions are low-paying and temporary and cannot alone support a household. As evidence of this, no father in the 2011 sample had given up farming for wage labor. However, from interviews with fathers in the community, child success is increasingly recognized as care-dependent and resource intensive in response to the emergence of a skills-based economy. Thus, we conclude that this change in the patterning of child success, coupled with few mating opportunities outside of marriage, incentivize fathers to funnel investments toward their children.

Limitations

While behavioral observation and time allocation data are a “gold-standard” in the study of behavior, this approach also has limitations. Because of the intensive time investment required for data collection, the sample of fathers for both time periods is small, potentially giving only a partial view of paternal behavior. To minimize bias, fathers included in the study were drawn from a community-wide census. One source of bias that we were not able to account for was migration-bias. Our data come from men who have chosen to remain in the community, which may select for particular kinds of men. And while not a limitation *per-se*, but because of our focus on fathers, we here leave out many other family members. For example, mother’s time budgets are changing as well. In 2011, mothers spent over 70% of their time in the home, an increase from 1992, with comparatively little time in other areas (Figure 3). This increase is in part due to older children spending more time in school and so are less available as helpers. While fathers spent more time at home in 2011 than in 1992, they still engaged in calorie and income generating activities outside of the home. Mothers have taken over more of the care of young children since 1992, and in particular spend more time in the direct care of infants (Kramer and Veile, 2018).

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- Cashdan, 1993; Kaplan and Lancaster, 2003; Geary, 2005; Marlowe, 2007; Gray and Anderson, 2010). To this point, cross-culturally, fathers provide between 16% and < 1% of the direct care received by a child (Kramer, 2010). Among the monogamous Maya, we find that incentives for intensified paternal investment, driven by the introduction of novel subsistence opportunities, are associated with fathers spending more time in the household, more time in domestic activities and more time interacting with their children. Thus, Maya fathers appear to repurpose found time by furthering investment in their families. These changes appear contingent on 1) increased efficiency in feeding offspring (indirect investment) such that more time is available for alternative activities; 2) limited opportunities to reinvest found time away from home (e.g., wage labor); 3) marginal benefits to invest in offspring (e.g., payoffs to education); 4) monogamy, which constrains mating effort. In sum, here, in response to changing requirements for offspring independence, we find fathers to be responsive and accordingly spending less time in activities not directly relevant to parenting effort.

CONCLUSION

Maternal investment is necessary for infants and young children to survive in all but the most modern of human societies (Kramer, 2010). In contrast, human paternal investment, and that of many other species, is facultatively expressed and dependent on a diverse array of individual, social, and ecological conditions (Westneat and Sherman, 1993), making it highly variable (Cashdan, 1993; Kaplan and Lancaster, 2003; Geary, 2005; Marlowe, 2007; Gray and Anderson, 2010). To this point, cross-culturally, fathers provide between 16% and < 1% of the direct care received by a child (Kramer, 2010). Among the monogamous Maya, we find that incentives for intensified paternal investment, driven by the introduction of novel subsistence opportunities, are associated with fathers spending more time in the household, more time in domestic activities and more time interacting with their children. Thus, Maya fathers appear to repurpose found time by furthering investment in their families. These changes appear contingent on 1) increased efficiency in feeding offspring (indirect investment) such that more time is available for alternative activities; 2) limited opportunities to reinvest found time away from home (e.g., wage labor); 3) marginal benefits to invest in offspring (e.g., payoffs to education); 4) monogamy, which constrains mating effort. In sum, here, in response to changing requirements for offspring independence, we find fathers to be responsive and accordingly spending less time in activities not directly relevant to parenting effort.

AUTHOR CONTRIBUTIONS

The coauthors collectively conceived the idea and edited the manuscript. RS and KK wrote the manuscript. KK collected the data, HD created the database, and RS performed the analyses.

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Changes in Behavior and Ultrasonic Vocalizations During Pair Bonding and in Response to an Infidelity Challenge in Monogamous California Mice

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Despite recent exciting research about pair bonding, little is known about how mammalian vocalizations change with the initiation and maintenance of pair bonding in monogamous species. Moreover, even less is known about the significance of pair bond resilience in the face of social challenges. In the strictly monogamous California mouse (*Peromyscus californicus*), we measured changes in ultrasonic vocalizations (USV) and other behaviors within male-female dyads over the course of pair bonding and characterized associations of USVs with affiliation and aggression. After 1 week of cohabitation, pairs exhibited decreased aggression and “bark” USVs, and increased “simple sweep” and “sustained vocalization” (SV) USV types. Accordingly, the number of barks was associated with aggression, whereas the number of simple sweeps and the number, call duration and bout size of SVs corresponded with affiliation. We then experimentally assessed the impact of an infidelity challenge (1 week cohabitation with an unfamiliar, opposite-sex, extra-pair individual) for both sexes on pair social behavior, acoustic behavior, and reproductive success. The infidelity challenge temporarily disrupted pair bond interactions during pair reunion, independent of which sex experienced the infidelity challenge, via both increases in aggression and barks, and a stunting of affiliation and SVs, compared to control pairs. Pair reproductive success, in the form of birth latency, litter size, pup survival and birth weight, did not differ between infidelity challenge pairs and controls. The quality of pair interactions, however, was associated with reproductive success: aggression during pair reunion across all pairs was associated with a lower likelihood of successfully producing a litter. Similarly, among infidelity challenge pairs, but not the controls, there was a positive association between pair affiliation and paternal care, and a negative association between pair aggression and paternal care. Overall, the infidelity challenge revealed a weak negative effect on reproductive success, but we speculate, based on our results, that greater resiliency of a pair bond can moderate negative effects of a social challenge.

Keywords: infidelity, pairbond, USVs, monogamy, California mouse, extra-pair, communication

INTRODUCTION

Among socially monogamous species in a variety of taxa, intersexual acoustic communication plays a key role in pair bond formation and maintenance (Geissmann and Orgeldinger, 2000; Smith et al., 2008; Hall, 2009). Investigation of one form of acoustic communication, ultrasonic vocalizations (USVs), has provided an emerging, valuable lens through which to examine social dynamics in rodents and other small mammals (Brudzynski, 2018). Rodent models of monogamy have been pivotal in our understanding of the regulation of mammalian pair bonding and mate fidelity (Wang and Aragona, 2004; Kingsbury et al., 2012; Lieberwirth and Wang, 2016), but USVs as they relate to pair bonding in monogamous rodents have not been examined until recently. Additionally, the elusive measure of pair bond quality has not been measured in the face of an infidelity challenge.

Mate fidelity is a characteristic of monogamy in the small subset of mammals that express monogamy (Emlen and Oring, 1977; Kleiman, 1977; Dewsbury, 1988). Among monogamous human couples, infidelity may weaken pair bonds (Fletcher et al., 2015) and is widely regarded as one of the most prominent factors influencing emotional distress and divorce (Atkins et al., 2001; Sweeney and Horwitz, 2001; Previti and Amato, 2004). Yet, very little is known about the impact of infidelity on monogamous social bonding in non-human animals and what mechanisms may characterize resiliency in response to this challenge to the integrity of the pair bond. Mated males and females of many monogamous species form strong social pair bonds that are often typified by prolonged association, close proximity, vocal signatures such as duetting, the exclusion of extraneous adults, and sexual fidelity (Kleiman, 1977; Mock and Fujioka, 1990; Geissmann and Orgeldinger, 2000; Dietrich-Bischoff et al., 2006; Martin et al., 2007). Several studies have highlighted negative relationships between extra pair copulations and fitness consequences in socially monogamous birds (for reviews see Choudhury, 1995; Griffith et al., 2002; Spoon et al., 2007; Culina et al., 2015; Schroeder et al., 2016 for a recent meta-analysis), but notably, these are correlational investigations. Other studies have examined the effects of pair separation on stress responses, as measured by the occurrence of distress behavior and/or increases in glucocorticoids in birds (Remage-Healey et al., 2003), primates (Fernandez-Duque et al., 1997; Shepherd and French, 1999; Ginther et al., 2001), and rodents (Starkey and Hendrie, 1998; Martin et al., 2006; Bosch et al., 2009; Sun et al., 2014). Overall, however, little is known about the impact of infidelity, or perceived infidelity, during this separation period on the dynamics of the pair bond upon reunion and on reproductive success measures. We used a longitudinal design to experimentally test the impact of an extra-pair co-housing treatment on pair behavior and acoustic communication in California mice (*Peromyscus californicus*). The treatment provided the opportunity of one individual of a pair to mate and/or form a bond with an extra-pair individual during a 1-week separation period and acted as an infidelity challenge to the pair.

The California mouse is an ideal system for studies of vocalizations and pair bonding because it is a strictly

monogamous species (Ribble, 1991) that forms permanent and stable pairs under field conditions (Dudley, 1974; Ribble and Salvioni, 1990; Gubernick and Teferi, 2000). However, when provided an opportunity in the laboratory, ~15% of males and females copulated outside the pair bond (Gubernick and Nordby, 1993), suggesting at least some capacity for extra-pair mating. Both parents care for the young (e.g., Gubernick and Alberts, 1987; Marler et al., 2003; Rosenfeld et al., 2013) and fathers contribute significantly to offspring survival (Gubernick and Teferi, 2000). Additionally, both male and female California mice produce USVs (Briggs and Kalcounis-Rueppell, 2011) and they produce similar USVs in the wild and the laboratory (Kalcounis-Rueppell et al., 2010). USVs occur at high levels in the laboratory between unfamiliar, opposite-sex individuals (Pultorak et al., 2015), between unfamiliar same-sex individuals (Rieger and Marler, 2018), and between bonded pair mates (Pultorak et al., 2017). Amounts of specific USV types produced between pairs separated by a wire mesh are predictive of later affiliative behavior (Pultorak et al., 2017). Furthermore, bonded females respond differently to playbacks of their male partner's USVs compared to an unfamiliar male's USVs when compared to background noise (Pultorak et al., 2017). Internal neurobiological changes are indirectly evident in males that have become bonded because testosterone injections inhibit USV production in pair bonded males but not sexually naïve males (Pultorak et al., 2015). Understanding the functions of USVs in this monogamous system may enhance our understanding of the functions of vocal signals in other systems in which long-term relationships are formed between individuals.

To understand our predictions, it is necessary to provide background for the general categorizations of USVs in California mice. We used four categories of adult vocalizations in California mice, adapted from previous laboratory (Pultorak et al., 2015, 2017) and field (Kalcounis-Rueppell et al., 2006, 2010; Briggs and Kalcounis-Rueppell, 2011) studies. These vocal categories include "simple sweeps," "complex sweeps," "sustained vocalizations (SVs)," and "barks," (spectral information provided in the Methods). Given previous work indicating that complex sweep and SV calls between partners separated by mesh wire predict later pair affiliation (Pultorak et al., 2017), and that SV calls are produced at high rates in the field among bonded pairs (Briggs and Kalcounis-Rueppell, 2011), we predicted that complex sweeps and SVs would increase as pairs form bonds. In contrast, bark calls [first described in *Peromyscus* in a field study (Kalcounis-Rueppell et al., 2006)] and aggression are positively associated, at least within same-sex interactions (Rieger and Marler, 2018). Thus, we predicted a decrease in barks as the pair bonds form. Finally, we predicted that an infidelity challenge would disrupt pair bonds, as indicated by a reduction in affiliation, complex sweeps and SVs and an increase in aggression and barks toward their original partner, as compared to pairs not exposed to an infidelity challenge.

We addressed three core questions in this study: (1) How does ultrasonic communication and behavior within pairs change during the formation of the pair bond? (2) What are the behavioral correlates of specific USV types emitted by pairs? (3) What are the consequences of an "infidelity" challenge,

via rehousing with an extra-pair, opposite sex conspecific, on subsequent pair ultrasonic communication, pair behavior, and measures of reproductive success? To address these questions, we assessed pair behavior and USVs during brief dyadic social interactions before and after an infidelity challenge or pair separation in a 28-day longitudinal design. We performed the infidelity challenge separately for both sexes, maintained a pair separation group and an undisturbed, no-separation pair group as controls. Following the dyadic behavioral testing regimen, we measured litter production (birth latency, litter size, mean pup weight, and pup survival) and paternal behavior during pup retrieval tests (latency to approach pup, huddling, licking and grooming) to assess pair reproductive success.

METHODS

Animal Use and Housing

We used 55 male and 55 female California mice (age >4 mo) reared in a colony in our laboratory at the University of Wisconsin-Madison. Animals were given water and food (Purina 5015TM mouse chow) *ad libitum* and housed in standard cages (48.3 cm × 26.7 cm × 15.6 cm) with 1–3 other same-sex conspecifics (minimum of 4 mo co-housing) prior to pairing. Colony and testing rooms were maintained at 20–23°C under a 14:10 light/dark cycle with lights on at 2,200 h. Animals used in pairs or extra-pair dyads shared no common ancestry for a minimum of two prior generations, were sexually naïve, and did not choose their partners (i.e., pairs were “forced”). All behavioral tests were conducted under red light within 3 h after the onset of the dark cycle, corresponding to the highest activity rates for *P. californicus* (Marler, unpublished data). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and were in adherence with the University of Wisconsin-Madison Research Animal Resource Committee (RARC) and Institutional Animal Care and Use Committee (IACUC; L0021-0-03-10).

Social Challenge Conditions and Timeline of Trials

Dyadic (male + female) behavioral social interaction trials were conducted once every 7 days over a period of 28 days (see **Figure 1** for a timeline diagram). Since previous data from our laboratory suggest that a majority of pairs copulate within approximately the first week of co-housing and are found to begin nesting together in this period (Gleason and Marler, 2010; Pultorak et al., 2017), we considered day 7 to represent the “pair development” phase. Behavioral trials for all pairs occurred at pair introduction (day 0) and pair development (day 7). On day 14 prior to the trial, pairs were randomly assigned to one of four social challenge conditions: (1) male infidelity challenge condition ($n = 11$ pairs), in which the male was separated from his mate and housed with an extra-pair unfamiliar female for 7 days (and the original female pairmate was singly-housed), (2) female infidelity challenge condition ($n = 11$ pairs), in which the female was separated from her mate and housed with an extra-pair unfamiliar male for 7 days (and the original male pairmate was singly-housed), (3) separation control condition

($n = 11$ pairs), in which both pair members were separated and singly-housed for 7 days, and (4) no-separation control condition ($n = 11$ pairs), in which the pair remained housed together, undisturbed. For social challenge conditions involving pair separation, members of a pair were housed in separate rooms, outside of their auditory and olfactory range.

We defined the “control supergroup” as all pairs in the separation control condition and no-separation condition ($n = 22$ pairs) and similarly, we defined the “infidelity supergroup” as all pairs in the male infidelity challenge condition and female infidelity condition ($n = 22$ pairs). Trials on day 14 for the control supergroup involved the established pair members, whereas trials on day 14 for the infidelity supergroup involved one pair member and the extra-pair (unpaired, sexually naïve, unfamiliar, and opposite-sex) individual. Immediately after the trial on day 14, the newly formed dyads among the infidelity supergroup were placed in a clean cage and housed together for 7 days. At pair reunion on day 21, trials were interactions of the original members of a pair (i.e., reunion of the pair for all social challenge conditions involving pair separation). These original pairs were then housed together again for the duration of the experiment. On day 28, a final trial (“pair re-establishment”) was conducted for all original pairs.

Dyadic Social Interaction Test Procedure

Each trial consisted of a 5-min behavioral interaction of male-female dyads in a large, neutral Plexiglas arena (90 cm long × 46 cm wide × 43 cm high) with aspen bedding. The male was placed in the arena 10 min prior to each trial, similar to previous work examining dyadic social interactions in California mice (Gleason and Marler, 2010; Pultorak et al., 2015), mimicking the female-biased dispersal pattern in this species (Ribble, 1991). Video recording (Panasonic SDR-SW20, Panasonic Corporation, Kadoma, Osaka, Japan) and audio recording (see below) were initiated simultaneously with the addition of the female.

Behaviors were scored by experienced observers blind to social challenge condition, and inter-rater reliability was assessed for 5% of the trials (intraclass correlation coefficient >0.90 for all measures). Since our primary questions concerned levels of affiliative and aggressive behaviors of the pair, we counted the total number of affiliative behaviors and aggressive behaviors of the dyad (male + female) for each trial. Affiliative behaviors included approaches, follows (continual pursuit of the other ambulatory animal at a slow consistent pace) and sniffs (investigation of the other stationary animal in nose-to-nose or nose-to-anogenital contact). These behaviors were categorized as affiliative and not just investigatory because they each negatively correlated with aggressive behaviors in analyses of all trials in the experiment (Spearman's rank correlation, $N = 213$, P -values ≤ 0.001). Aggressive behaviors included chases (movement at a rapid pace toward the other animal, often resulting in biting or wrestling) and wrestles (aggression develops into a tumble in which biting can occur). Behavioral measures used were defined in previous studies (Gleason and Marler, 2010; Pultorak et al., 2017). We provide more details of the raw behavior data, as well as USV data, for each phase of the experiment as **Supplemental Materials**.

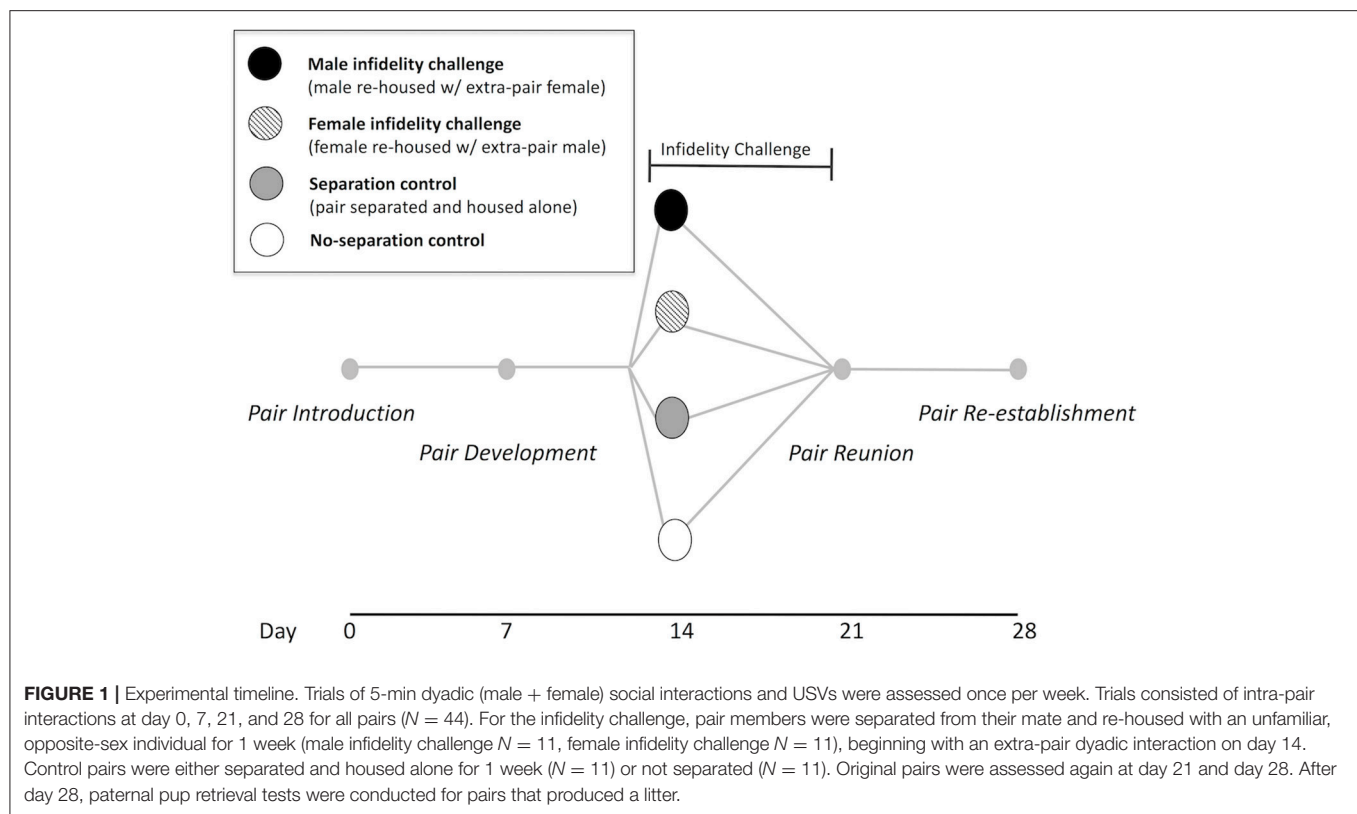


FIGURE 1 | Experimental timeline. Trials of 5-min dyadic (male + female) social interactions and USVs were assessed once per week. Trials consisted of intra-pair interactions at day 0, 7, 21, and 28 for all pairs ($N = 44$). For the infidelity challenge, pair members were separated from their mate and re-housed with an unfamiliar, opposite-sex individual for 1 week (male infidelity challenge $N = 11$, female infidelity challenge $N = 11$), beginning with an extra-pair dyadic interaction on day 14. Control pairs were either separated and housed alone for 1 week ($N = 11$) or not separated ($N = 11$). Original pairs were assessed again at day 21 and day 28. After day 28, paternal pup retrieval tests were conducted for pairs that produced a litter.

USV Recording and Analysis

USVs were recorded with a centrally located Emkay/Knowles FG series microphone capable of detecting broadband sound (10–120 kHz) via an Ultra Sound Gate USG416 interface (Avisoft Bioacoustics, Berlin, Germany). The microphone was placed in the middle of the arena along the back wall (45 cm from each side wall) at a height of 30 cm. Recordings were collected at a 250 kHz sampling rate with 16 bit resolution using RECORDER software (Avisoft Bioacoustics, Berlin, Germany). Spectrograms were produced with a 512 FFT (Fast Fourier Transform), high pass filter at 10 kHz, and 50% frame overlap using Avisoft-SASLab Pro sound analysis software (Avisoft Bioacoustics).

Since the vocalizer could not be determined, all USV measures reported are from the dyad (male + female). Counts of calls were done by experienced observers blind to condition and inter-rater reliability was assessed for 5% of the trials (intraclass correlation coefficient >0.90 for each USV type). Call durations of SV type USVs were extracted and exported for analysis. SV mean call duration (i.e., previously termed “mean syllable duration,” Pultorak et al., 2017 and altered based on Kalcounis-Rueppell et al., 2018) was calculated for each trial. We used a clustering program (“group.pl”) to automatically cluster SV calls into bouts (i.e., phrases) of 1–14 calls (i.e., syllables) per bout based on a maximum inter-syllable interval of 300 ms (i.e., twice the 150 ms peak of a distribution of inter-syllable intervals; for more detail see Pultorak et al., 2017). Mean bout size (i.e., “mean phrase size,” Pultorak et al., 2017), equivalent to the total number of SV calls

in the trial divided by the total number of bouts in trial, was calculated for each trial.

Categories of Ultrasonic Vocalizations

(1) Simple sweeps are one-syllable, typically downward frequency-modulated, short calls (<50 ms) with a peak frequency around 40 kHz. (2) Complex sweeps are also frequency-modulated but exhibit a much higher peak frequency (~ 100 kHz), a longer duration (<100 ms), and typically contain multiple inflection points. (3) SVs are relatively flat (i.e., little frequency modulation), exhibit a relatively long duration (~ 100 – $1,000$ ms) and a peak frequency around 20 kHz, and often occur in bouts (i.e., previously described as “phrases”) that vary in the number of calls (i.e., previously described as “syllables”; Kalcounis-Rueppell et al., 2018) in a given bout (Briggs and Kalcounis-Rueppell, 2011; Pultorak et al., 2017). (4) Barks typically start and end in the audible range (~ 12 kHz) with a peak around 20 kHz, and are broadband (as opposed to narrow), noisy calls, that are ~ 100 ms in duration or less. A more in-depth discussion of USV categories and relevant spectrogram figures can be found in Kalcounis-Rueppell et al. (2018).

Litter Production and Paternal Pup Retrieval Tests

Thirty-four of the 44 pairs produced a litter within the duration of the experiment (i.e., within 90 days of pair introduction at day 0). For each of these pairs, birth latency (number of days between day 0 and the birth of a litter), litter size and mean pup weight

in litter were measured on the day of birth, and proportion of litter survival to weaning (day 30) was recorded. Based on birth latency (the number of days from day 0 to the birth of a litter) and a gestation period of ~32 days (Gleason and Marler, 2010; Pultorak et al., 2017), we determined whether or not females were impregnated prior to the infidelity challenge (effects on results are examined later). On post-natal day 4, paternal pup retrieval tests were conducted using methods similar to Frazier et al. (2006) and Gleason and Marler (2010). Briefly, the male, female and all pups were moved from the home cage into a new cage placed outside the experimental room during the test ($N = 31$ pairs with pups surviving until the test on post-natal day 4). One pup was immediately randomly selected and placed in the home cage in the corner diagonal from the nest. After 90 s, the male was returned to the cage opposite the pup and a transparent lid with small air holes was placed on the cage to aid in observation. Video recording was initiated immediately to record paternal behavior. Interactions of the male with the pup were recorded for 10 min. We measured the latency to approach the pup, total duration spent huddling over the pup, and total duration spent licking and grooming the pup. After the trial, the female and remaining pups were returned to the home cage.

Statistical Analyses

Statistical analyses were performed in SPSS version 23 and graphs were produced using Graphpad Prism 5 (La Jolla, CA, USA). Due to technical failures or experimenter error, sample sizes were decreased from 44 to 43 pairs for the pair development phase (day 7), 43 pairs for behavioral analysis and 39 pairs for USV analysis for the pair reunion phase (day 21), and 39 pairs for the pair reestablishment phase (day 28). Due to ubiquitous non-normality (based on Shapiro-Wilk tests) of behavioral and USV measures, non-parametric tests were used unless otherwise stated. All group comparisons were performed using Mann-Whitney U or Kruskal-Wallis H tests, and repeated measures comparisons within pairs across two different relationship phases (e.g., changes from day 7 to day 21) were performed using Wilcoxon signed rank tests. When no statistically significant difference was found between the two control conditions or the two infidelity conditions, we examined differences between the pooled “supergroups.” To examine behavioral correlates (aggression and affiliation) of pair USVs (counts of each type), we pooled all trials across the relationship phases exclusively involving interaction of the original pairs (i.e., days 0, 7, 21, and 28) and used partial correlation to control for pair effects. For pairs producing SVs, we additionally examined correlations between behavior and SV features (mean call duration and mean bout size). Similarly, we used partial correlation to assess pair behavior consistency across phases and to assess whether behavior during the extra-pair interaction at day 14 corresponded to pair behavior at other phases. Spearman's rank correlation was used to examine whether pair behavior during reunion could predict paternal behavior during the pup retrieval test. We also used a binary categorical variable indicating whether or not aggression was present in a given trial (e.g., during the extra-pair interaction or during pair reunion). Associations of binary categorical variables were assessed using Chi-square tests

of independence. When conducting the same analyses within each of the four social challenge conditions separately for a given measure (e.g., change in affiliation from day 7 to day 21), or conducting analogous, pairwise correlations across multiple phases (e.g., day 0 \times day 7, day 7 \times day 21, day 21 \times day 28, day 0 \times day 28, etc.), we used Bonferroni corrections to minimize Type 1 error risk due to multiple comparisons. We otherwise used two-tailed tests with a significance level of $\alpha = 0.05$ for all analyses.

RESULTS

Impact of Pair Bonding on Pair Behavior and USVs (From Day 0 to Day 7)

From pair introduction phase (day 0) to pair development phase (day 7), there was a decrease in aggression (Wilcoxon signed rank test, $Z = -3.18$, $N = 43$, $P = 0.001$; **Figure 2A**), but no change in affiliation ($Z = -0.59$, $N = 43$, $P = 0.55$; **Figure 2B**). Pairs produced fewer barks ($Z = -2.21$, $N = 43$, $P = 0.03$) and more simple sweeps ($Z = 4.50$, $N = 43$, $P < 0.001$) and SV calls ($Z = 1.96$, $N = 43$, $P = 0.05$) on day 7 than on day 0 (**Figure 2C**), but showed no difference in the number of complex sweeps produced ($Z = 0.92$, $N = 43$, $P = 0.92$; **Figure 2C**). Of the subset of pairs that produced SVs at both time periods ($N = 7$), SV mean call duration increased from day 0 to day 7 ($Z = 2.37$, $N = 7$, $P = 0.018$; **Figure 2D**), but SV mean bout size did not change ($Z = -0.52$, $N = 7$, $P = 0.60$; **Figure 2E**).

Behavioral Correlates of USVs Within Pairs

Across all trials involving pair interaction, barks were positively correlated with aggression ($r_p = 0.22$, $N = 165$, $P = 0.004$; **Figure 3A**) and negatively correlated with affiliation ($r_p = -0.17$, $N = 165$, $P = 0.029$; **Figure 3B**). Simple sweeps were negatively correlated with aggression ($r_p = -0.22$, $N = 165$, $P = 0.006$; **Figure 3C**) and positively correlated with affiliation ($r_p = 0.49$, $N = 165$, $P < 0.001$; **Figure 3D**). Complex sweeps did not correlate with either affiliation or aggression (P -values ≥ 0.57). SVs positively correlated with affiliation ($r_p = 0.44$, $N = 165$, $P < 0.001$; **Figure 3E**), but did not correlate with aggression ($r_p = -0.06$, $N = 165$, $P = 0.47$). Among pairs that produced SVs, SV mean bout size positively correlated with affiliation ($r_p = 0.25$, $N = 82$, $P = 0.03$; **Figure 3F**) but not with aggression ($r_p = -0.16$, $N = 82$, $P = 0.17$), while SV mean call duration did not significantly correlate with affiliation ($r_p = -0.06$, $N = 82$, $P = 0.61$) or aggression (although there was a non-significant negative tendency; $r_p = -0.19$, $N = 82$, $P = 0.09$).

The presence of aggression was relatively rare (28 of 165 trials: nine for female infidelity pair trials, seven for male infidelity pair trials, nine for separation control pair trials, three for no-separation control pair trials). The presence of aggression was positively associated with the presence of barks ($\chi^2 = 38.6$, $N = 165$, $P < 0.001$) but not associated with the presence of simple sweeps ($\chi^2 = 0.89$, $P = 0.35$), complex sweeps ($\chi^2 = 0.66$, $P = 0.42$) or SVs ($\chi^2 = 0.001$, $P = 0.97$). Specifically, of 165 trials, aggression was observed in 71% of trials in which barks were produced (12 of 17 trials), but only 11% of trials in which barks were not produced (16 of 148 trials).

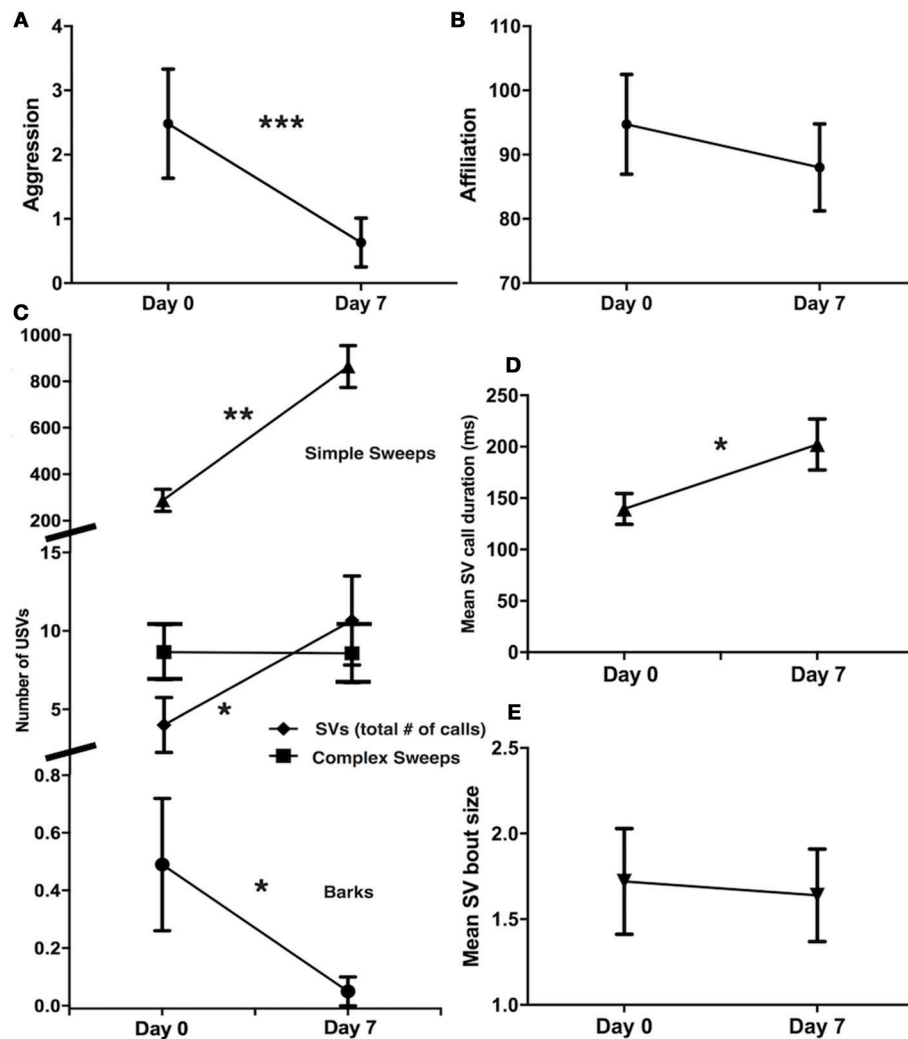


FIGURE 2 | Changes in aggression and USVs from pair introduction (day 0) to pair development (day 7). **(A)** Decrease in aggression ($N = 43$). **(B)** No change in affiliation ($N = 43$). **(C)** Decrease in barks, increase in simple sweeps and SVs, no change in complex sweeps ($N = 43$). **(D)** Increase in mean SV call duration ($N = 7$). **(E)** No change in mean SV bout size ($N = 7$). Mean \pm standard error shown, Wilcoxon signed rank tests, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Impact of Infidelity Challenge on Pair Behavior and USVs (During Pair Reunion on Day 21)

There were no differences across the four social challenge conditions in affiliation (Kruskal Wallis test, $H = 3.86$, $df = 3$, $P = 0.28$), aggression ($H = 5.42$, $df = 3$, $P = 0.14$), or any USV type (all P -values ≥ 0.16). Using the repeated measures design, we determined whether pairs showed behavioral or USV changes from day 7 to day 21 (i.e., pre- to post- social challenge treatment) within each social challenge condition (results presented in **Table 1**). Although there were patterns toward increased SVs in the separation control condition and female infidelity condition upon reunion, no changes in USVs or behavior were statistically significant (**Table 1**, all P -values ≥ 0.02 , Bonferroni corrected $\alpha = 0.002$).

Effects of the infidelity challenge, however, were apparent when comparisons of infidelity and control supergroups were made. The infidelity supergroup showed an increase in aggression [Wilcoxon signed rank test, $Z = 0.99$, $N = 21$, $P = 0.05$; **Figure 4A**] and barks ($Z = 2.38$, $N = 20$, $P = 0.018$; **Figure 4C**), but not affiliation ($P = 0.32$) or any other USV type (all P -values ≥ 0.06) from day 7 to day 21. Conversely, the control supergroup showed an increase in affiliation ($Z = 1.98$, $N = 22$, $P = 0.048$; **Figure 4B**) and in SVs ($Z = 2.27$, $N = 19$, $P = 0.02$; **Figure 4D**), but not aggression ($P = 0.85$) or any other USV type (all P -values ≥ 0.11) from day 7 to day 21. Similarly, a direct comparison of supergroups at day 21 revealed a non-significant tendency for increased aggression (Mann Whitney U -test, $U = 174$, $N_i = 22$, $N_c = 21$, $P = 0.054$) and barks ($U = 141$, $N_i = 19$, $N_c = 20$, $P = 0.065$) among infidelity challenge pairs as compared to control pairs, but no difference in affiliation

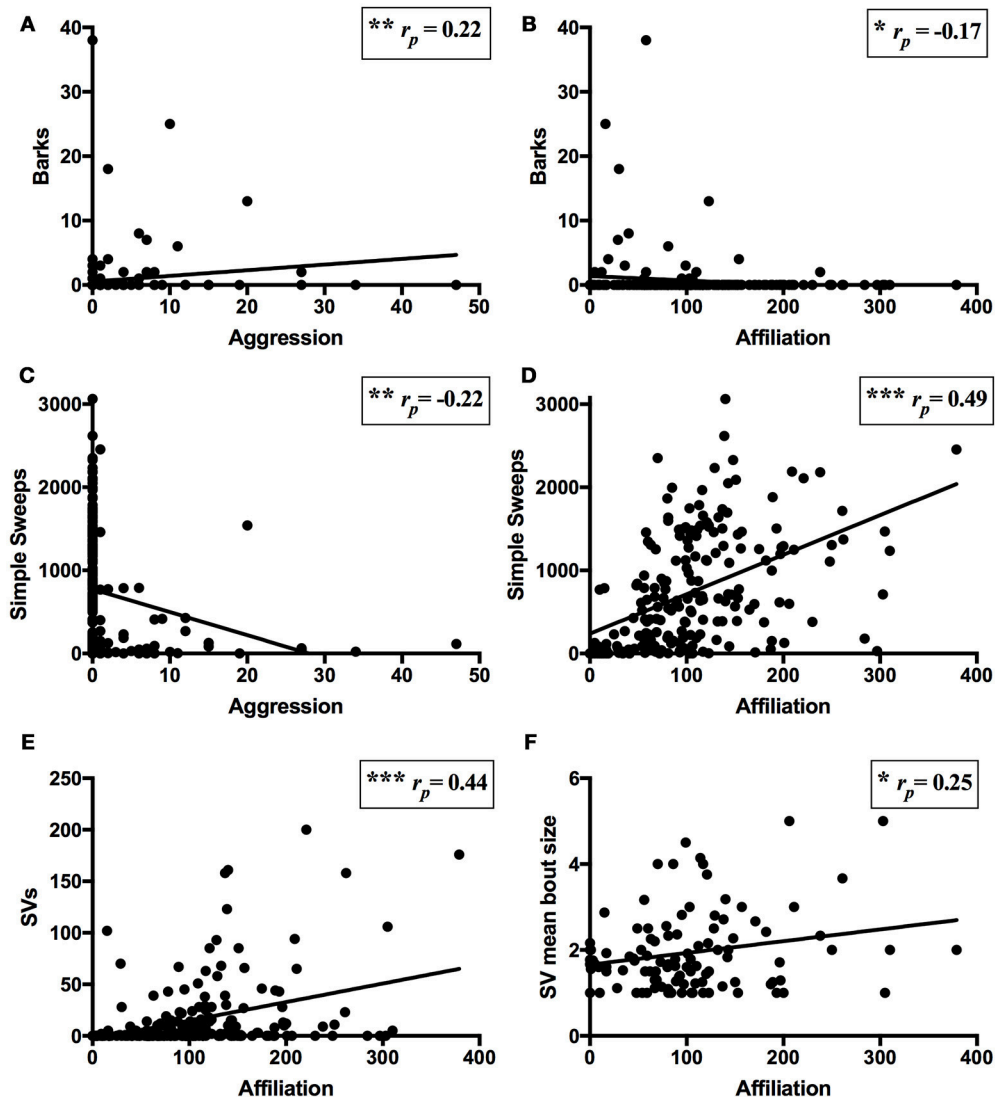


FIGURE 3 | Associations of USVs and pair behavior. Partial correlation (controlling for pair effects) between USVs and behavior for all trials within pairs over the course of the experiment [$N = 165$ for (A–E), $N = 82$ for (F)]. (A) Positive correlation of barks and aggression (i.e., chases and wrestles). (B) Negative correlation of barks and affiliation (i.e., approaches, follows, and sniffs). (C) Negative correlation of simple sweeps and aggression. (D) Positive correlation of simple sweeps and affiliation. (E) Positive correlation of SVs and affiliation. (F) Positive correlation of SV mean bout size and affiliation among trials in which SVs were produced. Lines of best fit shown. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

($U = 195$, $N_i = 22$, $N_c = 21$, $P = 0.39$) or any other USV type (all P -values ≥ 0.22).

Pair Behavior Consistency and Lack of Long Lasting Effects of Infidelity Challenges

There were no differences in affiliation or aggression (Kruskal-Wallis tests, all P -values ≥ 0.46) or USV counts across the four social challenge conditions (all P -values ≥ 0.34) on day 28. Similarly, there were no differences across supergroups in affiliation or aggression (all P -values ≥ 0.79) or USVs (all P -values ≥ 0.38) on day 28 (pair establishment phase). Partial correlations

for pair behavior across the relationship phases indicated patterns of behavioral consistency across the phases. Affiliation at day 28 positively correlated with affiliation at day 0 ($r_p = 0.52$, $N = 39$, $P = 0.001$) and day 7 ($r_p = 0.69$, $N = 39$, $P < 0.001$), and aggression at day 7 positively correlated with aggression at day 0 ($r_p = 0.53$, $N = 39$, $P = 0.001$) and day 28 ($r_p = 0.91$, $N = 39$, $P < 0.001$), but no other correlations for behavior across phases were statistically significant (all P -values > 0.003 , Bonferroni corrected alpha = 0.002). However, dyad behavior during the extra-pair interaction on day 14 did not correspond to pair behavior during any other phase ($N = 21$, all P -values ≥ 0.17 , Bonferroni corrected alpha = 0.003). Similarly, the presence of aggression (i.e., wrestles or chasing observed in trial) during extra-pair interaction on day

TABLE 1 | Behavior and USV changes from pair development phase (i.e., pre-social challenge treatment) at day 7 to pair reunion phase (i.e., post-social challenge treatment) at day 21 within each social condition.

	No-separation control			Separation control			Male infidelity challenge			Female infidelity challenge		
	Day 7	Day 21	N	P	Day 7	Day 21	N	P	Day 7	Day 21	N	P
Affiliation	92 ± 6	100 ± 7	11	0.45	86 ± 18	173 ± 35	11	0.06	101 ± 13	109 ± 22	11	0.48
Aggression	0 ± 0	0 ± 0	11	1.00	0.7 ± 0.6	1.9 ± 1.8	11	0.85	0.1 ± 0.1	1.1 ± 0.7	11	0.11
Barks	0 ± 0	0.1 ± .1	9	0.32	0.2 ± 0.2	1.3 ± 1.3	10	0.66	0 ± 0	2.8 ± 1.8	10	0.07
Simple Sweeps	876 ± 153	917 ± 232	9	0.68	976 ± 209	1317 ± 274	10	0.17	988 ± 160	631 ± 228	10	0.17
Complex Sweeps	6.6 ± 2.8	20 ± 6.0	9	0.08	6 ± 2.8	8.1 ± 3.0	10	0.80	13.2 ± 6.4	9.3 ± 3.7	10	0.72
SVs	9.9 ± 7.2	17 ± 8.8	9	0.69	12 ± 6.2	76 ± 25.4	10	0.02	12 ± 6.6	10 ± 4.8	10	0.92

Mean ± st. error shown. All *P*-values non-significant after Bonferroni correction (corrected alpha = 0.002).

14 was not associated with the presence of aggression during pair reunion on day 21 ($\chi^2 = 0.88$, $N = 21$, $P = 0.35$, **Figure 5A**) nor any other phase (all *P*-values >0.36).

Using Birth Latency to Estimate Timing of Pregnancy

Thirty four of 44 pairs produced a litter by the end of the experiment. Based on a gestation period of 32 days (Gleason and Marler, 2010; Pultorak et al., 2017), 22 of the females were estimated to have been impregnated prior to the infidelity challenge (i.e., pregnant prior to day 14), two were impregnated during the social challenge period, and 10 were impregnated after reunion with the partner. There was no significant difference in the likelihood to become pregnant prior to the infidelity challenge period across the four social challenge conditions ($\chi^2 = 1.82$, $N = 44$, $P = 0.61$) or across the control and infidelity supergroup ($\chi^2 = 1.46$, $N = 44$, $P = 0.23$). Of the two females impregnated during the social challenge period, one was from the no separation control and the other was from the female infidelity condition, indicating at least one case of extra-pair copulation.

Long Lasting Effects of Infidelity Challenge: Predicting Reproductive Success

Thirty-one of the 34 pairs with pups (all first time parents) successfully raised them until paternal testing day (post-natal day 4). There was no difference in the likelihood to produce a litter ($\chi^2 = 1.55$, $N = 44$, $P = 0.67$) or successfully raise pups surviving to paternal testing day ($\chi^2 = 2.07$, $N = 44$, $P = 0.56$) across the four social challenge conditions. There were no significant differences between the control supergroup and the infidelity supergroup in the likelihood to produce a litter ($\chi^2 = 0.52$, $N = 44$, $P = 0.47$), any aspect of litter production (birth latency, litter size, mean pup weight; Mann Whitney *U*-tests, all *P*-values ≥0.36) or any measures of paternal care (differences in latency to approach pup, duration of huddling over pup, or duration of licking and grooming pup; all *P*-values ≥0.11). Finally, there were no differences in litter production or paternal care between the two infidelity conditions (male infidelity vs. female infidelity; all *P*-values ≥0.44).

Reproductive success, as measured by aspects of litter production and paternal behavior, was predicted by pair behavior during the pair reunion phase (i.e., day 21). Pairs that successfully produced and raised offspring ($N = 31$) showed less aggression at day 21 (Mann Whitney *U*-test, $U = 108$, $P = 0.003$, **Figure 5B**) than pairs that did not ($N = 12$), although there was no difference in affiliation ($U = 149$, $P = 0.33$). Among pairs from the infidelity supergroup, paternal behavior was positively predicted by pair affiliation and negatively predicted by pair aggression at day 21. Specifically, pair affiliation was negatively correlated with the latency to contact the pup (i.e., high affiliation corresponded to fast paternal contact of pup) (Spearman's rank correlation, $r_s = -0.59$, $N = 14$, $P = 0.025$, **Figure 5C**), but did not correlate with huddling duration over the pup or licking and grooming (*P*-values >0.34, $N = 14$). Similarly, pair aggression at day 21 was negatively correlated with huddling duration over the pup ($r_s =$

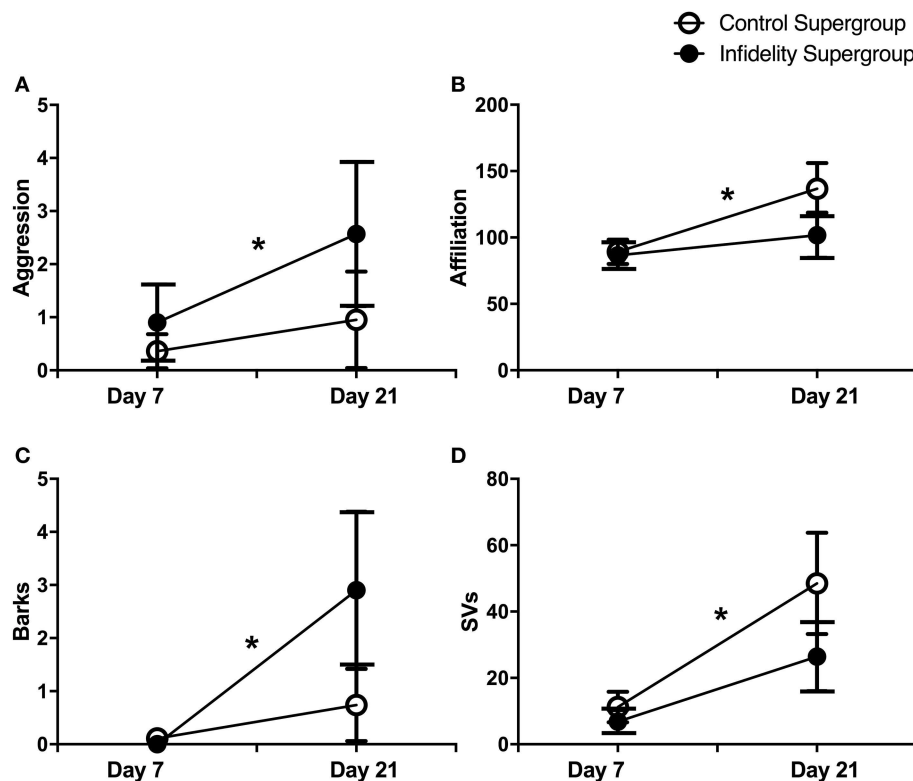


FIGURE 4 | Impacts of social challenge on pair behavior and USVs. Changes in aggression and USVs from pair development (day 7; pre-social challenge treatment) to pair reunion (day 21; post-social challenge treatment) shown for “control supergroup” (i.e., separation and no-separation control pairs pooled) and “infidelity supergroup” (i.e., male infidelity challenge and female infidelity challenge pairs pooled). **(A)** Increase in aggression for the infidelity supergroup ($N = 21$), but no change for the control supergroup ($N = 22$). **(B)** Increase in affiliation for the control supergroup ($N = 22$) but no change for the infidelity supergroup ($N = 21$). **(C)** Increase in barks for the infidelity supergroup ($N = 20$) but no change for the control supergroup ($N = 19$). **(D)** Increase in SVs for the control supergroup ($N = 19$), but no change for the infidelity supergroup ($N = 20$). Wilcoxon signed rank tests, $*P \leq 0.05$.

-0.56 , $N = 14$, $P = 0.038$), but did not correlate with the latency to contact the pup or with licking and grooming (P -values > 0.47 , $N = 14$). In contrast, among the control supergroup ($N = 17$), no paternal behaviors were correlated with affiliation (all P -values > 0.21 , $N = 17$) or aggression (all P -values > 0.23 , $N = 17$) during reunion (**Figure 5D**).

DISCUSSION

The present study contributes to our understanding of mechanisms of mammalian monogamy by characterizing changes in USVs and social behavior of pairs of California mice as they formed pair bonds and in response to a social challenge to that pair bond. This provides a valuable addition to our understanding of how USVs can change as two individuals form a strong bond and suggests that there may be specific USVs involved in maintaining pair bonds. In addition, even though the infidelity challenge lasted for one out of the 4 weeks of the study and temporarily disrupted the established normal pair bond behavior through an increase in aggressive USVs and behavior, there was no direct effect on pair reproductive success in this highly monogamous species. However, aggression during

reunion after the social challenge was associated with lower reproductive success. Pairs with higher aggression levels upon reunion showed a lower likelihood of successfully producing a litter, and among pairs that experienced the infidelity challenge, paternal behavior was positively predicted by pair affiliation and negatively predicted by pair aggression upon reunion with the original partner (maternal behavior was not measured). We speculate that pairs vary in their resilience to social challenges, such as that of the infidelity challenge, and this resilience influences reproductive success.

Behavior and USV Changes Associated With the Formation of a Pair Bond

The longitudinal design of the present study (**Figure 1**) allowed us to characterize changes resulting from the pair bonding process. As bonds formed, pairs expressed decreased aggression (chases and wrestles) and bark USVs (**Figure 2**), and although there was no change in affiliation (approaches, follows, and sniffs), the pairs expressed more simple sweeps, SV calls, and longer SV call durations (**Figure 2**). Simple sweeps, SV calls and SV call duration may therefore be USVs for pair bond maintenance, as discussed below.

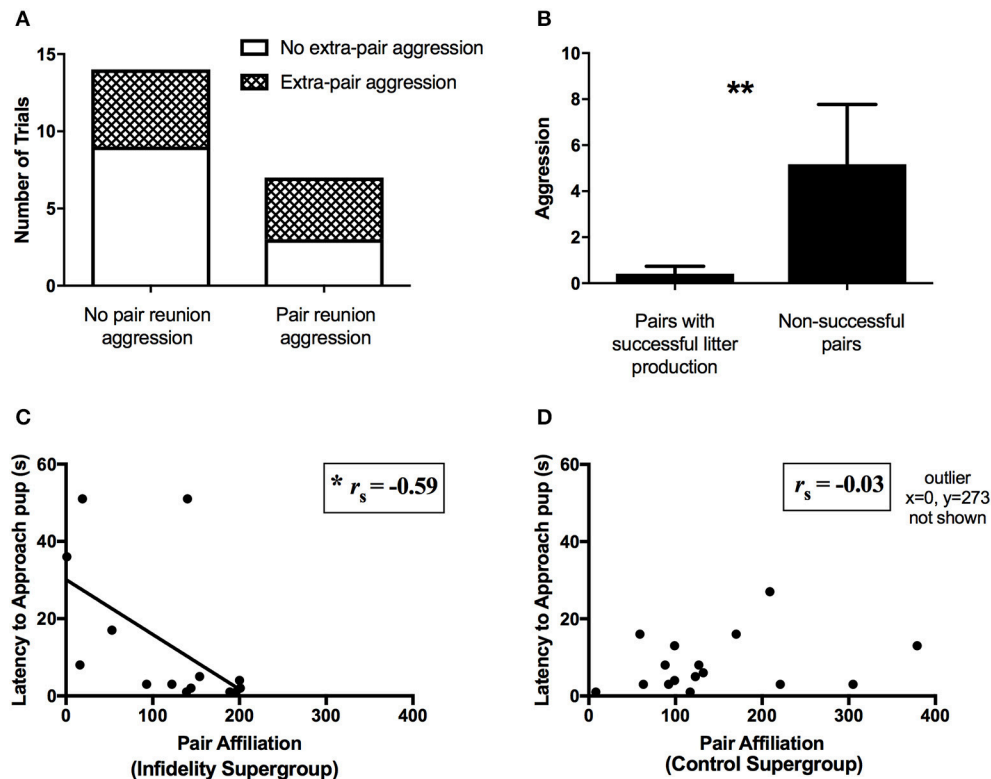


FIGURE 5 | Predictors of pair reproductive success. **(A)** No association between presence of aggression during the extra-pair interaction at day 14 and presence of aggression at pair reunion on day 21 (Chi square test of independence, $N = 21$, $P = 0.35$). **(B)** Pairs that successfully produced a litter (i.e., had pups and the pups survived to testing day on post-natal day 4, $N = 31$) showed less aggression at pair reunion than pairs who did not successfully produce a litter ($N = 12$) (Mann Whitney test, $**P < 0.01$). **(C)** Among the infidelity supergroup, pair affiliation at pair reunion was negatively correlated with latency to contact pup (i.e., high affiliation corresponded to fast paternal contact of pup) (Spearman's rank correlation, $N = 14$, $P = 0.025$, $*P < 0.05$). **(D)** Conversely, among the control supergroup, pair affiliation was not correlated with latency to contact pup (Spearman's rank correlation, $N = 17$, $P = 0.91$).

We predicted an increase of both SV calls and complex sweeps in bonded pairs, given previously observed production of SV calls in the field among bonded pairs (Briggs and Kalcounis-Rueppell, 2011) and associations of complex sweeps with pair affiliation in the laboratory (Pultorak et al., 2017), but only found support for the former and not the latter (see discussion below). Simple sweeps also increased as a result of bonding, and interestingly, although not statistically comparable, pair bonded males in a previous study produced fewer simple sweeps than did naïve (non-paired) males in response to novel females (Pultorak et al., 2015), suggesting that state changes as a result of bonding are manifest differently in intra-pair vs. extra-pair contexts. Changes in USV subtypes in response to bonding are broadly consistent with vocal repertoire and syntax changes concordant with pairing observed in socially monogamous birds (Hall, 2009) and primates (Snowdon and Elowson, 1999; Geissmann, 2002).

Associations Between USV Types and Pair Behavior

Simple sweeps and SVs (but not complex sweeps) emerged as indicators of pair affiliation, whereas barks emerged as indicators of aggression (Figure 3). Simple sweeps occurred in almost all

trials of the experiment, but totals increased as a result of pair bonding and were associated with a suite of affiliative behaviors (approaches, following, and sniffing). This finding supports the broad concept of a positive or “approach,” as opposed to “avoidant” (O’Connell and Hofmann, 2011) social behavioral role for simple sweeps. This finding also indirectly supports previous indications of a possible role for this vocal type in courtship since pair bonded males produce fewer simple sweeps compared to non-bonded males in response to extra-pair females in response to testosterone injection just prior to interaction (Pultorak et al., 2015). Minimally, simple sweep production appears to broadly indicate attraction toward the mate and may be associated with pair bond maintenance.

The number of SVs produced and SV mean call duration similarly increased as a result of pair bonding, but interestingly, SV mean bout size did not change (Figure 2). We predicted an increase in bout size given a field study indicating bouts of three calls (i.e., 3SVs) were more likely to occur when individuals were in the presence of a conspecific, whereas 1SVs were more likely to occur in isolation in the field (Briggs and Kalcounis-Rueppell, 2011). Consistent with the field study, we found that SV mean bout size positively correlated with affiliation (Figure 3)

but not with aggression. Rather than increasing the bout size, pairs seem to be lengthening each call (i.e., “syllable”) as the pair bond forms (**Figure 2**). This pattern is consistent with previous work revealing a positive correlation between female interest in the playback of her mate’s calls and the SV mean call duration of those calls (Pultorak et al., 2017). Likewise, among same-sex dyads, short SV call durations (i.e., closer to the durations of bark calls) are predictive of the intensity of aggression (Rieger and Marler, 2018).

Taken together, these findings reinforce the notion that changes in spectral and temporal features of the acoustic signal may inform important functional aspects of USVs between California mouse mates, akin to intersexual acoustic communication in other taxa. On a comparative level, aspects of spectral and temporal features are known to underlie “emotional states” in rats (*Rattus norvegicus*, Brudzynski, 2013), house mice (*Mus musculus*, Lahvis et al., 2011), and European starlings (*Sturnis vulgaris*, Alger et al., 2016). They can also signify quality in baboons (*Papio cynocephalus*, Fischer et al., 2004) and songbirds (Catchpole and Slater, 2008). Similarly, in *Mus*, USV spectral and temporal features can reflect individuality and kinship (Hoffmann et al., 2012) and these features are sensitive to changes in the social environment (Chabout et al., 2015). USVs are also used in monogamous species with pair bonds such as prairie voles (e.g., Lepri et al., 1988; Ma et al., 2014), as well as in affiliative calls by lemurs that form long-term relationships (review by Zimmermann, 2018). The trajectory of vocal change over the formation of the pair bond, however, has not been examined in these species. These studies suggest that vocalizations are indicating emotional state, at least, but have the potential to convey more complex information. Our current study has the most detailed analysis of USVs showing how USVs can change as a pair bond forms in contrast to investigating already formed pair bonds. Such studies will allow us to better understand the potential functions of each call type.

We predicted that “complex sweeps” would play a role in pair bonding since male complex sweeps predicted later affiliative behavior in a previous study (Pultorak et al., 2017). Our prediction was not supported; complex sweep production did not increase as a result of pair bonding (neither from day 0 to day 7 within all pairs nor from day 7 to day 21 within control pairs) and was not correlated with affiliation or aggression among pairs throughout the study. We can only speculate, but the previous association between complex calls and later affiliative behavior possibly occurred because calls may have been continually produced by males in the prior study involving a mesh barrier (Pultorak et al., 2017) in order to elicit approach from the female, consistent with findings in house mice (Chabout et al., 2015), whereas this was not the case when animals were able to fully interact in the present study. Another possibility is that complex sweeps might indicate a general level of behavioral arousal not unique to pair interactions. More investigation on this call type would be useful, yet difficulties arise given their comparatively rare production in the laboratory and low likelihood of being recorded by microphones in the wild because they have a very high frequency and attenuate rapidly.

Peromyscus bark calls have been identified in the wild (Kalcounis-Rueppell et al., 2006), and are readily observed during male-male and female-female aggression (Rieger and Marler, 2018). Our findings are consistent with these studies and suggest that California mice also use bark calls in male-female aggressive contexts. Overall, bark production was positively correlated with aggressive behavior and negatively correlated with affiliative behavior (**Figure 3**). Barks decreased during pair bond formation (**Figure 2**) and increased during reunion with the mate in the infidelity supergroup (**Figure 4**). Across all trials within pairs, aggression was observed in 71% of the trials for which barks were produced, as compared to only 11% of trials for which barks were not observed. However, the methodology of the present study did not allow us to determine the source (i.e., male or female) of the barks, so we cannot conclude whether they were primarily produced by males or females, or by aggressors or defenders. We suspect barks were produced primarily by females, and were most likely defensive, given previous findings that barks were found at higher rates in *P. californicus* female-female encounters than in male-male encounters, and corresponded most highly with defensive aggression (Rieger and Marler, 2018). Interestingly, one study of Siberian hamsters (*Phodopus sungorus*) similarly found that female-female aggressive encounters exhibited proportionally more “rattle” vocalizations than male-male aggressive encounters (Keesom et al., 2015). Analogous to the association of rattles with aggression, as opposed to other calls types in hamsters, the association of aggression with vocal behavior was unique to bark calls in *P. californicus*, as no other USV types were positively related to aggression. Indeed, the comparatively lower-frequency (components in the auditory range, i.e., <20 kHz) and “noisy” (as opposed to “narrow”) character of barks and rattles is consistent with competitive and territorial vocalizations in other taxa (Bradbury and Vehrencamp, 1998).

Impact of Infidelity Challenge and Isolation

After establishing what characterizes a bonded pair, we were able to test whether an infidelity challenge would disrupt pair bonds in this highly monogamous species by examining both aggressive and affiliative behaviors, as well as changes in the USVs. Interestingly, infidelity challenges impacted behaviors less than predicted. These changes were relatively mild, only being detected by pooled analysis of infidelity conditions (i.e., supergroups), and were only temporary since they returned to “normal” levels of pair bond behavior by day 28. In fact, pair behaviors at day 28 were predicted by pair behaviors at day 7 in an analysis of all pairs. Nonetheless, the infidelity challenge treatments increased aggression and barks with partners upon reunion, whereas the isolation and no-separation treatments increased affiliative behaviors and SVs with partners upon reunion, collectively (**Figure 4**), suggesting that the infidelity challenge had a stunting effect on the pair bonding process. It is possible that additional behaviors characteristic to pair bonding in rodents such as huddling, grooming, or side-by-side contact (Wang and Aragona, 2004; Ophir et al., 2008; Gleason et al., 2012) were influenced by the social challenge. However, we did not make observations when such behaviors might be seen (e.g.,

during inactive hours in home cages). Our observations were limited to brief, 5-min interactions in a neutral arena.

The 1-week isolation from the mate, both physically and acoustically, had surprisingly little effect on the behaviors measured, supporting the concept that pair bonds in California mice are highly stable. A previous study in Mongolian gerbils indicated pair-disruptive behavioral effects of 1-week separation and isolation on individuals (Hendrie and Starkey, 1998) and in California mice, stress from pair separation (as little as 2 days) is presumed to occur based on detrimental effects on wound healing rates in separated pairs as compared to control pairs that maintained contact (Gasper and DeVries, 2005; Martin et al., 2006). However, pair behavior in response to separation had not been previously assessed. In the present study, separation alone was not sufficient to disrupt normal pair behavior. Direct comparison of the separation controls and no-separation controls did not reveal differences, and pooled analysis indicated that control pairs were characterized by increased affiliation from day 7 to day 21, whereas pairs undergoing the infidelity challenge did not show this pattern. The precise mechanism through which this disruption may have occurred remains unknown and is ripe for further exploration.

One factor that could theoretically influence whether infidelity challenges or isolation influences the ease with which a pair bond could be disrupted is whether the females had become pregnant, either by the original “mate” or the “extra-pair mate.” We were limited in our ability to determine whether or not extra-pair dyads copulated during their 1-week co-housing period, but birth latency data suggest that only one female’s litter was sired by an extra-pair male. It is possible that pregnancy from the original mate could be blocked from exposure to the extra-pair male, as evidenced by the “Bruce effect” observed in rodents (Bruce, 1959), including some evidence in the closely-related *Peromyscus maniculatus* (Dewsbury, 1982), although reproductive behavior and physiology might substantially differ between the polygamous *P. maniculatus* and monogamous *P. californicus* (Insel et al., 1991). Given the similarity in copulation time based on birth latency estimates in the present study (50% of females by day 14) to similar *P. californicus* studies without extra-pair housing (53% by day 9, Pultorak et al., 2017; 54% by day 12, Gleason and Marler, 2010), the Bruce effect not likely a major determinant in the present study. Further, no difference was found in likelihood to become pregnant across conditions or across supergroups. More likely, dynamics within pairs determined whether, and how fast, offspring were produced. This idea is supported by evidence in indicating a strong relationship between pair affiliation (mate preference, huddling, grooming, close proximity) and short birth latencies (Gleason and Marler, 2010; Gleason et al., 2012). Nonetheless, the resultant experience from the infidelity challenge had observable effects on pair behavior upon reunion that did not occur in controls. Aggression may have been induced by unfamiliar odors of the extra-pair individual collected on the fur of the pair mate, but this is unlikely since extra-pair odors did not alter pair behavior in a separate study (Becker and Marler, unpublished data). A more likely possibility is that re-housed individuals started to form a new pair bond with the extra-pair individual. One question that

arises is whether California mice, or pair bonding species more broadly, can maintain multiple pair bonds simultaneously. Our implicit assumption was that the creation of a new bond would disrupt an old bond, but this may not necessarily be the case.

Classical sociobiological theory posits that there would be sex differences in response to threats to sexual fidelity (Trivers, 1972; Westneat et al., 1990; Clutton-Brock and Vincent, 1991). Fidelity may be actively imposed via mate guarding and harassment of the partner in both sexes (Wittenberger and Tilson, 1980), but males are expected to suffer greater fitness costs from partner infidelity due to paternity uncertainty (Trivers, 1972). Aggression might thus be predicted to be higher in cases of female infidelity over cases of male infidelity, but this was not found in the present study. Since we did not test paternity, we cannot definitively determine effects of paternal uncertainty. Interestingly, photoperiod-mediated infanticide inhibition can be triggered by ejaculation alone, at least in house mice (*M. musculus*; Perrigo et al., 1990), which could theoretically influence paternal behavior. Paternal behavior also might be influenced through the loss of a bond with the female partner. Although it cannot be ruled out, it is unlikely that paternity uncertainty played a major role in pup retrieval outcomes. If paternity uncertainty was negatively influencing paternal care, one might predict decreased paternal investment among potentially cuckolded males, but there were no significant differences in any measure of litter production or paternal care between the male infidelity and female infidelity conditions. It has been suggested that less behavioral sexual dimorphism should exist in monogamous species (Kleiman, 1977). Indeed, we found no significant differences in behavior or USVs in comparisons of female infidelity vs. male infidelity conditions at pair reunion (day 21).

Results from the present study suggest that resilience to an infidelity stressor is indicative of pair compatibility and may be associated with meaningful fitness benefits. A previous study in California mice revealed that pairings of “preferred” partners resulted in reproductive success increases over pairings of “non-preferred” partners (Gleason et al., 2012). The present study used randomized, forced pairings resulting in variation in pair compatibility. It is possible that if we had let individuals choose their mates instead of creating forced pairings that pair resilience to social challenges would have been even greater. Notably, variability in response to the infidelity challenge was predictive of reproductive success measures. Seven of the 21 pairs (33%) subjected to the infidelity challenge exhibited aggression at pair reunion at day 21 (as compared to 2 of 20 control pairs), and this aggression was associated with lowered reproductive success (Figure 5). Further, aggression at pair reunion was not associated with aggression during extra-pair interaction (day 14), indicating that aggressive behaviors were particular to dyads, not simply due to one aggressive individual across multiple contexts (Figure 5). Aggressive pairs at day 21 showed a longer birth latency than non-aggressive pairs (Figure 5), and paternal behavior (via latency to contact his pup) was negatively associated with the level of aggression at day 21, at least among pairs subjected to the infidelity challenge. Conversely, pair affiliation at day 21 was positively associated with paternal approach to the

pup (Figure 5). These effects are not trivial, given the strong link between fast and consistent production of litters (averaging over two litters per breeding season) and reproductive success in the wild (Ribble, 1992) as well as the importance of paternal care in this species (Cantoni and Brown, 1997; Gubernick and Teferi, 2000).

In conclusion, we characterized behavioral and acoustic changes during the development of a pair bond and in response to an infidelity challenge. We identified that simple sweeps and SV vocalizations were associated with affiliation, while bark vocalizations were associated with aggression, suggesting a role for acoustic changes in the formation and maintenance of rodent pair bonds. The current study reinforced the concept of the robustness of pair bonds in this strictly monogamous species (Ribble, 1991; Gubernick and Nordby, 1993). Even in this highly monogamous species, however, a social perturbation involving an extra-pair conspecific had the capacity to alter normal pair bond interactions. We speculate that pair resilience to a stressor or challenge may be indicative of pair bond quality and suggest that future studies further investigate this possibility. In a recent comprehensive meta-analysis of 81 studies on divorce (i.e., mate switching, typically between breeding seasons) in socially monogamous bird species, Culina et al. (2015) conclude that divorce is an adaptive response to low breeding success. However, one survey of monogamous mammal species failed to detect a significant impact of pair bond strength on rates of extra-pair paternity (Huck et al., 2014). Calls have been made for more experimental methods in this area across taxa (Uller and Olsson, 2008). A strength of the present study is that

it examines pair bond strength in relation to extra-pair activity by presenting a controlled social challenge manipulation in an animal model of monogamy that may not be feasible in field studies.

AUTHOR CONTRIBUTIONS

JP, CM, SA, and SL contributed to experimental design. AJ was critical in contributing to programming the software used in detection and recognition of ultrasonic vocalizations. JP and SA conducted statistical analyses. JP, CM, and SA contributed to manuscript writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2018.00125/full#supplementary-material>

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When to Cheat: Modeling Dynamics of Paternity and Promiscuity in Socially Monogamous Prairie Voles (*Microtus ochrogaster*)

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In many socially monogamous species, individuals form long-term pair bonds and males mate guard females. Such behavior is thought to help secure intra-pair fertilizations, the result of intra-pair copulations (IPCs), and ensure paternity. However, socially monogamous males are also often opportunistic and seek additional mating opportunities with other females, leaving their partner unguarded. The success associated with a male's decision to seek more mates over guarding his partner might be impacted by the activity of other males, specifically the proportion of other males leaving their territories to seek extra-pair copulations (EPCs). The amount of EPC-seeking males can impact the likelihood of a given male encountering an unguarded paired female, but also of being cuckolded (losing IPCs). It remains unclear under which conditions it is optimal to stay and guard or seek EPCs. Using field data from socially monogamous prairie voles (*Microtus ochrogaster*) to generate parameters, we used optimal performance modeling (Monte Carlo simulations) to ask when is it most reproductively advantageous for a bonded male to seek EPCs, despite the risk of losing IPCs. We defined three types of males: exclusive mating bonded males (true residents), non-exclusive mating bonded residents (roving residents), and unpaired males (wanderers). We first modeled the success of an individual male living in a context that incorporated only true and roving residents. We next added wandering males to this model. Finally, we considered the effects of including wandering males and unpaired females in our model. For all contexts, we found that as EPC-seeking in the population increases, the potential reproductive benefit for seeking EPCs increasingly outpaces the rate of cuckolding. In other words, we observe a shift in optimal strategy from true residents to rovers among paired males. Our models also demonstrate that reproductive fitness is likely to remain constant, despite the shift toward obtaining success via EPCs over IPCs. Our results show the dynamic nature of reproductive decision-making, and demonstrate that alternative reproductive decisions yield subtle but important differences despite appearing as balanced strategies.

Keywords: mating tactics, reproductive success, mate guarding, alternative reproductive tactics, model simulation

INTRODUCTION

Mating dynamics are influenced by many factors that include population density, number of competitors, number of potential mates, and available resources (Shuster and Wade, 2003). Over time, species evolve mating systems that maximize reproductive success given their life history and other ecological constraints (Shuster and Wade, 2003). Even within a species, individuals adopt various strategies to outcompete conspecifics for access to mates (Gross, 1996). Reproductive opportunities in the form of access to receptive females represent a limited resource for males, and as a result males engage in various strategies to maximize these opportunities (Emlen and Oring, 1977). Several behaviors that target ways for males to successfully acquire multiple mates have been described and range in the degree to which they involve male-directed or female-directed interactions (Hull and Rodriguez-Manzo, 2009). Another way males commonly attempt to maximize their own reproductive success at the cost of others is through mate guarding. This behavior is thought to have evolved as a countermeasure to contexts in which costs of female mate acquisition are high and males attempt to usurp other males (i.e., cuckoldry), females readily engage in multiple male mating, or both (Zamudio and Sinervo, 2000). Mate guarding is common across taxa in many species, and is observed in an array of mating systems including polygyny and social monogamy (Møller, 1985; Alberts et al., 1996; Jormalainen, 1998).

A variety of mating systems exist in many different forms across animals. Emlen and Oring (1977) have argued that social monogamy emerges when the ecological and social constraints, and the costs associated with them, are too much to maintain polygynous tactics. Thus, the shift toward social monogamy represents a shift from males attempting to monopolize several females toward monopolizing just one female. Interestingly, polygyny and promiscuity are the most common mating system among mammals, whereas monogamy of any form quite is rare (Kleiman, 1977; Lukas and Clutton-Brock, 2013). This suggests that the constraints that have resulted in mammalian monogamy are uncommon and this shift has only occurred a few times in mammalian evolution, making it all the more interesting to consider the forces that have led to such an outcome in this taxa.

Like all mating systems, social monogamy is rich with complex levels of variation in mating behavior and decisions (Mathews, 2002; Reichard and Boesch, 2003; Kokko and Morrell, 2005). For example, by definition, socially monogamous species seek outside mating opportunities while maintaining social fidelity (Lukas and Clutton-Brock, 2013). Taken together, this framework implies that males (and females) should—at some level—attend to the local and immediate social context to inform their mating decisions (i.e., to engage in monogamy or polygyny).

Although a social bond exists between a socially monogamous male-female pair, on average, both sexes will often engage in mating with individuals other than their pair partner. Several benefits to males mating with multiple females have been proposed, including increasing the quantity of potential successful fertilizations, and maximizing reproductive success through multiple mating (Trivers, 1972, but see Tang-Martinez and Ryder, 2005). Similarly, females mating with multiple males

is common (although the reasons for this may or may not be the same as those for males; Yasui, 1997; Tang-Martinez and Ryder, 2005; Blocker and Ophir, 2016). Nevertheless, under the context of females mating with multiple males and the assumption that males might maximize reproductive success through multi-female mating, socially monogamous males are faced with a poignant dilemma: they must weigh the decision to guard a pair partner to ensure paternity and diminish cuckolding, against the decision to leave a partner unguarded to seek extra-pair copulations (EPCs). As a result, a diverse array of behavioral, cognitive, physiological adaptations has evolved to aid in enabling some individuals to navigate this tradeoff. These responses might include responses to sperm competition (Birkhead and Møller, 1993), the ability to time quests for EPCs (Birkhead and Fletcher, 1995), the insertion of copulatory plugs (Ginsberg and Huck, 1989), and sequestering and herding females (Sherman, 1989), to name a few. Nevertheless, an important trade-off that males face between ensuring they fertilize the eggs of one female and attempting to fertilize the eggs of another female can be difficult to optimize. This is because the dynamic and fluid nature of the social environment presumably creates a backdrop on which the factors that define the limits of this trade-off are constantly changing.

Socially monogamous mating systems represent an enormous opportunity to explore the reproductive decision-making that occurs among individuals in a population. Although profoundly complex, the social dynamics within a socially monogamous pair are comparatively simple compared to the number of social interactions that are necessary when more than two individuals comprise a breeding unit, as is the case in other mating systems (polygynous, polyandrous, polygynandrous, etc.). The social context of any mating system is fraught with complexity, but the choice to remain with a partner or to pursue other partners is relatively simple in a socially monogamous mating system in which most individuals engage in some form of social pairing. It is from this perspective that we attempt to model social monogamy and the ways in which the social context potentially shapes the decision to remain a sexually exclusive partner, or to engage in multiple mating. To this end, we base our models on one of the best-understood examples of non-human mammalian social monogamy: the prairie vole (*Microtus ochrogaster*).

As briefly discussed above, individuals must make trade-offs that appear to balance competing strategies when determining the best mating decision. The life history of the prairie vole provides a compelling system for investigating reproductive decisions, as this species has a socially complex and nuanced socially monogamous mating system. Prairie voles exhibit pair bonds between male and female partners, and males engage in mate guarding presumably to maximize their paternity (Solomon et al., 2004). Despite the social arrangement associated with pair bonding, some males and females exhibit multiple-partner mating and/or mating outside the pair bond (Ophir et al., 2008). It is important to note that mixed-paternity litters are common among prairie voles (Solomon et al., 2004; Ophir et al., 2008; Rice and Ophir, Per Obs). Interestingly, males appear to demonstrate a predisposition to forming bonds initially (Blocker and Ophir, 2016), whereas females readily mate with multiple males (Wolff

et al., 2002). This evidence is consistent with the idea that males in particular are faced with the important dilemma of determining whether they should mate exclusively with one female or not.

The degree to which a male mate guards, compared to the degree to which he seeks outside mating opportunities, determines the broad categories for prairie vole mating tactics. In the field, males who strongly pair bond and guard both their territory and mate are known as residents (Getz et al., 1993). Yet, some residents appear to engage exclusively in intra-pair copulations (IPCs), whereas other males engage in EPCs or both IPCs and EPCs (Ophir et al., 2008). As such we distinguish between these two sub-types of the recognized “resident” tactic as either “true residents” or “roving residents” (see Ophir, 2017). Operationally, we define true residents as individuals that have formed a pair bond, share a home-range with the pair partner, and for whom all their paternity comes from in-pair fertilizations with that pair partner. Roving residents (or simply rovers), on the other hand, are defined as individuals that have formed a pair bond, share a home-range with the pair partner, and for whom their paternity comes from in-pair and extra-pair fertilizations. Furthermore, some individuals do not form pairs, adding a deeper level of complexity to the prairie vole mating system. These individuals live alone, occupy large home-ranges that are not defended, and intrude frequently into the territories of residents (Getz et al., 1993; Ophir et al., 2008). This tactic is referred to as “wandering” (Getz et al., 1993), and by definition male wanderers can only achieve paternity through EPCs and extra-pair fertilizations.

Traditionally, only the distinction between residents (collectively) and wanderers has been recognized and discussed (Solomon and Jacquot, 2002; Ophir et al., 2008). However, the difference in true resident and roving resident behavior creates an important dynamic in which any one or more of the three tactics might be favored at different moments in time (Okhovat et al., 2015). For instance, the resulting paternity gained by the mix of EPCs and IPCs of rovers potentially sets up an intermediate tactic in which these individuals neither maximize the benefits nor minimize the costs associated with the pure IPC tactic of true residents or the pure EPC tactic of wanderers. Based on the ecological constraints of the prairie vole mating system such as the stability and reproductive advantages of adopting a resident strategy over wandering, this intermediate roving tactic could be selected against (Phelps and Ophir, 2009). Nevertheless the existence and persistence of this intermediate tactic is particularly interesting because success is very likely dependent on the reproductive decisions of other individuals in the population. By leaving a partner unguarded, a rover becomes vulnerable to cuckolding from other rovers and wanderers. Therefore, we predict that roving is only beneficial when the probability of copulating with an unguarded female is relatively high, and the risk of being cuckolded is relatively low. The likelihood of encountering females, either guarded or unguarded, and being cuckolded should depend on whether other males seek EPCs.

We aimed to model the potential fitness payoffs of roving behavior and in doing so we attempt to assess under which social contexts roving behavior should be observed most or least. Some

models have addressed this choice of guarding vs. EPC seeking and shown that males mate guard more depending on the degree of female infidelity (e.g., Kokko and Morrell, 2005), others have shown that males mate guard more when there is a male skewed sex ratio and competition increases (e.g., Harts and Kokko, 2013). Here, in our model, the number of males in the population is the same, but the proportion of males engaging in roving behavior fluctuates. By manipulating the proportion of other males in a population that engages in a particular tactic, with only a few simple assumptions that are justified by actual prairie vole behavioral observations, we aim to identify population parameters that are influential in defining the emergence (and success) of roving. Specifically, our model asks: *At what point do reproductive benefits of roving outweigh the costs of potential cuckoldry?* Our goal was to identify the tipping point of rover success [i.e., at what proportion of roving vs. true residents in the population does roving become an advantageous (adaptive) tactic]. We approached this aim by beginning with an overly simple social context, and progressively added basic elements of social complexity. We also considered population size for each of the three progressive conditions we created (see below). In other words, we sought to determine when roving should emerge as a viable reproductive tactic.

MATERIALS AND METHODS

Our model was designed to assess the optimal decision-making for a hypothetical resident male based on variable social conditions. We began by creating an optimality model that simulated the probability of reproductive success for a single roving male (i.e., the “focal male”). The focal male could achieve reproductive success by mating within the pair bond, outside the pair bond, or both. Our model utilized a Monte Carlo simulation, which allowed us to quantify the ideal outcome of the focal male’s behavior, given various ecological parameters. Our model simulated the reproductive success that a rover could experience when the proportion of true residents and rovers varies. We based the probability of the subject encountering an unguarded female on the home-range size of a resident (true or rover) observed from radio tracking data in semi-natural enclosures (see Ophir et al., 2008). We ran simulations at pair population sizes of 6 (i.e., 6 males and 6 females total) based on Ophir et al. (2008). We also considered the outcome of population size by running simulations with 100, 200, 500, and 1,000 male-female pairs. Population distribution was estimated from Ophir et al. (2008), holding population density constant at 200 voles per ha (but see Getz et al., 1987; Ophir et al., 2008). We varied the population sizes but kept the proportion of animals per unit space constant because social dynamics do not necessarily scale linearly. For each population size, we ran 5,000 simulations for each percentage of roving (from 0 to 100%).

We designed the focal male to rove as our default because our aim was to determine under what social contexts (if any) that roving would ever be a superior tactic to being a true resident. We compared the focal male’s simulated reproductive success to a baseline measure of success typically achieved by

true residents. By our definition, a true resident cannot be cuckolded and will achieve all possible reproductive success via IPCs, but he cannot achieve any reproductive success via EPCs. Therefore, if the hypothetical (roving) focal male's simulated reproductive performance is above the (true resident) baseline, then the decision to rove has a higher probability for maximal reproductive success, indicating that a given male should adopt a roving tactic. However, if the focal male's simulated reproductive success is less than the baseline, then the decision to rove has a lower probability for maximal reproductive success, indicating that a given male should adopt a true resident tactic (see below for more details).

Layout of the Mating Field

When constructing our model, we started by creating a general layout of our mating environment where all of our simulations took place. An $N \times N$ square grid was composed of a number of "tiles" that equaled the product of the dimensions of the enclosure. For example, a 10×10 m space would have a grid of 100 m², or 100 tiles. In field experiments using prairie voles in semi-natural enclosures (Ophir et al., 2008), the size of the actual grid was 20×30 m, or 600 m² for 6 pairs of animals. The number of tiles in our simulated space for each simulation was held constant at 100 tiles per pair. Thus, a population with 1000 pairs was constructed of a 100,000 tile grid.

The simulations were structured with parameters indicating the location of each tile and a corresponding status for each tile: Empty, Guarded, or Unguarded. Radio telemetry data from Ophir et al. (2008) showed the average home-range size a pair occupied was roughly 40 m². Therefore, we limited an inhabited home-range for a pair to 40 individual tiles in our model. Encounter rates of females for the focal male and every other male utilized a random number generator from 1 to 100,000. Of these 100,000 tiles, hits were ordered as 1 to 40,000. If the focal male generated a number less than or equal to 40,000 at the start of a simulation, then it registered as a successful encounter of a home range. The total tile number decreased by 40 each time a home range was visited, making that home range unavailable thereafter. Thus, a male could encounter a female by landing on any of the 40 tiles constituting a single home range. We acknowledge that this is an oversimplification of mating behavior, as a male landing a single portion of the territory in nature would not guarantee encountering a female. However, because of the computational constraints of our model, we assume that landing on a tile within a territory will result in an encounter with the female on that territory. And if the female is unguarded on the territory, it will result in a copulation. During a "copulation search" in our simulation (see below), if a given tile on which the focal male explored was "inhabited" by a pair but the resident male of that tile left to seek EPCs (i.e., rove), then that tile was classified as "unguarded." Alternatively, if the resident male remained within the territory (i.e., a true resident), then the tile was considered inhabited and was classified as "guarded." If that tile was "uninhabited" by a pair, it was classified as "empty." The foundation of our simulation was based on probabilities of encountering an unguarded or guarded female to quantify reproductive success in order to observe how social context impacts reproductive success.

Scoring Scheme for Reproductive Success

Our model was designed to capture the tradeoff between increasing paternity by gaining EPC offspring at the cost of potentially losing IPC offspring. We assumed that by leaving the territory on a foray for additional mating opportunities (thereby leaving the female partner unguarded), a focal male ran the risk of losing IPC offspring due to cuckoldry. Ecologically these may or may not occur simultaneously and we acknowledge that the prospect of finding and achieving an EPC and the threat of being cuckolded are continuous variables in time. We also acknowledge that fertilization of pups within a litter is often attributable to a copulation (or a round of copulations closely linked in time). However, due to the limitations and structure of our Monte Carlo based model, we could only account for mating success of the hypothetical roving focal male in discrete serial events.

Furthermore, our model was also based on the premise that the average prairie vole litter size is four (Getz et al., 1993). Because the nature of the Monte Carlo method limited us to using discrete time points, we deconstructed the composition of the litter across time, such that for each IPC pup a male had to lose, he simultaneously gained one opportunity to foray for up to three EPCs, each of which could result in one pup. Thus, each male could gain up to 12 EPC chances that could result in up to 12 offspring, at the potential cost of four IPC offspring (**Figure 1**). Note that our simulated male only retained an IPC if he was not cuckolded while on a foray.

We use the term **Foray** to refer to each time that the focal male left his territory. Each foray resulted in what we refer to as a **Copulation Search**. A copulation search specifically refers to the three opportunities to gain up to three EPC offspring that a male has on each foray (**Figure 1**).

For simplicity, we assumed that a successful copulation (IPC or EPC) translated into a successful fertilization. However, we acknowledge that one copulation does not necessarily translate into fertilization. We recognize there are more complex possibilities due to sub-optimal mating events, sperm competition, and physiological conditions that lead to unsuccessful fertilization. For simplicity, we ignore these important sources of variation in fertilization outcomes, and focus on copulation as the key prerequisite of fertilization. As a result, our approximations of fitness rely solely on mating opportunity and the ratios of EPCs vs. IPCs.

On each foray, the focal male risked one IPC for three chances to successfully encounter females, but encountering an unguarded female was not guaranteed. If the focal male successfully encountered an unguarded female during one of the three chances in a copulation search, he gained one EPC. The choice of three EPCs per foray was partially arbitrary, but based on our intention to closely counterbalance the potential reproductive pay-offs and the risk-reward tradeoff of potentially losing an IPC for the chance at acquiring some number of EPCs. Importantly, we wanted to balance the number of potential EPCs with the number of potential IPCs to avoid over- or under-inflating the tradeoff value. Because the chance of IPC was high as long as the focal male did not attempt a foray, the incentive for EPC had to be large, but not guaranteed. Thus, our desired tradeoff of 3:1 should result in an average total fitness value of

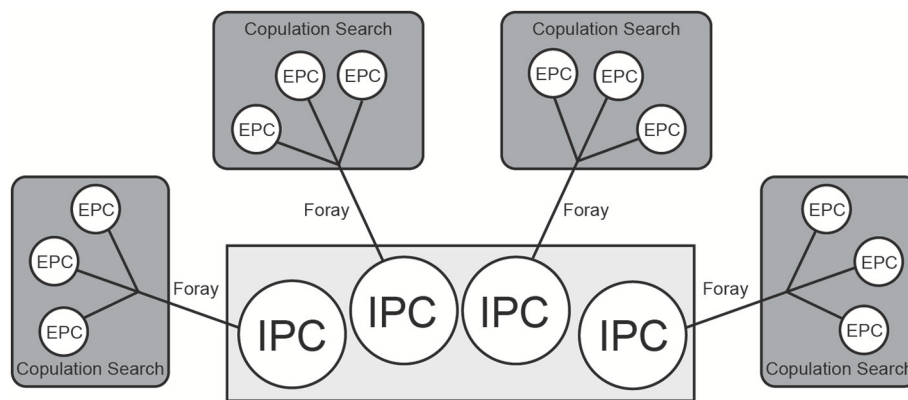


FIGURE 1 | Conceptual diagram of the model portraying the tradeoff between intra-pair copulations (IPC) and extra-pair copulations (EPC). The Monte Carlo method limited us to treating each of the four IPC-EPCs tradeoffs as discrete points in time. In each simulation, the focal male could gain a maximum of 12 EPC offspring (each representing an independent chance), at the potential cost of up to four IPC offspring. A foray refers to each time that the focal male left his territory and risked one IPC for up to three EPCs. Each foray resulted in a copulation search, which refers to the three opportunities to gain up to three EPC offspring.

approximately 3 to 5 pups (following 5,000 simulations), or about the average litter size to ensure biological plausibility.

Taken together, our model created four discrete time-points (forays), where the focal male could gain up to four offspring in each copulation search; three through EPCs and one through IPC. However, the simulated rove was not guaranteed to achieve any EPCs and could lose an IPC if cuckolded by another rove during the copulation search. Therefore, if the focal male never left the territory, then he was guaranteed to not be cuckolded. Using this tactic, the male would forgo all four copulation searches resulting in successful IPCs, but he would achieve no EPCs. If the male always left the territory, the best possible outcome would be 12 offspring from EPCs (see above and **Figure 1**). On the other hand, a roving male might achieve no EPCs on each of the four forays, and could be cuckolded at each turn, producing a total reproductive success of 0. Intermediate numbers of offspring could also be achieved if the focal male was only cuckolded some of the time and successfully achieved EPCs some of the time. Because each foray represented a single point in time, the focal male's female partner could not be visited by more than one male; she could only be visited by a cuckolding male, or no male on each turn. In the event that no male visited the partner, the focal male retained an IPC.

Formally, we calculated the number of total copulations by the simulated focal roving male (or reproductive success; R) using the equation: $R = E + I - C$. Here, E = EPC (or a mating with an unguarded female), I = IPC (or a guaranteed copulation due to successful mate guarding, or no rove intrusion), and C = Cuckold (or the number of times the simulated rove was cuckolded). As detailed above, the total R could vary between 16 ($E = 12$, $I = 4$, $C = 0$) and 0 ($E = 0$, $I = 4$, $C = 4$), and a true resident would yield an R of 4 ($E = 0$, $I = 4$, $C = 0$). Thus, roving can potentially maximize reproductive success only when $R > 4$. When $R = 4$, roving and true residency should be equivocal, and roving would be associated with fitness costs (loss of reproductive opportunities) when $R < 4$.

Statistical Model for Reproductive Success

As discussed above, each focal male had four chances to either rove (leave the territory) or mate guard (remain at the territory). Each time a focal male chose to rove, he had three chances to gain up to three EPCs. We calculated the focal male's R for each of those three EPC attempts by producing a value of E between 0 and 3 and a value of C either 0 or 1. The values of E and C were determined via the probability of events. For an $N \times N$ tile grid with T tiles ($N \times N = T$), only $T-1$ tiles were available to be visited by the focal male. Of those total possible tiles to visit, $T-1$ was divided into three groups: guarded, unguarded, or empty. The number of tiles that were inhabited and unguarded was TU . Thus, $TU/(T-1)$ was the probability of the focal male visiting an unguarded female, if he was roving on the first attempt of the three in a copulation search. The probability on the second attempt was $(TU-1)/(T-2)$. And the probability on the final attempt of the copulation search was $(TU-2)/(T-3)$. Each of the four forays, representing an opportunity to leave the territory to rove, was necessarily treated as independent of each other and therefore the probability of achieving an EPC if the focal male roved was reset to $(TU)/(T-1)$ to begin each search.

The different probabilities for each of the three possible EPCs within a copulation search accounted for the need to exclude the visited tiles during that search. Based on these probabilities, a random number was generated between 1 and the remaining unvisited tiles in that search ($[T-1]$ for the first attempt, $[T-2]$ for the second, and $[T-3]$ for the third). If the number generated was between 1 and the number of remaining unguarded tiles, the focal male was considered to have successfully mated and the value of E increased by one. If any other number was generated, E did not increase. This process repeated two more times for the search, adjusting for the shrinking number of total tiles and unguarded tiles. We reset the number of tiles for the next search and repeated this until all four forays were complete. Similarly, we used the same method to determine C for all roving males, not including the focal male if he was roving. Unlike R , however, the value of C could not be > 1 .

Recall, the goal of this model was to assess the value of roving compared to mate guarding. Thus, we used a baseline value of $R = 4$ as a benchmark to compare R of rovers. Our model was designed to quantify a given roving focal male's reproductive success when the percentage of rovers in the population varied. Thus, we varied the percentage of rovers from 0 to 100% in 10% increments. By varying the proportion of other males that engaged in roving, we were able to assess the threshold at which point a given male would benefit most by adopting a true resident tactic or a roving tactic given the average tactic of other males in the population.

We wanted to consider more complexity in our populations in the second iteration of the model (Condition 2) to better characterize the mating dynamics of prairie voles in the wild. To this end, we created a model as described above that also included male wanderers (i.e., males that remain unpaired and only acquire mates with unguarded females). In natural populations, the occurrence of wanderers varies from 10 to 40% (Thomas and Birney, 1979; Getz et al., 1993; Solomon and Jacquot, 2002; Ophir et al., 2008). We ran the entire model (5,000 simulations per roving percentage, 0 to 100%) with the addition of 10, 20, 30, or 40% wandering males in our Condition 2 simulations. The mechanics of the wandering males and their impact on the focal male used the same method to determine C for all roving males used in Condition 1 simulations. We predicted that adding wandering males would reduce R for the roving tactic because it would create greater male-male competition increasing the costs of leaving females alone.

In a final iteration of the model (Condition 3), we modified Condition 2 to account for an additional important social factor: availability of females. Typically, prairie vole sex ratios are relatively balanced overall (Getz et al., 1981). By adding additional male wanderers to the simulations in Condition 2, we created an unbalanced and male biased sex ratio that could profoundly impact the degree of competition, importance of mate guarding, and the ultimate R that any given male might achieve. Thus, in Condition 3 we simulated a balanced sex ratio that incorporated both resident and wandering males to avoid having an unnaturally skewed male to female sex ratio. To this end, we added unpaired and unguarded females to correspond to every male wanderer introduced in Condition 2. The mechanics of the added unpaired females were the same as the unguarded females in Conditions 1 and 2. As before, we ran the entire model (5,000 simulations per roving percentage, 0 to 100%) with the addition of 10, 20, 30, or 40% wandering males and the corresponding number of unpaired females in Condition 3 simulations. We predicted that adding unpaired females would restore any lost value of R observed in Condition 2 to levels comparable to those seen in Condition 1.

RESULTS

As stated above, each simulation was run 5,000 times at each percentage of roving (from 0 to 100%) in the population (6, 100, 200, 500, and 1,000 male-female pairs) to ensure that our measures of reproductive success were normally distributed.

To confirm this, a histogram was generated for each roving percentage in the population. As expected, all outcomes of the 5,000 simulations were normally distributed at each percentage of roving in the population. **Figure 2** presents the results of one such simulation at 60% roving with a population of 1,000 males and females as an example. All results are reported as the average reproductive success values. Because all pair populations exhibited the same patterns, we primarily focus on the simulations of the largest pair population size (1,000 pairs) below to eliminate redundancy. Nevertheless, results from other population simulation data are reported in **Supplementary Material**.

Condition 1

Our first model attempted to over-simplistically characterize the reproductive success of rovers given other male tactics in the population. **Figure 3A** presents the value for R , represented both as IPCs and EPCs, across the percentages of roving in the population. We used one-sample t -tests to compare the simulated focal male's R to the expected baseline of a true resident tactic ($R = 4$) for each column. T -test significance thresholds were adjusted for multiple comparisons using the False Discovery Rate (FDR) correction (Benjamini and Hochberg, 1995). Our results indicate that the focal male gained significantly more R than baseline [all $t_{s(4,999)} > 2.62$; $p < 0.0104$] in all but the 0–10% roving conditions. When no males in the population were roving (0% roving), the simulated focal male gained no EPCs, presumably because all the females in the population were always guarded. Also, when no males in the population roved, the simulated focal male retained all IPCs because no other males were seeking EPCs. As a result of these constraints, the simulated (roving) male could not achieve a reproductive success value other than 4 at 0% roving in the population, producing an outcome of $R = 4$ without variance. Although all the outcomes for R for the focal male at 10% roving were greater than baseline,

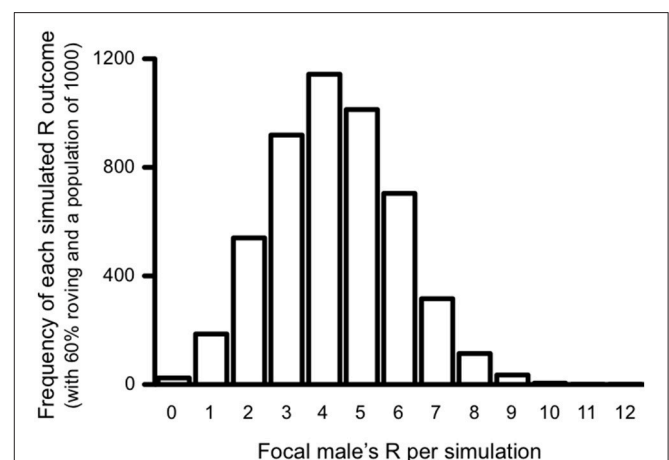
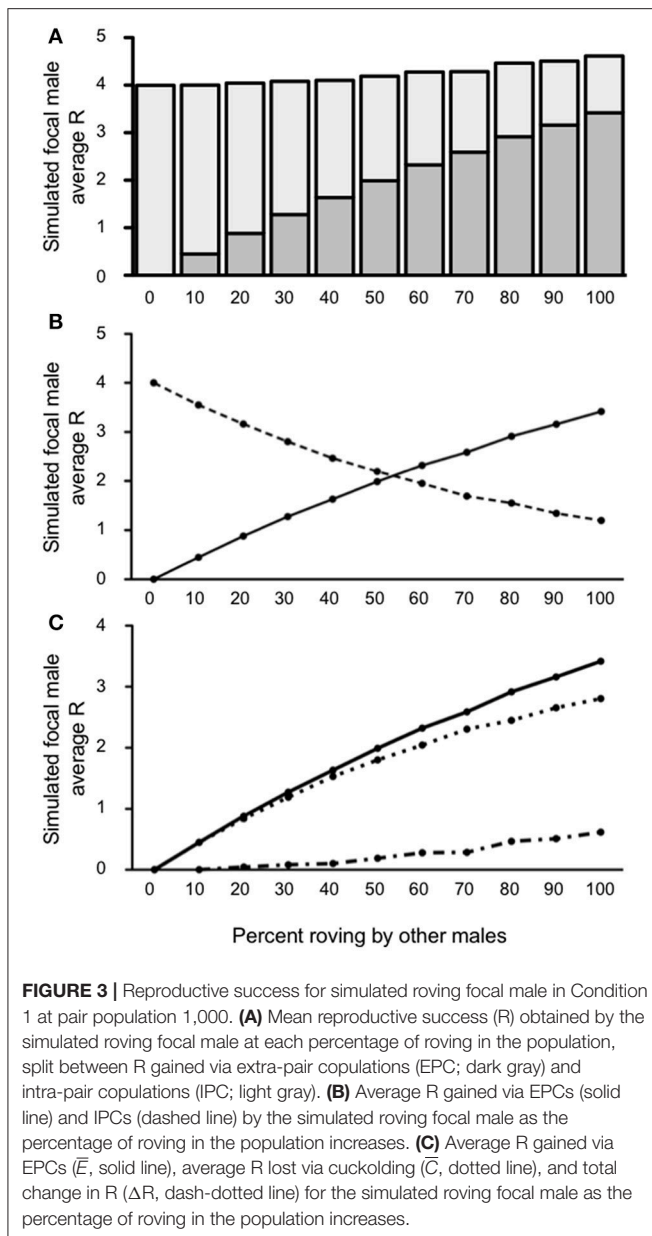


FIGURE 2 | Histogram of total reproductive success (R) outcomes for the simulated roving focal male after 5000 simulations. The histogram represents the simulation results for which 60% of the males in the population roved, and the pair population was 1,000.



the increase in the actual R gained was qualitatively marginal, and non-significant [$t_{(4,999)} = 0.08$; $p = 0.9347$]. At the other extreme, when 100% of the males in the population roved, the simulated focal male achieved the greatest R (4.614). This represents a 13.3% increase over the expected true resident R of 4. Interestingly, the composition of R was drastically different (more EPCs than IPCs) as the percentage of roving increased in the population (see **Figure 3B**).

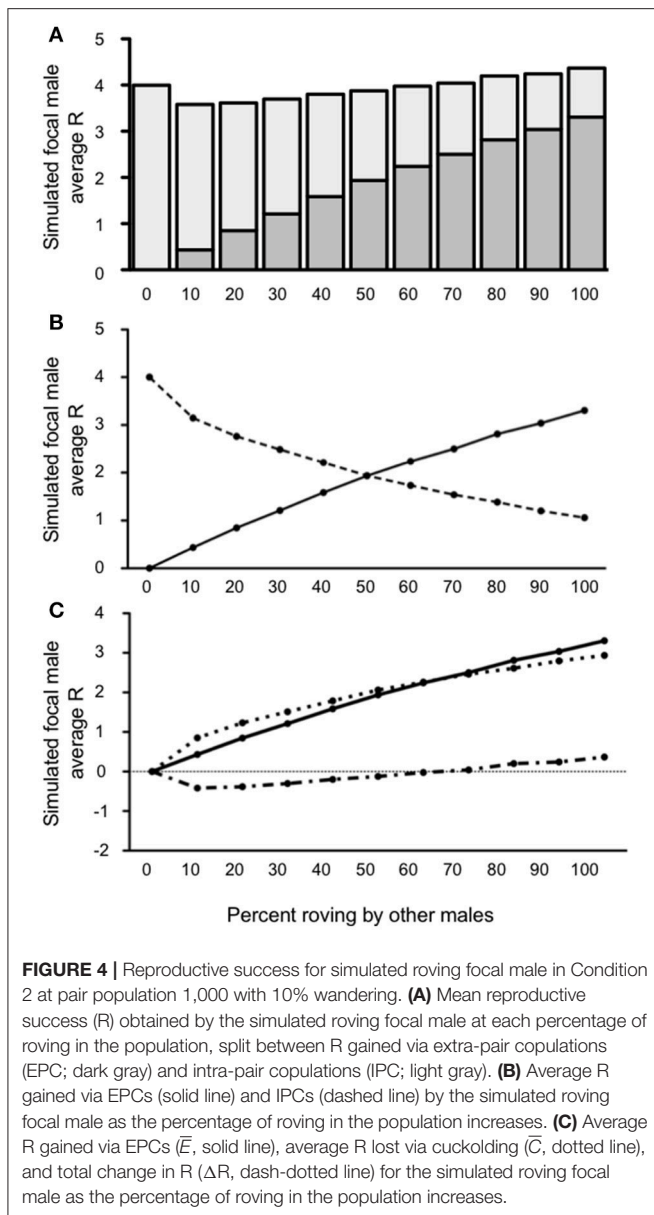
When 50% or less of males in the population roved, the majority of the simulated focal male's reproductive success resulted from IPCs (2.19–4.00) rather than EPCs (0.00–1.99). In contrast, when more than 50% of males in the population roved, most of the simulated focal male's reproductive success came from EPCs (2.32–3.41) rather than from IPCs (1.19–1.95).

The point at which EPC's contributed more to total R than IPCs occurred around 56% roving in the population. Despite this trade-off, the total R from both IPCs and EPCs was relatively constant, but slightly increased (see above). As a result of this relationship, the overall increase in reproductive success (ΔR) increased as a function of the relationship between the average acquired EPCs (\bar{E}), and the average amount of cuckolding (\bar{C}) (**Figure 3C**). Our model showed that when male roving was uncommon in the population, the \bar{E} and \bar{C} for the simulated focal male increased at similar rates. However, as male roving in the population became more common (i.e., higher percent of male roving), \bar{E} began to outpace \bar{C} . This result indicates that males benefit by adopting a roving tactic most when the proportion of other roving males in the population is relatively high.

Condition 2

We modified the original model to incorporate the influence of wandering males (at different proportions in the population) in a second iteration of our model. Using this framework, we created simulations for wanderers at four proportions (10, 20, 30, and 40% wanderers) and we report the results from the lowest (10%) and highest (40%) proportion of wanderers here; the model results for wandering at 20 and 30% are included in **Supplementary Material**. We predicted that increasing the presence of wanderers would decrease the simulated focal male's R due to the increased competition for unguarded females.

Like in condition 1, our model demonstrated that the simulated focal male's R varied as a function of the proportion of rovers in the population when 10% of the male population adopted a wandering tactic (a relatively low incidence of wandering) (see **Figure 4A**). Specifically, the optimal tactic was to be a true resident when there was a low incidence of wandering in the population and roving was uncommon. Adopting a roving tactic was beneficial, however, when the proportion of other rovers increased. The simulated focal male's R was <4 [all $t'_{s(4,999)} \geq 5.529$; all $p's \leq 0.0001$] when 50% or fewer of the males in the population roved, indicating that roving when most males are either wanderers or true residents does not benefit reproductive success. When 60 and 70% of the males in a population roved in the presence of 10% wanderers, the simulated roving male's R was equal to the baseline true resident reproductive success [$R = 4$; $t_{(4,999)} = 1.019$; $p = 0.308$ for 60%; $t_{(4,999)} = 1.733$; $p = 0.0831$ for 70%]. Notably, when roving in the population in the presence of 10% wanderers increased above 70%, the simulated roving male began to accumulate reproductive success that was greater than the true resident payoff of 4 [all $t'_{s(4,999)} \geq 8.157$; all $p's \leq 0.0001$]. Also like in Condition 1, the majority of copulations switching from IPCs to EPCs occurred between 50 and 60% roving (**Figure 4B**). However, Condition 2 differed from Condition 1 with respect to the relationship between \bar{E} and \bar{C} (**Figure 4C**). Specifically, \bar{C} was greater than \bar{E} for roving population percentages below 60%, resulting in a negative ΔR . Initially the rate of \bar{C} outpaced \bar{E} , but plateaued as the roving population reached 60%. Still, \bar{E} was smaller than \bar{C} when roving was relatively uncommon among males in the population. However, \bar{E} steadily increased as the percentage roving in the population increased.



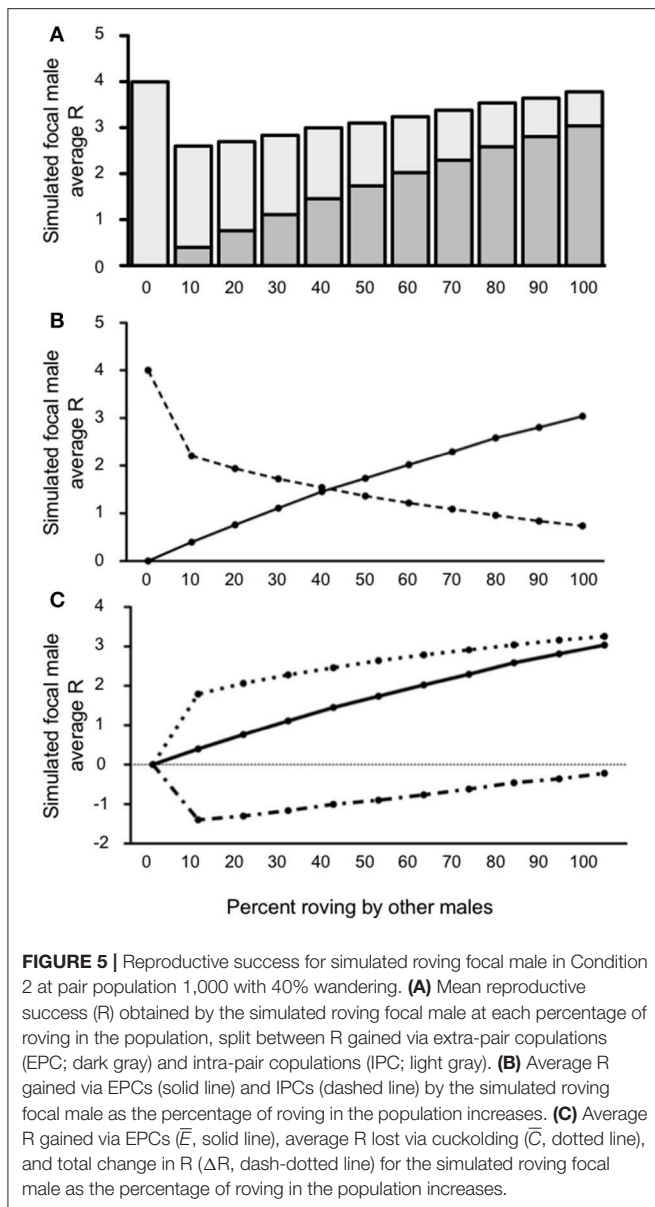
Interestingly, \bar{E} overtook \bar{C} as roving became more common in the population, indicating that roving would be beneficial for a given male (positive ΔR) when roving in the presence of a small proportion of wanderers (10%) becomes increasingly common.

The impact of wandering was most notable when the proportion of wanderers in the population was high. Indeed, when wandering was relatively common (40% wanderers in the population), the simulated focal male achieved less reproductive success than baseline (true residents, $R = 4$) regardless of the proportion of other rovers in the population above 0% [all $t_{(4999)} \geq 9.441$; all p 's ≤ 0.0001]. The one exception to this was when no roving (0%) occurred and the simulated focal male's R was always 4, identical to that of a true resident (Figure 5A). In other words, when wandering was common,

there appeared to be no reproductive benefit to roving, and there was usually a reproductive cost. Furthermore, the reproductive costs associated with roving were greatest when the proportion of roving among other males in the population was between 0% and 50%. The point at which IPCs contributed to R less than EPCs occurred much earlier in this simulated scenario than we found in Condition 1 or when wanderers were relatively uncommon (10% wanderers in the population). In this case, EPCs began to account for the majority of the simulated focal male's R when 40% of the population roved (Figure 5B). Moreover, \bar{C} increased rapidly throughout the simulations (Figure 5C), such that \bar{C} was very large when roving was relatively rare (i.e., low percentages of roving) and continued to increase steadily as more males in the population began to rove. The \bar{E} also increased as the proportion of rovers increased in the population, thereby leaving more and more females unguarded. The ΔR slowly increased as \bar{E} also increased, but \bar{E} never surpassed \bar{C} in this scenario and ΔR therefore remained negative. Taken together, the results from this model showed that when wandering is common (40% wanderers in the population) the optimal reproductive tactic is to adopt true residency, regardless of the roving percentages in the population.

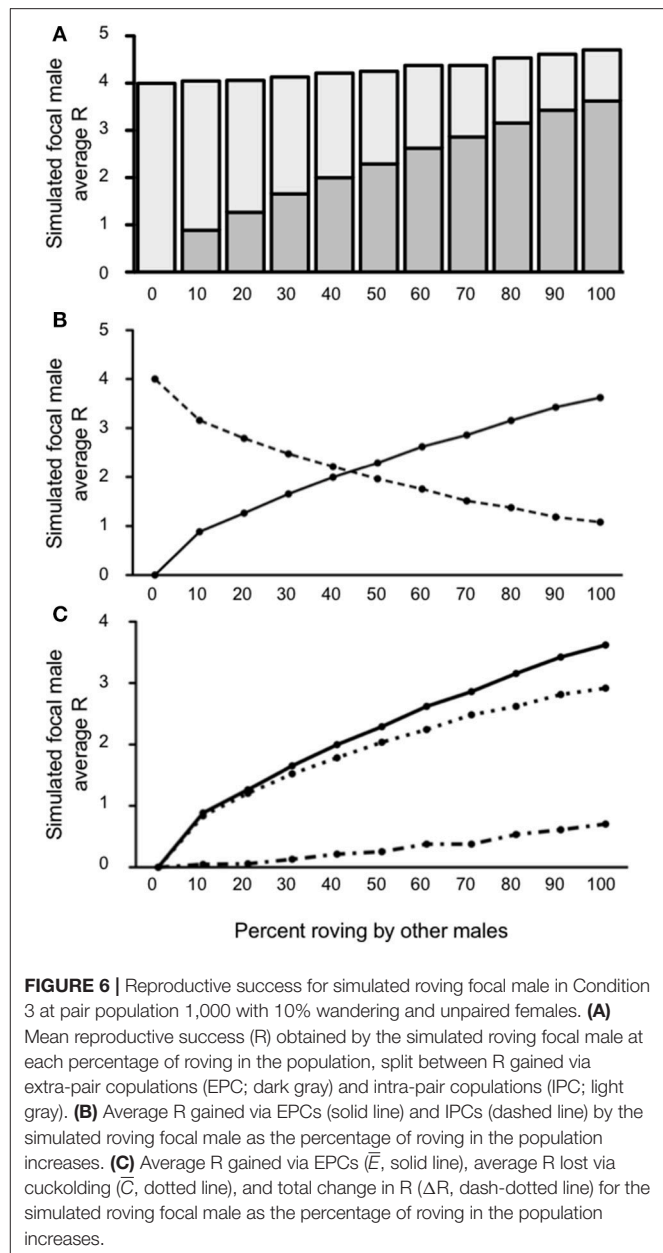
Condition 3

In a final set of simulations we incorporated the social contexts discussed in Conditions 1 and 2, again with a focus on accounting for low (10%) and high (40%) rates of wandering in the population, but now adding unpaired females to represent a more equitable sex ratio in the population. Under this context, we found that at low levels of wandering (10% wanderers in the population), the decision to rove was a successful tactic for the simulated focal male, regardless of the proportion of roving by other males in the population from 10 to 100% [all $t_{(4,999)} \geq 2.799$, all p 's ≤ 0.0051 ; see Figure 6A]. As we observed before, when no other males roved (0% rovers in the population) the simulated focal male always achieved the same reproductive fitness if he roved as he would if he adopted true residency (where $R = 4$). Despite these statistical differences, the simulated focal male's R was qualitatively only marginally better than the true resident baseline ($R = 4$) when the proportion of other males in the population that roved was 50% or less. Specifically, when 50% of the males in the population roved $R = 4.25$ for the simulated focal male, representing a small-scale fitness advantage, but one that could be functionally important over time. Moreover, as the proportion of roving by other males in the population increased beyond 50%, the focal male's R also increased. When the proportion of other males that roved reached 100%, the simulated focal male's reproductive success peaked at $R = 4.70$. Notably, the point at which the simulated focal male's IPCs contributed less to R than his EPCs occurred when 50% or more of the other males in the population roved (Figure 6B). This total positive change in R was best observable by the result indicating that \bar{E} began to outpace \bar{C} (Figure 6C). These results demonstrate that the addition of unpaired females at low levels of wandering (10%) produced very similar outcomes as Condition 1 and seemed to restore an overall balance between which tactic (roving or true residency) resulted in the maximal

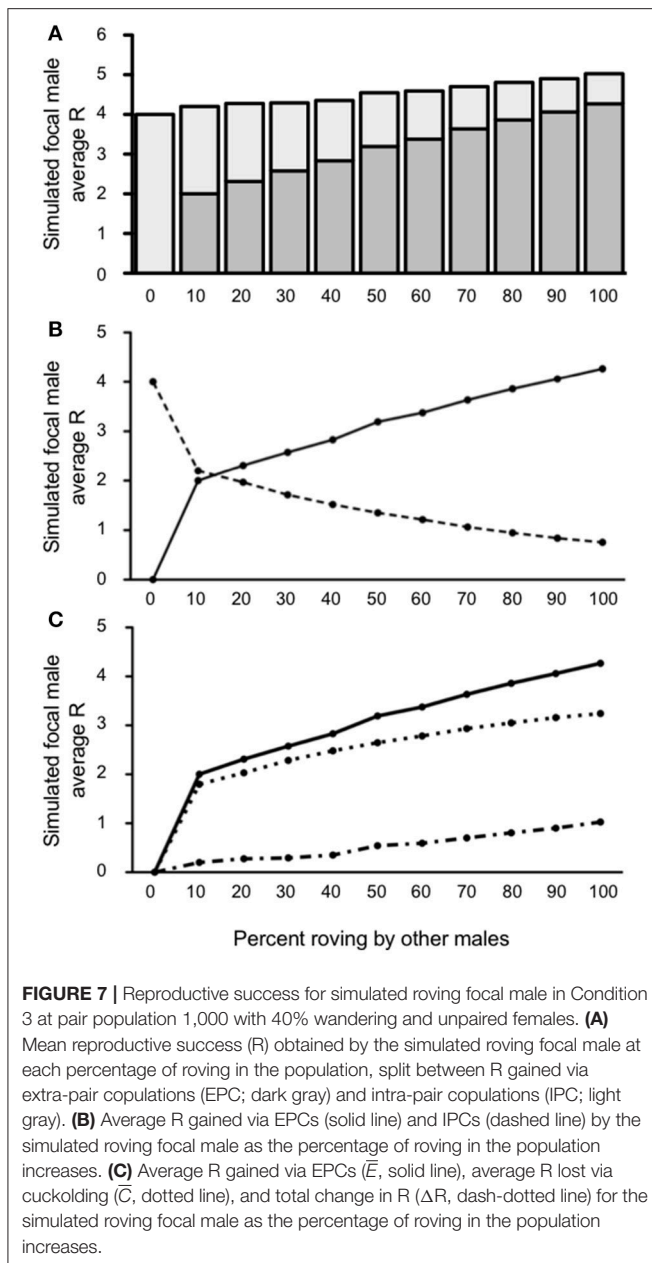


reproductive pay-off for the simulated focal male depending on the proportion of other males that decided to rove.

High levels of wandering (40%) in the presence of a balanced sex ratio greatly increased the reproductive success of the simulated focal male (**Figure 7A**). Just like when wandering was uncommon (10%, see immediately above), the simulated focal male's R was significantly >4 so long as at least some other males in the population also roved [10–100%; all $t_{(4,999)} \geq 8.719$; all p 's < 0.0001]. The increase in R was more pronounced when the proportion of other roving males increased. For example, when 100% of other males in the population were rovers, $R = 5.02$ for the simulated focal male. Not surprisingly, it was under this context where our model predicted the highest rates of EPCs by the simulated focal male than in any other condition for which we ran simulations. Indeed, the model indicated that



when wandering is high and a balanced sex ratio provided some proportion of unpaired females, the focal male lost more IPCs on average, but he also gained more reproductive success via EPCs to compensate and surpass those losses. Notably, this shift in the source of reproductive success (IPC to EPCs) occurred at the earliest point for all conditions and scenarios we modeled—occurring between 10 and 20% of other males' roving in the population (**Figure 7B**). Because the simulated focal male was able to compensate for the loss of IPCs with additional EPCs, the rate of \bar{E} outpaced \bar{C} throughout the simulation resulting in a consistently positive ΔR (**Figure 7C**). Taken together, our model predicted that at high levels of wandering (40%) and in the presence of additional females in the population, the simulated



focal male has a high probability of benefiting from adopting a roving tactic, and reproductive success should continually increase as the rate of roving in the population also increases.

DISCUSSION

Taken together, our models demonstrated that the decision to rove is strongly dependent on the social environment and the degree to which other males have adopted roving and/or wandering alternative tactics. In general, the more common roving becomes in a population, the greater the average fitness payoff is likely to be if a given male decides to rove in kind. The point at which the pay-off to switch to roving from true

residency tends to occur is when half or more of the males in the population rove. Whereas the presence of wanderers in the population increased the net reproductive pay-off of guarding partners and the ultimate value of adopting true residency, the availability of females in the population had the opposite effect. The consistent pattern across all of our simulations showing that reproductive success (R) for roving increases as the proportion of roving by other males increases is noteworthy. This is because although rates of cuckolding increased as male roving became more common (representing a potential fitness cost for the simulated focal male), the simulated focal male's reproductive success from EPCs also increased, and at a rate that outpaced cuckolding.

A Putative Context in Which an Intermediate Strategy Might Evolve

Most mating systems that have alternative tactics usually have two dominant forms. Frequently this is observed as the "territorial"/"sneaker" dynamic (Oliveira et al., 2008). The rarity for more than two tactics to occur in a system is often explained by disruptive selection operating against the intermediate tactics. This would certainly be a more powerful explanation when prominent morphological differences (particularly those that are dictated by developmental pathways) are associated with the alternative tactics. Our model offers potential insight into the ways in which behaviorally based intermediate tactics might evolve. Specifically, our model supports the idea that the social context contributes to the costs and benefits of engaging in the intermediate mating tactic of roving. The behaviorally flexible nature of the tactic in this system is an underlying necessity for this intermediate tactic to be successful. As expected, some population parameters of our model limited the reproductive payoffs associated with roving, resulting in this tactic being detrimental. For example, when wandering was relatively common (40% wanderers in the population) and approximated the rate of wandering observed in some field studies (Thomas and Birney, 1979; Getz et al., 1993), roving was associated with a loss in fitness relative to remaining exclusive and guarding a partner. This was particularly true when the sex ratio was skewed toward more males (i.e., a male biased sex ratio; Condition 2). Similarly, roving tended to be more costly than true residency with a male-biased sex ratio, even when wandering was relatively rare (10% wanderers in the population) and approached a rate that is just under what has been observed in the wild (Ophir et al., 2008). However, under this scenario the presumptive cost of roving was relaxed as roving in the population among other males increased beyond 60%. Still, under a male-biased context with the threat of cuckoldry from other resident males in the population and wanderers present, the fitness costs to roving should limit the frequency of this tactic. Despite these outcomes from our model (particularly under Condition 2), and the theoretical logic that underlies them, roving persists in free-living populations of prairie voles (Solomon et al., 2004; Ophir et al., 2008) suggesting that the conditions that lead to selection against roving must be uncommon, or understudied. Indeed a context with a more equitable sex ratio (like those modeled

in Condition 3) is probably more representative of the natural contexts in which the male reproductive decision-making takes place (see below). Importantly, our model demonstrated that the decision to rove should be flexible and contingent on the social context. It also demonstrated that several social contexts not only permitted the viability of roving, but in many cases that roving was associated with a net benefit over true residency. Indeed, our model indicates that although selection should operate against roving among male prairie voles under some contexts, there are several other contexts in which this “intermediate” tactic can be quite successful.

Balanced Outcomes of Reproductive Success

In a few cases, our model indicated that the reproductive success of the simulated focal male when roving was equivalent to that of true residents. This was true in Condition 1 at 10% roving, and Condition 2 at 60 and 70% roving, for example. Although this outcome did not account for the majority of scenarios we modeled, it did indicate that under some cases the pay-offs of roving would be no better than to mate guard as a true resident. Under these conditions, there are some additional considerations that could bias males to decide to either rove or remain exclusive. For example, our model did not account for the energetic costs associated with guarding or with roving and these would certainly impact the decision of which tactic to adopt. Venturing outside the safety of the territory and home range to engage in EPCs should increase predatory risks and the potential for aggressive encounters with other males, which might bias males to avoid roving when all else is equal. On the other hand, our model did not account for conditions where males could seek EPCs with minimal cost by roving only after intra-pair fertility was secured. Some examples include when the female is past receptivity, pregnant, or caring for pups. Perhaps the incidences of roving and EPCs would be higher than predicted in natural populations when considering these factors. Another consideration is that roving might benefit males if increasing genetic diversity (Hasselquist et al., 1996) or avoiding the potential costs associated with placing “all eggs in one basket” (from predation or disease for example, Krokene et al., 1998) are important factors in a system. Surely factors like these and others that our model did not consider could bias males’ reproductive decisions. Importantly, second order fitness payoffs should be considered if/when the reproductive payoffs are equivalent. Wolff and Macdonald (2004) argued that when all else is reproductively equal, males that remain at the nest and invest in offspring will ultimately outperform males that invest less in their offspring. Engaging in a tactic that enables more paternal care is more likely to produce offspring with greater survivability, if for no other reason other than spending more time at the nest increases the probability that pups will be defended, groomed, thermoregulated, etc. Thus, even if the reproductive costs of successfully fertilizing offspring for a partner or stranger are equivalent for rovers and true residents, the investment in own offspring could provide greater fitness payoffs for true residency and outweigh the payoffs of roving. In support of this notion,

pups raised without fathers demonstrate behavioral and neural phenotypes that could produce offspring that are less prepared for success as adults (Wang and Novak, 1992, 1994; Ahern and Young, 2009; Prounis et al., 2015).

For every iteration of our model, we found a point where reproductive success from EPCs began to contribute more to the simulated focal male’s total R than the reproductive success gained from IPCs. This is an interesting finding considering that previous models have found that males should increase mate guarding as male competition increase in order to preserve paternity (Harts and Kokko, 2013). Our model brings to light an alternative tactic to maximize paternity in the face of increased male competition; to shift to predominantly seeking EPCs. Despite the fact that our simulated focal males gained paternity from EPCs, they also suffered reproductive costs from cuckolding, which limited the average total success that our simulated focal males stood to gain as rovers. This tradeoff is seen in many species, particularly in synchronous breeding conditions, where males gain much of their EPCs when their mate is also fertile and most susceptible to cuckolding (Stutchbury and Morton, 1995; Grunst et al., 2017). If in our simulation \bar{E} did not outpace \bar{C} , then a true resident strategy would be more advantageous and the costs of roving would not outweigh the benefits. Thus, the switch in composition of R represents a potential switch for which rovers may benefit more by primarily pursuing EPCs. In other words, this switch-point captures the trade-off that rovers face: having half of copulations outside a pair ensures some paternity in the event of nest destruction, while potentially raising the young of another male is disadvantageous.

Optimizing Strategy or Merely Getting Lucky

Our model considered the reproductive pay-offs of roving. However, it is unclear if roving is the default tactic in nature. Mixed paternity has been observed in field experiments (Solomon et al., 2004; Ophir et al., 2008), providing strong evidence that prairie voles commonly adopt roving and/or wandering strategies. Even if residency (broadly defined) is the preferred or default tactic among prairie voles, no study of which we are aware has attempted to characterize the frequency of roving residents to true residents, or whether one has a clear reproductive advantage over the other. The current study attempts to predict the contexts in which roving and true residency should be observed, the frequencies at which they should be found, and estimate the potential reproductive pay-offs of the two tactics when they are found. Still, little is known about the individual decision to pursue each tactic. The information that an animal relies upon to best inform mating decisions is often incomplete. It is for this reason that assessment of the social context (however complete or flawed it might be) should serve as a valuable and relatively easily acquired source of information on which inferences about the population could be based. Social information could, thereby, serve as grounds on which reproductive decisions could be based (Jarrige et al., 2015).

Similarly, mating decisions can result in behavioral reinforcement that perpetuates previous decisions. For example, if a male successfully mates with a female other than his partner (regardless of if she is unpaired, or paired and unguarded), the decision to seek EPCs in the future should presumably be reinforced. Likewise, if a resident male encounters and expels several EPC-seeking intruders while mate guarding, he is likely to continue mate guarding. Conversely, regularly encountering other EPC-seeking males while searching for EPCs might indicate to a given male that the risk of being cuckolded is high, and encourage that male to return to his territory. Although mate guarding could plausibly offset the risk of cuckoldry, our model indicates that males should continue seeking EPCs when other EPC-seeking males are common in order to offset the high risk of cuckoldry. Similarly, low rates of intrusions might inform a mate guarding resident male that risk of cuckoldry is low, in turn increasing the probability that that male will search for EPC opportunities.

Whatever the mechanisms that account for the decisions males make, we believe that the social environment offers a rich set of information that individual animals can and should use to assess the costs and benefits of adopting a particular tactic at a given moment in time. For example, in the lekking lesser wax moth, *Achroia grisella*, males change mating behavior depending on the perception of other male competition (Jarrige et al., 2015). When the experimenters included another male observer during mating (perception of increased competition), the focal male mated the female more frequently allocating more sperm than when no observer was present (Jarrige et al., 2015). Additionally, a similar conceptual approach, relying on information in the social environment, has been used to review extra-pair paternity in birds (Maldonado-Chaparro et al., 2018). Maldonado-Chaparro et al. (2018) argue that the local social environment (information about a pair partner) and the extended social environment (individuals in the population) contribute to individual mating decisions.

Finally, we believe that effort aimed at assessing the behavioral mechanisms and the modes by which social information is

gathered and processed is tremendously important if we are to ever fully begin to understand the cognitive ecology that subserves reproductive decision-making. Ultimately, the extent to which mating tactics are flexible and individuals are sensitive to social information will serve as one of the pillars upon which the foundation of understanding the dynamics of mating systems is broadly built. It is our hope that the current study highlights the potential importance of social information on reproductive decision-making, the adoption of mating tactics, and the mating systems that ultimately emerge from them.

AUTHOR CONTRIBUTIONS

MR conceptualized the experiment, developed the experimental design, analyzed data, and wrote the manuscript. LR created the ecological model, ran all simulations, and collected the raw data. AO conceptualized the experiment and wrote the manuscript.

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Longitudinal Trajectories and Inter-parental Dynamics of Prairie Vole Biparental Care

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For altricial mammalian species, early life social bonds are constructed principally between offspring and their mothers, and the mother-offspring relationship sets the trajectory for offspring bio-behavioral development. In the rare subset of monogamous and biparental species, offspring experience an expanded social network which includes a father. Accordingly, in biparental species fathers also have the potential to influence trajectories of offspring development. Previous semi-natural and laboratory study of one monogamous and biparental species, the prairie vole (*Microtus ochrogaster*), has given insight into the role that mothers and fathers play in shaping behavioral phenotypes of offspring. Of particular interest is the influence of biparental care in the development of monogamous behavior in offspring. Here, we first briefly review that influence. We then present novel research which describes how parental investment in prairie voles changes across sequential litters of pups, and the extent to which it is coordinated between mothers and fathers. We use approximately 6 years of archival data on prairie vole parenting to investigate trajectories and inter-parent dynamics in prairie vole parenting. We use a series of latent growth models to assess the stability of parental investment across the first 4 litters. Our findings suggest that prairie voles display sexually dimorphic patterns of change in parental behavior: mothers' investment declines linearly whereas fathers' pattern of change is characterized by initial decline between litters 1 and 2 with subsequent increase from litters 2 to 4. Our findings also support a conclusion that prairie vole paternal care may be better characterized as compensatory—that is, fathers may compensate for decline in maternal investment. Opposing trends in investment between mothers and fathers ultimately imply stability in offspring investment across sequential litters. These findings, combined with previous studies, generate a hypothesis that paternal compensation could play an important role in maintaining the development of monogamous behavioral phenotypes in individual offspring and across cohorts of those offspring. Understanding longitudinal and inter-individual dynamics of complex social behaviors is critical for the informed investigation of both proximate and ultimate mechanisms that may subserve these behaviors.

Keywords: monogamy, prairie vole, biparental care, latent growth model, structural equation model

INTRODUCTION

Social bonds formed in early life are particularly influential in the development of adult social behaviors; early life experiences have incredible potential to shape individual variation (Meaney, 2001). Of particular importance to bio-behavioral development is the role of the mother and the social relationship between her and her offspring in altricial mammals. Of the 3–5% of monogamous mammalian species (Kleiman, 1977), many display biparental care (infant care by both parents), and the dynamics of this parenting are of particular interest given the high frequency of biparental care in humans. It is generally agreed that paternal care (and therefore biparental care) emerged after monogamy (Lukas and Clutton-Brock, 2013, 2014; Opie et al., 2013, 2014). Biparental care is demonstrated in a range of mammals, including but not limited to rodents (e.g., prairie voles, California mice, white-footed mice, etc.) (McGuire and Bemis, 2007), canids (e.g., Maned wolves, red foxes, African wild dogs, etc.) (Malcolm, 1985), and primates (e.g., titi monkeys, common marmoset, Goeldi's monkey, humans, etc.) (Schradin et al., 2003; Fernandez-Duque et al., 2009; Bales and Jarcho, 2013).

Under conditions of biparental care, developing young have an expanded early life social network, allowing mothers to distribute the labor of parental investment and allowing offspring the benefit of a slower and safer development (Hrdy, 2009). In biparental rodent species, offspring may benefit from improved rates of survival and growth (McGuire and Bemis, 2007). Among biparental canids, young benefit from increased defense and provisioning (Malcolm, 1985). In biparental primates, particularly arboreal New World monkeys, fathers play an important role in the transport of offspring (Tardif, 1994; Fernandez-Duque et al., 2009). The relative role of fathers can be quite extensive, such as in the case of the titi monkey (*Callicebus moloch*), in which fathers do the majority of infant transport and in which infants show extensive distress upon separation from the father, but not mother (Hoffman et al., 1995).

The way in which maternal and paternal investment changes across time (i.e., across sequential births or litters) varies by sex and species (McGuire and Bemis, 2007), and changes in parental investment are typically considered in terms of new vs. experienced parents, or in other words primiparous vs. multiparous parents. Some studies report that multiparous female rats and mice (notably, both generally monoparental species), when rearing pups alone, are more responsive to pups than primiparous conspecifics (Kinsley, 1994), while others report no difference (McGuire and Bemis, 2007). However, when presented with a sexually mature male conspecific, multiparous female Norway rats in post-partum estrus more effectively switch between maternal and copulatory behaviors than primiparous mothers, as in part indicated by more effective pup retrievals (Gilbert et al., 1984). Previous study of the biparental prairie vole is conflicted, either demonstrating that multiparous females display more parental care than primiparous females (Wang and Novak, 1994a) or that primiparous females display more parental care than multiparous females (Stone and Bales, 2010). Paternal care either does not change (Wang and Novak, 1994a) or is greater in primiparous than multiparous prairie vole fathers (Stone and Bales, 2010). In the biparental coppery

titi monkey, infants reared by multiparous mothers are more likely to survive than those reared by primiparous mothers, although neither infant growth rate nor maternal behavior are shown to be different between primiparous and multiparous mothers (Jarcho et al., 2012). In humans, first-time parents of both sexes show more arousal to cues of infant crying than non-parents and experienced parents (Boukydis and Burgess, 1982).

Notably, previous study of the effect of parity on parental behavior has been primarily conducted in mothers, with little research on the effect of parity on paternal care or on the interplay between maternal and paternal care. A synthesis of the findings in biparental species would indicate that parity has no effect on parental care (Jarcho et al., 2012), that more parental experience begets more parental attention and care (Boukydis and Burgess, 1982; Wang and Novak, 1994a), or that parental experience yields a decrease in parental care (Stone and Bales, 2010). Here, we briefly review evidence from one model monogamous and biparental species, the prairie vole (*Microtus ochrogaster*), suggesting an important role of paternal care in the development of the monogamous behavioral phenotype. We then consider the connection between parental experience and parental behavior using a novel application of latent growth curve modeling.

The prairie vole is a socially monogamous arvicoline rodent native to the North American Midwest (for review on taxonomy, conservation, and distribution, see Laerm and Ford, 2007). Field observations of prairie voles are relatively difficult, as the species navigates their environment along running paths in tall grass and nests in underground burrows (Gier and Cooksey, 1967). The dominant mating system among prairie voles is monogamy, with family units consisting of the breeding female and male along with their offspring, of which the majority will remain in their natal nest living with parents and other siblings for life (Getz and Carter, 1980; Getz et al., 1981, 1987, 2003, 2005; McGuire et al., 1993; McGuire and Getz, 2012). Under natural conditions, the average tenure of a breeding pair is short (approximately 42 ± 14 days) with termination most often due to the death of one or both partners (Getz and Hofmann, 1986); it is unlikely that new pair bonds are formed following the loss of a mate (Carter et al., 1997; Pizzuto and Getz, 1998).

More direct observation of mating and parenting behaviors was facilitated by the successful integration of prairie voles into the laboratory in the late 1960s (Gier and Cooksey, 1967). Ovulation in female prairie voles is induced in the presence of male prairie voles (Carter et al., 1980), and both sexes demonstrate incest avoidance (McGuire and Getz, 1981). Gestation for the species is 20–21 days, and successive litters of pups may be born every 21–24 days (Gier and Cooksey, 1967). Prairie vole mothers and fathers both demonstrate a high frequency of parental behavior in laboratory and in seminatural conditions (Hartung and Dewsbury, 1979; Thomas and Birney, 1979; Solomon, 1993; Lonstein and de Vries, 1999; McGuire et al., 2007). The pattern of prairie vole parental care is sexually dimorphic, with mothers investing more time in direct pup-directed behaviors and nest maintenance than fathers (Solomon, 1993; McGuire et al., 2007; although, see Hartung and Dewsbury, 1979).

Biparental care in prairie voles persists throughout the pre-weaning period (post-natal days 0–21), and maternal behavior (e.g., brooding, nursing, and grooming) and time in nest is greatest in the perinatal period and declines across the pre-weaning period (McGuire and Novak, 1984). Natural variation in frequency and type of prairie vole parenting behavior in the perinatal period has been demonstrated to have significant consequences for bio-behavioral development of offspring (Perkeybile et al., 2013; Arias Del Razo and Bales, 2016). Directly observable developmental consequences result from natural variation in the quantity of parental care given by prairie vole parents to their offspring (i.e., pups)—that is, pups reared by low contact parents develop more quickly than conspecifics reared by high contact parents, as demonstrated through the advent of developmental milestones (i.e., opening of eyes, eating solid food, leaving the nest autonomously, etc.; Perkeybile et al., 2013; although, see Wang and Novak, 1994b). Increased parental contact promotes social affiliation (Arias Del Razo and Bales, 2016), and the behavioral phenotypes of monogamy (e.g., partner preference formation) are also facilitated by increased parental contact (Bales et al., 2007; Ahern and Young, 2009; Stone and Bales, 2010). Natural variation in prairie vole parental behavior induces differences in the size of pup cortical fields (Seelke et al., 2016a), intrinsic connections within the primary somatosensory cortex (Seelke et al., 2016b), as well as neuroendocrine function (Perkeybile and Bales, 2016). For a review of possible mechanisms behind these effects, see Perkeybile and Bales (2017).

While the developmental consequences of variation in parental care are becoming increasingly understood, the dynamic processes that result in observable patterns of parental behavior remain understudied. One might hypothesize that, in rodents, parental behavior remains consistent across litters, that is, parental behavior does not significantly vary from one litter to the next. One might also hypothesize that parental behavior in a monogamous, biparental species ought to be characterized as a dyadic process with extensive coordination and mutual-reliance between partner parents. Under seminatural conditions, pups reared under biparental care are left unattended less often than conspecifics reared under mother only conditions, suggesting some level of coordination between mothers and fathers (McGuire et al., 2007); however, previous study of maternal care under conditions of paternal absence also presents little evidence for maternal compensation for paternal loss, suggesting that parenting in prairie vole mothers may function independently of the paternal behavior of their partner (McGuire et al., 2007; Ahern et al., 2011). Still, there remains little empirical evidence to either support or reject these conceptualizations of prairie vole parenting.

In this study, we seek to explore two behavioral processes with the potential to alter developmental trajectories of monogamy in offspring: the nature of parenting across litters; and, the nature of parenting between partner parents. In the case of the former, we consider if parental care changes from the first litter and across a series of subsequent litters, or if parental care does in fact remain consistent across litters. For the latter process, we consider the extent to which individual parents' behaviors

are influenced by those behaviors of their partner. Here, we hypothesize consistency of parental care across litters, and we hypothesize that parenting behavior in prairie voles can be characterized as a coordinated process.

Latent Growth Curve Models (LGMs) are a useful way to conceptualize and analyze hypothesized processes of change, including change in means (McArdle and Epstein, 1987). LGMs can be applied, even using incomplete data, for analysis of processes that display no growth (level-only) and/or linear or non-linear models that include both an intercept and slope (Ferrer et al., 2004). These models can incorporate covariates (both time-varying and time-invariant) to examine the effect of external factors on the process (McArdle and Epstein, 1987). Ultimately, these models can also be expanded to accommodate multivariate processes (McArdle, 1988, 2009; Ferrer and McArdle, 2003; Bollen and Curran, 2006).

Here, we attempt to use all of these methods to better characterize the nature of prairie vole parenting as it unfolds across a pair's first 4l. We consider models of no growth and change at the level of the mother, father, and dyad; and we attempt integration of covariates of parental age and litter size. Ultimately, such a characterization is needed to ascertain what potential there might be for parental care to directly influence behavioral phenotypes of monogamy (e.g., partner preference, selective aggression, etc.) in offspring. Because offspring phenotypes of monogamy are directly influenced by parental care, characterization of change in parental care elucidates our understanding of how phenotypes of monogamy may or may not vary from one litter to the next. This study explores the stability of parental care, a moderator of monogamous phenotypes, to better inform our understanding of prairie vole parenting as a process.

The use of LGMs to analyze longitudinal trajectories of biparental care in prairie voles is, to the best of our knowledge, novel. Estimates of trajectories of biparental care produced using LGMs take into account within-parent trajectories across subsequent litters, which should yield a more reliable prediction of a trajectory generalizable across all observed individuals (Bollen and Curran, 2006). This approach contrasts with cross-sectional methods used in previous studies on the effect of parity on prairie vole parental care. Moreover, where previous studies have compared primiparous and multiparous mothers, our study uses a litter-to-litter approach to capture a more detailed, dynamic process. Finally, this study also attempts to bring both maternal and paternal care into the context of the biparental dyad, i.e., how maternal and paternal care compare and contrast across subsequent litters.

METHODS

Research Questions

Here, the two behavioral processes we sought to investigate were explored in a series of questions. A fundamental question concerned the true unit of analysis—that is, should the level of analysis be *the individual* or *the dyad*? We first considered if, when treated as independent actors, male and female parents demonstrate unique patterns of change across four sequentially

reared litters. Further, we considered if change can be best characterized with a model of no growth, linear growth, or non-linear growth. A model of no growth could be indicative of either constant (e.g., invariant) parenting or an inability to identify a mean trajectory followed by all parents. Support for a linear growth model would indicate an approximately equal growth or decline of the mean parental behavior across litters. A non-linear growth model would indicate growth or decline of the mean parental behavior in an unequal way across litters. We made the same considerations of change at the level of the dyad, using a model that considers the dyad as two covarying individuals—that is, we considered an alternative model in which the level of analysis is the individual (either male or female parent), but in which some interaction between partner parents is permitted through time-varying covariances.

Subjects and Laboratory Conditions

All data were collected from the prairie vole colony at the University of California, Davis over a period of approximately 6 years. One-hundred forty-one parenting dyads were selected from archival data on the basis that no experimental manipulation had been applied to the dyad or their pups and that observations of parenting behavior had been made upon the dyad during post-natal day (PND) one through three. All subjects were descendants of wild prairie voles that were originally caught near Champaign, Illinois and continually outbred to maintain genetic diversity, and included new genetic stock from another captive colony in 2015. Animals were maintained on a 14:10 light-dark cycle with lights on at 06:00. Water and food (high-fiber Purina rabbit chow) were provided *ad libitum*. Breeder pairs and their offspring were maintained and observed in large, polycarbonate cages (44 × 22 × 16 cm). Each cage had aspen wood bedding (i.e., Sani-Chips), and cotton was provided for nesting material. Humidity was controlled and room temperature maintained near 70°F. All pups were weaned from the home cage on PND20, and subsequent litters of pups were not exposed to older siblings. Home cages were left undisturbed beyond weekly cage changes and three daily checks of food and water.

Litter size for each cage was recorded at PND1 and corrected at weaning in the event of a miscount. Corresponding information on litter size in each observed litter and the age of each parent at the time of birth of their first litter was also found in laboratory archives and recorded when available. The mean number of pups per litter across all measured litters (1–4) was 4.75 ($SD = 1.47$); the number of pups per litter ranged from 1 to 8. At the time of birth of their first litter, mothers' mean age was 99.56 days ($SD = 26.56$); the range of maternal age at first litter was 64 to 180 days. At the same time point, the fathers had a mean age of 145 days ($SD = 73.00$); the range of paternal age at first litter was 51–422 days.

When measures of parental behavior were (in some cases) available for many litters, litters one through four were used in this study. This decision was both practical and theoretical. Practically, the availability of observational data beyond litter four was increasingly sparse. Under natural conditions, prairie vole dyads are unlikely to produce more than four litters of pups before the death of one or both parents, as the average

life expectancy of both male and female prairie voles is short (approximately 50–80 days), with most breeding pairs surviving only 1–2 months (Getz and Hofmann, 1986; Getz et al., 1997, 2000; Thomas and Wolff, 2004). In laboratory conditions, animals may live over 2 years and breeding pairs may produce well in excess of 10 successive litters.

Behavioral Measures

Parental care observations were collected through live focal sampling by graduate students and undergraduate research assistants who were trained and validated according to the ethogram presented in Perkeybile et al. (2013). Observers sat approximately 1–2 feet from the home cage, and observations were recorded on laptop computers using behavioral software (www.behaviortracker.com). For each litter, both mother and father were simultaneously observed for 20 min focal samples during PND1–3. Mothers were distinguished from fathers using individual characteristics (e.g., size, color, etc.) in addition to observations of pup attachment to nipples or evidence that nursing had occurred (e.g., swollen nipples or milk-wetted fur). Variation in parental behavior in this perinatal period has been predictive of pup bio-behavioral outcomes (Perkeybile et al., 2013). The perinatal period is also the period in which the most extensive parental care is shown, and it is a period in which, prior to fur growth, pups have little ability to thermoregulate (Gebczynski, 1981; Blake, 1992). The observed home cage was left undisturbed on a metal cage rack with overhead coverage from the rack above. Observations were not conducted on days on which cage changes occurred.

The primary outcome measure was a composite score of pup-directed behaviors (PDBs), which was calculated for each respective litter from the focal sampling output. The number of seconds spent in a variety of pup-directed behaviors (i.e., nursing, licking and grooming, physical contact, etc.) were summed across each focal sample, added across all focal samples for each respective litter, and then divided by the total number of focal samples collected (between two and four) for a mean value of pup-directed behavior observed for each parent in the perinatal period of each respective litter. In all, 93.2% of composite scores were generated from four focal samples, 4.1% from three focal samples, and 2.6% from two focal samples with a mean of 3.91 (median = 4) focal samples per composite score of PDBs. Some behaviors were not considered mutually exclusive (e.g., nursing and licking), thus allowing for summed totals of PDB to exceed 1,200 s; and maternal and paternal care were often contemporaneous.

Missing Data

The mean number of litters observed per breeder pair was 2.13 (median = 2 litters). Across all 141 breeding pairs and across all four time points, 303 litters were observed; Thus, of the 564 potential opportunities for observation (i.e., across all 141 breeder pairs at four time points), there were 261 missing observations, due to attrition across the 4 litters. A complete summary of the distribution of missing observations (by litter) is provided in **Table 1**. The number of missing observations in the data increased as the litter number increased from 19 in litter 1 to

TABLE 1 | Descriptive statistics for pup-directed behaviors, number of litters observed, and number of litters left unobserved (of the 141 total observed pairs) across litters and by litter.

Variable	Min	Mean	Max	SEM	Nobs	Nmissing
Maternal PDB	250.0	1055.0	1522.0	14.5	303	261
Litter 1	385.0	1100.7	1489.0	21.0	122	19
Litter 2	346.2	1066.0	1508.0	24.0	95	46
Litter 3	278.3	1032.7	1380.0	32.7	53	88
Litter 4	250.0	1051.0	1522.0	53.1	33	108
Paternal PDB	0.0	628.5	1366.0	17.7	303	261
Litter 1	0.0	622.3	1218.0	26.9	122	19
Litter 2	19.0	594.1	1230.0	31.7	95	46
Litter 3	11.0	641.1	1366.0	43.8	53	88
Litter 4	15.0	730.0	1286.0	52.5	33	108

108 in litter 4. Data were not missing because of active researcher selection for any particular behavioral trait(s). This behavioral paradigm was designed originally as a behavioral diagnostic to classify new parents as low-, medium, or high-contact parents, and the diagnostic was originally designed such that generally only the first two litters of a pair were observed. However, in some circumstances, later litters (i.e., litters 3 and 4) had been opportunistically observed. The choice to halt observation after two litters or to continue observation in later litters was not determined by any behavioral characteristic of the pairs observed. For some pairs, these observations were not necessarily in consecutive litters (due to inconvenience, logistic difficulty, etc. of observation timing). For example, for some pairs there are observations for litters 1 and 3, rather than litters 1 and 2; and, for others there were observations for litters 1–4. Thus, we believe it is reasonable to assume data to be missing completely at random (MCAR), and we do not expect missing observations to introduce bias into the estimated model parameters.

Model Specification

In this study, we explored three separate clusters of models. The first cluster contains two identical sets of models for mothers and fathers. The second cluster adds to the cluster 1 models both a time-varying covariate for age and a time-varying covariate for litter size. The third cluster allows for time-varying covariance between parenting partners—that is, if a significant covariation exists between maternal and paternal care, and how that covariation exists across successive litters. The level of analysis was primarily exploratory, with the primary interest being in model selection based on comparative indices of model fit, i.e., what pattern of change best describes the observed data on parental care across successive litters. Within each cluster, models of *no growth*, *linear growth*, and *non-linear growth* were compared in a structural equation modeling framework (see Kline, 2016 for further reading) to determine which growth pattern best fit observed data from mothers and fathers independently (i.e., independent maternal and paternal models), and mothers and fathers within the context of one-another (i.e., a maternal-paternal bivariate model). The models run for

mothers and fathers could not be compared directly to each other given different data were used for the generation of their respective models. However, model parameters for each sample can be interpreted and compared (yet informally) across samples. Path diagrams representing the respective models are found in (Figures 3A–C) along with detail for their interpretation. For further reading on these techniques, we recommend Bollen and Curran (2006).

Model Cluster 1: Independent Maternal and Paternal Models

There were three models in this cluster: a No-Growth Model, a Linear Growth Model, and a Non-linear Growth Model (see Figure 1A). All three models include an observed outcome measure of a composite score of pup-directed behaviors for each litter (1–4).

The No-Growth Model for the maternal parent is therefore expressed as:

$$X_{[t]n} = x_{[0]n} + e_{[t]n}$$

$$x_{[0]n} = \mu_{x[0]} + d_{x[0]n}$$

where $X_{[t]n}$ is the observed score for the outcome variable (i.e., PDBs) at any given point, t (i.e., litter 1–4), $x_{[0]n}$ is an individual's intercept (i.e., PDB for litter 1), and $e_{[t]n}$ is the residual variance; μ is a fixed group mean, and d represents the variation in such mean across individuals. Whereas the no-growth model predicts only a starting value (i.e., the intercept) and no further change, this model is expanded upon in the Linear Growth Model and the Non-linear Growth Model to include an individual's slope (i.e., pattern of change in PDBs from litter 1 onward). Thus, the general model is:

$$X_{[t]n} = x_{[0]n} + B_{[t]} \cdot x_{sn} + e_{[t]n}$$

$$x_{[0]n} = \mu_{x[0]} + d_{x[0]n}$$

$$x_{[s]n} = \mu_{x[s]} + d_{x[s]n}$$

where $B_{[t]}$ represents a set of coefficients expressing the shape of the curve. These coefficients can be fixed to test various hypotheses of growth. For example, for a linear growth model, the coefficients can be fixed as = 0, 0.33, 0.67, 1, such that the effect of parity on the outcome of PDBs is constrained to a linear pattern. Alternatively, some of the $B_{[t]}$ can be estimated from the data to detect non-linear changes, thus to test the Non-linear Growth Model, which is also often referred to as a latent basis model. For this, the first and last loading (leading from x_s to the PDBs for litters 1 and 4, respectively) can be set to 0 and 1, respectively, and the loadings for litters 2 and 3 are left to be freely estimated from the data.

Model Cluster 2: Independent Maternal and Paternal Models With Covariates

Cluster two expanded on the models in cluster one with the addition of covariates for parental age at the birth of their first litter and litter size for each litter (see Figure 1B). There were similarly three models in this cluster: a No-Growth Model, a Linear Model, and a Non-linear Growth Model. All models

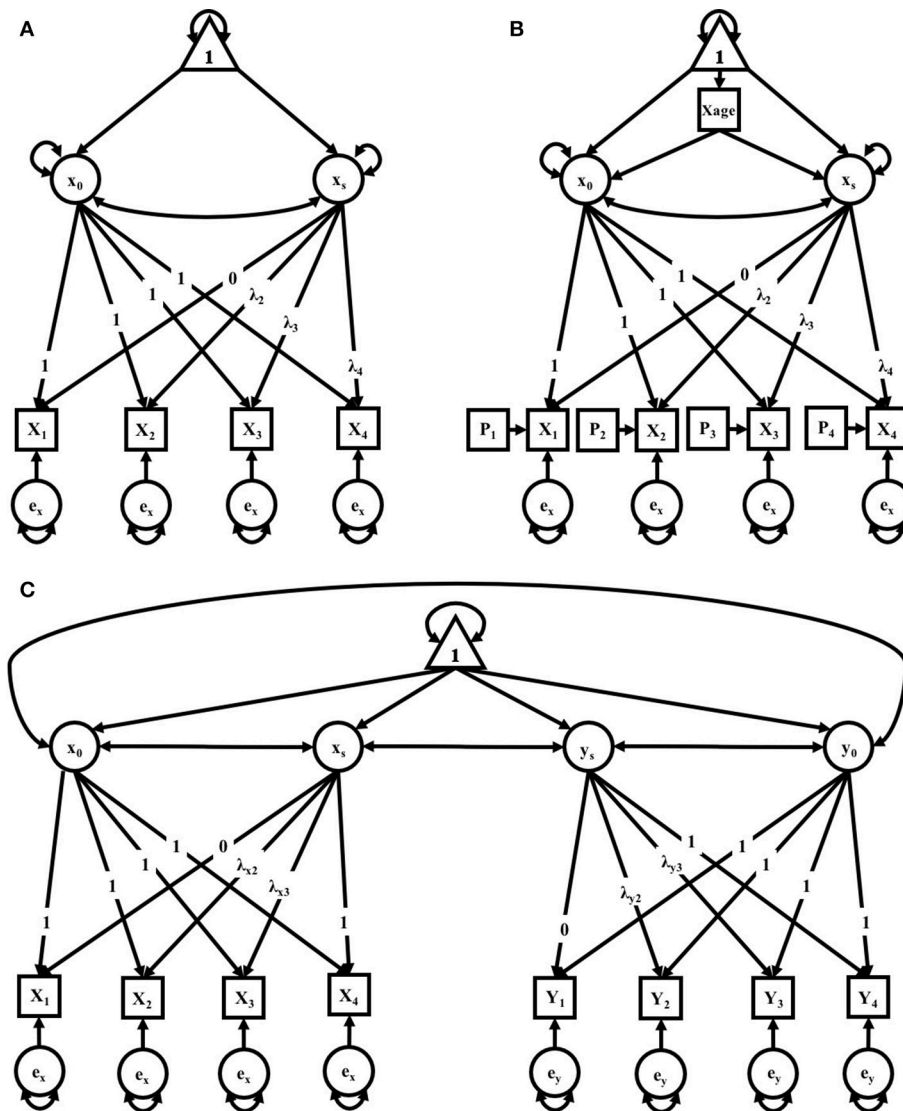


FIGURE 1 | (A–C) path diagrams for Clusters 1–3. Path diagrams are visual representations of model parameters and their relationships, in which each type of model parameter is provided a graphical symbol, i.e., squares or rectangles are used for observed variables (i.e., indicators), circles are used for latent variables and error terms, straight arrows for hypothetical causal or direct effects, and curved arrows for covariances (Kline, 2016). In all path diagrams presented here **(A–C)**, composite scores of pub-directed behaviors (PDBs) for each litter (1–4) are represented as sequential squares (from left to right) around indicators by X_t or Y_t , where t = litter. Each represented composite score (e.g., X_t or Y_t) has an error term, e_x or e_y , which represents variance not explained by the composite scores, including variance due to measurement error. Elements of regression, intercept and slope, are represented by x_0 and x_s , respectively, and circumscribed to represent their status as latent variables, each with their own covariance and a covariance between the two. Triangles containing the number 1 represent the inclusion of a term for the analysis of means. As the intercept for each model does not change across time, straight arrows from the intercept factor to each time point are labeled with the number 1, indicating a constraint on estimation of the regression between the intercept and each time point. Straight arrows from the slope factor (x_s or y_s) are variably constrained, according to the growth pattern in consideration. Thus, for the no growth model, regression paths from the slope factor to indicators at all time points are constrained to 0; for the linear growth model, regression paths from the slope factor to indicators are constrained to 0, .33, .67, and 1 for litters 1, 2, 3, and 4, respectively; and for the non-linear growth model, only the regression path from the slope factor to litter 1 is constrained (to 0) and all others are freely estimated, as represented by the term λ_t . Path diagram **(A)** represents models tested in Cluster 1, the Independent Maternal and Paternal Models, which includes only the common parameters outlined above. Path diagram **(B)** represents models tested in Cluster 2, the Independent Maternal and Paternal Models with Covariates, which expands upon the model given for Cluster 1 with the addition of a time-invariant covariate for parental age (X_{age}) and time-varying covariates for litter size (P_t), both given in squares. Path diagram **(C)** represents models tested in Cluster 3, the Maternal-Paternal Bivariate Model, which expands upon the model given for Cluster 1 by presenting models for change in maternal and paternal care in parallel with double headed arrows representing covariance between the two models, and therefore covarying trajectories of change between mothers and fathers.

included an observed measure for each litter (1–4), each with its own residual and time-varying covariate (P_t) to account for litter size. Both models also accounted for parental age with the inclusion of an exogenous, time-invariant covariate for age (X_{age} , Y_{age} , respectively). In the models generated for the combined dyad, both exogenous covariates for age are included. The model for which time does not contribute to a pattern of growth for the maternal parent is expressed as:

$$X_{[t]n} = x_{[0]n} + P_{[t]n} + X_{age_n} + e_{[t]n}$$

$$x_{[0]n} = \mu_{x[0]} + d_{x[0]n}$$

Model Cluster 3: Maternal-Paternal Bivariate Model

Cluster 3 took the same elements from the first cluster to form a bivariate growth model, which estimates two individual models (maternal and paternal) simultaneously. This third cluster of models allows for covariation between the female and male parent such that the intercepts and slopes of the two covary. Here, again, factor loadings could be fixed to = 0, .33, .67, 1, or left open and allowed to vary freely in order to form the Non-linear Growth Model (see **Figure 1C**); specifically, maternal factor loadings were fixed for a linear model while paternal factor loadings were fixed for a non-linear growth model, according to the best fitting models in Cluster 1. Either could be modified, as in cluster 2, to include either or both time-invariant and/or time-varying covariates. This model affords new parameter estimates, including the covariance between slopes of each parent (i.e., the extent to which changes are related), as well as the covariance between the parents' intercepts.

Statistical Analyses

All models were fit with the package *lavaan* (Rosseel, 2012) in R (R Core Team, 2017) using full information maximum likelihood (FIML). All behavioral scores were divided by 100 to put all measures in the same metric and aid convergence. Standard measures of model fit (chi-square difference test, CFI, TLI, RMSEA) and information criteria [AIC_i , $\Delta_i(AIC)$, and $w_i(AIC)$] were used to evaluate the models.

“Good fit” is first characterized, here, by a p -value above 0.05, an indication that the hypothesis of exact model fit is not rejected. Ideal Comparative Fit Index (CFI; Bentler, 1990) and Tucker-Lewis Index (TLI; Tucker and Lewis, 1973) scores are >0.95 (Hu and Bentler, 1999). Better Root Mean Square Error of Approximation (RMSEA; Steiger, 1990) scores are below 0.080. A chi-square difference test can be used to determine significant differences (improvement) in fit between two models that are nested, that is, when one model can be represented as a more constrained sub-model of the other. Thus, our no growth model is nested within linear growth model, which is in turn nested within the non-linear growth model.

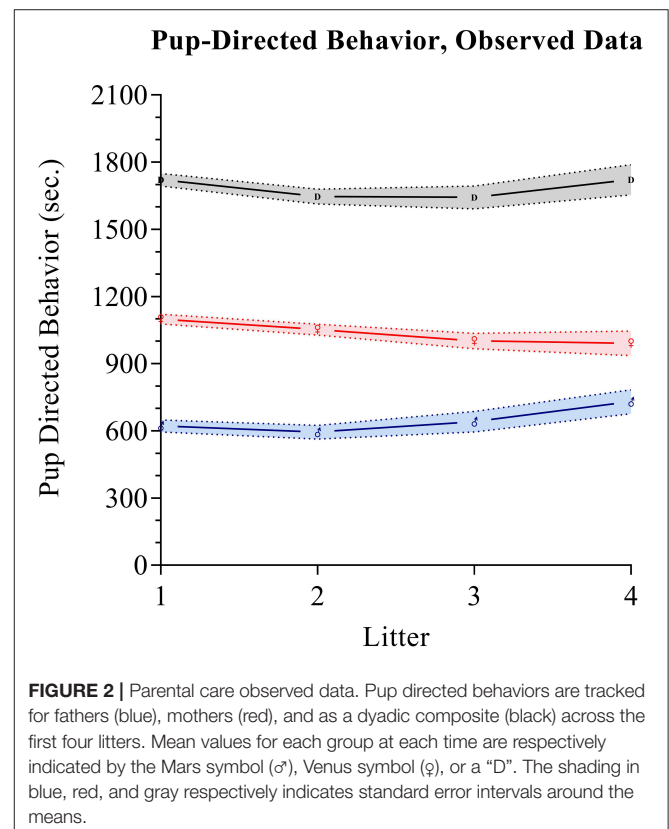
The additional measure of fit, Akaike's Information Criterion (AIC_i), was generated as well as transformations of AIC_i , including $\Delta_i(AIC)$, the change in AIC between each model and the best candidate model, and Akaike Weights [$w_i(AIC)$], which can be interpreted as a probability that a model is the best in its set (Wagenmakers and Farrell, 2004). All fit indices for Cluster 1 and Cluster 3 can be found in **Table 3**.

In some cases, there was an occurrence of a *Heywood Case*, an instance in which there are parameter estimates of illogical value (Chen et al., 2001; Kolenikov and Bollen, 2012). Here, such cases were restricted to the production of negative slope variances; thus, where the model with negative variances demonstrated significant improvement of model fit over alternative models, the variance and all covariances for the slope parameter were fixed to zero and treated as a “corrected” model. Corrected latent base models are comparable to no-growth models, as the no-growth models are nested within the latent base model; model comparison between corrected latent base models and linear models is, however, impossible for lack of nesting.

RESULTS

Descriptive Statistics

Maternal pup-directed behaviors have a mean value of 1,055 ($SD = 251.8$) with a range of 250–1,522. Maternal PDBs appear close to normally distributed with a slight negative skew and kurtosis. Paternal PDBs have a mean value of 628.5 ($SD = 307.9$) with a range of 0–1,366. Paternal PDBs appear to be normally distributed with positive skewness and kurtosis. Combined dyad PDBs (i.e., the sum of maternal and paternal PDBs) have a mean value of 1,684 ($SD = 335.9$) with a range of 585.8–2606.0. Dyad PDBs are normally distributed. The slope of plotted observed means across the four measured litters for maternal PDB, paternal PDB, and combined dyad PDB appear flat-to-negative, flat-to-positive, and flat-to-positive, respectively (see **Figure 2**).



Correlation coefficients between maternal and paternal care care at each time point are presented in **Table 2**.

Independent Maternal and Paternal Models

For analyses of maternal care, the exact-fit hypothesis was not rejected for no-growth [$\chi^2_M(11) = 18.521, p = 0.070$], linear [$\chi^2_M(8) = 9.923, p = 0.318$], and latent base [$\chi^2_M(6) = 10.194, p = 0.117$] models, giving first evidence that all three models could fit the observed data. A chi-square difference test shows that the addition of a linear growth parameter significantly improves model fit compared to the no-growth model [$\chi^2_D(3) = 9.229, p = 0.026$] (see **Table 3, Figure 3A**). The non-linear growth model, however, does not significantly improve model fit over the no-growth model [$\chi^2_D(5) = 8.328, p = 0.139$]. CFI, TLI, RMSEA, and AIC_i show better fit for the linear model over the no-growth model, and w_i(AIC) sets the conditional probability that the linear model is the best fitting model of the set at 0.778.

For analyses of paternal care, the exact-fit hypothesis is not rejected for no-growth [$\chi^2_M(11) = 17.246, p = 0.101$], linear [$\chi^2_M(8) = 15.021, p = 0.059$], and latent base [$\chi^2_M(6) = 6.537, p = 0.366$] models, giving first evidence that all three models could fit the observed data; however, the non-linear growth model demonstrated negative variance while also displaying better

relative fit (as assessed by CFI, TLI, RMSEA, and AIC_i) than either the no-growth and linear models. For a corrected non-linear growth model, the exact-fit hypothesis is also not rejected [$\chi^2_M(8) = 5.565, p = 0.585$] and the corrected latent base model shows improvement of model fit compared to the no-growth model [$\chi^2_D(3) = 10.681, p = 0.014$] (see **Table 3, Figure 3B**). The conditional probability that the corrected non-linear growth model is the best fitting model of the set is 0.912.

Independent Maternal and Paternal Models With Covariates

For both instances (maternal care and paternal care), the addition of covariates controlling for age and litter size yielded models with exceptionally poor fit. Cluster 2 models yield estimates of intercept and slope that are comparable, yet further from the observed data, to those from models in Cluster 1.

Maternal-Paternal Bivariate Model

For analyses of parental care in a corrected bivariate process, in which the trajectory for maternal care is fixed as linear and the trajectory for paternal care is fixed as non-linear, the exact-fit hypothesis is not rejected [$\chi^2_M(24) = 30.616, p = 0.165$]. The result of negative slope variance for paternal care and subsequent correction for the Heywood Case means results for slope covariance between maternal and paternal care are uninterpretable. The covariance of intercepts for maternal and paternal care is -0.057 ($p = 0.93$) (see **Table 3, Figure 3C**).

DISCUSSION

Parenting Changes Over Time

We hypothesized that prairie vole parental care does not vary from one litter to the next. Our results depart from this hypothesis of consistency. Contrary to previous observations that indicated increased parental care in multiparous mothers (Wang and Novak, 1994b), our findings suggest that maternal care is best described as having a negative trajectory, with a decline across litters (see **Figures 3A,C**). Differences in methodology

TABLE 2 | Correlation coefficients for measures of pup-directed behaviors across litters (1–4) by individual (Female, X; Male, Y).

	X1	X2	X3	X4	Y1	Y2	Y3	Y4
X1	1.00							
X2	0.391	1.00						
X3	0.312	0.361	1.00					
X4	0.235	−0.033	0.257	1.00				
Y1	−0.346	0.063	0.005	−0.116	1.00			
Y2	0.028	−0.318	0.112	−0.422	0.314	1.00		
Y3	−0.059	0.081	−0.251	−0.056	0.448	0.237	1.00	
Y4	−0.440	0.014	−0.126	−0.235	0.630	0.457	0.506	1.00

TABLE 3 | Indices of model fit.

Group	Model	χ^2	DF	P	CFI	TLI	RMSEA	AIC _i	Δ_i (AIC)	w _i (AIC)
Mothers	No Growth	18.521	11	0.070	0.687	0.829	0.070	1400.279	3.23	0.155
	Linear	9.929	8	0.318	0.946	0.960	0.034	1397.049	0	0.778
	Non-linear	10.194	6	0.117	0.825	0.825	0.070	1401.951	4.90	0.067
Fathers	No Growth	17.246	11	0.101	0.766	0.872	0.063	1524.841	4.68	0.088
	Linear	15.021	8	0.059	0.737	0.803	0.079	4319.349	2799.20	0
	Non-linear	6.537	6	0.366	0.980	0.980	0.025	4314.865	2794.71	0
	CNL	6.565	8	0.584	1.000	1.040	0.000	1520.160	0	0.912
Bivariate	Linear/CNL	30.616	28	0.165	0.935	0.924	0.044	2880.914	–	–

Rows in bold indicate the model with best comparative fit (as determined through comparative fit indices) for each observed group [Mothers, Fathers, or the Dyad (Bivariate)]. Models include patterns of no growth, linear growth, non-linear growth, corrected non-linear (CNL) growth and/or a Linear/CNL Mix. Analyses of Cluster 2 are not given; for the mother, father, and dyad, the addition of covariates of litter size and parental age yielded models with exceptionally poor fit/non-converging models. In order from left to right, model fit indices presented are chi-square statistic (χ^2), degrees of freedom (DF), p-value (P), Comparative Fit Index (CFI), Tucker-Lewis Index (TLI), Root Mean Square Error of Approximation (RMSEA), Akaike's Information Criterion (AIC_i), Δ_i (AIC), and Akaike Weights [w_i(AIC)].

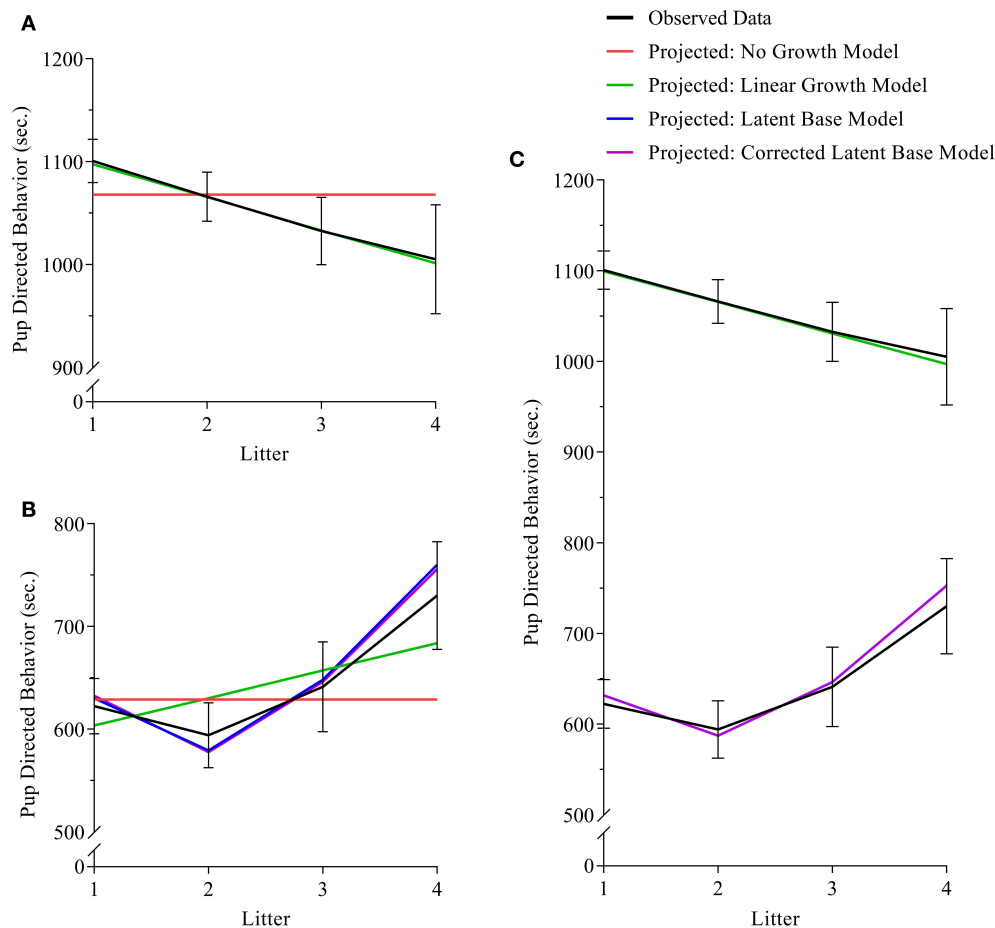


FIGURE 3 | (A–C) (A) maternal, (B) paternal, and (C) bivariate dyadic models of pup-directed behavior. In all sub-figures: black lines indicate the plotted means of the sample data; red lines indicated the plotted means of the calculated no-growth model; green lines indicate the plotted means of the calculated linear model; blue and purple lines indicate the plotted means of the uncorrected and corrected latent base models, respectively. In **Figure 1C**, the black line in the lower half of the figure indicates the means of sample data for fathers, and the black line in the upper half of the figure indicates the means of sample data for mothers. Black error bars represent standard error.

may explain these differences, particularly the use of cross-sectional vs. mixed-longitudinal analysis in the former and current studies, respectively, as well as significant differences in sample size. Previous study of parental change and parity in male and female prairie vole parents from litter 1 and 2 (using longitudinal methods) also find a decline in parental care from litters 1 and 2 (Stone and Bales, 2010). Moreover, our findings of decline in maternal care with parental experience aligns more closely with the human literature (Boukydis and Burgess, 1982). The mechanism behind a decline in care for neonates across subsequent litters is not particularly clear. We hypothesize that mothers may become more efficient in their investment with parenting experience; alternatively, reduced sensitivity to pup cues may play some role, as could the effect of aging. *Post-hoc* investigation of the individual behaviors that compose the composite score for PDBs show that decline in maternal care is reflected in time nursing (Supplementary Table 1, Supplementary Figure 3); a similar decline is observed in time spent in the nest

(Supplementary Table 1, Supplementary Figure 1), which is not a component of the composite score for PDBs.

Paternal care is best described as having an initial decline from the first to second litter and a subsequent uptake in paternal activity from litter 2 through 4 (see **Figures 3B,C**). The comparison of mothers' and fathers' respective patterns of parental care highlights their opposing trajectories (**Figures 2, 3C**). A pattern of initial decline followed by an increase in paternal behavior could be explained by competing factors; that is, one responsible for the decline, and another which counteracts the decline. Similar mechanisms behind maternal care decline could be responsible for paternal care decline, including an improved paternal efficiency, reduced sensitivity, or a broad effect of aging. We would then hypothesize that paternal care increases following an initial decline in order to compensate for maternal decline in investment in of their offspring. *Post-hoc* investigation of paternal care shows that the paternal pattern of decline and subsequent incline is reflected in paternal time in

nest (Supplementary Table 1, Supplementary Figure 2), which is not a component of the composite score for PDBs. The increase of PDBs appears to be driven largely by an increase in huddling and non-huddling contact (Supplementary Table 1, Supplementary Figures 5, 7, respectively). Other individual parental behaviors are displayed in Supplementary Figures 4, 6, 8–11.

Compensatory Fathers

The models of individual change for mothers and fathers fit quite well and suggest opposing trends in parental care between mothers and fathers from litters 2 to 4. The general stability seen in the composite of maternal and paternal behavior (Figure 2) may be a consequence of opposing trends, where when mothers decline in maternal care across time, fathers display compensatory behavior to fill an apparent void. We hypothesize that the increase of paternal care could be a response intended to decrease the amount of time pups are left unattended on the nest, or more simply that fathers are aware of unattended pups and act to ameliorate the pups' condition. A potential mechanism by which fathers become aware of unattended pups is through pup ultrasonic vocalization, to which male prairie voles are responsive (Rabon et al., 2001). The mechanism behind paternal motivation to respond to ultrasonic vocalization may be mediated through stress, as pup-vocalizations may be stress inducing and male prairie voles have been demonstrated to increase parental care when stressed (Bales et al., 2006). Moreover, the initial decline and subsequent increase of paternal care parallels previous trends of weight loss and subsequent recovery in fathers across their first 31 of pups (Campbell et al., 2009). This suggests energetics may play an important role in the patterns of paternal behavior.

One challenge to the hypothesis of independent actors is the observation of “forced baby sitting”—an behavior in which mothers or fathers may push one another back into the nest—, which, while anecdotal, we and others have observed in prairie voles under laboratory conditions (although, not seen in McGuire et al., 2007) and empirically observed in other vole species (e.g., *M. socialis guentheri*; Libhaber and Eilam, 2002); thus, it is possible that mothers increasingly encourage paternal behavior through forced baby sitting with each successive litter.

Consequences for Offspring

Responsive fathers may play an important role in stabilizing early life experiences for offspring, particularly offspring of later litters which experience less maternal care. Without the stabilizing influence of fathers, pups in later litters might experience significantly less direct parental care than those of earlier litters. Despite shared genetics, we could then expect differential adult behavioral phenotypes in siblings of different litters if fathers cannot or do not stabilize the parental environment.

In prairie voles, increased parental investment may result in higher survival rate in the laboratory (Wang and Novak, 1994a), although other studies would suggest no such effect in the laboratory setting (McGuire et al., 1992; McGuire et al., 2007; Wang and Novak, 1992). Under more challenging circumstances, the conferred benefit of paternal care on pup survival may be more pronounced in some biparental species, such as under

conditions of cold temperature (in California mice, Gubernick et al., 1993), presence of predators (in prairie voles, Getz et al., 1992), or increased effort to access food (in California mice, Gubernick et al., 1993; Cantoni and Brown, 1997). High contact parenting is also associated with slower development, as indicated through the achievement of developmental milestones of eye opening, leaving the nest, and eating solid food (Perkeybile et al., 2013). Contrasts between high- and low-contact parents also indicate variation in neuroendocrine (Perkeybile and Bales, 2016) and cortical development (Seelke et al., 2016a); for example, pups receiving high tactile contact develop greater intrinsic and more localized connections in the primary somatosensory area than their low-contact counterparts (Seelke et al., 2016b).

Of particular relevance here is the expression of monogamy in adulthood, which has been linked to early life experience of parental care. Experimental manipulations of the family unit during the neonatal period induce increased parental behavior, an effect that resulted in facilitated partner preference formation in manipulated (higher contact) female offspring, but inhibited partner preference formation in non-manipulated (lower-contact) female offspring (Bales et al., 2007). High contact parenting as a result of natural variation also promotes social behavior (e.g., physical contact) when compared to medium- and low-contact parenting (Arias Del Razo and Bales, 2016). These effects are demonstrated to have intergenerational effects on parenting and alloparenting behaviors (Stone and Bales, 2010; Arias Del Razo and Bales, 2016). After paternal deprivation, male and female offspring reared with their mother only show deficits in pair-bond formation, thus indicating that paternal care facilitates partner preference formation (Ahern and Young, 2009).

Another potential stabilizing factor not considered here is the presence of alloparental care from non-dispersed siblings. The presence of fathers and alloparental siblings is associated with decline in maternal care and time spent in the natal nest as well as increased maternal locomotion, eating, and drinking (Wang and Novak, 1992). Pups reared in the presence of a mother, father and alloparents are left unattended less frequently than those reared with only a mother (Solomon, 1991). While well reviewed by Kenkel et al. (2017), more research on the effects of alloparental care on early life development is needed.

Limitations and Future Directions

A major limitation of this study is the relatively small sample size of 141 dyads (282 individuals), which is compounded by a high rate of missing data. As discussed earlier, the missing data are likely to be missing completely at random, which means that they have little potential to introduce systematic bias into the results. However, missing data translate directly into loss of power and loss of precision in the estimation. Continued data collection, particularly in later litters (e.g., litters 3 and 4) would be particularly beneficial to future analyses. Another benefit of an increased sample size would be the ability to utilize multiple groups models to consider the classification of “high contact” and “low contact” parents—that is, parents who show stability in the extremes of parenting over time. It should also be noted that

our analyses do not provide information as to whether observed change from one litter to the next is statistically significant, but rather that one pattern of change fits the observed data significantly better than another. Whether or not these changes in parental behavior translate into significant differences in pup bio-behavioral development is not studied here; however, the hypothesis that parity affects pup bio-behavioral development is testable.

Another major limitation of this study is its having been done with individuals exclusively from a single laboratory colony that had been outbred several generations prior from an ancestral population in natural conditions. The removal of the study population from natural environmental cues could result in patterns specific to laboratory conditions, just as could any laboratory study of this species. However, the amount of control on external conditions (e.g., *ad libitum* provisioning of food and water, no threat of predation or natural disaster, etc.) aids in our identification of this latent process of change in parental behavior that might otherwise be masked by confounding environmental factors. Finally, it should be noted that the age of the parents observed for this study is significantly older than what would be seen in the wild. It is unlikely that in the wild, pairs would live to produce more than 21 or to begin parenting at such an advanced age. Nevertheless, given the longevity of voles in the laboratory, these findings are particularly useful for those who study the species in the laboratory setting.

CONCLUSIONS

This study provides valuable information for our understanding of the process of parenting in a monogamous species. We find evidence, here, that prairie vole parenting is indeed a process of change, rather than a constant. Our findings support previous findings of sexual dimorphism in the parental behaviors of prairie voles, and our findings extend the conceptualization of sexual dimorphism to patterns of change in parental behaviors across litters. Moreover, we find evidence for a potentially important role of fathers in the maintenance of monogamous behavior in offspring. These results generate new hypotheses that can and should be tested with further research. Thus, we conclude that prairie vole parenting is a dynamic process of two individuals, each with their own potential to dramatically alter trajectories of bio-behavioral development in offspring. Understanding longitudinal and inter-individual dynamics of

complex social behaviors and their development is critical for the informed investigation of both proximate and ultimate mechanisms that may subserve these very behaviors.

ETHICS STATEMENT

Protocols for general husbandry and any studies generative of data used here and collected from the standing vole breeding colony were reviewed and approved by the Institutional Animal Care and Use Committee (IACUC) at the University of California, Davis, and complied with National Institutes of Health ethical guidelines as set forth in the Guide for Lab Animal Care.

AUTHOR CONTRIBUTIONS

FR designed and executed all aspects of this work under the advisement of MR, EF, and KB. All authors participated in writing and editing of this article.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2018.00073/full#supplementary-material>

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Dopamine Modulation of Reunion Behavior in Short and Long Term Marmoset Pairs

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One major neurobiological substrate regulating social processes is dopamine (DA). DA is implicated in social behavior in species as diverse as fish and birds, and has an established role in regulating relationships between mates in socially monogamous rodents. Marmoset monkeys display traits associated with social monogamy including high rates of affiliation, biparental care, distress upon separation, and aggression toward strangers; several of these behavioral patterns change throughout the development of relationships. This temporal change may represent changing demands, as pairs are likely to jointly face new experiences (e.g., parenthood) throughout pairing. We investigated the role of DA and pairing length on social behavior during reunion after separation from the mate. Marmosets were removed from their home environment and treated with agonists and antagonists for the D1 and D2 receptor subtypes. They were exposed to a novel environment containing an opposite-sex stranger and their pair mate, and then reunited with their mate in the home enclosure. Marmosets in long term pairs exhibited higher levels of food sharing during reunion than marmosets in short term pairs, with females in long term pairs sharing food more than males; no sex difference was observed in short term pairs. Subjects in short term pairs spent more time grooming their mate than receiving grooming during reunion, while marmosets in long term pairs displayed similar amounts of both initiated and received grooming. DA treatment altered pair-level behavior. When females received either a D2 agonist or antagonist, short term pairs spent less time in proximity, compared to when males received the same treatments. In long term pairs, treatment of females with either a D1 agonist or antagonist resulted in pairs spending less time in social proximity than when males were treated. These findings suggest that the function of the DA system in mate behavior may be similar between rodents and primates, with the D1 system modulating the expression of behavior in long term pairs and the D2 system regulating behavior in short term pairs. Furthermore, these results supplement a large body of work suggestive of deep evolutionary roots of the DA system in regulating social behavior.

Keywords: social monogamy, pairing length, social relationships, formation, mating system

INTRODUCTION

A close, selective, though not necessarily exclusive, social and sexual relationship with a single partner is a hallmark of social monogamy. There are several behavioral components of social monogamy, all of which reference this relationship between partners. Within the construct of social monogamy there is variability both within, and especially among, species in the specific social and behavioral components that are displayed (Díaz-Muñoz and Bales, 2015; Tecot et al., 2016). In nonhuman primates, social monogamy is associated with a host of behavioral traits, including a selective social preference for the mate over other conspecifics, biparental care, and aggression toward same- or opposite-sex conspecifics (French et al., 2017). Of particular interest are several phenomena associated with separation of the mating pair, which include distress upon separation from the mate, social buffering of stressful experiences while in the presence of the mate, and high rates of affiliative behavior upon reunion with the mate after a period of social separation (French et al., 2017).

Marmoset monkeys (*Callithrix* spp.) display many characteristics associated with social monogamy. These features include social buffering of stress responses by the presence of the pair mate (Smith et al., 1998; Rukstalis and French, 2005; Cavanaugh et al., 2015), affiliation toward the mate (Ågmo et al., 2012), biparental care (Snowdon, 1996; Ziegler et al., 2009), and aggression toward same-sex conspecifics (Evans, 1983; Ross et al., 2004; Ross and French, 2011). However, marmosets do not display a strong selective social preference for their mate in standard partner preference tests (Smith et al., 2010; Cavanaugh et al., 2014), and they also demonstrate high levels of social and sexual interest in opposite-sex strangers (Cavanaugh et al., 2014; Mustoe et al., 2015). In addition, there is variability in group demography in wild marmosets, ranging from single pair and offspring to multimale/multifemale groups (Digby, 1999; Sousa et al., 2005). Thus, marmosets demonstrate traits that are associated with social monogamy, as well as flexible and conditional social responses in ways that resemble the complexities of human “social monogamy” (Chapais, 2013).

One behavioral trait that may be particularly important to the stability of a mating pair is the degree to which pairs re-establish their relationship during reunion after a period of separation, stress, or disruption. Separation from social partners is often accompanied by behavioral signs of distress, and increased glucocorticoid concentrations (Smith et al., 1998; DeVries et al., 2003; Hennessy et al., 2009; French et al., 2012; Ziegler and Crockford, 2017). Monogamous male titi monkeys demonstrate differential brain activation in regions associated with the regulation of social behavior (limbic and striatal) during separation from a mate, and release of the neuropeptide oxytocin upon reunion with the mate (Hinde et al., 2016), indicating physiological responses to both separation from, and reunion with, a mate. In marmosets, separation from a mating partner and short- or long-term exposure to a novel environment is associated with elevated hormonal stress responses (cortisol increases) (Smith et al., 1998; Cavanaugh et al., 2016). Furthermore, levels of affiliation are higher between

mates after a separation, compared to pre-separation levels, suggesting that elevated rates of affiliative behavior upon reunion in marmosets is an important mechanism for down-regulating the negative affect and stress response associated with partner separation (Shepherd and French, 1999; Cavanaugh et al., 2018). High rates of affiliative behavior upon reunion among other classes of social relationships in marmosets is also associated with regulation of the arousal associated with separation from close social contacts. Juvenile marmosets that engage in high levels of affiliation during reunion after social isolation demonstrate a faster return to baseline glucocorticoid levels (Taylor et al., 2015), highlighting the importance of reunion behavior across social contexts in marmosets.

The notion that reunion behavior modulates stress responses to separation is supported by the observation that marmosets experiencing a stressor *with* their partner exhibit no difference in affiliative behavior upon reunion from pre-stressor levels (Smith et al., 1998). This suggests that in marmosets when a mate is present during a stressor, behavioral and physiological responses during the stressor are reduced (e.g., social buffering), and the need to downregulate stress upon reunion in the home enclosure is hence less important (Cavanaugh et al., 2016). The duration of separation also shapes the nature of affiliative interactions upon reunion. Marmoset pairs separated for an extended period of time (7 days) showed elevated pair-directed affiliation upon reunion, while short separations (5–15 min) did not increase rates of affiliative behavior (Duarte et al., 2017), suggesting that longer separations require larger behavioral responses during reunion, presumably to aid in re-establishment of the social relationship. Together, these data suggest that high rates of affiliative interactions with significant social partners after a period of separation has important consequences for regulating the biobehavioral responses associated with social separation. Thus, reunion after separation represents a time at which individuals in the pair are engaging in behavior to reduce behavioral and endocrine components of the stress response and to re-establish social relationships.

The expression of reunion behavior with a pair mate may be dependent on the phase of the relationship. The underlying relationship between mating partners in socially monogamous rodents has been delineated into two phases: formation and maintenance. Each of these phases is associated with distinct behavioral traits, as well as neurobiology, in rodent models of social monogamy (i.e., prairie voles) (Young and Wang, 2004; Curtis et al., 2006; Lim and Young, 2006; Young et al., 2008, 2011; Aragona and Wang, 2009). Social preference for the mate is a key marker of pair bond formation, and in voles is observed after 24 h of cohabitation (Williams et al., 1992), while selective aggression toward conspecifics is considered a marker of pair bond maintenance and is tied to onset of mating with a mate (Carter et al., 1995). While the phases of pair formation and maintenance in prairie voles appear to follow a strict and short timeline, primates tend to show longer and more variable transitions in relationships (Maninger et al., 2017). Patterns of behavior between mates in marmosets shift across time, including levels of sexual behavior (typically, high in the beginning and lower with increased length of pairing) and affiliative social

behavior across pairing (typically, lower in the beginning and increasing with pairing length) (Schaffner et al., 1995; Ågmo et al., 2012; c.f. Evans and Poole, 1984). Thus, while there are differences in affiliative behavior in marmosets between short and long term pairs, there is no clear behavioral marker of an “established” pair. Furthermore, social monogamy is theorized to have evolved from an environment in which females were highly dispersed and males experienced fitness benefits from guarding and maintaining a relationship with a single female (Lukas and Clutton-Brock, 2013). Thus, male and female mates experience a suite of different evolutionary pressures in terms of mating success. While males may benefit from engaging in as many sexual encounters as possible given the minimal cost associated with sperm production, they also benefit from continuous presence near their female mates (e.g., mate guarding, proximity maintenance) to reduce the risk of her engaging in extra pair copulations. Especially in species that exhibit paternal care, it is critically important, from an energetic perspective, that males raise offspring genetically related to them. It is therefore likely that males and females will display different behavioral profiles from one another at both initial and later stages of a relationship.

The neurotransmitter dopamine (DA) has been identified as a key player in decision making and social behavior in species as diverse as invertebrate leeches, fish, birds, and mammals (O’Connell and Hofmann, 2011). Of particular note is the role that DA plays in the formation and maintenance of bonds between mating partners in rodents. DA is a neurobiological regulator of the reward system, and its role in associative learning may facilitate its involvement in social behavior (Aragona et al., 2003; Curtis et al., 2006; Brom et al., 2014). The DA system has five receptor types that can be divided into two subfamilies of receptors: D1-like (D1 and D5), and D2-like (D2, D3, and D4). These subtypes differentially regulate bond formation and maintenance in prairie vole pairs (Curtis et al., 2006; Aragona and Wang, 2009): activation of the D2 system facilitates selective social preferences and thereby *formation* (Wang et al., 1999; Gingrich et al., 2000; Aragona et al., 2003, 2006; Edwards and Self, 2006) and activation of the D1 system regulates selective social aggression associated with bond *maintenance* (Aragona et al., 2006). In prairie voles, bond formation is accompanied by an upregulation of D1 receptors in the nucleus accumbens, a brain region central to the reward system (Aragona et al., 2006). To date, there has not been a systematic assessment of the role of the D1 and D2 system in regulating the formation and maintenance of attachments in socially monogamous nonhuman primates.

There is, however, some evidence for the importance of the DA system in mediating social relationships in primates. D1 receptor binding in monogamous male titi monkeys is increased after pairing with a female in the lateral septum, a brain region associated with motivation, reward, and reinforcement (Hostetler et al., 2016), suggesting that pairing with a social partner may alter the expression of D1 receptors. Genetic variation in a DA receptor in humans is associated with variability in measures of fidelity and sexual promiscuity (Garcia et al., 2010), and brain regions associated with DA show increased activation in human males treated with oxytocin in response to viewing images of

a romantic partner (Scheele et al., 2013), indicating that other neural systems may be working with, or through, the DA system to induce social effects. General cooperative behaviors even outside of a pairing context in humans appears to be mediated through activation of brain regions rich in DA and involved in reward processing (Rilling et al., 2002). Furthermore, blocking either D1 or D2 receptor types in macaques, a polygynous primate, reduced attention toward a social stimulus (Yamaguchi et al., 2017), indicating that both the D1 and D2 systems function in assessing social stimuli in nonhuman primates. While there is evidence indicating that the DA system influences social behavior in primates, it is unclear to what extent the DA system has a conserved role in regulating relationships in socially monogamous primates in relatively new vs. well-established pairs.

The current study assessed the ways in which reunion behavior after separation in marmosets was influenced by manipulation of the D1 and D2 signaling systems, and whether the effects of DA manipulation differed as a function of the length of the social relationship between pair mates. Marmoset pairs cohabiting for 8 weeks (short-term) or 3 years (long-term) were physically separated from pair mates and housed in a novel environment for 60–75 min, and affiliative behavior upon reunion was quantified. D1 and D2 receptor activation was pharmacologically manipulated with selective receptor agonists and antagonists. If the role of the DA system in relationship dynamics in marmosets is similar to voles, then we expected that manipulation of the D2 system would alter reunion behavior in short term, but not long term pairs, while manipulation of the D1 system would alter reunion behavior in long term, but not short term pairs.

MATERIALS AND METHODS

Subjects

A total of 20 marmosets (*Callithrix jacchus*) were used in this study. Subjects included animals in short term ($n = 7$ pairs, average pair length = 8.76 weeks, $SD = 3.07$ weeks), and long term ($n = 5$ pairs, average pairing length = 3.07 years, $SD = 1.25$ years) pairs. None of the pairs had parental experience with their current mate, and one female in the study had previous parental experience. Four animals were repaired and studied both in a short term and a long term pair context, but the remaining subjects were studied in only one pairing context. Both members of a pair served as subjects on different days of testing, with a minimum of 3 days between tests as a treated focal animal. Marmosets were housed at the Callitrichid Research Center at the University of Nebraska at Omaha. Animals were housed in enclosures with minimum dimensions of $101 \times 76 \times 160$ cm.

Marmosets received a daily diet of a prepared commercial marmoset food (Zupreem®) supplemented by fresh fruits, vegetables, yogurt, apple sauce, eggs, and mealworms. The production of offspring was prevented by either surgical vasectomy of the male or monthly treatment of the female with the luteolytic agent Estrumate® (Merck). Hormonal states of the subjects are not anticipated to be highly impacted by these procedures and treatments. Surgical vasectomy is not

known to reduce testosterone levels, and estrumate produces a normative nonconceptive ovarian cycle, with post-ovulatory progesterone levels equivalent to those of untreated females (Hodges et al., 1988; Mustoe et al., 2012). Additional information regarding animal care can be found in Schaffner et al. (1995). This study was carried out in accordance with the PHS Policy on the Humane Care and Use of Laboratory Animals. The protocol was approved by the University of Nebraska Medical Center/University of Nebraska at Omaha Institutional Animal Care and Use Committee (protocol # 15-033-05-FC).

Drug Treatments

Subjects were treated with one of five treatments: D1 agonist (SKF 38393, 0.05 mg/kg), D1 antagonist (SCH 23390, 0.01 mg/kg), D2 agonist (Quinpirole, 0.05 mg/kg), D2 antagonist (Raclopride 0.03 mg/kg), or saline vehicle. Treatment order was counterbalanced among subjects. Thus, each marmoset received five treatments and served as an untreated pair mate five times for a total of 10 exposures to the testing paradigm. Treatment doses were selected based on a systematic dose-response study conducted in our lab that identified doses at which motoric side effects were not observed (Carp, unpublished data). Injections were given intramuscularly in a volume of 0.5 mL/kg. These compounds have been documented to cross the blood brain barrier. Both raclopride (Farde et al., 1986) and SCH 23390 (Hostetler et al., 2016) are regularly utilized in PET imaging studies. Quinpirole is able to cross the blood brain barrier (Kostrzewa et al., 1993). It is unclear how well SKF 38393 penetrates the blood brain barrier (Kamien and Woolverton, 1985), however, intramuscular administration does alter neuronal activity (Boraud et al., 2001). Therefore, peripheral administration of all compounds are anticipated to produce effects through central activation. All treatments were purchased from Sigma Aldrich and prepared in sterile saline and kept frozen at -20°C until day of treatment. As per recommendations from the manufacturer, D1 and D2 antagonist treatments were reconstituted from stock every 30 days, while the D1 and D2 agonist treatment solutions were reconstituted every 90 days.

Reunion Observations

Subjects were removed from their home enclosure and administered a treatment, housed alone in a small transport cage in an isolated room for 30 min during the drug uptake period, and then placed in a novel T-shaped enclosure in a separate room for 30–45 min. During the time in the T-enclosure, the marmoset had simultaneous visual, auditory, olfactory, and limited tactile access to their untreated mate and to an untreated unfamiliar opposite-sex marmoset in stimulus cages at each end of the T-portion of the cage [for more details on the preference testing apparatus, see (Cavanaugh et al., 2014) and (Smith et al., 2010)]. The T maze is a novel environment for subjects, and simultaneous separation from a mate, and exposure to a novel environment results in a reliable stress response in marmosets (Smith et al., 1998). After this procedure, the treated marmoset and mate were reunited in their home enclosure. Interactions between males and females were recorded for 10 min (long-term pairs) or 15 min (short-term pairs), and included rates of food sharing, approaches to partner, instances of initiating

TABLE 1 | Ethogram of marmoset (*Callithrix jacchus*) behavior recorded during reunion observations.

Behavior	Definition
Proximity ^{a,b}	Mates are within approximately 30 cm of each other, excluding the tail
Contact ^{a,b}	Mates are in physical contact with each other, excluding the tail
Huddle ^{a,b}	Mates are inactive and in side-by-side contact
Approach ^a	Individual enters within approximately 30 cm of their mate
Leave ^a	Individual is within 30 cm of their mate and moves outside of this range
Grooming ^{a,b}	Manipulating the fur of the mate with either hands or teeth
Solicit Grooming ^a	Individual presents an orientation of body or head in a position for grooming
Food sharing ^a	Offering or allowing the mate to take a food object without aggression
Mount ^a	Male places one or two hands on back of female with pelvic thrusting

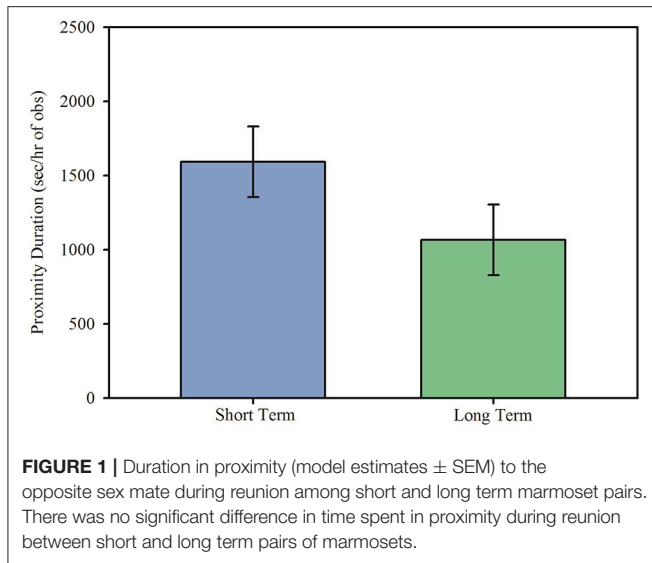
^aIndicates the behavior was recorded for number of occurrences.

^bIndicates the duration of the behavior was recorded.

and receiving grooming, and durations of grooming and time spent in social proximity. Definitions for the behavioral patterns are found in **Table 1**. Duration of separation and reunion were different because data were collected for two projects, one with short term and one with long term pairs. To correct for the different observation lengths, all behaviors were converted to duration or count per hour of observation for data analysis purposes. This correction assumes that the rates of recorded behavior did not vary across the observation period.

Data Analysis

To assess the effects of treatment, sex, and pair type (short term or long term) we used a Linear Mixed Model analysis that nested marmoset ID within Pair ID. This nesting allowed us to account for the non-independence of marmosets being tested in both the short term and long term pairing context. Because age at testing varied between social conditions, this measure was included as a covariate. For behavior that could be exhibited by either the treated marmoset or the untreated mate, factors were added to include behavior initiated and received. As such, our template model is as follows: Behavior = **DA Treatment × Sex × Pair Type × Initiate/Receive** + Age + error(Pair ID) + error(Subject ID) + error(residual), with those factors in bold as the tests of our hypotheses, and those in italics added when grooming behavior was analyzed. We calculated a Hinde index for approach and leave behavior of subjects using the following equation: [Number of Subject Approaches/(Number of Subject Approaches + Number of Pair Mate Approaches)] – [Number of Subject Leaves/(Number of Subject Leaves + Number of Pair Mate Leaves)]. This index allows for a simultaneous measure of responsibility of both initiation (approach) of proximity and breaking proximity (leave) by the subject. *Post hoc* probing was conducted only if significant main effects or interactions were obtained. Statistical tests were conducted with Fisher's tests and a Satterthwaite approximation for degrees of freedom. Cohen's *d* effect sizes for *post hoc* Fisher's *t*-tests were calculated using model estimated marginal means and standard errors, and



standard deviations were calculated from standard errors using Satterthwaite approximated degrees of freedom +1 to estimate n . ANOVA tables for all reported analyses can be found in Supplementary Tables S1–S4.

RESULTS

Effects of Length of Relationship on Reunion Behavior

Social Proximity

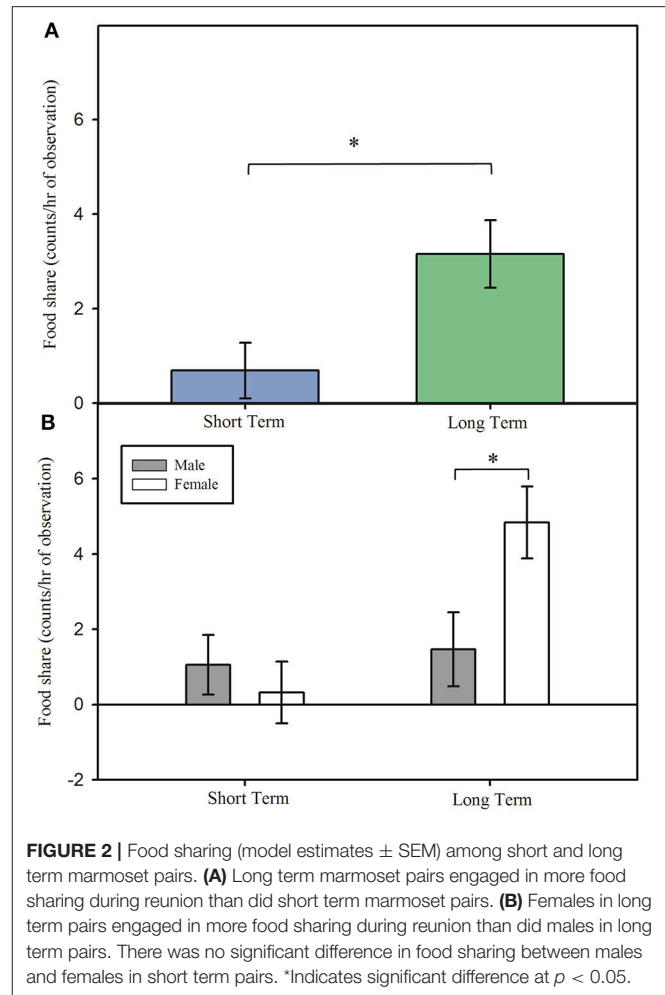
After a social stressor involving partner separation and exposure to an opposite-sex stranger, marmosets in short and long term pairs behaved differentially upon reunion. Marmosets in both short and long term pairs spent similar amounts of time in proximity during reunion, **Figure 1**; main effect: $F_{(1, 14.11)} = 2.69$, $p = 0.123$, but differed in the specific behavior patterns associated with close spatial proximity.

Food Sharing

Marmosets in long term pairs engaged in higher levels of food sharing upon reunion than did marmosets in short term pairs, **Figure 2A**; main effect: $F_{(1, 14.90)} = 6.17$, $p = 0.025$. There was also a sex difference observed in long term, but not short term, pairs of marmosets in frequency of food sharing, interaction effect: $F_{(1, 11.98)} = 5.84$, $p = 0.032$. In long term pairs of marmosets, females engaged in higher levels of food sharing during reunion than did male marmosets, **Figure 2B**; *post hoc*: $t_{(12.1)} = 2.59$, $p = 0.024$, 95% CI [0.009, 0.103], $d = 0.695$. However, in short term pairs of marmosets females and males displayed no difference in their rate of food sharing, **Figure 2B**; *post hoc*: $t_{(12.2)} = -0.66$, $p = 0.519$, 95% CI [-0.052, 0.028], $d = -0.181$.

Grooming

Although overall duration of grooming did not differ in reunion between short term and long term pairs, **Figure 3A**; main effect:

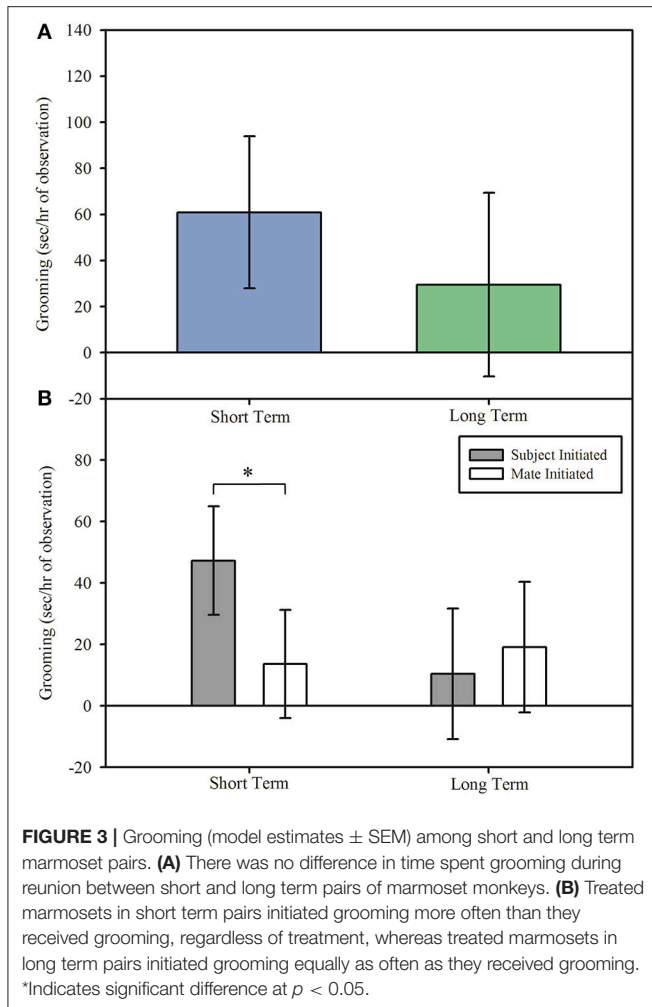


$F_{(1, 14.798)} = 0.33$, $p = 0.576$, the duration of grooming initiated by subjects or mates differed by pair length, interaction effect: $F_{(1, 215.99)} = 4.87$, $p = 0.028$. Regardless of DA treatment, treated marmosets in short term pairs spent longer grooming their mate than their mate spent grooming them upon reunion, **Figure 3B**; *post hoc*: $t_{(216)} = 2.72$, $p = 0.007$, 95% CI [0.154, 0.967], $d = 0.450$. However, treated subjects and their mates in long term pairs displayed no difference in the duration of grooming during reunion after separation, **Figure 3B**; *post hoc*: $t_{(216)} = -0.59$, $p = 0.556$, 95% CI [-0.625, 0.337], $d = -0.095$.

Effects of Dopamine Treatment on Reunion Behavior

Dopamine Effects in Short Term Pairs

During reunion, marmoset pairs spent similar amounts of time in proximity regardless of DA treatment, main effect: $F_{(4, 96.00)} = 1.91$, $p = 0.114$. However, time in proximity differed between short and long term pairs based on DA treatment and whether the male or female received the treatment, interaction effect: $F_{(4, 96.00)} = 2.50$, $p = 0.047$. During reunion, male and female marmosets in short term pairs spent similar amounts of time in proximity when they received a saline treatment, **Figure 4A**;



post hoc: $t_{(70.70)} = -0.29$, $p = 0.772$, 95% CI $[-11.471, 8.556]$, $d = -0.047$. However, marmosets in short term pairs spent less time in proximity during reunion when females were treated with either a D2 receptor agonist, **Figure 4A**; *post hoc*: $t_{(70.70)} = -2.04$, $p = 0.045$, 95% CI $[-20.237, -0.213]$, $d = -0.333$, or a D2 receptor antagonist, **Figure 4A**; *post hoc*: $t_{(70.70)} = -2.18$, $p = 0.032$, 95% CI $[-20.973, -0.946]$, $d = -0.356$, compared to when males received the same treatment. Additionally, pairs spent less time in proximity when females were treated with a D2 receptor agonist compared to when females were treated with saline, *post hoc*: $t_{(96.0)} = -2.29$, $p = 0.024$, 95% CI $[-19.530, -1.399]$, $d = -0.336$. No other treatments were significantly different from saline. Short term pairs spent similar amounts of time in proximity when either males or females were treated with a D1 agonist, **Figure 4A**; *post hoc*: $t_{(70.8)} = 0.48$, $p = 0.634$, 95% CI $[-7.607, 12.407]$, $d = 0.078$, or D1 antagonist, **Figure 4A**; *post hoc*: $t_{(70.8)} = -0.37$, $p = 0.716$, 95% CI $[-11.842, 8.175]$, $d = -0.060$.

Dopamine Effects in Long Term Pairs

A different pattern of treatment effects was observed in long term pairs. There was no sex difference in time spent in proximity in long term pairs when males and females were treated with saline,

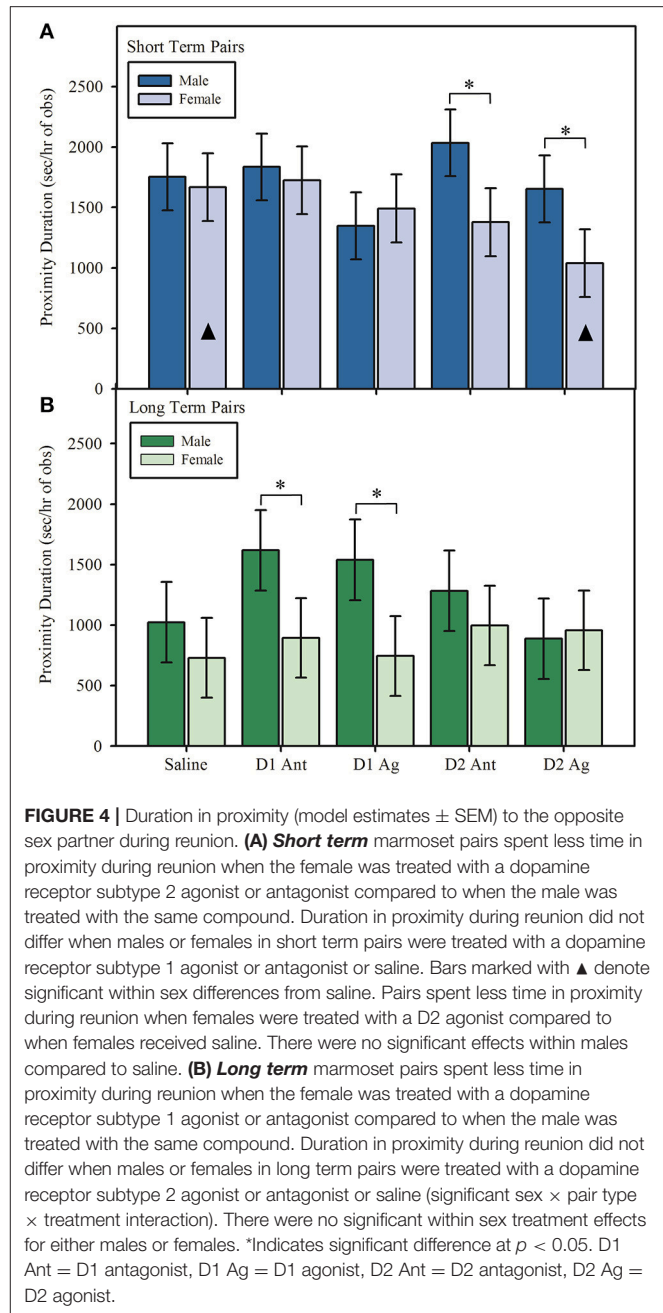


Figure 4B; *post hoc*: $t_{(71.1)} = -0.83$, $p = 0.412$, 95% CI $[-16.704, 6.925]$, $d = -0.134$. However, male and female marmosets in long term pairs spent less time in proximity when females received treatment with either a D1 agonist, **Figure 4B**; *post hoc*: $t_{(71.00)} = -2.23$, $p = 0.029$, 95% CI $[-25.061, -1.415]$, $d = -0.365$, or D1 antagonist, **Figure 4B**; *post hoc*: $t_{(71.00)} = -2.03$, $p = 0.046$, 95% CI $[-23.880, -0.238]$, $d = -0.329$, compared to when males received the same treatment. Long term marmoset pairs spent similar amounts of time in proximity upon reunion when males and females were treated with a D2 agonist, **Figure 4B**; *post hoc*: $t_{(71.00)} = 0.19$, $p = 0.846$, 95% CI $[-10.663, 12.971]$, $d = 0.031$, or D2 antagonist, **Figure 4B**; *post hoc*: $t_{(71.00)} = -0.81$, $p = 0.421$, 95% CI $[-16.615, 7.028]$, $d = -0.131$.

Responsibility for Proximity Maintenance

The Hinde index revealed no effect of DA treatment on the rate at which treated subjects were initiating and breaking proximity with their mates, main effect: $F_{(4, 96.00)} = 0.88$, $p = 0.477$, suggesting that the observed differences in proximity behavior were not attributable to changes in approach or leave behavior by the subject.

DISCUSSION

Reunion in marmoset pairs constitutes an important time for assessing affiliative behavior. We noted several differences in the ways in which pairs housed together for differing lengths of time interact upon reunion. Marmosets in long term pairs engaged in higher levels of food sharing than did marmosets in short term pairs. Females in long term pairs demonstrated higher rates of food sharing than their mates, while males and females shared food at equal rates in short term pairs. It has been hypothesized that in social settings in which females have multiple mating partner options, males should share food with females at high rates in order to enhance the chance for mating opportunities (Jaeggi and Van Schaik, 2011). However, in our study females in long term pairs were observed to share food more often than males. Though the social context in the current study differs from that in Jaeggi and Van Schaik (2011), females were reunited with their mate after exposure to a strange male. Presumably, males are cognizant of the odors/sounds of the other marmoset in the testing room and therefore may be more likely to behave during reunion as if their female mate had additional mating opportunities. In a comparative analysis of food sharing in primate species whose groups are composed of a single adult male, high rates of male-to-female food sharing predominantly occurs in socially monogamous species (Jaeggi and Van Schaik, 2011), however, that study did not measure female-to-male instances of food sharing. Food sharing is a behavior that is sensitive to the context of the pair (i.e., pregnancy). Monogamous male and female owl monkeys share food at equal rates, however, male-to-female food sharing increases when females are lactating compared to when they are cycling or pregnant, while female-to-male food sharing occurs at equal rates regardless of reproductive status (Wolovich et al., 2010). Though male-to-female food sharing may facilitate reduced energy expenditure by females and shortened interbirth interval (Wolovich et al., 2010), underlying proximate and ultimate causes of female-to-male food sharing are less clear.

Marmosets in short term pairs displayed a different pattern of grooming compared to that observed in long term pairs. Grooming behavior was altered such that rather than initiating and receiving comparable levels of grooming, as in long term pairs, treated marmosets in short term pairs spent more time grooming their partners upon reunion than their partner spent grooming them. This difference in behavior may indicate that while in long term pairs the context of the separation (e.g., experience as the treated subject vs experience as the untreated mate) does not change the expression of grooming, members of short term pairs are sensitive to the experimental context. Thus,

in short term pairs, treated subjects engaged in longer duration of grooming than did untreated mates during reunion, thereby displaying a behavioral difference dependent on experimental experience. In prairie voles, the opposite effect is found: separated voles receive, rather than initiate, higher rates of grooming from their partners (Burkett et al., 2016). These contrasts point to potentially important species differences in the roles of initiated vs. received sociality upon reunion in regulating and reestablishing relationships after separation.

There was no difference in the total amount of time spent in proximity between short term and long term pairs. Though there are documented differences in normative levels of affiliation as measured by sexual behavior, time in proximity, and overall time spent grooming in marmoset pairs dependent on length of pairing (Evans and Poole, 1984; Schaffner et al., 1995; Ågmo et al., 2012), we did not find these differences expressed during reunion. Thus, while marmosets in short and long term pairs may use slightly different strategies to reestablish their relationship upon reunion (e.g., initiation of grooming and rates of food sharing), they spent similar amounts of time in proximity. The pattern of change in behavior dependent on the actions of both members of the pair is largely consistent across findings in the current study. Both food sharing and grooming (behaviors that differed between short and long term pairs in reunion) can only occur when both members of the pair engage in the appropriate dyadic interaction. This dependence on both partners highlights the complexities of studying pair-level interactions and the behavioral richness of dyads.

The DA system appears to be involved in the way that pairs behave during reunion, with DA treatment affecting pair-level interactions. Marmoset pairs, of both short and long term, spent similar amounts of time in proximity upon reunion under saline conditions regardless of whether the male or female was treated. However, alteration of the D2 system, either through receptor agonism or antagonism, altered this pattern in short term pairs, with pairs spending less time in proximity when females received treatment compared to when males received the same treatment. D1 treatments produced different effects in long term pairs, such that pairs spent less time in proximity when the female was treated with either a D1 receptor agonist or antagonist compared to when males received the same treatment. Furthermore, short term pairs spent less time in proximity when females were treated with a D2 agonist compared to when females were treated with saline, indicating that the sex difference observed between males and females was likely due to a decrease in proximity when females were treated. Though other treatments did not produce significant differences from saline, this suggests that at least in short term pairs, treatment of females may yield differences in the way in which pairs regulate social proximity. Male marmosets increase proximity regulation as their mate progresses through pregnancy (Evans and Poole, 1984), suggesting that pairs may be primed to be sensitive to alterations in female physiology, and our data suggest that DA signaling in females may be included in changes in female physiology that alter pair social dynamics. DA, particularly D2 agonists, also reduce prolactin release in marmoset monkeys (Almond et al., 2006), indicating the potential for DA treatments to have off-target effects on

other hormonal systems. Given the known role of prolactin (PRL) in facilitating parental behavior (Ziegler et al., 2009) and parent-infant bonding, it is likely that DA-PRL interactions may have meaningful implications for behavior between mates. This may provide another mechanism through which marmoset females are more sensitive to manipulation of the DA system than males. While overall proximity duration was affected by both DA treatment and sex, other measures, such as initiating and breaking proximity did not differ among DA treatment conditions. Future research should evaluate aspects of individual behavior that may underlie the observed differences in pair-level behavior. In the current study individual initiation and breaking of proximity (the Hinde index) was not able to explain observed differences of time spent in proximity. However, other measures of social interest, such as social gaze, a measure known to be important in directing human social behavior (Frischen et al., 2007), may help to illuminate the behavioral mechanisms through which pairs are altering interactions in response to DA treatment.

It is also worth noting that the same pattern of change in social proximity to the partner during reunion is observed when marmosets are treated with *either* the agonist or antagonist, suggesting that pairs may be responding to an *alteration* of DA signaling rather than enhancement or inhibition of the system. The similarity in agonist and antagonist effects stands in contrast to research in other species indicating differential effects of agonist and antagonist treatment. One potential explanation for the similarity in effect is differential efficacy of some of the compounds. The D1 receptor agonist (SKF 38393) has been documented to have a lower efficacy in primate than in rodent brain tissue, and in both rodents and primates the efficacy of the agonist is lower than that of DA itself (Arnt et al., 1988; Pifl et al., 1991). Additionally, there is evidence of a U shaped dose-response curve for agonists of the D1 system (Cai and Arnsten, 1997), indicating the potential that observed effects are dose-dependent. Therefore, at least within the D1 system, it is possible that the effects of the agonist and antagonist are both producing effects less potent than if DA were acting alone.

The consistency of findings across pair types (D2 manipulation altering behavior in short term pairs, and D1 manipulation altering behavior in long term pairs) indicates that there may be dynamic shifts in behavior that affect the dyadic nature of pair interactions dependent on pairing length and DA subsystem. Research in prairie voles has indicated a role for the D2 system in measures of relationship formation (Gingrich et al., 2000; Aragona et al., 2003, 2006), and the D1 system in measures of relationship maintenance (Aragona et al., 2006). Thus, it is interesting to note that social proximity in short term pairs of marmosets is changed by manipulation of the D2 system, and social proximity in long term pairs of marmosets is changed by manipulation of the D1 system, as would be predicted if the DA system has a conserved role in pair behavior during reunion.

DA itself is an evolutionarily conserved neurotransmitter with widespread effects on regulating behavior. Though commonly recognized as having a role in motoric function, DA also

has known roles in decision making and social behavior (O'Connell and Hofmann, 2011). DA receptor distribution has been characterized in cichlid fish and D1 and D2 receptors are found in regions homologous to those associated with social behavior in other vertebrate species (O'Connell et al., 2011). The effect of DA on mate behavior is not limited to mammals. DA has been associated with male courtship and pairing behavior in monogamous zebra finch birds (Huang and Hessler, 2008; Goodson et al., 2009), and higher levels of DA and its metabolites are found in paired than unpaired zebra finches (Banerjee et al., 2013). Furthermore, immediately early gene markers indicated increased neuronal activity of dopamine rich brain regions after pairing compared to unpaired finches (Banerjee et al., 2013). Together, these studies highlight the conserved nature of DA in facilitating both social behavior generally, and regulating interactions between mates.

There is further evidence for the role of DA in primate pair interactions from studies on humans. Subjects looking at pictures of a partner with whom they considered themselves to be in love showed increased activation of brain regions rich in DA, compared to looking at pictures of an acquaintance (Fisher et al., 2005). This indicates that the DA system may be selectively important in romantic attachments rather than overall sociality. Additionally, genetic variability in the DA system has been linked to differences in human sexual behavior. Variation in a D2-like receptor has been associated with human male sexual desire and arousal (Ben Zion et al., 2006), as well as self-reported levels of fidelity and promiscuity (Garcia et al., 2010). Though DA has a role in modulating sociosexual relationships, it is not the only regulatory neurotransmitter that impacts sociality in mammals. Other neural systems, especially oxytocin and vasopressin, interact with dopaminergic signaling to facilitate social behavior (Johnson and Young, 2015). Thus, research on the specific roles of the D1 and D2 systems in primate pair behavior is necessary in order to inform not only the independent role of the dopaminergic system, but the potential co-modulatory effects with other neural systems. Specifically, the current study indicates that DA subsystems do maintain a role in regulating reunion behavior in a primate species displaying social monogamy. These findings fit into the larger emerging evolutionary notion that there are neurobiological systems, including those involving dopamine signaling, conserved across vertebrate species that may play crucial roles in regulating sociality.

AUTHOR CONTRIBUTIONS

SC: designed the study, carried out experiments, organized the dataset, and wrote the first draft of the manuscript; JF and SC: obtained funding for the project; JT and SC: performed statistical analyses and interpreted analyses; JT, SW, and JF: contributed to and revised the manuscript. All authors read, revised and approved the final version of the submitted manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpsy.2018.00046/full#supplementary-material>

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Why Monogamy? A Review of Potential Ultimate Drivers

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The existence of monogamy in animals is perplexing from an evolutionary perspective. If individuals: (1) have the opportunity to mate with more than one individual and (2) doing so provides fitness benefits (e.g., indirect benefits, increased mating success or fecundity), why does monogamy ever occur in animals? To address this question, we must examine how the potential benefits and costs of monogamy differ between the sexes and how such costs and benefits interact with factors including resource availability, offspring need, parental care, and mating dynamics (i.e., the costs and benefits associated with acquiring mates and mate availability). In this review, I examine the interplay between parental and offspring dynamics, resource availability and mate distribution, and mating dynamics. In doing so, I highlight the life history and ecological conditions under which monogamy is expected vs. not. I then discuss areas of research that are needed to enhance our evolutionary understanding of monogamy. In particular, enhanced understanding of monogamy will come from: (1) more explicit consideration that the factors that lead to the origin of monogamy vs. the maintenance of monogamy might differ and (2) identifying how potential interactions among factors influence the origin and/or maintenance of monogamy.

Keywords: monogamy, parental care, parental investment, sexual selection, life history, mating system

MONOGAMY IS AN EVOLUTIONARY CONUNDRUM

Multiple mating is frequently associated with fitness benefits in both sexes. For example, Bateman (1948) found that male reproductive success is often limited by the number of female mates that a male acquires; as such, males are predicted to increase their lifetime reproductive success by mating with multiple females (Bateman, 1948; Jones and Ratterman, 2009). The expectation that male reproductive success is highly dependent on male mating success has been used to explain male multiple mating in a range of taxonomic groups (Jones and Ratterman, 2009). Likewise, females frequently benefit from mating with multiple males. For instance, a meta-analysis in insects revealed that multiple mating provides direct benefits to females in terms of increased egg production and fertility (Arnqvist and Nilsson, 2000). Similarly, extra-pair paternity, which is a proxy for multiple mating, was associated with higher hatching success, and hence greater female reproductive success, across 113 bird species (Reding, 2015). Female multiple mating can also in some, but not all, cases be associated with infanticide avoidance (Hrdy, 1979) or indirect benefits (Blomqvist et al., 2002; García-González and Simmons, 2005).

Given that multiple mating is often associated with fitness benefits, the existence of monogamy is perplexing from an evolutionary perspective. Indeed, if individuals: (1) have the opportunity to mate multiply and (2) doing so provides fitness benefits (e.g., increased reproductive success;

see also Thonhauser et al., 2014; for review of relevant hypotheses), why does monogamy ever occur in animals? To address this question from an ultimate perspective, we must consider whether multiple mating is always possible and explore the costs and benefits of multiple mating. If multiple mating is possible, monogamy would most generally be expected to occur when there are no benefits of multiple mating or when there are costs of multiple mating. Understanding how monogamy can be beneficial to individuals, and hence, persist in populations requires that we consider: (1) how the benefits and costs of monogamy differ between the sexes and (2) how such costs and benefits interact with factors such as resource availability, offspring need, parental care, and mating dynamics.

In this review, I focus on the ultimate causes of monogamy in animals. I first discuss operational definitions and classic hypotheses of monogamy; I then discuss more recent work that has focused on the evolutionary interplay between parental and offspring dynamics, resource availability, and mating dynamics.

MONOGAMY: WHAT'S IN A NAME AND WHAT DO WE SEE IN NATURE?

Monogamy occurs when individuals have one mate for their entire lifetime or some specified period of time, and monogamy has been classified as a mating system in which neither sex is able to monopolize additional members of the opposite sex (Emlen and Oring, 1977). Historically, monogamy was thought to occur primarily in birds, and Lack (1968) initially estimated that more than 90% of birds were monogamous. However, as molecular tools became more accessible, researchers began to discover that many species that were once thought to be monogamous mate multiply. For instance, in one of the first studies on this topic, Gowaty and Karlin (1984) found that at least 5% of male and 15% of female eastern bluebirds (*Sialia sialis*) were caring for at least one offspring that was not genetically theirs; such research was surprising at the time because eastern bluebirds were thought to be monogamous. Such studies led to a distinction between genetic and social monogamy (Gowaty, 1996). Social monogamy occurs when a male-female pair cohabit and/or form a pair bond for some specified period of time; social monogamy does not assume that the male-female pair is exclusive with regard to mating. In contrast, genetic monogamy assumes that a male-female pair is exclusive for some specified period of time with regard to mating and fertilization, although the pair doesn't necessarily pairbond.

The distinction between social and genetic monogamy has led to a range of studies that have revealed unique combinations of genetic and social monogamy. For instance, the largemouth bass (*Micropterus salmoides*) is socially monogamous and exhibits near-genetic monogamy (DeWoody et al., 2000). Likewise, long-eared owls (*Asio otus*) are socially and genetically monogamous (Marks et al., 1999). Similarly, Kentish plovers (*Charadrius alexandrinus*) tend to primarily, but not always, exhibit social and genetic monogamy (Küpper et al., 2004). In contrast, in the prairie vole (*Microtus ochrogaster*), most males form pairbonds and cohabit with a single female but

also engage in extra-pair mating; thus, most, but not all, individuals engage in social but not genetic monogamy (Ophir et al., 2007, 2008a,b). In the pot-bellied seahorse (*Hippocampus abdominalis*) the opposite trend has been observed: despite social promiscuity (e.g., promiscuous courtship) and a lack of pairbonding, genetic monogamy has been observed (Wilson and Martin-Smith, 2007). Mating systems have also been found to be dynamic (e.g., Forsgren et al., 2004; Wilson and Martin-Smith, 2007), suggesting that in some systems, individuals that are socially and/or genetically monogamous at one point in time might adopt a different strategy under different ecological conditions. Indeed, genetic monogamy occurs across a range of animals, but there is often inter-specific variation in the extent to which genetic monogamy occurs (Table 1).

When we focus on understanding the occurrence of monogamy in nature, it is important to recognize that a mating system is a descriptor of population- or species-level dynamics. Individuals themselves can exhibit strategies that are consistent with a given mating system, and these individual-level strategies that are associated with a given mating system (e.g., a particular propensity to engage in monogamous courtship, monogamous mating, multiple mating) are traits that can experience and respond to selection. That is, such traits can evolve. In contrast, the mating system of a population is not a trait and can therefore not evolve in a biological sense; a mating system can change on short and long time scales and across spatial contexts, and a mating system can create selection pressures, but ultimately traits are what evolve biologically. In considering the factors that are hypothesized to influence monogamy (discussed below), it is important to keep in mind that mating systems are influenced by traits, which can evolve, and that a mating system can create selective pressures that lead to future evolution of relevant traits. This evolutionary interplay and feedback between mating systems and traits is likely key to understanding the variation in mating dynamics that exist in nature, and hence, key to understanding the occurrence of monogamy.

CLASSIC PERSPECTIVES ON MONOGAMY

Resources, Parental Care, and Sexual Selection Matter

Emlen and Oring (1977) were not the first to study mating systems (Darwin, 1888; Verner and Willson, 1966; Orians, 1969; Bartholomew, 1970), but the synthetic conceptual framework of mating systems that they developed was remarkably influential. Emlen and Oring (1977) hypothesized that there is a link between mating system and sexual selection and suggested that sexual selection will be relatively slight in monogamous systems (Figure 1). They emphasized that understanding diversity in mating systems requires that we understand the factors that influence sexual selection. Specifically, they suggested that sexual selection will be influenced by the "ability of a portion of the population to control the access of others to potential mates" and that monogamy will occur when there is "economic defendability of a mate" (Emlen and Oring, 1977; Figure 1). Emlen and

TABLE 1 | Examples of monogamy in nature.

Animal type	Example of monogamy
Fish	The bonnethead shark (<i>Sphyrna tiburo</i>) tends to exhibit within-litter genetic monogamy, despite the ability to store sperm, although in 19% of cases, litters were sired by multiple males (Chapman et al., 2004).
Amphibian	The mimic poison frog (<i>Ranitomeya imitator</i>) is the first known example of a socially and genetically monogamous amphibian (Turnulty et al., 2013).
Reptile	The Australian lizard (<i>Egernia stokesii</i>) lives in stable groups of breeding pairs, and genetic monogamy is the most common mating strategy, although some litters had multiple paternity (Gardner et al., 2002).
Bird	Florida scrub-jays (<i>Aphelocoma coerulescens</i>), who breed cooperatively, are genetically monogamous in nearly all cases, although there are rare exceptions in which males have two female mates (Quinn et al., 1999).
Mammal	The Azara's owl monkey (<i>Aotus azarae</i>) is a pair-living primate with bi-parental care that exhibits genetic monogamy (Huck et al., 2014).

Oring (1977) noted that critical non-mate resources will vary spatially and temporally and that this can affect the spatial and temporal distribution—and hence the defendability—of potential mates (**Figure 1**). They additionally predicted a link between bi-parental care and monogamy and noted that monogamy is most likely to occur when the potential for or the benefit of multiple mating is low (**Figure 1**). They hypothesized that under such conditions, individuals can increase their fitness by remaining with their current mate and increasing offspring survival.

More recent work (discussed below) has demonstrated that co-evolutionary feedback can occur and lead to patterns that are more complex than those initially predicted (e.g., we now know that sexual selection isn't always slight in monogamous systems; Jones and Hunter, 1993). Indeed, as noted by Wittenberger and Tilson (1980), no single hypothesis alone is sufficient to explain monogamy; instead a series of hypotheses and an understanding of when each should apply is required to understand monogamy (Wittenberger and Tilson, 1980). Nonetheless, the relatively simple verbal arguments of Emlen and Oring (1977) highlighted the key role that sexual selection, resources, and parental care can play in influencing monogamy.

The Role of Female Benefits in Monogamous Mating Systems

Wittenberger and Tilson (1980) expanded the conditions under which monogamy is expected. They focused more explicitly on the role that female fitness benefits have in maintaining monogamy and hypothesized that monogamous mating systems require: (1) female benefits of monogamous pair bonds that cannot be obtained in the absence of monogamy; (2) the ability of females to assess the mated status of males; and (3) a lack of male desertion. They additionally hypothesized that monogamy is most likely to occur when: (1) male parental care is essential and non-shareable among offspring; (2) the benefits of mating with a superior polygynous male do not outweigh the costs of polygyny

that is associated with reduced parental care; (3) males achieve the greatest fitness benefits by mating with and defending a single female; (4) aggression by females occurs; and (5) increased competition for resources and/or increased predation associated with multiple female mates occurs (Wittenberger and Tilson, 1980). Importantly, these hypotheses are inter-related and not mutually exclusive.

In the years following the work of Emlen and Oring (1977) and Wittenberger and Tilson (1980), numerous authors refined the conditions under which monogamy is expected (e.g., Greenlaw and Post, 1985; Björklund and Westman, 1986; Mock and Fujioka, 1990). Many of these early studies that focused explicitly on monogamy utilized verbal arguments that were largely based on our knowledge of mating systems at the time (but see, e.g., mathematical models by Parker and Macnair, 1978 and McLean and Manning, 1985). Many of these early hypotheses have now been tested or expanded upon empirically and/or by using mathematical modeling. Below, I review the insights that such work has provided.

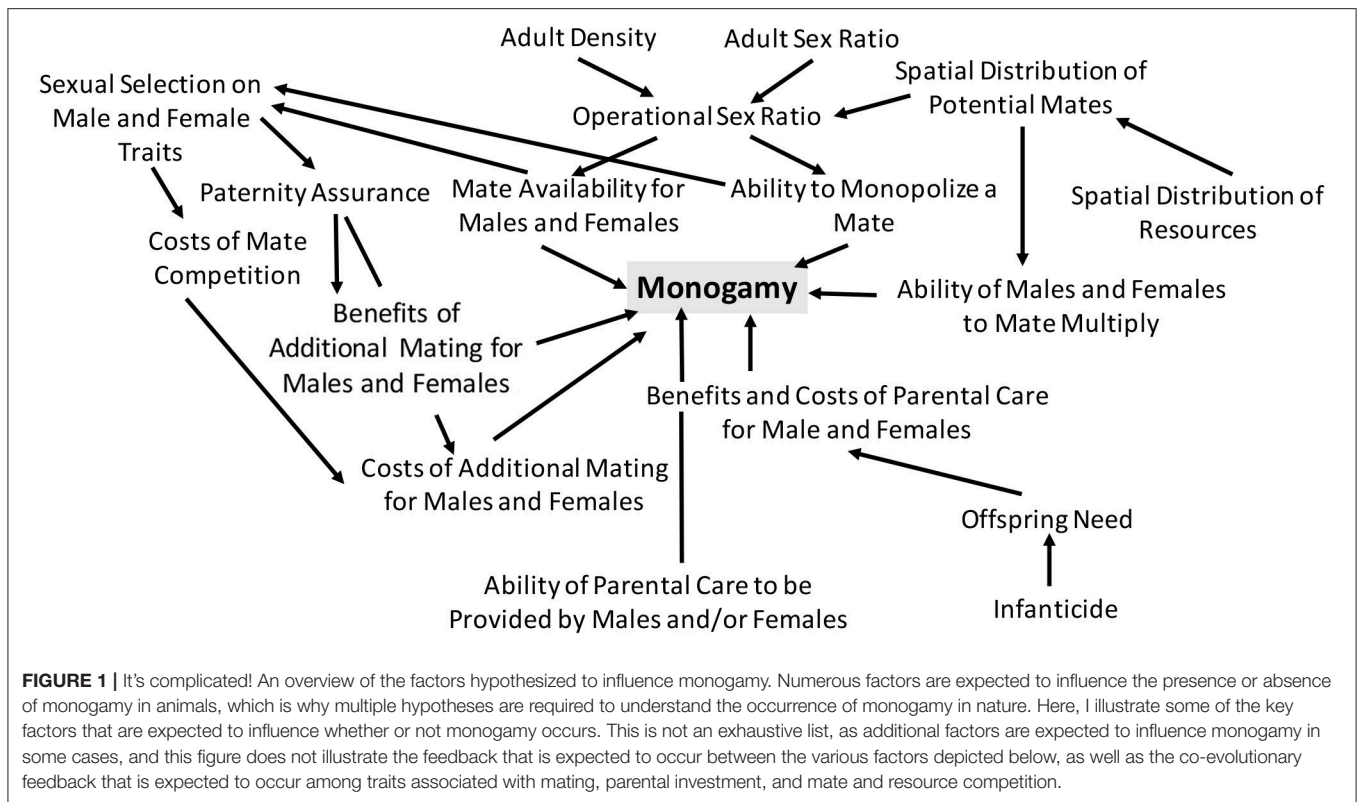
RECENT PERSPECTIVES ON THE ORIGIN AND MAINTENANCE OF MONOGAMY

Parental Care Can Matter

A frequent prediction of early work is that paternal care is associated with monogamy (Emlen and Oring, 1977; Wittenberger and Tilson, 1980; Gowaty, 1996; **Figure 1**). Indeed, some theoretical work has found that paternal care influences the occurrence of monogamy. Iwasa and Harada (1998) found that monogamy can occur when parental ability is the same between parents if females choose their mates and males invest in paternal care. If females and males vary in quality (i.e., fecundity and parental ability), this can lead to assortative mating and monogamy, although the mating dynamics will depend on the costs of care to males and variation in female fecundity (Iwasa and Harada, 1998). In animals, monogamy is often associated with bi-parental care, but whether bi-parental care precedes or follows the evolution of monogamy is debatable (reviewed in Brotherton and Komers, 2003 and discussed in section “But, Is Bi-parental Care Really Necessary for Monogamy?” below).

Co-evolutionary Dynamics Matter

More recent work has suggested that understanding the origin and persistence of any mating system, including monogamy, requires that we develop a framework that accounts for interactions among mating dynamics, parental investment, and costs of care, and mating (**Figure 1**). The likelihood of paternal care, which as discussed above is in some cases predicted to influence monogamy, is affected by a range of factors, including the costs and benefits of caring vs. competing for mates (**Figure 1**). Kokko and Jennions (2008) developed a model focused on sex roles that accounted for feedback associated with the costs and benefits of caring vs. competing for mates. Their work revealed that when providing parental care is associated with higher mortality than competing for mates, individuals of the deserting sex (i.e., the sex that provides no care) will become more common in the population and in turn have difficulty



finding a mate; under such a scenario, across evolutionary time, we would expect (1) bi-parental care to be more likely and (2) for males and females to differ relatively little in the amount of care provided (Kokko and Jennions, 2008). While monogamy was not explicitly focused on in the modeling work of Kokko and Jennions (2008), if bi-parental care is associated with monogamy (see above), we might expect monogamy to be more likely in systems in which parental care is associated with high adult mortality.

But, Is Bi-parental Care Really Necessary for Monogamy?

While bi-parental care and monogamy commonly co-occur (reviewed in Brotherton and Komers, 2003), some researchers have questioned whether bi-parental care is necessary for, or rather a consequence of, monogamy. In humans, Schacht and Bell (2016) found that mate guarding rather than paternal care leads to monogamy, as monogamy allows males to maintain high paternity. Likewise, Lukas and Clutton-Brock (2013) suggested that in non-human mammals, male care is a consequence rather than a cause of monogamy. They instead suggested that monogamy is caused by low female density and the inability of males to defend multiple females. However, Dobson et al. (2010) found that socially monogamous and non-monogamous mammals have similar local densities and home ranges, suggesting that local density and home range area might not be a primary driver of monogamy in all mammals. Instead, Dobson et al. (2010) suggested that the origin of monogamy

in mammals is caused by a range of factors. In primates, Opie et al. (2013) found a correlation between social monogamy, female home range, and bi-parental care; however, their research suggests that infanticide is likely the key factor that leads to a shift toward social monogamy in primates.

In some cases, paternal care is decoupled from monogamy. In extreme cases, males die after mating and are thus unable to provide paternal care. Fromhage et al. (2005) found that monogyny can be favored in the absence of male care when monogyny increases paternity if the sex ratio is male biased. Thus, while bi-parental care and monogamy frequently co-occur, it does not appear that bi-parental care is always a pre-requisite for the origin or maintenance of monogamy. Indeed, in some cases mate guarding and paternity assurance can directly favor monogamy.

In summary, bi-parental care commonly co-occurs with monogamy, but the role that bi-parental care plays in driving the origin of monogamy is unclear, particularly in mammals.

Interactions Between Ecology and Parental Care Can Lead to Monogamy

While bi-parental care is not always essential for monogamy, parental care and offspring need can in some cases interact with ecological factors to drive the origin of monogamy. For instance, Brown et al. (2010) found that in frogs, a single ecological factor (breeding pool size) is related to the origin of care. In poison frogs, they found that feeding of offspring co-evolved with the use of small pools and that feeding behavior was associated with

the origin of bi-parental care, as bi-parental care is essential to offspring survival in small (but not large) pools. Molecular and field analyses revealed that social and genetic monogamy occur in *Ranitomeya imitator*, a species that utilizes small pools, but not *Ranitomeya variabilis*, a species that uses large pools, suggesting that an ecological factor (pool size) led to the co-evolution of bi-parental care and monogamy in *R. imitator* (Brown et al., 2010). These results highlight the important interactions that can occur between ecological factors, parental care, offspring need, and monogamy.

PUTTING IS ALL TOGETHER: WHAT DRIVES THE ORIGIN AND MAINTENANCE OF MONOGAMY?

Decades of empirical and theoretical research suggest that there is no single factor that drives monogamy across animals. This is perhaps not surprising given the immense variation in life history, evolutionary history, and ecological factors in animals. Numerous studies, however, have demonstrated that the following likely influence monogamy: (1) spatial and temporal distribution of females, (2) parental care costs and benefits, (3) offspring need, (4) infanticide, (5) costs and benefits of multiple mating, (7) mate competition, (8) paternity assurance, (9) the potential for mate guarding, and (10) resource use (Figure 1). This is a broad list, and the relative importance of each factor likely varies across systems. Additionally, the factors above are likely to interact. For example, ecology can affect mate distribution and offspring need; infanticide can affect offspring need; costs of parental care will influence mate availability, which will in turn affect benefits of mate searching. Additional research on such interactions warrants further attention (discussed below).

WHAT'S NEXT?

I suggest that there are two primary areas of research that are needed to more fully understand monogamy from an ultimate

perspective. First, we need to recognize that the factors that promote the origin vs. the maintenance of monogamy might differ (see discussion in Gowaty, 1996). Within animals, it will be important to better understand if the factors that promote the origin of monogamy are the same (or different) than those that promote the maintenance of monogamy.

Second, it will be critical to better understand how life-history, ecological, and mating factors interact to influence monogamy. As mentioned earlier, monogamous mating dynamics can create selective pressures that influence evolutionary trajectories; for example, West (2014) found that the evolution of large brain size is associated with social but not genetic monogamy in birds. Likewise, Jašarević et al. (2013) found that monogamy can influence the evolution of female life histories in mammals. Further, previous work has found that mate guarding, male attractiveness, and paternity can interact in complicated ways to influence social monogamy (Kokko and Morrell, 2005). Recent studies have begun to focus on the interplay between such factors, but there is still more work to do in identifying the interactions (rather than the individual factors) that lead to the origin and maintenance of monogamy. Focusing on such interactions will likely also be necessary to better understand how monogamy varies within a population and through time. Indeed, understanding variation in the propensity to be monogamous within and across individuals of a population has received relatively little attention from an ultimate perspective and warrants future attention.

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The author confirms being the sole contributor of this work and approved it for publication.

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Socio-Ecological Disruptions at Critical Periods During Development Alter Stress Responses and Hippocampal Dendritic Morphology of Prairie Voles: Implications for Social Monogamy

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Emotions are often associated with the evolution of monogamy. For example, fear of cuckoldry has been recently proposed as the driving force for human monogamy. We used prairie voles (*Microtus ochrogaster*) as a model of human behavior to study how stress reactivity is shaped by socio-ecological disruptions experienced as neonates and as subadults. We hypothesized that social disruptions would have a greater impact on the vole's stress levels than ecological disruptions, and that females would be more susceptible to the experience than males. At 6 days postpartum, the housing conditions were manipulated to have offspring raised by: (1) both parents under a protective cover (NoDisrupt); (2) Both parents uncovered (EcoDisrupt); (3) Mother alone covered (SocDisrupt); (4) Mother alone uncovered (SocEcoDisrupt). To experience disruptions as subadults, offspring were weaned then housed either alone (Isolate) or with a same-sex sibling (Social). As adults, each offspring was placed in an open-field arena and tested over 3 consecutive days to measure its behavior in response to an empty space (Day1), a same-sex vole in a container (Day2), and an empty container (Day3). The brain of a subgroup of subjects was processed for Golgi staining to assess the impact of disruptions on hippocampal dendritic morphology in adulthood. Males that experienced social disruption in early life displayed lower stress levels on Day2 of testing than males and females in other groups. This effect was only evident in males that did not experience social disruptions as subadults. Socio-ecological disruptions at postpartum had an unanticipated impact on the hippocampus of the voles. The apical dendrites of the CA3 neurons in male and female voles that experienced either social or ecological disruptions in early life and remained socially isolated as subadults were longer than those in undisturbed voles. Our results suggest that social disruptions experienced in early life modulate the male's stress-related behaviors and may thus influence his monogamous tendencies. Exposure to disruptions may also impact the memory circuits of the brain that monogamous animals use to make mating decisions.

Keywords: paternal deprivation, early-life environmental disruptions, socio-spatial memory circuit, social monogamy, adolescence, social isolation, HPA-axis

INTRODUCTION

The evolutionary pressure that led humans and other mammals to form monogamous relationships is an enigma (Wittenberger and Tilson, 1980; Henrich et al., 2012). Given the low cost of reproduction for male mammals, they should maximize their fitness by pursuing as many females as possible (Clutton-Brock and Parker, 1992; Kappeler, 2013), but not all of them do (Lukas and Clutton-Brock, 2012). Males of a few species across a broad range of taxa display pair-living and copulate with their partner rather than with novel females (Lukas and Clutton-Brock, 2013). Although some of these males occasionally come in contact with other females and engage in extra-pair copulations (Solomon and Jacquot, 2002; Cohas and Allaine, 2009; Streatfeild et al., 2011), most share a home range with one female for an extended period of time and some even participate in parental care (Reichard, 2003). Studies from a variety of species that have attempted to explain why some males forgo their mating opportunities to invest in their family have produced contradictory results (Dobson et al., 2010). While the conflicting data continues to puzzle the evolutionary biologists (Kappeler, 2013), the research has provided neurobiologists with multiple avenues to explore the underlying physiological mechanisms that may maintain social monogamy within a population.

The neurobiology of social monogamy is studied from multiple angles. Some have focused on the biology of attachment in monogamous species as a rewarding emotion that keeps sexual partners in close proximity of each other and fosters paternal care (Lim et al., 2004; Young and Wang, 2004; Young, 2009; Young et al., 2011; Burkett and Young, 2012; Johnson and Young, 2015). This line of research, which has been immensely fruitful in discovering the neurochemistry of selective partner preference and social bonding, has been based on the theory that the evolution of monogamy was driven by the need for males to invest in paternal care, thus making bonding an adaptive behavior (Geary, 2000; Fraley et al., 2005; Young et al., 2011). However, others have viewed the problem of monogamy as a male tactic to maximize his fitness in environments where access to mates is limited and where he could be cuckolded into caring for another male's progeny (Phelps and Ophir, 2009; Ophir, 2017). This approach that is focused on cognition is more in line with the theory that the pressure driving the evolution of monogamy was mate guarding or resource scarcity instead of paternal investment (Schacht and Bell, 2016). Accordingly, individuals choose a mating strategy to increase their fitness and lower their chances of being cuckolded by processing social and spatial information within a given space. That information enables them to identify and remember the location of potential mates and their competitors. Additionally, a unified model of emotions and cognition controlled by the so called "social decision-making network" has been proposed to show how animals could evaluate their social environment when deciding whether to remain attached to a single mating partner, mate outside the relationship or seek many partners (Ophir, 2017). A key brain region in this model is the hippocampus, which along with the retrosplenial cortex, anterior thalamus, and septal nuclei is part of a network for forming spatial and social memories, and

is also a main accessory area of the mesolimbic reward circuitry (Ikemoto, 2010; O'Connell and Hofmann, 2011; Ophir, 2017).

If social monogamy is a cost-benefit assessment evolved to enhance fitness, then it is likely to be entangled not only with the positive emotion of attachment, but also with stress that can affect decisions making. In real life, when individuals are challenged with physical threats or face uncertainty, neither humans nor other animals weigh all alternatives to choose the best strategy and their cognitive abilities can be affected by their stress responses (Giora, 1987; Lima, 1998; Porcelli and Delgado, 2017; Summers et al., 2017). Although several studies have examined the role of stress in monogamy, most have focused on how stress influences or is impacted by partner preference and paternal care (DeVries et al., 1996; Bosch et al., 2009; Hostetler and Ryabinin, 2013; Hyer and Glasper, 2017; Kowalczyk et al., 2018). Our aim in the current study was to examine the development of stress reactivity in a socially monogamous rodent that displays alternative reproductive tactics in nature to understand how stress might shape an individual's decision-making processes associated with reproductive strategies.

To investigate the development of stress reactivity in a monogamous species, we looked at studies in other rodents. Research in rats has shown that the rearing environment in early life impacts the developing brain to shape the adult stress responses, cognition, and reproductive behavior (Liu et al., 2000; Cameron et al., 2008; Kundakovic and Champagne, 2015). However, the process is complex and depends on multiple factors including the offspring genotype, sex, and social interactions experienced later in life (Daskalakis et al., 2013). We used prairie voles as an animal model of social monogamy to examine the impact of early rearing environment and later social experience on stress reactivity of male vs. female offspring. Prairie voles are one of the rare mammalian species that display socially monogamous relationships and biparental care in captivity and in nature (Getz et al., 1981; Oliveras and Novak, 1986; Terleph et al., 2004). Like humans, prairie voles are designated as a socially monogamous species because the adult male and female pairs show a preference to live together but do not mate exclusively (Carter et al., 1995; Strassmann, 2003; Solomon et al., 2004; Streatfeild et al., 2011). Laboratory studies have shown that when male prairie voles are given the opportunity to access multiple mates, they show a preference to mate with only one of them (Blocker and Ophir, 2016). Although pair-bonded males are attentive to the sensory stimuli of other sexually-receptive females (Parker et al., 2011; Rodriguez et al., 2013), when given a choice, they prefer to remain in contact with their mate rather than a novel female (Blocker and Ophir, 2016). This suggests that males may be predisposed to forgo a desire to seek other mates once they form a pair bond.

Nevertheless, observations of prairie voles under natural and semi-natural settings have shown that the behavior of both males and females is dynamic and can shift from exclusive mating with a single partner to occasional mating with a novel conspecific (Solomon and Jacquot, 2002; Ophir et al., 2008; McGuire and Getz, 2010). For example, wild male prairie voles are reported to switch their mating tactics from being residents that share a home range with a single female to being wanderers that visit multiple

nests (Solomon and Jacquot, 2002; Ophir et al., 2008). Given that the reproductive advantage of monogamy vs. polygamy for prairie voles is equivocal (Mabry et al., 2011; Okhovat et al., 2015), it is unclear why some male voles choose a pair-living tactic while others do not and why some males switch their tactic. An insight into this conundrum might be found by examining the stress responses of voles when they encounter conspecifics and must decide to form a monogamous bond or to copulate outside the relationship. It is possible that stress reactivity of prairie voles affects their decision-making processes when exploring their mating options in unpredictable environments.

By varying the social and ecological conditions of the natal nest, we attempted to identify the early-life factors that might contribute to the predisposition of male and female voles for responding to stress. We hypothesized that the anxiety level shown by adult voles in presence of a conspecific would differ based on their sex, whether they were exposed to either social or ecological disruptions in their early-life environment, and if they experienced additional disruptions by being socially isolated as subadults later in life. Given that the hippocampus can be reshaped by stress throughout life (McEwen and Magarinos, 2001) and is a key brain region within the so called “social decision-making network” (Ophir, 2017), we examined the dendritic morphology of its neurons to determine the impact of disruptions experienced in early life superimposed on disruptions experienced in later life. As voles are social animals that sometimes live in groups and are raised by both parents (McGuire and Getz, 1995), we predicted that social disruptions would increase the anxiety levels of adult offspring more than ecological disruptions. Based on previous research in prairie and mandarin voles showing that females are more sensitive than males to manipulations of their social environment such as paternal deprivation and social isolation (Ruscio et al., 2009; Yu et al., 2012), we also predicted that our female subjects would be more susceptible to the impact of postpartum disruptions than males. Given the adverse effects of social isolation in voles (Scotti et al., 2015), we expected the early-life disruptions to have a greater negative effect on the stress reactivity and neuronal development of voles that were isolated as subadults than the socially-housed voles that remained with their same-sex sibling.

MATERIALS AND METHODS

Subjects

The subjects were the F2 generation of prairie-vole breeding pairs that are maintained in the animal facility at Lehman College. The breeding colony was formed from descendants of wild-caught voles that were originally captured in east-central Illinois, U.S.A. We minimize inbreeding in our colony by monitoring the relatedness of males and females that we select for breeding. All voles in our facility are housed in standard clear plastic cages (48 × 27 × 20 cm) and supplied with nesting material to simulate their natural habitat. Voles are underground burrowers that occupy a variety of habitats including ungrazed pastures, hay fields, and alfalfa fields (Cole and Batzli, 1979; Mankin and Getz, 1994). They prefer to live in areas of thick rather than sparse vegetation; they use vegetation as both food and cover

(Lin and Batzli, 2001). They are more likely to disperse from areas of no vegetative cover (Lin et al., 2006). Given that voles are considered as pests, a way to control their population is to mow their vegetative cover (Carter and Getz, 1993; O'Brien, 1994). To create a protective and familiar environment for them in the lab, we first place a layer of ~5 cm of moistened peat moss at the bottom of their cage then fill the cage to the top with straw. Water and food, consisting of a mixture of sunflower seeds, rabbit chow, and cracked corn are available *ad libitum*. The colony animals are kept in rooms with fluorescent lighting and at temperatures around 20–25°C. The light:dark of the room is set at 14:10 with lights on at 6:00 a.m. The offspring of our breeding colony serve as experimental subjects. They are weaned at 20 days then transferred to a separate room where they are housed with their same-sex siblings under a protective cover of straw until adulthood. All experimental and stimulus animals used in the study were at least 60-days-old, were sexually inexperienced at the beginning of the experiment, were raised by both parents. They were removed from their natal nest before their mother gave birth to another litter.

All applicable national and institutional guidelines for the care and use of animals were followed. Animal care and all procedures performed were in accordance with the ethical standards of Lehman College and were approved by the Lehman College Institutional Animal Care and Use Committee.

Housing Manipulations

We used a total of 64 adult males and 64 adult females that we separated from their same-sex siblings to create four sets of breeding pairs ($N = 16$ pairs for each of four conditions), whose offspring served as our experimental subjects. The animals selected for breeding were between 60 and 120 days old. They were unrelated and unfamiliar to each other. Each male was held in a wire mesh cylindrical container (10 × 7.7 cm) with some food. The container was capped and placed in the cage of a female for 24 h, so the partners would become accustomed to one another's sensory stimuli. The male was then released into the female's cage and the pair was left undisturbed, except for cage cleaning, until the birth of their first offspring. At 6 days postpartum, the cages of the breeding pairs were manipulated to expose offspring to early-life disruptions that they may experience in nature such as loss of their father, protective cover or both their father and their protective cover. A total of 16 family units were left undisturbed and served as control (NoDisrupt). The NoDisrupt offspring were reared by both parents under a protective cover of straw. In the 16 family units whose ecological condition was disrupted (EcoDisrupt) the protective cover was permanently removed leaving the mother and the father to raise the young with only the peat moss at the bottom of the cage and a handful of loose straws. In the 16 family units whose social condition was disrupted (SocDisrupt), the father was permanently removed leaving the mother to raise the young under the protective cover of straw. In the 16 family units whose social and ecological conditions were disrupted (SocEcoDisrupt), the father and the protective cover were permanently removed leaving the mother to raise the young alone with only the peat moss at the bottom of the cage and a handful of loose straws. All

family units were then left undisturbed until the offspring were 20 days of age. To expose offspring to later-life disruptions, the subadults at weaning were sexed and housed either with a same sex-same sibling (Social) or housed alone (Isolate). The Social and Isolate groups were housed under a protective cover of straw until adulthood.

Anxiety Testing

Between 60 and 70 days of age, the Social and Isolate adult offspring from each family unit and of each sex were tested for their anxiety level in an open-field arena for 3 consecutive days. The open-field test is a common procedure where behavioral and physiological reactions such as immobility, leaving the preferred periphery of the arena to enter the center or defecation and urination are regarded as increased anxiety (Prut and Belzung, 2003). A day before testing, all subjects were placed alone in a new cage. The cage holding the Social or the Isolate vole was transferred to a brightly-lit room where an open-field testing box was placed directly under the fluorescent light. The square box ($72 \times 72 \times 36$ cm) was made of four white plywood sides and a Plexiglas bottom that was marked to divide the area into 12 equally-sized squares (18×18 cm each). An extra square was drawn in the center of the box at the intersection of the four middle squares. The subject's cage was left on a cart for 20 min for the animal to acclimate to the testing room. Each subject was then gently picked up by an experimenter and released at the same corner of the testing arena. A video camera attached to the ceiling above the open-field arena was turned on a minute before testing began. After releasing the animal, the experimenter left the room. Each subject was video-taped for 10 min and its behavior was later scored for the duration of time spent in the side squares, in the middle squares, in the center square, locomotion, autogrooming, freezing (remaining stationary), and rearing (standing on hind legs) by experimenters blind to the testing conditions. On day 1, the subject was tested in an arena that was empty. On day 2, the subject was tested in an arena containing an unfamiliar and unrelated stimulus animal of the same sex. The stimulus animal was held in a capped wire-mesh cylindrical container (10×7.7 cm) that was placed in the center square and attached to the Plexiglas floor with Velcro. On day 3, the subject was tested in an arena containing an empty capped wire-mesh cylindrical container that was similarly placed in the center. The open-field test was designed to determine the animal's tendency for overcoming its anxiety and risk moving from the arena's sides and explore its center. Previous studies in our lab have shown that prairie voles do not attend to or explore empty containers unless these containers have a stimulus animal within them (Parker et al., 2011). To ensure that our subjects would have an incentive to explore the arena, we tested them over 3 days with and without a social stimulus. On day 2 and 3 of the behavioral testing sessions, we also measured the time subjects spent investigating the container that had a stimulus conspecific or remained empty. However, because we found no differences in the time spent in the center of the arena and the time spent investigating the container, we are only reporting the time in the center. Following each testing session, the animal was returned to its cage and the number of fecal boli and urine puddles were

counted. The arena was cleaned to remove the excreta, sprayed with 70% alcohol to remove all odors, and allowed to dry in between testing sessions.

Brain Analysis

To determine how the brain is impacted by disturbances experienced early in life superimposed on those experienced later in life, we examined the dendritic morphology of neurons in the CA3 regions of the hippocampus of Isolate adult offspring that had experienced Social or Ecological disruptions in early life vs. the Social adult offspring that experienced no disruptions in early life. Following the behavioral tests, 16 brains from Isolate subjects (4 brains of each sex from the SocDisrupt and 4 brains of each sex from the EcoDisrupt groups) and 8 brains from Controls (4 brains of each sex from the NoDisrupt group that were socially housed after weaning) were placed in a Golgi-Cox solution. To stain the neurons, we followed the instructions in the SuperGolgi Kit by Bioenno LifeSciences (Bioenno Tech, LLC Santa Ana, California). After immersing the whole brain in Golgi solution then buffer, we sectioned it on a vibratome at $200 \mu\text{m}$, mounted the sections, and completed the staining process on gel-coated slides. The slides were coded prior to image analysis with the Neurolucida morphometry software (MBF Bioscience). The images were acquired on a Zeiss Axiophot 2 microscope equipped with a motorized stage and a video camera, and the stained neurons were traced using a $40\times/1.4\text{N.A.}$, Plan-Apochromat oil immersion objective. An experimenter blind to the testing conditions measured the average length of the apical dendrites of selected neurons in the CA3 area identified on the rat atlas (Paxinos and Watson, 2013). Of the 24 brains that were processed, 3 did not stain clearly to be used in the analysis (1 male and 1 female brain from the EcoDisrupt group and 1 female brain from the SocDisrupt group). For the remaining animals, 3 adjacent neurons were selected from each hemisphere and analyzed for a total of 6 neurons per brain. The selected neuron had to satisfy two criteria: (1) reside within the pyramidal layer of the CA3 region of the designated hippocampus region; (2) be adjacent to each other.

Statistical Analysis

For all statistical analysis, we used the IBM SPSS Statistics software for Macintosh, Subscriptions. Prior to running the statistical analysis, we used the Shapiro-Wilk's test to determine if the data were normally distributed and used the Levene's test to check for homogeneity of variance. Some of the data did not pass those tests. The data that did not pass those tests were log, square-root or cube-root transformed. For the behavioral data, we used a three-way ANOVA with sex, group, and condition as between-subject variables to test for differences on each of the three testing days and used partial eta-squared (η^2) as a measure of effect size. For the brain data, we used a two-way ANOVA with sex and conditions as between-subject variables. For significant *P*-values at <0.05 , *post-hoc* analysis was conducted with the Holm-Bonferroni method. At weaning, a total of 102 offspring raised under four different conditions were assigned to the Social group and 93 were assigned to the Isolate groups (see **Tables 1, 2** for sample sizes). We had missing data on Day 2 (a SocEcoDisrupt

TABLE 1 | ANOVA results for the main effects.

Condition	NoDisrupt		EcoDisrupt		SocDisrupt		SocEcoDisrupt	
Group	Social-Isolate		Social-Isolate		Social-Isolate		Social-Isolate	
Sample size	16♂12♀-13♂9♀		10♂12♀-13♂11♀		12♂12♀-13♂10♀		14♂14♀-12♂11♀	
	Sex		Group		Condition			
DAY 1								
Locomotion	$F_{(1, 177)} = 10^{**}$	$\eta_p^{2=} 0.05$	$F_{(1, 177)} = 0.1$	$\eta_p^{2=} 0.001$	$F_{(3, 177)} = 1.0$	$\eta_p^{2=} 0.02$		
Autogroom	$F_{(1, 177)} = 8.9^{**}$	$\eta_p^{2=} 0.05$	$F_{(1, 177)} = 0.2$	$\eta_p^{2=} 0.001$	$F_{(3, 177)} = 2.0$	$\eta_p^{2=} 0.03$		
Freezing	$F_{(1, 177)} = 5.2^*$	$\eta_p^{2=} 0.03$	$F_{(1, 177)} = 1.3$	$\eta_p^{2=} 0.007$	$F_{(3, 177)} = 3.4^*$	$\eta_p^{2=} 0.06$		
Rearing	$F_{(1, 177)} = 1.3$	$\eta_p^{2=} 0.007$	$F_{(1, 177)} = 0.05$	$\eta_p^{2=} 0.000$	$F_{(3, 177)} = 3.0^*$	$\eta_p^{2=} 0.05$		
Sides	$F_{(1, 177)} = 0.90$	$\eta_p^{2=} 0.005$	$F_{(1, 177)} = 0.6$	$\eta_p^{2=} 0.003$	$F_{(3, 177)} = 1.9$	$\eta_p^{2=} 0.03$		
Middle	$F_{(1, 177)} = 1.1$	$\eta_p^{2=} 0.006$	$F_{(1, 177)} = 1.0$	$\eta_p^{2=} 0.005$	$F_{(3, 177)} = 1.4$	$\eta_p^{2=} 0.02$		
Center	$F_{(1, 177)} = 0.1$	$\eta_p^{2=} 0.001$	$F_{(1, 177)} = 1.9$	$\eta_p^{2=} 0.01$	$F_{(3, 177)} = 1.0$	$\eta_p^{2=} 0.02$		
DAY 2								
Locomotion	$F_{(1, 174)} = 0.4$	$\eta_p^{2=} 0.003$	$F_{(1, 174)} = 0.5$	$\eta_p^{2=} 0.003$	$F_{(3, 174)} = 1.1$	$\eta_p^{2=} 0.02$		
Autogroom	$F_{(1, 174)} = 5.9^*$	$\eta_p^{2=} 0.03$	$F_{(1, 174)} = 0.8$	$\eta_p^{2=} 0.005$	$F_{(3, 174)} = 3.0^*$	$\eta_p^{2=} 0.05$		
Freezing	$F_{(1, 174)} = 3.3$	$\eta_p^{2=} 0.02$	$F_{(1, 174)} = 82^{**}$	$\eta_p^{2=} 0.3$	$F_{(3, 174)} = 2.3$	$\eta_p^{2=} 0.04$		
Rearing	$F_{(1, 174)} = 0.01$	$\eta_p^{2=} 0.000$	$F_{(1, 174)} = 2.0$	$\eta_p^{2=} 0.001$	$F_{(3, 174)} = 1.2$	$\eta_p^{2=} 0.02$		
Sides	$F_{(1, 174)} = 23^{**}$	$\eta_p^{2=} 0.1$	$F_{(1, 174)} = 2.7$	$\eta_p^{2=} 0.02$	$F_{(3, 174)} = 1.4$	$\eta_p^{2=} 0.02$		
Middle	$F_{(1, 174)} = 5.0^*$	$\eta_p^{2=} 0.03$	$F_{(1, 174)} = 2.1$	$\eta_p^{2=} 0.01$	$F_{(3, 174)} = 2.2$	$\eta_p^{2=} 0.04$		
Center	$F_{(1, 174)} = 23^{**}$	$\eta_p^{2=} 0.1$	$F_{(1, 174)} = 2.2$	$\eta_p^{2=} 0.01$	$F_{(3, 174)} = 1.0$	$\eta_p^{2=} 0.02$		
DAY 3								
Locomotion	$F_{(1, 174)} = 7.8^{**}$	$\eta_p^{2=} 0.04$	$F_{(1, 174)} = 2.0$	$\eta_p^{2=} 0.01$	$F_{(3, 174)} = 1.5$	$\eta_p^{2=} 0.03$		
Autogroom	$F_{(1, 174)} = 10^{**}$	$\eta_p^{2=} 0.06$	$F_{(1, 174)} = 0.04$	$\eta_p^{2=} 0.000$	$F_{(3, 174)} = 2.2$	$\eta_p^{2=} 0.04$		
Freezing	$F_{(1, 174)} = 7.0^{**}$	$\eta_p^{2=} 0.04$	$F_{(1, 174)} = 0.05$	$\eta_p^{2=} 0.000$	$F_{(3, 174)} = 1.5$	$\eta_p^{2=} 0.02$		
Rearing	$F_{(1, 174)} = 7.7^{**}$	$\eta_p^{2=} 0.04$	$F_{(1, 174)} = 0.1$	$\eta_p^{2=} 0.001$	$F_{(3, 174)} = 1.7$	$\eta_p^{2=} 0.03$		
Sides	$F_{(1, 174)} = 2.4$	$\eta_p^{2=} 0.01$	$F_{(1, 174)} = 0.6$	$\eta_p^{2=} 0.004$	$F_{(3, 174)} = 3.0^*$	$\eta_p^{2=} 0.05$		
Middle	$F_{(1, 174)} = 1.4$	$\eta_p^{2=} 0.008$	$F_{(1, 174)} = 0.6$	$\eta_p^{2=} 0.004$	$F_{(3, 174)} = 1.7$	$\eta_p^{2=} 0.03$		
Center	$F_{(1, 174)} = 2.2$	$\eta_p^{2=} 0.01$	$F_{(1, 174)} = 0.7$	$\eta_p^{2=} 0.004$	$F_{(3, 174)} = 2.0$	$\eta_p^{2=} 0.03$		

*Indicates significant differences at $p < 0.05$. **Indicates significant differences at $p < 0.01$.

male) and on Day 3 (a NoDisrupt male). Also, the excreta of a EcoDisrupt female was not collected after the behavioral testing. The data for one NoDisrupt Isolate female were removed because they were outliers, and the data for one SocEcoDisrupt female could not be analyzed because the video-recordings were distorted. We had missing data on Day 2 (a NoDisrupt male and a SocDisrupt female) and on Day 3 (a SocDisrupt female and a SocEcoDisrupt male). Also, the excreta of one SocEcoDisrupt male was not collected after the behavioral testing. For differences in frequency of excreta by subjects within the testing arena, we first categorized the counts as High if there were more than 3 and as Low if there were <3 excrements then used Fisher's exact probability test to analyze the data for each testing day.

RESULTS

Behavior in Open-Field Test

The three-way ANOVA results for the main effects are shown in **Table 1** and for the interaction effects are shown in **Table 2**. There were no significant three-way interactions among sex, group, and conditions. However, for some of the behavioral measures on

each testing day, we found significant main effects and two-way interactions.

On Day1, there were significant main and interaction effects for time spent on locomotion, autogrooming, freezing, and Rearing, but there were no differences in time spent on the Sides, Middle or Center of the arena. For locomotion and freezing, there was a significant group by condition effect. In the NoDisrupt condition, the Social subjects spent more time on locomotion ($P = 0.004$) and less time on freezing ($P = 0.002$) than the Isolate subjects. For autogrooming and rearing, there was a significant sex by group effect. Isolate females groomed themselves more ($P = 0.0001$) and spent less time on rearing ($P = 0.004$) than Isolate males.

On Day2, there were significant main effects for autogroom and time spent in the arena's center and middle. Females across groups and conditions groomed themselves more and spent less time in the center and middle sections of the arena than males. The NoDisrupt subjects had the highest mean for autogrooming that differed significantly with those in the SocEcoDisrupt condition ($P = 0.04$). For Freezing, there was a significant sex by condition effect. The SocDisrupt males spent less time freezing than the SocDisrupt females ($P = 0.0001$). For

TABLE 2 | ANOVA results for the interaction effect.

	Sex X Group		Sex X Condition		Group X Condition		Sex X Group X Condition	
DAY 1								
Locomotion	$F_{(1, 177)} = 0.2$	$\eta^2 = 0.001$	$F_{(3, 177)} = 0.6$	$\eta^2 = 0.01$	$F_{(3, 177)} = 3.5^*$	$\eta^2 = 0.06$	$F_{(3, 177)} = 0.9$	$\eta^2 = 0.02$
Autogroom	$F_{(1, 177)} = 8.0^{**}$	$\eta^2 = 0.04$	$F_{(3, 177)} = 0.9$	$\eta^2 = 0.02$	$F_{(3, 177)} = 0.6$	$\eta^2 = 0.009$	$F_{(3, 177)} = 0.4$	$\eta^2 = 0.007$
Freezing	$F_{(1, 177)} = 1.3$	$\eta^2 = 0.007$	$F_{(3, 177)} = 0.4$	$\eta^2 = 0.007$	$F_{(3, 177)} = 3.0^*$	$\eta^2 = 0.05$	$F_{(3, 177)} = 0.4$	$\eta^2 = 0.007$
Rearing	$F_{(1, 177)} = 9.9^*$	$\eta^2 = 0.05$	$F_{(3, 177)} = 0.6$	$\eta^2 = 0.01$	$F_{(3, 177)} = 0.4$	$\eta^2 = 0.006$	$F_{(3, 177)} = 1.5$	$\eta^2 = 0.02$
Sides	$F_{(1, 177)} = 0.5$	$\eta^2 = 0.003$	$F_{(3, 177)} = 0.6$	$\eta^2 = 0.01$	$F_{(3, 177)} = 0.08$	$\eta^2 = 0.001$	$F_{(3, 177)} = 1.8$	$\eta^2 = 0.3$
Middle	$F_{(1, 177)} = 0.05$	$\eta^2 = 0.000$	$F_{(3, 177)} = 0.4$	$\eta^2 = 0.007$	$F_{(3, 177)} = 0.2$	$\eta^2 = 0.004$	$F_{(3, 177)} = 2.2$	$\eta^2 = 0.4$
Center	$F_{(1, 177)} = 1.5$	$\eta^2 = 0.008$	$F_{(3, 177)} = 0.2$	$\eta^2 = 0.004$	$F_{(3, 177)} = 0.09$	$\eta^2 = 0.002$	$F_{(3, 177)} = 1.3$	$\eta^2 = 0.02$
DAY 2								
Locomotion	$F_{(1, 174)} = 2.9$	$\eta^2 = 0.02$	$F_{(3, 174)} = 1.0$	$\eta^2 = 0.02$	$F_{(3, 174)} = 1.1$	$\eta^2 = 0.02$	$F_{(3, 174)} = 1.0$	$\eta^2 = 0.02$
Autogroom	$F_{(1, 174)} = 2.1$	$\eta^2 = 0.01$	$F_{(3, 174)} = 1.2$	$\eta^2 = 0.02$	$F_{(3, 174)} = 0.9$	$\eta^2 = 0.02$	$F_{(3, 174)} = 2.2$	$\eta^2 = 0.04$
Freezing	$F_{(1, 174)} = 0.6$	$\eta^2 = 0.004$	$F_{(3, 174)} = 3.6^*$	$\eta^2 = 0.06$	$F_{(3, 174)} = 1.0$	$\eta^2 = 0.02$	$F_{(3, 174)} = 0.4$	$\eta^2 = 0.008$
Rearing	$F_{(1, 174)} = 0.1$	$\eta^2 = 0.001$	$F_{(3, 174)} = 1.6$	$\eta^2 = 0.03$	$F_{(3, 174)} = 3.8^*$	$\eta^2 = 0.06$	$F_{(3, 174)} = 0.6$	$\eta^2 = 0.009$
Sides	$F_{(1, 174)} = 1.6$	$\eta^2 = 0.009$	$F_{(3, 174)} = 2.9^*$	$\eta^2 = 0.05$	$F_{(3, 174)} = 2.7^*$	$\eta^2 = 0.04$	$F_{(3, 174)} = 0.5$	$\eta^2 = 0.009$
Middle	$F_{(1, 174)} = 0.05$	$\eta^2 = 0.000$	$F_{(3, 174)} = 1.4$	$\eta^2 = 0.02$	$F_{(3, 174)} = 1.7$	$\eta^2 = 0.03$	$F_{(3, 174)} = 0.7$	$\eta^2 = 0.01$
Center	$F_{(1, 174)} = 1.2$	$\eta^2 = 0.007$	$F_{(3, 174)} = 2.4$	$\eta^2 = 0.04$	$F_{(3, 174)} = 2.0$	$\eta^2 = 0.03$	$F_{(3, 174)} = 0.4$	$\eta^2 = 0.007$
DAY 3								
Locomotion	$F_{(1, 174)} = 0.7$	$\eta^2 = 0.004$	$F_{(3, 174)} = 1.3$	$\eta^2 = 0.02$	$F_{(3, 174)} = 1.3$	$\eta^2 = 0.02$	$F_{(3, 174)} = 0.2$	$\eta^2 = 0.004$
Autogroom	$F_{(1, 174)} = 5.7^*$	$\eta^2 = 0.03$	$F_{(3, 174)} = 0.9$	$\eta^2 = 0.02$	$F_{(3, 174)} = 0.8$	$\eta^2 = 0.01$	$F_{(3, 174)} = 0.3$	$\eta^2 = 0.005$
Freezing	$F_{(1, 174)} = 0.4$	$\eta^2 = 0.002$	$F_{(3, 174)} = 1.8$	$\eta^2 = 0.03$	$F_{(3, 174)} = 1.7$	$\eta^2 = 0.03$	$F_{(3, 174)} = 0.3$	$\eta^2 = 0.006$
Rearing	$F_{(1, 174)} = 0.5$	$\eta^2 = 0.003$	$F_{(3, 174)} = 1.2$	$\eta^2 = 0.02$	$F_{(3, 174)} = 0.3$	$\eta^2 = 0.006$	$F_{(3, 174)} = 0.5$	$\eta^2 = 0.008$
Sides	$F_{(1, 174)} = 0.001$	$\eta^2 = 0.000$	$F_{(3, 174)} = 0.3$	$\eta^2 = 0.005$	$F_{(3, 174)} = 0.8^*$	$\eta^2 = 0.05$	$F_{(3, 174)} = 0.4$	$\eta^2 = 0.007$
Middle	$F_{(1, 174)} = 0.02$	$\eta^2 = 0.000$	$F_{(3, 174)} = 0.9$	$\eta^2 = 0.02$	$F_{(3, 174)} = 1.0$	$\eta^2 = 0.02$	$F_{(3, 174)} = 0.8$	$\eta^2 = 0.01$
Center	$F_{(1, 174)} = 0.07$	$\eta^2 = 0.000$	$F_{(3, 174)} = 0.3$	$\eta^2 = 0.006$	$F_{(3, 174)} = 2.8^*$	$\eta^2 = 0.05$	$F_{(3, 174)} = 0.8$	$\eta^2 = 0.01$

*Indicates significant differences at $p < 0.05$. **Indicates significant differences at $p < 0.01$.

Rearing, there was a significant group by condition effect. In the SocDisrupt condition, the Isolate subjects spent more time on rearing than the Social subjects ($P = 0.003$). For time spent on the arena's sides, there was a significant sex by condition and a group by condition effect. Males spent much less time on the arena's sides than females in the SocDisrupt ($P = 0.0001$) and the SocEcoDisrupt ($P = 0.001$) conditions. Although males in the NoDisrupt group also showed a similar tendency ($P = 0.05$), those in the EcoDisrupt condition did not differ from females (Figure 1).

On Day3, there were significant sex differences in locomotion, freezing and rearing. Males were more active than females. They spent more time in locomotion and rearing and less time freezing than females. For Autogrooming, there was a significant sex by group effect. Isolate females spent more time grooming themselves than Isolate males ($P = 0.0001$). For time spent on the arena's sides and center, there were significant group by condition effect. In the EcoDisrupt group, the Isolate subjects spent more time in the center ($P = 0.02$) and less time in the arena's sides ($P = 0.01$) than the Social subjects.

The amount of excreta left in the arena on Day 2 of testing differed significantly in Isolate males ($N = 50$, $P = 0.001$, Fisher's exact test) and females ($N = 41$, $P = 0.02$, Fisher's exact test) but not in Social males ($N = 52$, $P = 0.49$) and females ($N = 49$, $P = 0.40$). Isolate males in the EcoDisrupt and SocDisrupt groups and Isolate females in the SocDisrupt groups urinated and defecated

more in presence of a stimulus animal than voles on other days (Table 3).

Dendritic Morphology

For the length of the apical dendrites in the CA3 area of the hippocampus (Figure 2a), we found a significant effect of condition [$F_{(2,15)} = 13.7$, $P = 0.001$, $\eta_p^2 = 0.6$]. The apical dendritic length in the pyramidal neurons was longer for the SocDisrupt ($P = 0.001$) and for the EcoDisrupt (0.02) than for the Control subjects (Figures 2b–d). There were no significant sex [$F_{(1,15)} = 0.1$, $P = 0.341$, $\eta_p^2 = 0.07$] or interactions effects [$F_{(2,15)} = 1.4$, $P = 0.29$, $\eta_p^2 = 0.15$].

DISCUSSION

We disrupted the social and ecological rearing environment of prairie-vole offspring during the first week of life when rodent brains are rapidly growing and are susceptible to modifications by experience (Bandeira et al., 2009; Kundakovic and Champagne, 2015). The results were contrary to our predictions. Exposure to disruptions early in life had an anxiolytic effect, but the impact on males was greater than on females. Social disruption created by removal of the father, even in the absence of protective cover, was more effective in reducing anxiety than other conditions. The effect was noticeable in males on Day 2 of testing when a same-sex stimulus animal was placed in the center of the

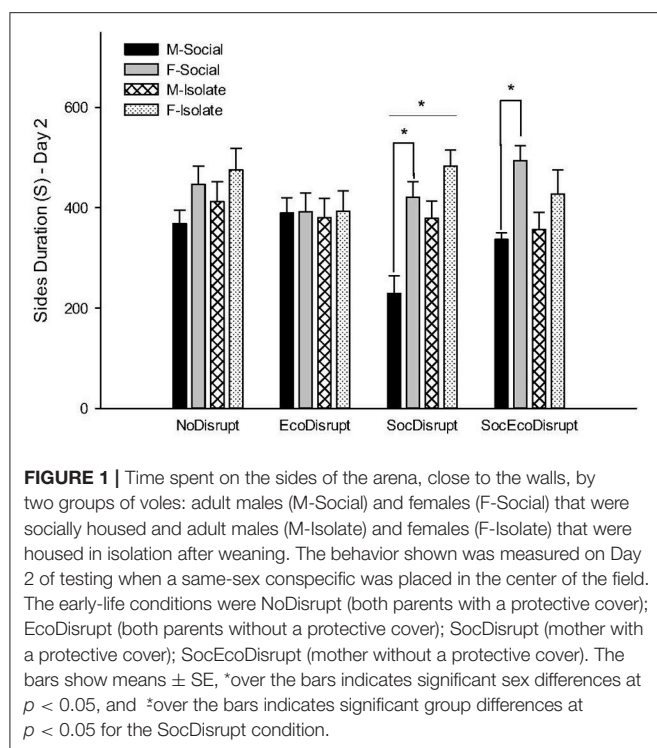


TABLE 3 | Frequency of excretion by Singly-housed (Isolate) subjects in the open-field arena.

Condition	Low	High	Low	High	Low	High
Male	Day 1	NS[†]	Day 2	$P = 0.001$	Day 3	NS
NoDisrupt	12	1	13	0	11	2
EcoDisrupt	12	1	7	6	10	3
SocDisrupt	9	4	6	7	7	6
SocEcoDisrupt	10	1	10	1	11	0
Female	Day 1	NS	Day 2	$P = 0.02$	Day 3	NS
NoDisrupt	8	1	9	0	9	0
EcoDisrupt	11	0	9	2	10	1
SocDisrupt	8	2	4	6	8	2
SocEcoDisrupt	10	1	8	3	8	3

[†] Fisher's Exact Probability Test for each testing day.

arena. Male offspring having experienced the loss of their father were more likely to risk moving from the arena's sides to the center for investigating a social object compared to males and females in other groups. Confronting the subjects with an empty container that was previously housed with a stimulus animal on Day 3 reduced the Social males' tendency to move away from the sides and investigate the inanimate object in the arena's center while increasing the Isolate voles' propensity to move to the center. Exposing the male and female voles to social isolation in early life increased the subjects' anxiety-related behaviors in adulthood, but the experience had a greater impact on females than on males. Social isolation enhanced the emotionality of both sexes in response to the social stimulus as evidenced by their increased defecation and urination on Day 2 and reduced

the anxiolytic effect of social disruption in males. Although the Isolated voles showed sex differences in their behavior and appeared to be more anxious than social voles, examination of their dendritic morphology indicated that both social and ecological disruptions induced growth rather than retraction of dendrites in the hippocampus.

Our results are contrary to some of the previous research in monogamous rodents. In mandarin voles, removal of the father immediately after birth or separation of young from their littermates increased adulthood anxiety levels measured in an empty open-field testing arena (Jia et al., 2009). Exposure of mandarin voles to paternal loss as neonates also lowered their sociality, particularly in females. As adults, the subjects were less parental, less likely to investigate novel conspecifics, and the females were less likely to show partner preference (Jia et al., 2011; Yu et al., 2012; Cao et al., 2014). In California mice, removal of the father 3 days postpartum had no effect on the anxiety of the adult offspring tested in an empty open-field arena, but the subjects showed reduced social interactions and increased aggression (Bambico et al., 2015). In prairie voles, removal of the father a day after birth had no effect on the anxiety levels of adult offspring tested on the elevated plus maze but increased their social affiliation toward a conspecific (Tabbaa et al., 2017). However, with removal of the father 2 days before birth, the adult offspring displayed delayed partner preference and were less parental. They showed indications of reduced anxiety in an empty open-field testing arena and on an elevated plus maze (Ahern and Young, 2009; Ahern et al., 2011). Collectively, these studies suggest that social disruption created by the father's removal has a negative impact on sociality but a variable effect on stress reactivity. The stress results are understandable in light of a vast literature indicating that the outcome of early-life disruptions in mammals depends on multiple factors including its timing, severity, and testing procedure (Macri et al., 2011; Chen and Baram, 2016). For example, there is evidence that moderate disruptions of the rearing environment produce offspring that are hyposensitive, whereas severe disruptions produce offspring that are hypersensitive to threats as adults (Macri and Wurbel, 2007; Coutellier et al., 2008). Furthermore, exposure to stress-induced changes during postnatal days 3–4 can result in hypersensitivity, whereas the same changes introduced on postnatal days 7–8 can result in hyposensitivity to stress later in life (Van Oers et al., 1998). By removing the father or the cover at postnatal day 6, we think we created a moderately stressful environment that prairie-vole family units may experience in nature as they occupy surface nests or because their protective cover might be reduced by mowing. When confronted with a conflicting situation as adults, only SocDisrupt males that were socially-housed had sufficiently reduced stress reactivity for overcoming their anxiety of open spaces to approach and investigate a stranger.

Multiple hypotheses may explain why we found the SocDisrupt males to show reduced anxiety following the loss of their father. It is possible that their mother altered her maternal behavior when we removed her partner on postpartum day 6. Many studies have found the mother to be the source of modifications in stress reactivity of offspring when disruptions to

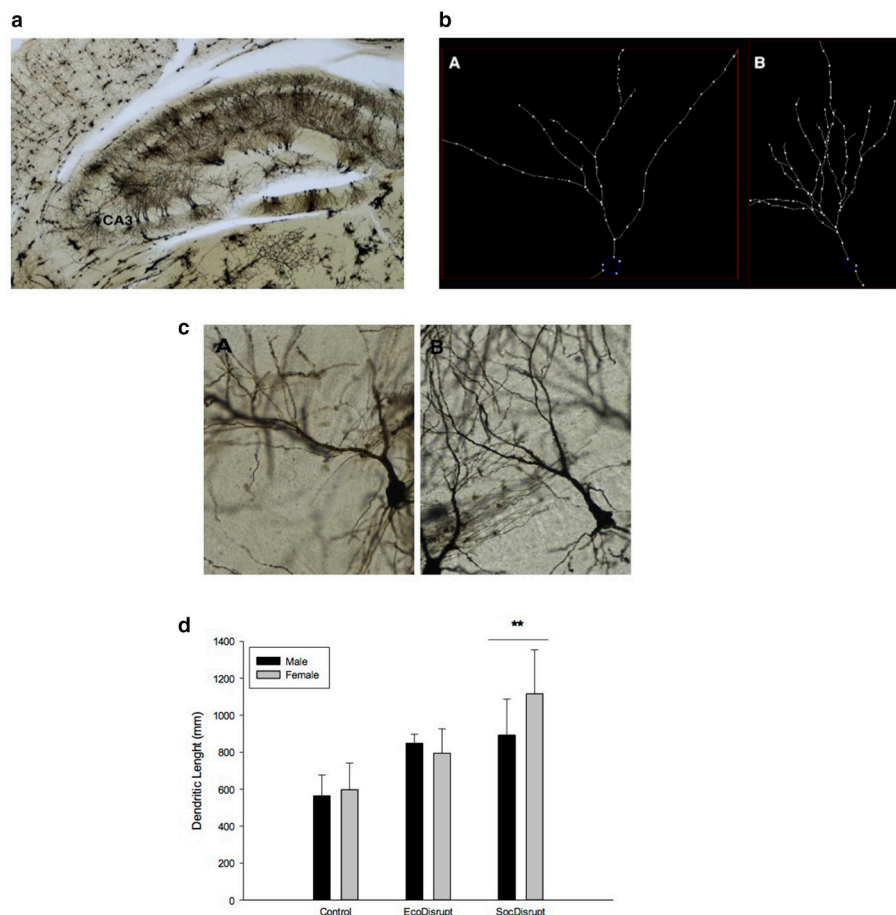


FIGURE 2 | (a) Photomicrograph showing CA3 area of the hippocampus of a prairie vole prepared with Golgi Stain. **(b)** Reconstructed CA3 neuron in the hippocampus showing the apical dendrites in a representative animal from **(A)** Control and **(B)** SocDisrupt group. **(c)** Photomicrograph of the CA3 neuron in the hippocampus showing the apical dendrites in a representative animal from **(A)** Control and **(B)** SocDisrupt group. **(d)** Group differences in apical dendritic length of neurons in the CA3 region of the hippocampus. The conditions were Control (adult offspring raised by both parents under a protective cover and housed with a same-sex partner after weaning), EcoDisrupt (adult offspring raised by both parents without a protective cover and housed alone after weaning); SocDisrupt (adult offspring raised by mother alone with a protective cover and housed alone after weaning). The bars show means \pm SE and **over the bars indicate significant group differences at $p < 0.01$.

the maternal environment are introduced at critical points during development (Curley and Champagne, 2016). Laboratory studies in uniparental species such as rats and mice have shown that when the mother is confronted with foraging demands, removal of nesting materials or predator threats, she alters her nest attendance and active maternal care thus changing the activity of her offspring hypothalamic-pituitary-adrenal (HPA) axis in a sex-specific manner (Ivy et al., 2008; Coutellier et al., 2009; Mashoodh et al., 2009). Hence, it is possible that the behavior of prairie-vole mothers in our study altered her adult sons' stress responses. Although we did not record the mother's behavior following the father's removal, we think this is an unlikely scenario because previous studies under laboratory or semi-natural conditions in prairie and mandarin voles have shown that the mother does not compensate when the father is removed from the nest (McGuire et al., 2007; Jia et al., 2009; Ahern et al., 2011). However, because voles are biparental, it is possible that reduction in total overall

care that is usually provided by both parents affected the sons' behavior later in life (Ahern and Young, 2009).

Alternatively, the sons themselves may have sensed and reacted to the changes in their social environment as we abruptly removed their father. Their father's absence may have caused a shift in how the HPA axis and the sympathetic nervous system balance the subjects' risk-taking tendencies in adulthood (Del Giudice et al., 2011). That change may have mobilized the voles in our study to move from the safety zones to the center of the arena where a social stimulus was placed. It is also plausible that the father's removal in our study altered the activity of the mother's HPA-axis, and that change was transferred to her young through lactation. Prairie voles form a pair bond shortly after mating, and separation of the partners increases their levels of plasma corticosterone (Bosch et al., 2009; McNeal et al., 2013). Rodent studies have shown that maternal corticosterone can be transferred to young via milk to affect regulation of HPA axis

and behavior of the offspring (Casolini et al., 1997; Catalani et al., 2011). Unlike uniparental species in which only the mother creates the early social environment of the young, in biparental species such as prairie voles, the father also contributes to that social environment and his absence can have either a direct or an indirect effect on the offspring brain and behavior (McGuire et al., 2007; Ahern et al., 2011).

Disruptions in life can affect offspring not only in early phases of their lives but also during adolescence (Weintraub et al., 2010). There is evidence that exposure of subadults to social disruptions can alter their behavior so they can adapt to their environment (Sachser et al., 2011). To determine how later experience affects prairie vole offspring that were exposed to social or ecological disturbances, we isolated half of them and examined their behavior and hippocampal dendritic morphology in adulthood. Our behavioral results were consistent with past research showing that chronic isolation activates the subjects' sympathetic drive and enhances their anxiety and depression-like behaviors (Grippe et al., 2007; Ruscio et al., 2009). Our subjects showed signs of increased emotionality in presence of a social stimulus within the open-field arena and the male's mobilization to the center for investigating a conspecific was diminished following isolation.

However, we found changes in the length of hippocampal neurons that were contrary to our expectations. Previous research in a number of species have shown that hippocampal CA1-CA3 neurons are particularly susceptible to stress and atrophy in response to chronic stress including social isolation (McEwen, 1999; McEwen and Magarinos, 2001; Silva-Gómez et al., 2003). In our subjects, both males and females that had experienced either social or ecological disruptions as neonates and social isolation as juveniles displayed increases in the dendritic length of their CA3 neurons. However, our data are consistent with a recent study in California mice showing that social isolation enhances cell survival and proliferation in the hippocampus (Ruscio et al., 2015). Chronic social isolation in prairie voles also increase estrogen receptors in the medial amygdala (MEA) and the bed nucleus of stria terminalis (BST) of males, decrease corticotropin-releasing hormone (CRH) receptor type 1 but increase CRH receptor type 2 in the hippocampus (Pournajafi-Nazarloo et al., 2009; Perry et al., 2016). Given that CRH-R1 and CRH-R2 have been found to differentially modulate dendritic growth of hippocampal neurons (Sheng et al., 2012), it is possible

that these receptors along with estrogen receptors may mediate alterations of the hippocampal neuronal structure in response to moderate environmental disruptions experienced during offspring development of monogamous species. Combined, the increased dendritic length of the hippocampal neurons and the anxiolytic effects of paternal absence on sons that we observed in prairie voles suggest that moderate stress during development may be adaptive. The experience might prepare offspring to counter stressful challenges such as the perils of exposure to predators or the risk of leaving the social group as ecological variables change and affect their decision to opt for a resident vs. a wanderer strategy (Solomon, 2003; McGuire and Getz, 2010).

The hippocampus has recently been proposed to be part of a socio-spatial memory circuit that is entangled with the pair-bonding network where neuropeptides such as vasopressin and oxytocin act to influence prairie vole's decision for remaining with a single partner, moving away to mate outside the relationship or adopting a non-monogamous mating tactic (Ophir, 2017). We have shown that disruptions of the neonatal environment at critical periods during development alters the anxiety profile of individuals to affect their risk-taking tendencies and enhance hippocampal neuronal growth. These changes in behavior and brain of voles in response to stress experienced during development may modify how they integrate socio-spatial information about the position of their mates and competitors in space and thus the decision to remain monogamous.

AUTHOR CONTRIBUTIONS

OA-N designed and conducted the behavioral study. NR assisted with conducting the behavioral experiments. JD conducted the brain staining and analysis. SC, FA, and MC analyzed the behavioral data, MB oversaw the study and wrote the manuscript.

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Imaging, Behavior and Endocrine Analysis of “Jealousy” in a Monogamous Primate

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Understanding the neurobiology of social bonding in non-human primates is a critical step in understanding the evolution of monogamy, as well as understanding the neural substrates for emotion and behavior. Coppery titi monkeys (*Callicebus cupreus*) form strong pair bonds, characterized by selective preference for their pair mate, mate-guarding, physiological and behavioral agitation upon separation, and social buffering. Mate-guarding, or the “maintenance” phase of pair bonding, is relatively under-studied in primates. In the current study, we used functional imaging to examine how male titi monkeys viewing their pair mate in close proximity to a stranger male would change regional cerebral glucose metabolism. We predicted that this situation would challenge the pair bond and induce “jealousy” in the males. Animals were injected with [¹⁸F]-fluorodeoxyglucose (FDG), returned to their cage for 30 min of conscious uptake, placed under anesthesia, and then scanned for 1 h on a microPET P4 scanner. During the FDG uptake, males ($n = 8$) had a view of either their female pair mate next to a stranger male (“jealousy” condition) or a stranger female next to a stranger male (control condition). Blood and cerebrospinal fluid samples were collected and assayed for testosterone, cortisol, oxytocin, and vasopressin. Positron emission tomography (PET) was co-registered with structural magnetic resonance imaging (MRI), and region of interest analysis was carried out. Bayesian multivariate multilevel analyses found that the right lateral septum ($\text{Pr}(b > 0) = 93\%$), left posterior cingulate cortex ($\text{Pr}(b > 0) = 99\%$), and left anterior cingulate ($\text{Pr}(b > 0) = 96\%$) showed higher FDG uptake in the jealousy condition compared to the control condition, while the right medial amygdala ($\text{Pr}(b > 0) = 85\%$) showed lower FDG uptake. Plasma testosterone and cortisol concentrations were higher during the jealousy condition. During the jealousy condition, duration of time spent looking across at the pair mate next to a stranger male was associated with higher plasma cortisol concentrations. The lateral septum has been shown to be involved in mate-guarding and mating-induced aggression in monogamous rodents, while the cingulate cortex has been linked to territoriality. These neural and physiological changes may underpin the emotion of jealousy, which can act in a monogamous species to preserve the long-term integrity of the pair.

Keywords: monogamy, mate-guarding, mating-induced aggression, testosterone, lateral septum, cingulate cortex, vasopressin, cortisol

INTRODUCTION

Shakespeare's "green-eyed monster" has been written about for centuries (Shakespeare, 1988), but the scientific study of jealousy is relatively young. Jealousy is an aspect of romantic relationships that works to maintain the relationship, but which can develop into intimate partner violence when unrestrained (Buss, 2002; Neal and Edwards, 2015). Jealousy may have given a fitness advantage to humans in our ancestral environment; current evidence shows that culture also plays a role (Harris, 2003). The emotion of jealousy is a form of social rejection that occurs when another individual (partner, parent, etc.) appears to devalue a relationship because of an outside third party (Leary, 2015). Because jealousy is an emotion that often occurs in the context of reproductive relationships, it is relevant to our understanding of the evolution and neurobiology of pair bonds.

The neural basis of jealousy in humans is not well understood in part because eliciting jealousy requires complex social interactions which may be difficult to create in a laboratory setting (Harmon-Jones et al., 2009). However, a large body of studies has suggested that social rejection of various types is mediated by the anterior cingulate cortex (Eisenberger, 2015). A recent functional magnetic resonance imaging (fMRI) study asked participants to imagine that an early stage romantic partner "did not prefer" them over a romantic rival. This jealousy condition provoked activation in the dorsal and ventral striatum (dopaminergic areas), as well as the cingulate cortex (Sun et al., 2016). Dopamine agonist therapy is also associated with delusional jealousy in Parkinson's patients (Poletti et al., 2012).

Investigating the neurobiology of jealousy in non-human primates that form pair bonds is an important step in understanding the evolution of monogamy. Male sexual "jealousy" was studied in the context of rhesus monkey consortships using positron emission tomography (PET) imaging (Rilling et al., 2004). Rhesus monkeys are not socially monogamous, but do form short-term consortships in which a male guards an estrus female (Manson, 1997; Palombit, 2014). When rhesus males viewed their consort next to a stranger male, they had increased [^{18}F]-fluorodeoxyglucose (FDG) uptake in areas including the right amygdala and right superior temporal sulcus; plasma testosterone concentrations also increased (Rilling et al., 2004). Theoretically, a threat to a long-term reproductive and affiliative relationship might be even more salient than a threat to a short-term sexual consortship, because it is an attachment bond and there are more resources to lose (Ellis and Weinstein, 1986). Unlike rhesus monkeys, titi monkeys are socially monogamous and form long-term pair bonds, and thus might even have stronger "jealousy" reactions than rhesus monkeys (which only form consortships).

Social monogamy is displayed by a small minority of mammals, usually estimated at 3–5% of mammalian species (Kleiman, 1977; Lukas and Clutton-Brock, 2013; Diaz-Munoz and Bales, 2016; Tecot et al., 2016). In socially monogamous animals, the development of an adult attachment relationship or "pair bond" is associated with the onset of mate-guarding in both males and females (Mason, 1966; Winslow et al., 1993; McGuire and Getz, 1998; Fernandez-Duque et al., 2000; Bowler et al., 2002;

Getz et al., 2003; Fisher-Phelps et al., 2016; Tabbaa et al., 2016). This behavior helps maintain the relationship through aggression toward both same- and opposite-sex individuals. The pair bond is a construct encompassing a preference for the familiar partner, distress upon separation, and the ability of the pair mate to buffer stress (Mason and Mendoza, 1998). As such, it is very similar to a human romantic relationship (Hazan and Shaver, 1987; Sbarra and Hazan, 2008) and the pair mates might be expected to feel jealousy if a third party threatened that relationship. While the neurobiology of pair bonding has been best studied in a rodent model, the socially monogamous prairie vole (*Microtus ochrogaster*), the many potential differences between rodent and primate nervous systems make a primate model for pair bonding desirable as well (Phillips et al., 2014; Bales et al., 2017).

Titi monkeys (genus *Callicebus*) are small, arboreal primates which display social monogamy (including "jealousy" behavior) both in the field (Mason, 1966; Spence-Aizenberg et al., 2016; Van Belle et al., 2016) and in the laboratory (Mason, 1974; Mendoza and Mason, 1997; Carp et al., 2016). For example, in the wild, a male was observed placing himself in between his female pair mate and intruding male, and physically restraining his female pair mate to keep her from moving toward an "intruder" male (Mason, 1966). Wild titi monkeys of both sexes respond to conspecific playbacks by duetting and approaching the speaker, which may function as both territorial and mate defense (Caselli et al., 2015). Both males and females show strong arousal reactions toward outsiders, including tail-lashing and arched-back displays, and restraint of the pair mate to keep her/him away from the stranger, although males have stronger reactions than females (Cubiciotti and Mason, 1978; Fernandez-Duque et al., 2000). This jealousy reaction can be duplicated in a laboratory context either with live intruders (Fernandez-Duque et al., 2000) or by introduction of a mirror in which the pair sees their own reflections (Fisher-Phelps et al., 2016). Titi monkeys provide an ideal non-human primate to examine a challenge to the pair bond that could elicit a "jealousy" response. Ellis and Weinstein (Ellis and Weinstein, 1986) proposed that three conditions are necessary for eliciting jealousy: (1) an attachment relationship between two individuals, (2) valued resources that are part of the attachment bond, and (3) intrusion by a third individual that is perceived by one partner as wanting to become a receiver of resources. Titi monkeys fit these criteria since the (1) adult male and female form an attachment relationship with each other (unlike most other monkeys), and (2) titi monkeys naturally respond to "intruders" in the wild and captivity.

In addition to the potential neural changes associated with jealousy, we were also interested in the potential hormonal changes. In the rhesus monkey study, males who viewed their consort next to a stranger male had an increase in plasma testosterone concentrations (Rilling et al., 2004). While testosterone is the hormone most often associated with male jealousy or mate-guarding (Wingfield et al., 1990; Gray et al., 2017), there is also evidence for the role of vasopressin in aggression from both animals (Winslow et al., 1993; Ferris and Delville, 1994; Stribley and Carter, 1999; Gobrogge and Wang, 2016; Simmons et al., 2017) and humans (Marshall, 2013). Vasopressin and oxytocin are also involved in the neurobiology

of pair bond formation (Numan and Young, 2016). A role for cortisol in jealousy is also plausible based on its responses to challenging social situations (Breuner and Hahn, 2003; Casto and Edwards, 2016; Beehner and Bergman, 2017; Mendoza, 2017).

In the current study, we examined potential changes in the neural and hormonal substrates in response to a challenge to the pair bond of male titi monkeys, using the previously mentioned rodent, rhesus monkey, and human studies as our guides for the outcome measures. We exposed our subjects to two conditions in which they viewed either (1) their female pair mate next to a stranger male (jealousy condition) or (2) a stranger female next to a stranger male (control condition). We expected to see increased [^{18}F]-fluorodeoxyglucose (FDG) uptake in the lateral septum; this could be due to up-regulation of dopamine D1 receptors as has been observed in monogamous prairie voles who mate-guard (Aragona et al., 2006; Resendez et al., 2016) and titi monkeys who were recently paired (Hostetler et al., 2017). We also examined other areas implicated in jealousy in rodents (i.e., posterior cingulate cortex, medial amygdala, anterior hypothalamus), rhesus monkeys (i.e., insular cortex, superior temporal sulcus, Rilling et al., 2004), or humans (i.e., anterior cingulate, nucleus accumbens, caudate, putamen, ventral pallidum, Sun et al., 2016). While we do not specifically know the distribution of androgen receptors in titi monkeys, we did have a strong *a priori* prediction of increased plasma testosterone concentrations, because of testosterone's association with mating-related aggression and competition (Gray et al., 2017; Wingfield, 2017). Similarly, we predicted increases in plasma hormone concentrations of cortisol, oxytocin, and vasopressin due to their association with social challenge (Mendoza, 2017).

METHODS

All experimental procedures were approved by the Animal Care and Use Committee of the University of California, Davis, and complied with National Institutes of Health ethical guidelines as set forth in the Guide for Lab Animal Care.

Subjects

Subjects were eight captive-born adult male titi monkeys (*Callicebus cupreus*) housed at the California National Primate Research Center (CNPRC) in Davis, CA. Subjects were a mean age of 7.7 years old (median 7.0, range 4.0–12.8), and were living with their female pair mates for a mean of 2.5 years (median 1.7, range 0.7–9.9). All subjects were parents of offspring living in the cage. Animals were fed twice daily (0,830 and 1,330 h) a diet consisting of New World monkey chow, rice cereal, banana, apples, raisins, and baby carrots and water was available *ad libitum*. Further details of husbandry and training are available elsewhere (Tardif et al., 2006).

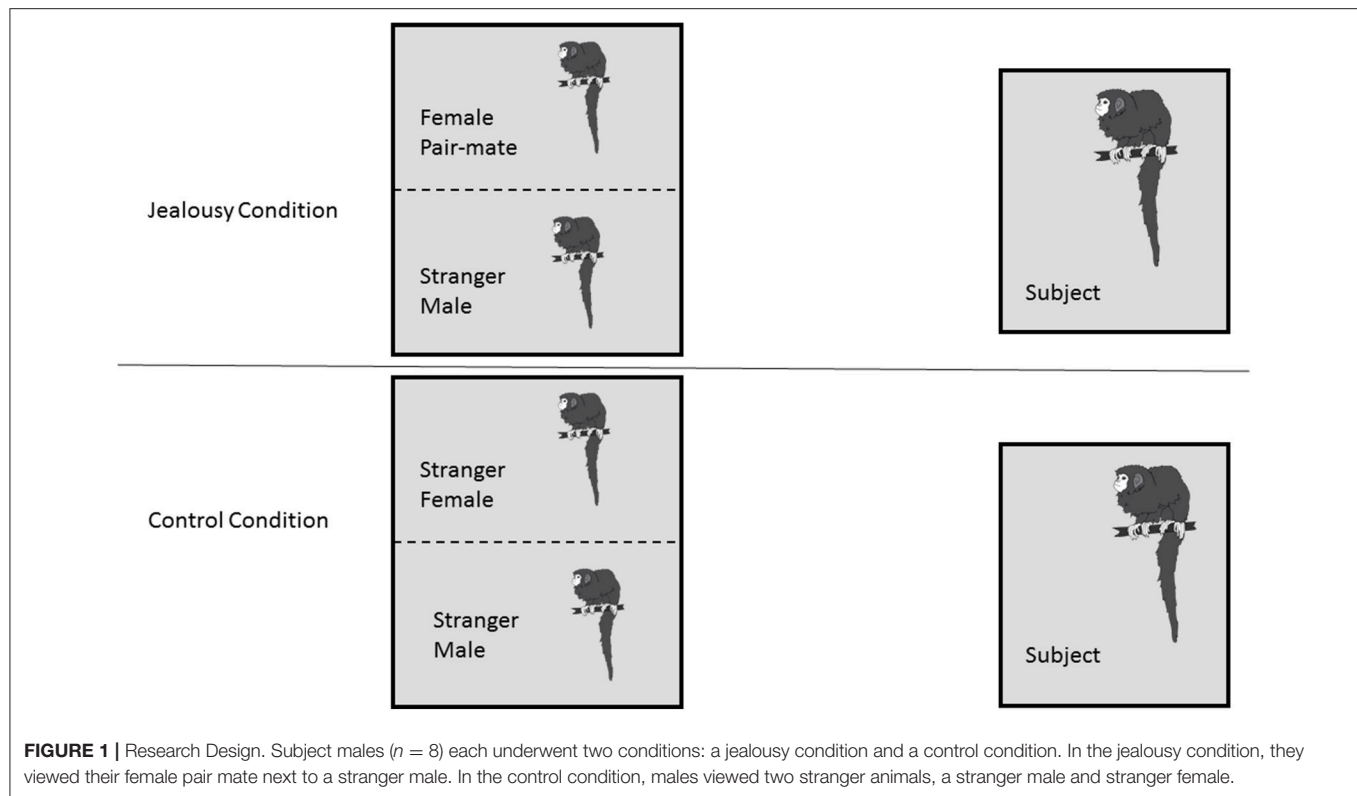
Experimental Design and PET Scanning with FDG

Functional imaging was used to examine how males viewing their pair mate in close proximity to a stranger male would differ in their regional cerebral glucose metabolism compared to viewing a stranger male next to a stranger female in adjacent

cages. Subjects, pair mates and young offspring (less than 1 year old) were relocated to a metabolism room 48 h prior to their positron emission tomography (PET) scan. As in our previous PET studies (Bales et al., 2007; Hinde et al., 2016; Maninger et al., 2017), animals were relocated prior to the scan in order to reduce the possible effect of novel housing on brain metabolism. Animals were fasted 6–12 h prior to the scan, with water available throughout the pre-scan period. On the day of the scan, all of the animals were caught and removed from the cage. The subject was manually restrained while he received a bolus injection of [^{18}F]-fluorodeoxyglucose (FDG, PETNET Solutions, Sacramento, CA, up to 2 mCi/kg IV, administered in a volume of <2 ml) into the saphenous vein.

Following the FDG injection, the male was put back in his cage alone (since his pair mate and offspring were removed) for the 30 min conscious uptake period, where he had visual access to another cage that housed two animals separated by a wire mesh. In the jealousy condition, the two animals in the viewing cage were the subject's female pair mate and a stranger male (Figure 1). The stranger was a male who was unfamiliar to the subjects. Viewing a stranger male adjacent to his female pair mate was designed to challenge the pair bond and induce "jealousy" in the male subjects. In the control condition, there was a stranger female and a stranger male monkey (note that this was a different animal from the jealousy condition) in the viewing cage. Because titi monkeys are territorial animals when paired and can show aggression to opposite-sex strangers (Fernandez-Duque et al., 2013), the male and female in the viewing cage were separated by a wire mesh in order to prevent any physical aggression (and potential wounding) between the unfamiliar animals. This was important because there were no humans in the room during the FDG uptake period to stop any fights. During the control condition, the female pair mate was moved out of the testing room. The offspring were moved out of the testing room for both the control and jealousy conditions. A camera was placed at the side of the subject's cage and the male was filmed during the uptake period for 30 min, while all of the humans left the room. Each of the eight males experienced both the jealousy and control conditions on separate days; there was a mean of 5.2 weeks (range 3–6.3) between testing days. The order of conditions was counter-balanced, such that four males experienced the jealousy condition before the control condition and four males experienced the control condition before the jealousy condition.

After the FDG uptake period, subjects were anesthetized with ketamine (25 mg/kg IM) and administered medetomidine (0.05 mg/kg IM). After the subject was sedated, a 1 ml blood sample was collected from the femoral vein and put into a heparin-containing tube, and a sample of cerebrospinal fluid (CSF) was collected and put on ice. In order to ensure that hormonal outcomes were not influenced by the considerable disturbances involved prior to collection of blood samples, care was taken to ensure that the time of day was comparable for a given subject tested in each condition. Testing started between 0,800 and 0,839 h for the first subject, and the second subject was tested approximately 1.5–2 h later. Cortisol concentrations for males tested in the first (earlier) group averaged 94.1 ± 5.8 $\mu\text{g/dl}$, while males tested in the later group averaged 55.7



± 7.2 $\mu\text{g/dl}$. While time of day was correlated with cortisol concentrations ($r = -0.575$), this effect of circadian rhythm was accounted for in the design of the study by carrying out both of an individual's scans (control and jealousy) in the same time grouping (early or late). For example, both of 32878's scans were carried out in the early group, and both of 31716's scans were carried out in the late group. We also measured the duration of time between capture of the subject following FDG uptake until blood and CSF sample collection (i.e., "disturbance time"). Disturbance time for blood samples was a mean of 5.22 min (median 4.80, range 1.72–16.15) after capture and sedation (raw data in Appendix 1). This disturbance time was not statistically correlated with plasma cortisol concentrations ($r = 0.102$). CSF samples were collected a mean of 9.50 min (median 9.88, range 5.75–13.13) after capture and sedation (raw data in Appendix 1; no statistical analysis on CSF data was carried out).

Following collection of blood and CSF samples, an endotracheal tube was placed and a catheter was placed in the saphenous vein in order to administer IV fluids (lactated ringers solution, 10 ml/kg/h). Atipamazole was used to reverse medetomidine, and anesthesia was maintained with isoflurane (1–2%), while the male was positioned on the scanner bed feet first and the brain of the animal was positioned in the center of the scanner. PET imaging was performed on a microPET P4 scanner (Siemens Preclinical Solutions, Knoxville, TN). Image acquisition began a mean of 69.49 (SD ± 7.52) minutes post-FDG administration, and static PET scans were acquired for 60 min. Anesthesia was maintained throughout the scan. Animals were

housed in metabolism cages for 24 h after scanning, at which time radiation was decayed to background levels and animals were returned to their home cages.

MRI Scanning

Structural magnetic resonance imaging (MRI) scans were conducted in a GE Signa LX 9.1 scanner (General Electric Corporation, Milwaukee, WI) with a 1.5 T field strength and a 3" surface coil. Each male was fasted 8–12 h before the procedure. At the start of the procedure, the male was sedated with ketamine (10 mg/kg IM) and medazolam (0.1 mg/kg IM), and an endotracheal tube was placed. A catheter was also placed in the saphenous vein in order to administer fluids as necessary. Anesthesia was maintained with isoflurane (1–2%) while the male was positioned in the MRI scanner. Each scan lasted approximately 20 min and consisted of a 3D SPGR pulse sequence in a coronal plane. Images of the entire brain were collected using the following parameters: echo time TE = 7.9 ms, repetition time TR = 22.0 ms, flip angle = 30.0° , field of view = 8 cm, number of excitations = 3, matrix = 256×256 , and slice thickness = 1 mm. As a precautionary measure, the male's EtCO₂, oxygen saturation, heart rate and blood pressure were monitored throughout.

PET and MRI Coregistration, Quantification of FDG Uptake

We determined which regions of interest (ROIs) to quantify based on three groups of studies: rodent studies of aggression (lateral septum, medial amygdala, posterior cingulate cortex, and anterior hypothalamus), the Rilling rhesus monkey study

of consortship (superior temporal cortex, insular cortex), and human studies of social pain and jealousy (anterior cingulate cortex, nucleus accumbens, ventral pallidum, caudate, and putamen) (Figure 2).

ROI structures were individually drawn on each subject's MRI image, for both left and right hemispheres, using landmarks as a guide, in Siemen's Inveon Research Workplace software (IRW, Siemens Healthcare, USA). ROIs were drawn prior to co-registrations with the PET image, so they were drawn blind with regard to PET image/FDG uptake and to experimental condition. The same ROIs were used for both the jealousy and control conditions. Static PET images were reconstructed with a 3DRP reconstruction protocol. MRI images were co-registered with PET scan images using the automatic rigid registration algorithm in IRW and checked visually for registration accuracy. Mean activity for the PET images were determined in IRW by applying ROIs defined on the MRI images to the PET images. Data are presented in proportions of whole brain activity, which was calculated by dividing the mean activity in the ROI (in units of microcuries per cubic centimeter) by mean activity of whole brain ROI.

Behavioral Coding

Males were filmed during the 30 min FDG uptake period. After all of the PET scans were completed, the videos were scored by a trained coder (T.S.) who was blind to experimental condition and validated against previous scoring done in the laboratory. Videos were scored on Behavior Tracker 1.5 (behaviortracker.com) for duration of the behaviors in the ethogram (see Table 1). Behaviors included lip smacking (an affiliative behavior), tail lashing (an arousal behavior), arching (an arousal behavior), as well as looking across at the stimulus cage, locomotion, chewing, drinking, and "off camera." Data analyses were performed on the total duration of each behavior (i.e., the absolute length of time the behavior was performed).

Blood Sampling and Hormone Analysis

Blood and CSF samples were collected after animals were sedated for the PET scan following the FDG uptake period, and placed on ice. Blood samples in heparin-containing tubes were centrifuged at 3,000 RPM for 15 min at 4°C. Plasma was aliquoted, and plasma and CSF samples were stored at -70°C until assay. CSF samples were assayed for oxytocin (OT) and vasopressin (AVP). Plasma samples were assayed for testosterone, cortisol, OT, and AVP. While the veterinarians collected as many CSF samples as possible, often they were unable to get a sample due to the small size of the animals (male subjects weighed a mean of 1.3 kg, median 1.2, range 1.1–1.6). Therefore, we present CSF values in Appendix 1, but did not have an adequate sample size to analyze them statistically.

AVP and OT concentrations were estimated in duplicate using commercial enzyme immunoassay kits (Enzo Life Sciences, Farmingdale, NY) previously validated for titi monkeys. Assay sensitivity was 2.34 pg/ml for AVP and 15.55 pg/ml for OT. Intra- and inter-assay coefficients of variation (CV) were 3.36 and 14.34% respectively for AVP, and 10.62 and 12.78%, respectively

for OT. Plasma cortisol and testosterone concentrations were estimated in duplicate using commercial radioimmunoassay kits (Siemens Healthcare, Malvern, PA). Prior to cortisol assay, plasma samples were diluted 1:4 in PBS gel buffer. Cortisol assay procedures were modified with the addition of 0.5 and 2.35 µg/dl concentrations of standards along with the provided range of 1.0–49 µg/dl. Assay sensitivity was 0.261 µg/dl. Intra- and inter-assay CV were 3.20 and 6.26%, respectively. Prior to testosterone assay, plasma samples were diluted 1:2 in PBS gel buffer. Testosterone assay procedures were modified with the addition of 57 and 197.5 ng/dl concentrations of standards along with the provided range of 24–1,667 ng/dl. Testosterone assay sensitivity was 4.58 ng/dl. All samples were run in the same assay and intra-assay CV was 1.02%.

Data Analysis

All models were fitted in a fully Bayesian multivariate multilevel framework for several reasons. First, due to our small sample size and large number of outcomes, multivariate models could not be estimated with least squares or maximum likelihood methods. Bayesian multivariate methods allowed for estimation of hypothesized regions of interest that included numerous correlated outcomes in one model. In addition, Bayesian multilevel methods fully account for uncertainty across levels of hierarchically structured data (McElreath, 2015), which was important due to our within-subjects design. Third, Bayesian methods allow for incorporating prior information into the model which improves precision of the parameter estimates (Gelman et al., 2008; Kruschke and Vanpaemel, 2015; see Supplementary Material for model details). Finally, parameter estimates have probabilistic interpretations, which allows for estimating the probability of a positive or negative experimental effect (Zucker et al., 1997; Lee, 2011).

In total, we fit five multivariate multilevel models. The first three models were based on hypothesized brain regions previously implicated as modulating jealousy-like behavior in different species: (1) mate-guarding in rodents; (2) jealousy or social pain in humans; and (3) bilateral regions from the rhesus monkey study. The next two multivariate multilevel models assessed hormonal and behavioral differences. The final models were exploratory, in that outcomes were determined from our results. These final models were not multilevel, but multivariate examining correlations between look duration and hormones as well as FDG uptake in ROIs (for the jealousy condition only). For these models, we standardized the predictors and response variables so that the estimates were on r scale (correlation coefficient). All model based estimates are provided in Tables 2–6, whereas the raw means and standard deviations are provided with the model checks (Appendix 2).

Variance was partitioned into two components (Gelman and Hill, 2007): (1) the variance (σ_u^2) between subjects (i.e., varying intercepts); and (2) the residual variance (σ_e^2). As a measure of residual variance explained by subject, we computed intra-class correlation coefficients (ICC) (Quene and Van Den Bergh, 2004). Each multivariate model included one fixed effect, which provided a contrast from the control group. The parameter

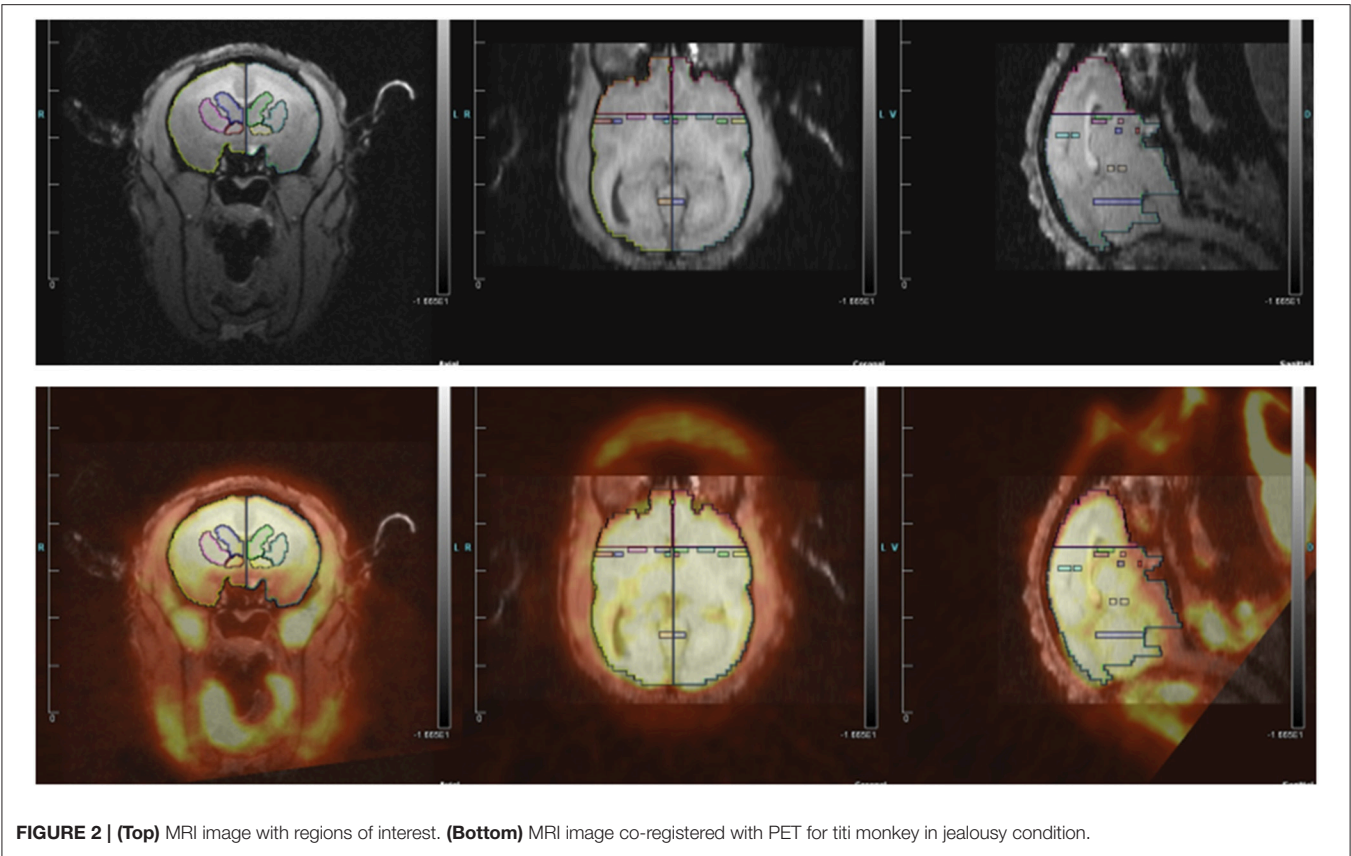


FIGURE 2 | (Top) MRI image with regions of interest. (Bottom) MRI image co-registered with PET for titi monkey in jealousy condition.

TABLE 1 | Ethogram.

Behavior*	Definition
Look Across	Male's eyes gaze in the direction of the stimulus cage.
Lip smack	Male makes rapid lip movement accompanied by smacking sound.
Arch	Male raises dorsal surface of his back. May be accompanied by piloerection. (This behavior along with tail lash are "arousal behavior")
Tail lash	Male whips his tail back and forth laterally. (This behavior along with arch are "arousal behavior")
Locomotion	Male moves at least one body length.
Chew/pick bandage	Male manipulates bandage (which covers his injection site) with his mouth or hands.
Drink	Male drinks water. Begins when mouth touches lixit and ends when drinking terminates.
Off camera	Male is out of view of the camera.

*All behaviors were analyzed as total durations.

estimates were summarized with 95% credibility intervals (*CrI*) that, by definition, have a 95% probability of containing the true parameter (Morey et al., 2015). Bayesian methods provide probabilistic estimates that allow for explicit statements about likely values for the *true* treatment effect. We thus computed posterior probabilities of a positive or negative effect ($\Pr(b > 0)$ and $\Pr(b < 0)$) (Gelman, 2013; Greenland and Poole, 2013).

This is not possible with classical methods, since parameters are assumed to be fixed point estimates (probability distributions cannot exist). Posterior probabilities $>80\%$ are reported in the results section, but all estimates are provided in tables. The 80% figure was chosen merely as a convenient figure in order to simplify the reporting of the results. Finally, an effect size parameter (δ_T) was obtained from dividing the estimate (*b*) by the square root of the variance components summed ($\sqrt{\sigma_u^2 + \sigma_e^2}$) (Hedges, 2007). Interpretation of (δ_T) follows Cohen's *d* (Cohen, 2009; small = 0.2, medium = 0.5, large = 0.8).

The jealousy condition for one male was not usable for technical reasons, thus the final sample size was 8 control scans and 7 jealousy scans, for 8 total subjects. Due to the complexity of the multivariate multilevel models, we examined fit with posterior predictive checks and posterior predictive *p*-values (Gelman et al., 1996; de la Horra and Rodriguea-Bernal, 1999). Here, the fitted model was used to simulate data, from which a properly specified model will provide replications that look like the observed data and non-extreme *p*-values ($0.95 > p\text{-value} > 0.05$). For most models, the posterior predictive *p*-values indicated that model fit was adequate (Appendix 2).

All computation was done in R (Team, 2016).The package *brms* (Buerkner, 2015), a front end to the probabilistic programming language *Stan* (Stan_Development_Team, 2015), was used to fit all regression models (all R script and data are available upon request).

TABLE 2 | Multivariate multilevel model estimates for regions of interest implicated by rodent studies as modulating mate-guarding behavior.

ROI		<i>b</i>	Post. SD	95% CrI	δ_T	Pr (<i>b</i> > 0)	Pr (<i>b</i> < 0)
LS-L	Intercept	0.96	0.03	0.87, 1.02	–	–	–
	Jealousy	–0.02	0.04	–0.08, 0.06	–0.18	31%	69%
LS-R	Intercept	0.91	0.03	0.85, 0.97	–	–	–
	Jealousy	0.04	0.03	–0.02, 0.10	0.55	93%	7%
AH-L	Intercept	0.67	0.03	0.61, 0.74	–	–	–
	Jealousy	0.01	0.04	–0.07, 0.10	0.14	63%	37%
AH-R	Intercept	0.69	0.03	0.62, 0.76	–	–	–
	Jealousy	–0.04	0.04	–0.12, 0.05	–0.35	20%	80%
PCC-L	Intercept	1.07	0.01	1.01, 1.09	–	–	–
	Jealousy	0.04	0.02	0.01, 0.07	1.02	98%	2%
PCC-R	Intercept	1.09	0.02	1.05, 1.14	–	–	–
	Jealousy	0.01	0.03	–0.05, 0.06	0.05	55%	45%
MeA-L	Intercept	0.70	0.03	0.64, 0.75	–	–	–
	Jealousy	–0.01	0.03	–0.07, 0.06	–0.04	44%	56%
MeA-R	Intercept	0.70	0.03	0.64, 0.76	–	–	–
	Jealousy	–0.03	0.03	–0.10, 0.03	–0.40	16%	84%

Intercept is the model estimate for the control condition. Jealousy is the difference from the control condition—the jealousy effect. Post. SD is the posterior standard deviation of the estimate. These estimates were all obtained from the same model. Interpretation of (δ_T) follows Cohen's *d* (small = 0.2, medium = 0.5, large = 0.8).

A Note on Interpretation of Results

The use of Bayesian statistics remains relatively uncommon. This may be seen as a limitation when comparing our results to the extant literature. Indeed, our use of Bayesian methods has different goals than typically pursued: we did not focus on rejecting a null hypothesis. Instead, our analysis sought to quantify the most probable values for the “true” effect of jealousy on regional cerebral glucose metabolism, hormones and behavior in titi monkeys. This is not possible with classical methods (e.g., ANOVA) in which evidential quantities (e.g., *p*-values) are in reference to counterfactual sampling procedures. When inferring from our results, the posterior probabilities can be directly interpreted as probabilities (how probability is used in everyday language). The present approach does not include thresholds (i.e., cut-offs, but of course a probability of 99% provides stronger evidence than 85%, assuming equal prior odds). A meaningful probability can be determined in light of theory, past research, the quality of this study (including limitations), and the reported results (Harrell and Shih, 2001; Gelman, 2013; Greenland and Poole, 2013; Gelman et al., 2014; Kruschke, 2014).

RESULTS

FDG Uptake

Our first multivariate multilevel model simultaneously estimated areas implicated by rodent studies as modulating mate-guarding behavior: the lateral septum (LS), anterior hypothalamus (AH), posterior cingulate cortex (PCC), and medial amygdala (MeA). The probability of a positive effect of jealousy condition on FDG uptake in the right LS was 93% (*b* = 0.04, *CrI* = [–0.02–0.10],

TABLE 3 | Multivariate multilevel model estimates for regions of interest shown to be associated with jealousy and social pain in humans.

ROI		<i>b</i>	Post. SD	95% CrI	δ_T	Pr (<i>b</i> > 0)	Pr (<i>b</i> < 0)
AC-L	Intercept	1.06	0.02	1.04, 1.10	–	–	–
	Jealousy	0.05	0.03	–0.01, 0.10	0.79	96%	4%
AC-R	Intercept	1.08	0.02	1.04, 1.12	–	–	–
	Jealousy	0.01	0.02	–0.04, 0.05	0.09	60%	40%
Ca-L	Intercept	1.13	0.03	1.07, 1.18	–	–	–
	Jealousy	–0.01	0.03	–0.08, 0.06	–0.14	36%	64%
Ca-R	Intercept	1.06	0.03	0.99, 1.13	–	–	–
	Jealousy	0.04	0.03	–0.03, 0.09	0.41	90%	10%
P-L	Intercept	1.18	0.02	1.14, 1.23	–	–	–
	Jealousy	0.02	0.02	–0.03, 0.06	0.26	79%	21%
P-R	Intercept	1.15	0.04	1.06, 1.24	–	–	–
	Jealousy	–0.02	0.05	–0.12, 0.08	–0.19	31%	69%
NAcc-L	Intercept	0.96	0.05	0.86, 1.06	–	–	–
	Jealousy	0.02	0.06	–0.10, 0.12	0.27	76%	24%
NAcc-R	Intercept	0.89	0.03	0.83, 0.96	–	–	–
	Jealousy	0.02	0.04	–0.05, 0.09	0.11	62%	38%
VP-L	Intercept	0.83	0.04	0.76, 0.90	–	–	–
	Jealousy	0.05	0.04	–0.04, 0.13	0.38	88%	12%
VP-R	Intercept	0.79	0.03	0.72, 0.85	–	–	–
	Jealousy	0.03	0.03	–0.03, 0.10	0.45	86%	14%

Intercept is the model estimate for the control condition. Jealousy is the difference from the control condition—the jealousy effect. Post. SD is the posterior standard deviation of the estimate. These estimates were all obtained from the same model. Interpretation of (δ_T) follows Cohen's *d* (small = 0.2, medium = 0.5, large = 0.8).

$\delta_T = 0.55$; **Figure 3A**) and, similarly, 99% in the left PCC (*b* = 0.04, *CrI* = [0.01–0.07], $\delta_T = 1.02$; **Figure 3B**), while there was some evidence for reduced uptake in the right MeA (Pr(*b* < 0) = 85%, *b* = –0.03, *CrI* = [–0.10–0.03], $\delta_T = –0.40$; **Figure 3A**). The posterior probabilities for the other comparisons were below 80% and are reported in **Table 2**. Notably, the amount of variation explained by subject across outcomes ranged from 9% (left AH: ICC = 0.09, *CrI* = [0.00–0.44]) to 42% (right LS: ICC = 0.42, *CrI* = [0.004–0.87]).

Our second multivariate multilevel model examined several cortical areas that were shown to be associated with jealousy or social pain in human studies [anterior cingulate cortex (AC), caudate (Ca), putamen (P), nucleus accumbens (NAcc), and ventral pallidum (VP)]. The probability of a positive effect of jealousy condition on FDG uptake in the left AC was 96% (*b* = 0.05, *CrI* = [–0.01–0.10], $\delta_T = 0.79$), while there was some evidence for reduced uptake in the right Ca (Pr(*b* > 0) = 90%, *b* = 0.04, *CrI* = [–0.03–0.10], $\delta_T = 0.41$), right VP (Pr(*b* > 0) = 86%, *b* = 0.05, *CrI* = [–0.03–0.13], $\delta_T = 0.38$), and the left VP (Pr(*b* > 0) = 88%, *b* = 0.04, *CrI* = [–0.03–0.13], $\delta_T = 0.38$). According to the posterior predictive checks, model fit was adequate. The other comparisons are provided in **Table 3**. The amount of residual variation explained by subject across outcomes ranged from 13% (left VP: ICC = 0.13, *CrI* = [0.00–0.56]) to 53% (right Ca: ICC = 0.53, *CrI* = [0.02–0.89]).

TABLE 4 | Multivariate multilevel model estimates for regions from the rhesus monkey study.

ROI		<i>b</i>	Post. SD	95% CrI	δ_T	Pr (<i>b</i> > 0)	Pr (<i>b</i> < 0)
IC-L	Intercept	1.09	0.03	1.03, 1.14	–	–	–
	Jealousy	–0.01	0.03	–0.07, 0.04	–0.16	27%	73%
IC-R	Intercept	1.07	0.03	1.02, 1.13	–	–	–
	Jealousy	0.01	0.03	–0.05, 0.06	0.09	63%	37%
ST-L	Intercept	1.01	0.05	0.91, 1.12	–	–	–
	Jealousy	0.01	0.04	–0.07, 0.09	0.07	62%	38%
ST-R	Intercept	1.04	0.11	0.84, 1.25	–	–	–
	Jealousy	0.02	0.07	–0.11, 0.15	0.06	62%	38%

Intercept is the model estimate for the control condition. Jealousy is the difference from the control condition—the jealousy effect. Post. SD is the posterior standard deviation of the estimate. These estimates were all obtained from the same model. Interpretation of (δ_T) follows Cohen's *d* (small = 0.2, medium = 0.5, large = 0.8).

TABLE 5 | Multivariate multilevel model estimates for plasma hormone concentrations.

ROI		<i>b</i>	Post. SD	95% CrI	δ_T	Pr (<i>b</i> > 0)	Pr (<i>b</i> < 0)
OT	Intercept	509.65	67.16	378.36, 647.11	–	–	–
	Jealousy	23.01	68.26	–120.78, 155.07	0.13	65%	35%
AVP	Intercept	263.17	25.60	212.61, 316.62	–	–	–
	Jealousy	17.72	29.51	–42.55, 75.83	0.25	74%	26%
Cortisol	Intercept	75.67	9.32	56.76, 93.98	–	–	–
	Jealousy	10.13	7.35	–4.83, 24.48	0.41	92 %	8 %
Testosterone	Intercept	410.88	160.66	129.45, 723.02	–	–	–
	Jealousy	190.17	129.97	–85.38, 440.42	0.48	93%	7%

Intercept is the model estimate for the control condition. Jealousy is the difference from the control condition—the jealousy effect. Post. SD is the posterior standard deviation of the estimate. These estimates were all obtained from the same model. Interpretation of (δ_T) follows Cohen's *d* (small = 0.2, medium = 0.5, large = 0.8).

The third multivariate multilevel model estimated bilateral ROIs from the rhesus monkey study [insular cortex (IC) and superior temporal sulcus (ST)]. This model produced negligible probabilities for an effect of jealousy, and residual variation attributed to subjects was minimal (all instances <5%). Importantly, posterior predictive check indicated a misfit between the observed and the model implied standard deviations (Appendix 2; **Table 4**). Assuming equal variances was problematic, but unfortunately a heteroskedastic model could not be fit (due to an already complex model).

Hormones

Our multivariate multilevel model estimated plasma hormone concentrations of oxytocin (OT), vasopressin (AVP), cortisol, and testosterone in the jealousy condition compared to the control condition. There was a positive effect ($\text{Pr}(b > 0) = 93\%$) of jealousy condition on plasma testosterone ($b = 190.17$, $\text{CrI} = [-85.38-440.42]$, $\delta_T = 0.48$) as well as similar evidence ($\text{Pr}(b > 0) = 92\%$) for a positive effect on plasma cortisol ($b = 10.13$, $\text{CrI} = [-4.83-24.48]$, $\delta_T = 0.40$). Posterior

TABLE 6 | Multivariate multilevel model estimates for behaviors (duration).

Behavior		<i>b</i>	Post. SD	95% CrI	δ_T	Pr (<i>b</i> > 0)	Pr (<i>b</i> < 0)
Tail lash	Intercept	1.41	1.81	–2.20, 4.90	–	–	–
	Jealousy	0.14	0.18	–0.23, 0.51	0.03	75%	15%
Arch	Intercept	15.45	8.07	–0.58, 31.15	–	–	–
	Jealousy	–10.51	9.88	–29.60, 9.75	–0.49	13%	87%
Look across	Intercept	145.72	45.57	55.98, 239.23	–	–	–
	Jealousy	6.28	54.11	–101.40, 116.81	0.05	55%	45%
Lip smack	Intercept	3.01	5.38	–7.66, 13.50	–	–	–
	Jealousy	7.60	5.90	–4.19, 19.75	0.55	90%	10%
Locomotion	Intercept	261.85	87.39	78.18, 437.65	–	–	–
	Jealousy	–14.51	104.07	–222.03, 195.26	–0.06	44%	56%
Chew	Intercept	123.73	42.85	40.55, 280.42	–	–	–
	Jealousy	–19.81	59.22	–139.99, 99.02	–0.17	37%	63%

Intercept is the model estimate for the control condition. Jealousy is the difference from the control condition—the jealousy effect. Post. SD is the posterior standard deviation of the estimate. These estimates were all obtained from the same model. Interpretation of (δ_T) follows Cohen's *d* (small = 0.2, medium = 0.5, large = 0.8).

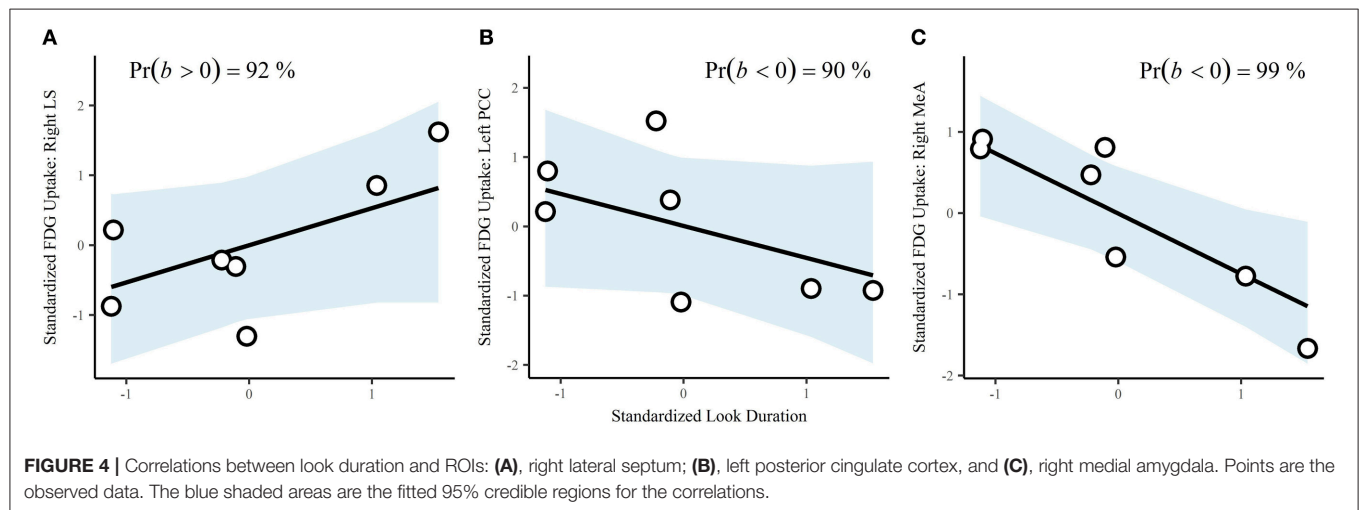
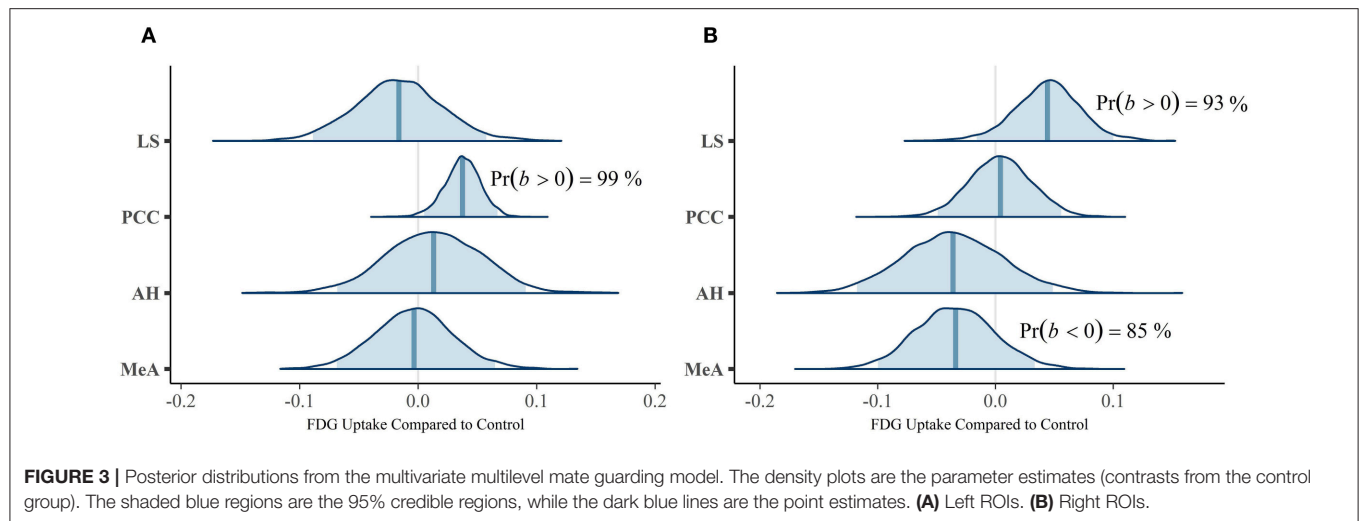
predictive checks indicated that the model adequately described the observed data. The amount of residual variation explained by subjects ranged from 17% (AVP: ICC = 0.17, $\text{CrI} = [0.00-0.67]$) to 63% (cortisol: ICC = 0.62, $\text{CrI} = [0.03-0.92]$). Plasma OT and AVP concentrations had lower probabilities (65 and 74%, respectively) for differences between conditions (**Table 5**; also presented are model estimates and confidence intervals).

Behavior

The multivariate multilevel model estimated differences in total durations of behavior between the control and jealousy conditions (for ethogram see **Table 1**). Due to excessive zeroes, drinking and time off camera were not analyzed. There was some evidence for a positive effect ($\text{Pr}(b > 0) = 90\%$) of jealousy condition on lip smacking duration ($b = 7.60$, $\text{CrI} = [-4.19-19.75]$, $\delta_T = 0.55$). The residual variance explained by subject ranged from 14% (chewing: ICC = 0.14, $\text{CrI} = [0-0.59]$) to 99% (tail lashing: ICC = 0.99, $\text{CrI} = [0.97-1.0]$). All estimates are reported in **Table 6**.

Correlations: Jealousy Condition

Durations of behaviors were standardized prior to analysis, resulting in correlations (*r*). Look duration via a single-level multivariate model was positively correlated with cortisol ($b = 0.63$, $\text{CrI} = [-0.07-0.98]$, $\text{Pr}(b > 0) = 97\%$). The correlation with testosterone was also positive, but the interval was very wide ($b = 0.31$, $\text{CrI} = [-0.67-0.94]$, $\text{Pr}(b > 0) = 78\%$). Using a single-level multivariate model to investigate associations between behavior and brain region of interest, we found that look across duration had a probability of a positive correlation on FDG uptake in the right LS of 92% ($b = 0.53$, $\text{CrI} = [-0.32-0.97]$; **Figure 4A**). There were substantial negative correlations with look duration in the left PCC ($b = -0.46$, $\text{CrI} = [-0.97-0.35]$, $\text{Pr}(b < 0) =$



90%; **Figure 4B**) and the right MeA ($b = -0.74$, $CrI = [-0.99$ to $-0.22]$, $Pr(b < 0) = 99\%$; **Figure 4C**).

The probability of a negative correlation between plasma testosterone and FDG uptake in the right MeA was 96% ($b = -0.57$, $CrI = [-0.97-0.07]$), 48% for the right LS ($b = -0.03$, $CrI = [-0.84-0.80]$), and 79% for the left PCC ($b = -0.57$, $CrI = [-0.93, 0.60]$). There were negative correlations between cortisol concentrations and FDG uptake in the left PCC ($b = -0.19$, $CrI = [-0.91, 0.70]$, $Pr(b < 0) = 72\%$), and right MeA ($b = -0.54$, $CrI = [-0.97, 0.22]$, $Pr(b < 0) = 93\%$). There was a positive correlation between cortisol concentrations and FDG uptake in the right LS ($b = 0.31$, $CrI = [-0.66, 0.94]$, $Pr(b > 0) = 81\%$), but the interval was very wide.

DISCUSSION

After seeing his female pair mate next to a stranger male, male titi monkeys showed increased FDG uptake in the right lateral septum (LS), left posterior cingulate cortex (PCC) and

left anterior cingulate (AC), and decreased uptake in the right medial amygdala (MeA) compared to the control condition. Our subjects also had higher plasma testosterone and cortisol concentrations and spent more time lip smacking in the jealousy condition compared to the control condition. In the jealousy condition, the amount of time looking at the pair mate next to a stranger male was associated with higher plasma cortisol concentrations. These neural and physiological changes may underpin the emotion of jealousy, which can act in a monogamous species to preserve the long-term integrity of the pair.

We now have multiple lines of evidence suggesting that the lateral septum plays a role in both pair bond formation and pair bond maintenance in titi monkeys. The lateral septum is innervated by vasopressin fibers in many mammalian species, including a number of primate species (Ragen and Bales, 2013). In titi monkeys it contains oxytocin receptors but not vasopressin receptors (Freeman et al., 2014), suggesting that any actions of vasopressin in that area are mediated through oxytocin receptors (Barberis and Tribollet, 1996). In addition, it receives

dopaminergic input from the ventral tegmental area (Sheehan et al., 2004). In our initial cross-sectional study comparing pair bonded males to males that were housed alone, FDG uptake in the lateral septum was statistically different between the two groups, with a difference of 9% (Bales et al., 2007). Dopamine D1 receptor binding in the lateral septum of male titi monkeys is also statistically significantly up-regulated 4–9 weeks following pair bonding (Hostetler et al., 2017). In socially monogamous prairie voles, up-regulation of D1 receptors is associated with the onset of mate-guarding, although in that case the sensitive neural area is the nucleus accumbens (Aragona et al., 2006). The lateral septum also plays an important role in social memory (Everts and Koolhaas, 1999) and in the preference formation aspects of pair bonding (Liu et al., 2001). The lateral septum also modulates stress in many species, via an oxytocinergic mechanism (Singewald et al., 2011; Guzman et al., 2013), and stress can modulate the process of social bonding (DeVries et al., 1996). In this study, the medium-large effect size that we found suggests not just a long-term change in dopamine neurochemistry (Hostetler et al., 2017), but also a strong involvement in acute responses to a threat to the pair bond.

In the present study we also found higher FDG uptake in the left posterior cingulate cortex in the jealousy condition, as well as evidence for a positive effect in the left anterior cingulate. In semi-free-ranging prairie voles, higher vasopressin receptor binding in the posterior cingulate was associated with higher fidelity to the partner (Ophir et al., 2008), which theoretically could be related to a stronger pair bond or more time spent in proximity mate-guarding. The fact that we also found evidence for higher FDG uptake in the anterior portion of the cingulate (and that the effect sizes for both posterior and anterior were large and remarkably similar in magnitude) suggests that our “jealousy” condition affects the left cingulate cortex as a whole, and is not just confined to the posterior cingulate. There are well-studied associations between anterior cingulate cortex and socially painful situations (Eisenberger, 2015), which fits with the view of jealousy as social rejection.

Our study found lateralized effects of the jealousy condition on regional cerebral glucose metabolism, such that male titi monkeys showed increased FDG uptake in the right lateral septum (LS), left posterior cingulate cortex (PCC) and left anterior cingulate (AC), and decreased FDG uptake in the right medial amygdala (MeA) in the jealousy condition compared to the control. Lateralized effects have also been found in human studies of jealousy or other forms of social exclusion. In a human study on jealousy using electroencephalogram (EEG) to measure electrical activity of the brain, jealousy evoked by a computerized ball-tossing game was associated with greater relative left frontal activation (Harmon-Jones et al., 2009). In that study, the authors concluded that their left frontal activation finding was consistent with jealousy being associated with approach motivation. This finding was interpreted within long-standing research in human emotion that greater left-sided brain activity is associated with approach behavior and predominantly positive affect, while relative greater right-sided activity is associated with avoidance behavior and negative emotions (Davidson and Fox, 1982).

Like our male titi monkeys, Takahashi et al. (2006) found men who read about infidelity showed functional magnetic resonance imaging (fMRI) changes in the amygdala and the cingulate cortex (Takahashi et al., 2006). Takahashi et al. (2006) found that men who read statements about sexual infidelity had increased fMRI activation in the right amygdala (as well as other areas), while men who read statements about emotional infidelity had greater fMRI activation in the left and right cingulate cortex (as well as other areas). Unlike Takahashi and colleagues, who found right and left activation of the cingulate cortex with jealousy, Sun and colleagues (Sun et al., 2016) found that the left posterior cingulate gyrus fMRI activation was associated with romantic jealousy and the left anterior cingulate gyrus was associated with romantic happiness. Using EEG, fMRI and regional cerebral glucose metabolism PET/MRI methods allow us to visualize what areas of the brain are associated with behavior and social scenarios, but they do not allow us to know what types of receptors are being activated or what neurotransmitters are changing in the brain. Future research on jealousy using PET with specific radiotracers could allow us to measure changes in neurotransmitter availability and potentially in release in this model (Hostetler et al., 2017). While it is commonly assumed that lateralization is a human trait, brain (and behavior) asymmetries are not the exception but the norm, and can be found in all taxa of the animal kingdom (Gunturkun and Ocklenburg, 2017).

We found lower probabilities that our experimental condition affected plasma hormone concentrations of OT (65%) or AVP (74%), and a small effect size for AVP. Some human studies have found relationships between elevated plasma oxytocin levels and socially painful situations such as troubled romantic relationships (Taylor et al., 2010) or other types of relationship distress (Taylor et al., 2006), mainly in women. In contrast to women, higher levels of plasma vasopressin, but not oxytocin, were associated with relationship problems in men (Taylor et al., 2010). Although we did not find large differences in our peripheral measure of plasma OT and AVP peptide hormones, this does not mean that central nervous system changes in OT and AVP did not occur. Plasma and other peripheral measures of these peptide hormones are considered imperfect reflections of central nervous system levels (Freeman et al., 2016). An additional explanation for why we did not find a larger effect for plasma OT or AVP is the timing of when we collected blood samples from our subjects. While sampling blood following the 30 min FDG uptake period was reasonable timing to see effects of steroids such as testosterone and cortisol (Mendoza, 2017), it would almost certainly be past the peak timing to see effects of a behavioral stimulus on plasma oxytocin (Kenkel et al., 2012). Lastly, these blood samples also were taken after animals were sedated, so they do not represent “baseline” blood samples.

As predicted, there were positive associations between the jealousy condition and plasma steroid hormone concentrations of testosterone and cortisol. Testosterone concentrations were measurably higher in the jealousy condition, with a small to medium effect size. This increase is not surprising given testosterone's association with mating-related aggression

(Wingfield et al., 1990; Wingfield, 2017). The “challenge hypothesis” predicts that androgens should respond acutely to social challenges, and then return to baseline in order to avoid adverse effects of steroids (Wingfield et al., 1990). This has been generally supported in the literature, including that on non-human primates (Bales et al., 2006) and humans (Archer, 2006). Cortisol was marginally higher during the jealousy condition (92% probability of a true effect), and it was significantly correlated with the time that the subject spent gazing at his pair mate and the stranger male, suggesting that this stimulus does constitute a social stressor (Mendoza, 2017). The increased time spent lip smacking during the jealousy condition compared to the control condition was possibly affiliative behavior directed toward his pair mate, an attempt to get her attention, or a form of self-soothing behavior. We did not tape the stimulus pair, so we do not know what specific behavior our subject was viewing. This is a limitation of the current study which should be corrected in future studies.

We also cannot say definitively that the subjects in our experiment experienced the emotion of “jealousy.” Similarly, with humans we would need verbal confirmation that participants experienced this emotion. In particular, since the pair mate was separated from the stranger by a barrier, the stimulus may have been less potent for the subject than if the pair mate and stranger had full access to each other. The higher testosterone concentrations experienced by our male subjects when viewing their pair mate next to a stranger, as well as the positive correlations between duration of time spent looking across at them and both cortisol concentrations and FDG uptake in the lateral septum, do suggest that this situation may have been viewed as a challenge to the pair bond or sexual relationship. However, it is worth noting that the emotion we attribute to the subjects was not shown unambiguously through behavior.

A neural model of pair bonding in titi monkeys is beginning to coalesce, and the available evidence suggests both similarities and differences to the current, rodent-based model (Gobrogge and Wang, 2015; Numan and Young, 2016). When forming pair bonds, both prairie voles and titi monkeys recruit neural areas rich with oxytocin and/or vasopressin receptors and involved in social memory (such as the lateral septum), and dopaminergic areas involved in reward (such as the nucleus accumbens) (Bales et al., 2017). The involvement of these two systems suggests that the initial pair bond formation, and subsequent mating, serve both as learning and as positive reinforcing stimuli, involving the neural systems involved in other motivated behaviors (Tops et al., 2014). The maintenance phase of pair bonding is thought to be based on negative reinforcement; i.e., avoidance of aversive stimuli such as separation (Resendez et al., 2016), and to involve the opioid and dopamine systems as well. The lateral septum in titi monkey brain contains oxytocin receptors (Freeman et al., 2014), dopamine D1 receptors (Hostetler et al., 2017), dopamine D2 receptors (Bales, unpublished data), and both μ and κ opioid receptors (Ragen et al., 2015). Thus, the lateral septum appears to be a hot-spot for both the

formation and the maintenance of pair bonding in male titi monkeys. The neural substrates of primate pair bonding thus appear to involve the same principles and neurochemistry, but differing neural areas, as rodent pair bonding. Based on current mammalian phylogenies, it is likely that monogamy evolved multiple times (Lukas and Clutton-Brock, 2013), and it is therefore not surprising for the details of neurobiological mechanism to differ. Convergent evolution on nonapeptide mechanisms, however, seems likely given the outcomes of this and other studies.

Previous findings, as well as the present study, have suggested an important role for the lateral septum. Future research might focus on this area and particularly on interactions between the oxytocin, dopamine, and opioid systems, in order to continue dissecting the underpinnings of pair bonding in primates. Special attention will need to be paid to other potential differences from rodents, such as the longer time that it takes for primates to form a pair bond (Rothwell, unpublished data). Studying these neural substrates of social bonds may give us important clues with which to approach health and welfare problems such as addiction (Tops et al., 2014), autism (Anagnostou et al., 2014), and partner violence (Marshall, 2013). Finally, they may help inform us as to the evolutionary origin and maintenance of monogamy as a social system.

AUTHOR CONTRIBUTIONS

KB, SM, and WM designed the study and obtained the funding. The animal experiments were carried out by NM and TS. SC and DR oversaw the methodology and analysis of the imaging data. DW performed the statistical analysis. NM and KB wrote the paper and all authors edited the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fevo.2017.00119/full#supplementary-material>

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