CHAPTER FIVE

Variation, plasticity, and alternative mating tactics: Revisiting what we know about the socially monogamous prairie vole

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Contents

1. Introduction

Species' mating systems are often characterized as either monogamous or non–monogamous, and this distinction has enabled comparative investigations that have advanced our understanding of the neurobiological basis of

specific reproductive behaviors like pair bonding and parental behavior (Bester-Meredith, Young, & Marler, 1999; Goodson, 2013; Goodson & Bass, 2001; Walum & Young, 2018; Young et al., 2019; Young, Gobrogge, Liu, & Wang, 2011; Young & Wang, 2004). However, such dichotomous characterization ignores the fact that species often exhibit variation in reproductive decision-making, at times displaying mating decisions outside of the species' normative mating system (i.e., alternative mating tactics) (Oliveira, Taborsky, & Brockmann, 2008). In fact, recent application of molecular tools to field research has highlighted the prevalence of alternative mating tactics, such as the decision to engage in extra-pair copulations within predominantly monogamous mating systems, (Carter & Perkeybile, 2018; Gowaty & Karlin, 1984; Hughes, 1998; Klug, 2018; Solomon, Keane, Knoch, & Hogan, 2004).

The presence of alternative mating tactics within otherwise monogamous mating systems offers a rich yet underappreciated avenue of inquiry. On the one hand, alternative mating tactics can either occur as distinct evolutionarily stable phenotypes whereby pair-bonded individuals breed exclusively with a single partner (i.e., are genetically monogamous), or engage in extra-pair copulations (i.e., are only socially monogamous) (Oliveira et al., 2008). On the other hand, the expression of alternative mating tactics can be context dependent (i.e., plasticity), in which individuals' phenotype can be reversible or irreversible (Brockmann, 2001). It remains unclear whether the specific ecological, social, and spatial selection pressures that impact mating systems, also shape the evolution and expression of alternative mating tactics, and the potential for plasticity therein.

In this article, we will review our increasing knowledge of alternative mating tactics in the prairie vole (*Microtus ochrogaster*). Studies on this socially monogamous rodent have been instrumental to our understanding of neurobiological mechanisms that underlie pair bonding, selective aggression, and parental behavior. Research on this species also has much more to offer in terms of understanding the neurobiology of alternative mating tactics, reproductive decision-making, and the plasticity therein. To contextualize these findings, we will first provide an overview of the social, ecological, and spatial pressures that influence the evolution of mating systems. We will then review evidence for variation in reproductive decisions within typically-defined monogamous and non-monogamous rodent species. We focus specifically on the contributions of comparative laboratory-based research on voles, which have fundamentally enhanced our understanding of the neurobiology underlying monogamous behaviors. We will then argue that this

work has overlooked the rich variation in monogamous behaviors these organisms express, and will highlight insights from field studies that capitalize on the neurobiological bases of alternative mating tactics. Finally, we will suggest future areas of research with great promise and potential to address whether, and how, plasticity inherent to alternative mating tactics allows individuals to respond to relevant social, ecologic, and spatial pressures.

2. Mating systems

2.1 Mating system evolution: Social, spatial, and ecological demands

In simplified terms, mating systems are often defined by the modal number of mates with whom males and females of a given population engage (Shuster & Wade, 2003). This way of categorizing mating decisions creates four general categories of mating systems: polygyny (one male, multi-female reproductive units), polyandry (one female, multi-male reproductive units), polygynandry (inclusive of promiscuity, multi-male/multi-female reproductive units, and other forms of polygamy), and monogamy (one male, one female reproductive units) (Wittenberger, 1979). Although, mating systems can be effectively defined in terms of mating decisions, they are instead often conceptualized in terms of socio-spatial behaviors.

Navigating the social world is an integral component of reproduction. Although social behaviors encompass more than reproductive behaviors, natural selection places a strong pressure on ways in which animals can enhance reproductive success through their behavior. Indeed, much of our understanding of behavioral ecology has been based on the factors that contribute to reproductive success, and the social interactions that facilitate it. As interpreted through parental investment theory, Emlen and Oring (1977) argue the potential for polygyny in a species is contingent on the ability of the least-investing sex (usually males, Eens & Pinxten, 2000) to monopolize resources (by establishing large territories, for example) that attract the most-investing sex (usually females). In fact, access to resources and the size and exclusivity of territories are measures often used to help define mating systems (Emlen & Oring, 1977; Trivers, 1972). For example, mammalian monogamy is most likely to evolve when females occupy small but exclusive home ranges, thereby increasing the difficulty for males to monopolize multiple females (Komers & Brotherton, 1997).

Indeed, mating decisions (and the mating systems that emerge from them) depend substantially on the ability of males to consider the defendable

resources located within a given territory, the number of mating partners they are capable of monopolizing, and the activity of their mate(s) and neighbors (Emlen & Oring, 1977; Shuster & Wade, 2003). Based on their best estimate of the status of their own body condition and social context, individuals should make mating decisions that will maximize their probabilities of reproductive success. It follows that individual mating decisions should reflect the social landscape in which animals find themselves, and the assessment of these factors will largely depend on an animal's success in integrating social and spatial information (i.e., the identity and location of potential mates or competitors). Inherent in this and most theories of the evolution of mating systems is an emphasis on the importance of space use in reproductive decision-making, and therefore the dependence of mating systems on socio-spatial memory and cognition (Ophir, 2017).

Another key aspect of reproductive success is offspring survival. The relationship between mating systems and the presence of biparental care (i.e., post-zygotic investment from both mates) is diverse and complex (Emlen & Oring, 1977; Lott, 1984). Historically, researchers have hypothesized that species that demonstrate promiscuous sexual relationships should exhibit little or no biparental care, whereas species that display monogamous sexual relationships should be more likely to show biparental care (Clutton-Brock, 1991; Trivers, 1972). Relatedly, non-monogamous mating systems are thought to have evolved in habitats where the most-investing sex (i.e., females) have plentiful access to resources to raise young alone, and where population densities support access to multiple mates for the least-investing sex (i.e., males) (Kleiman, 1977; Lukas & Clutton-Brock, 2013). Under the socioecological conditions where maternal care is sufficient for survival of the offspring, males can best maximize their reproductive success by seeking multiple copulations, rather than expending effort on one female mate and her offspring.

In contrast, monogamous mating systems are hypothesized to be associated with restrictive habitats, and to coincide with selective affiliation for a mate, biparental care, and selective aggression in the form of territoriality or mate-guarding (Clutton-Brock, 1991; Kleiman, 1977; Trivers, 1985). This suite of social behaviors likely serves to mitigate fitness costs associated with challenging breeding conditions (e.g., decreased access to mates, compromised offspring survivorship because of a patchy resource base, high predation risk, or increased offspring energy needs). For males, social monogamy likely augments reproductive success by providing regular access to postpartum mating opportunities with a known breeding female,

increased paternity certainty, and enhanced offspring survivorship (Kleiman, 1977). For females, the presence and reliably non-agonistic attendance of a male partner likely reduces the energetic demands typified by uniparental care, including sole guarding of pups from aggressive infanticidal conspecifics, and elevated metabolic activity to ensure adequate thermoregulation of the litter during colder months (Clutton-Brock, 1991; Van Schaik & Kappeler, 1997; Wolff & MacDonald, 2004).

2.2 Variation and flexibility in mating systems

Although mating systems are traditionally defined by "species-typical" suites of reproductive decisions, variation in these reproductive decisions commonly arises, and can serve as a foundation for the evolution of alternative mating tactics (Oliveira et al., 2008). Inherent in the evolution of alternative mating tactics, however, is the ability for individuals to incorporate cues from their ecological and social landscapes, and to express different tactics accordingly (Oliveira et al., 2008; Ophir, 2017). This is in contrast to alternative mating *strategies*, which typically represent stable traits within individuals, and that persist in a population over evolutionary time via balancing selection (Dominey, 1984; Gross, 1996; Shuster & Wade, 2003; Shuster, Willen, Keane, & Solomon, 2019).

Variation in reproductive decisions (i.e., alternative mating tactics) are often driven by changes in socioecological constraints that influence the location of mating and parenting effort across time and/or geographic populations (Eisenberg, 1966; Emlen & Oring, 1977). Some characteristically monogamous species can opportunistically exploit the "polygyny potential" of different environments that afford increased access to multiple mates, for example, through fluctuations in population density or through control of seasonal resources. White-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculatus*) well-illustrate this flexibility: although they are commonly described as promiscuous or polygynous (respectively), their mating systems can range from promiscuity to facultative monogamy (Wolff, 1989). In contrast, some characteristically monogamous species will adopt promiscuous traits under circumstances in which one sex no longer retains the capacity to monopolize multiple mates or control access to resources, and/or when environmental circumstances are such that paternal contributions are required to mitigate offspring mortality (e.g., California mice, *P. californicus* and Oldfield mice, *P. polionotus*) (Foltz, 1981; Ribble, 2003).

Numerous field studies strongly support the idea that changes in socio-ecological conditions influence the common reproductive decisions for a species or population (Lott, 1991). Some, studies have shown that non-monogamous characteristics can arise in typically monogamous rodent species. For example, monogamous alpine marmots (*Marmota marmota*) show higher rates of extra-pair paternity when living in densely distributed populations (Goossens et al., 1998). Similarly, beavers (*Castor canadensis*) are known to exhibit polygyny under high-density populations (Busher, Warner, & Jenkins, 1983).

Conversely, monogamous behaviors are also known to arise concomitantly with socioecological changes in typically non-monogamous species. For example, bushy-tailed woodrats (*Neotoma cinerea*) are monogamous in landscapes lacking suitable den sites (Topping & Millar, 1998), and hoary marmots (*Marmota caligata*) are monogamous under low-density food conditions (Armitage, 1999). The presence of biparental care has also been reported for several species of typically non-monogamous rodents. For example, free-living deer mice (Mihok, 1979), white-footed mice (Schug, Vessey, & Underwood, 1992), and hoary marmots (Barash, 1975) exhibit paternal care during colder months of the year, often while living with more than one adult female. It has been suggested that facultative paternal care has evolved as a means to offset offspring mortality during winter breeding. This type of within species variation in social organization is likely enhanced in small rodents by their seasonally unpredictable habitats (Eisenberg, 1966).

3. Comparing mating systems among vole species

Our understanding of mating systems, both theoretically and practically, has progressed considerably over recent decades. Among mammals, various forms of polygamy (usually polygyny) are quite common, whereas monogamy is rare—occurring in less than 5% of mammalian species (Kleiman, 1977; Lukas & Clutton-Brock, 2013). That said, monogamy is relatively prevalent in primates (Kappeler & Pereira, 2003), canids (Moehlman, 1989), and rodents (Carter & Getz, 1993; Gubernick & Teferi, 2000; Komers & Brotherton, 1997; Reichard & Boesch, 2003). Comparative studies among species of *Microtus* voles has substantially contributed to our understanding of the factors that drive species to transition between mating systems. Specifically, work on the evolution of mating systems has identified prairie voles and meadow voles (*Microtus pennsylvanicus*) as

model species for the study of monogamy and polygamy, respectively (Carter & Perkeybile, 2018; Getz, McGuire, Pizzuto, Hofmann, & Frase, 1993; Insel & Young, 2000; Ophir, Campbell, Hanna, & Phelps, 2008; Ophir, Wolff, & Phelps, 2008; Solomon et al., 2004). Indeed, meadow voles and prairie voles have been characterized as representing two extreme ends of the monogamy-polygamy continuum for rodents. Because these species are closely related, share the same habitat, and have been the subjects of numerous comparative neuroendocrine investigations (Insel, Wang, & Ferris, 1994; Oliveras & Novak, 1986; Wang, Ferris, & De Vries, 1994; Wang & Insel, 1996; Wang & Novak, 1994; Wang, Smith, Major, & De Vries, 1994; Wang, Young, Liu, & Insel, 1997), they make excellent candidates for investigating mechanisms that shape mating systems.

3.1 Reproductive ecology of prairie voles and meadow voles

Broadly, New World arvicoline rodents (including meadow and prairie voles) are found between 40° and 70°N latitude, and experience rapid fluctuations in population density (Taitt & Krebbs, 1985; Wolff, 1985). Unlike some mammals, voles do not hibernate or experience torpor, and consequently undergo marked physiological and behavioral changes to promote thermoregulation during winter (Wunder, 1985). The primary breeding season for *Microtus* generally occurs during warmer months of the year, but breeding may continue year-round (Keller, 1985). Because *Microtus* voles inhabit a geographic range that is characterized by unpredictable seasonal changes, Wolff (1985) argued that these species have evolved the ability to exhibit flexible behavioral strategies to offset fitness costs associated with changing environmental, and therefore, social parameters.

Given that meadow and prairie voles are closely related congeners, differences in their ecology and mechanisms of reproduction can reveal factors that contribute to the different evolutionary outcomes in mating systems. Meadow voles inhabit grassland regions in the northern half the continental United States and Canada, where males typically maintain large overlapping and diffuse ranges encompassing several adult females, with females maintaining mutually exclusive territories (Madison, 1980). Female meadow voles generally provide sole parental care of pre-weanling offspring, and juveniles disperse immediately upon weaning (Madison, 1980). For these reasons, meadow voles are commonly described as polygynous or promiscuous (Madison, FitzGerald, & McShea, 1984; McShea, 1990; McShea & Madison, 1984; Webster & Brooks, 1981).

Somewhat complicating the story, meadow voles have also been observed living in communal groups and showing high tolerance for conspecifics in the winter, and even forming selective partner preferences toward familiar conspecifics of the opposite-sex under winter-like contexts in the laboratory (Madison et al., 1984; Parker, Phillips, Kinney, & Lee, 2001) (see below).

Prairie voles are primarily native to the tall grassland prairies of eastern and central North America. Accordingly, prairie voles and meadow voles are partially sympatric. Despite their shared ecology, prairie voles differ from meadow voles in a number of important ways. For example, prairie voles form pair bonds year-round, and establish highly territorial long-term mating associations in the field (Getz, Carter, & Gavish, 1981; Getz & Hofmann, 1986; Getz et al., 1993). Indeed, males aggressively exclude intruding males from their territories and maintain minimal home range overlap with neighbors (Getz & Hofmann, 1986; McGuire & Getz, 1998). Male and female prairie vole pairs are often live-trapped together, and engage in joint nest construction and parental care (Getz et al., 1981, 1993; Thomas & Birney, 1979).

3.2 Studying monogamous behaviors in laboratory settings

Prairie voles have become a predominant species for investigating monogamous behavior in the laboratory, in part because they are amenable to captivity and express behaviors consistent with monogamy under these conditions (Thomas & Birney, 1979). For example, male prairie voles in the lab engage in nest construction and maintenance, and provide direct paternal care for pre-weanling young in captivity (Gruder-Adams & Getz, 1985; Wilson, 1982). Monogamous social relationships can be formally characterized in the lab by measuring selective partner preferences in a two-choice apparatus (Insel & Hulihan, 1995; Williams, Catania, & Carter, 1992; Winslow, Hastings, Carter, Harbaugh, & Insel, 1993). Insel and Hulihan (1995) defined a selective partner preference as occurring when a subject spends twice as much time in lateral contact (or huddling) with a familiar partner than with an unfamiliar conspecific. More often, selective partner preferences have simply been defined as a statistically significant preference for a familiar over unfamiliar partner (Carter & Perkeybile, 2018; Williams et al., 1992). Based on either criterion, the partner preference effect is traditionally considered robust for both female and male prairie voles. However, recent work has highlighted striking variation in the strength of partner preferences (Vogel, Patisaul, Arambula, Tiezzi, & McGraw, 2018).

When pair bonds do form after 24 h of cohabitation or mating, longer cohabitation periods do not increase the strength of this preference (Insel & Hulihan, 1995; Williams et al., 1992; Winslow et al., 1993). Physical copulation facilitates the formation of a partner preference; 6 h of cohabitation paired with copulation can also establish a partner preference (Insel & Hulihan, 1995; Williams et al., 1992). Interestingly, the relative strength of a pair bond can be predicted by whether or not a pair produces fertilized embryos (Curtis, 2010). Assessment of pair bonds in the lab can extend beyond measuring the preference for a familiar conspecific of the opposite-sex. Indeed, an increase in stranger-directed aggression (often assessed using a resident-intruder paradigm) is often closely associated with pair bonding behavior. Such selective aggression has been observed shortly after a partner preference is established and can be directed to both male and female conspecifics (Winslow et al., 1993).

Initial comparative work in voles contrasted prairie voles with the non-monogamous montane vole (*Microtus montanus*). Unlike prairie voles, male montane voles do not form selective opposite-sex partner preferences following 24 h of mated cohabitation (Shapiro, Austin, Ward, & Dewsbury, 1986). In female montane voles, 24 h of mated cohabitation does induce partner preferences, but these preferences do not persist following separate cohabitation (after the initial 24 h of mated cohabitation), when females are re-tested for partner preferences 7 or 14 days later.

Partly due to sympatry (and the resulting similarity in the native ecology) with prairie voles, meadow voles have largely supplanted montane voles as the representative "non-monogamous vole species." Meadow voles do not naturally provide paternal care, do not share exclusive nesting sites or territories with one conspecific of the opposite-sex, and males often sire multiple litters with mixed paternity (Boonstra, Gilbert, & Krebs, 1993; Shapiro & Dewsbury, 1990; Wolff, 1985). Salo, Shapiro, and Dewsbury (1993) showed that male-female pairs of prairie voles show significantly more huddling than either meadow or montane voles, which do not differ. This result suggests that prairie voles are more affiliative with familiar partners than are either of these non-monogamous congeners, for which male-female huddling is relatively uncommon (Salo et al., 1993).

Surprisingly, much of the original work characterizing the lack of pair bonding in montane voles has not been conducted with meadow voles. To the best of our knowledge, Lim et al. (2004) is the only study that directly showed that male meadow voles do not form partner preferences with females following a 24 h period of cohabitation (Lim et al., 2004).

By contrast, many other studies that have investigated conspecific preferences in non–monogamous meadow voles paint a far more complicated picture. Meadow voles will form preferences for familiar conspecifics of both sexes following 24 h of cohabitation (with or without copulation), and males demonstrate increased aggression toward unfamiliar conspecifics (Beery, Loo, & Zucker, 2008; Lee et al., 2019; Ondrasek et al., 2015; Parker & Lee, 2003; Parker, Phillips, & Lee, 2001). Even more provocative is the result showing that male meadow voles show significant preferences for familiar females after only 6 h of cohabitation (Stetzik et al., 2018). Much of this work has gone on to demonstrate that variation in day length (simulating winter/non–breeding conditions or summer/breeding conditions) impacts familiarity preference formation for males and especially females (Beery, 2019). This has been interpreted as evidence supporting the hypothesis that preferences for familiarity facilitate the overwintering behavior that is characteristic of meadow voles (Beery, 2019). The preferences for familiarity in meadow voles are, in all probability, functionally different than the selective preferences for a familiar mate in prairie voles. Results such as these raise questions about how laboratory partner preference tests should be interpreted, and how they relate to measures of monogamy and polygamy in nature.

3.3 Variation in monogamous behaviors in field settings

The differences between laboratory studies comparing the behavior of meadow voles and prairie voles have received a great amount of attention, in both public and academic circles, largely due to the compelling narratives that this work has provided. However, it should be noted that this work has overshadowed preexisting work in the lab and field demonstrating that vole parental care, breeding, and mating systems are really quite flexible. For example, male meadow voles exhibit considerable paternal behavior under some circumstances (Hartung & Dewsbury, 1979; Parker & Lee, 2001, 2002; Storey & Snow, 1987). Although summer is the primary reproductive season for meadow voles, reproduction can occur year-round (Keller, 1985). Indeed, up to 50% of meadow vole females were found with litters in the field in the autumn and winter of several years (Tamarin, 1977), and 100% of females sampled were seen to continue breeding during unusually warm winters (Webster & Brooks, 1981). Furthermore, meadow voles are frequently found living in extended maternal family groups in early fall (Madison et al., 1984), with social nesting and breeding activity overlapping

in late fall, such that reproductive adult males nest and sleep with females and pre-weanling young in monogamous–like groups (Madison et al., 1984).

The degree to which, or even if, meadow voles engage in facultative monogamy during the colder months of the year remains unknown. However, McShea (1990) reported that winter conditions in communal nest sites promote the development of social bonds in otherwise socially intolerant animals. Thus, Madison (1980) has suggested that "under suboptimum conditions, paternal care and the attendant bonding may emerge as the best fitness strategy for the individuals concerned." Indeed, dyads of female meadow voles are known to exhibit communal nursing in the winter (McShea & Madison, 1984), which reinforces the claim that meadow voles may demonstrate social preferences for familiar individuals as a function of photoperiodic seasonal fluctuations (Beery, 2019; Beery et al., 2008; Parker & Lee, 2003; Parker, Phillips, & Lee, 2001).

Variation and flexibility in social systems is also well documented among prairie voles. Indeed, most free-living prairie voles live in monogamous mating pairs year-round. However, single mother family units, male-female pair units, and male-female extended family units (in which juveniles do not disperse, but rather stay at the nest and provide alloparental care toward subsequent litters) occur at approximately equal frequencies (Carter & Getz, 1985; Getz et al., 1981). Moreover, during autumn, prairie voles have been observed to form larger philopatric communal groups consisting of 10–12 animals, in which they continue breeding throughout the winter particularly when winters are mild, as is often the case in southern locations (Keller, 1985). Although these nesting constellations usually consist of mating pairs and their juvenile offspring, prairie voles can exhibit polygamy under such breeding conditions (Getz, Hofmann, & Carter, 1987).

Between-population differences in social organization are also evident among prairie voles. This variation can be attributed to populations living under different social contexts like population density or can be attributed to abiotic ecological contexts (Carter, Getz, & Cohen-Parsons, 1986). For example, prairie voles exhibit polygyny in the more xeric habitat of eastern Kansas (Fitch, 1957). Furthermore, in the laboratory, prairie voles from Kansas show less alloparental care as juvenile animals, and adult males engage in less paternal behavior when compared with their Illinois counterparts (Roberts, Cushing, & Carter, 1998). Similarly, Mabry, Streatfeild, Keane, and Solomon (2011) demonstrated potential variation in social monogamy among different populations of prairie voles living in Kansas and Indiana, although in these cases the variation appeared to be attributable to variation

in the native ecology (Mabry et al., 2011). However, in a series of studies conducted using two geographically distinct populations (Illinois and Tennessee) of prairie voles in the same conditions (i.e., the laboratory or outdoor semi-natural field enclosures in TN), virtually no between-populations differences were found (Ophir, Phelps, Sorin, & Wolff, 2007).

Taken together, these studies demonstrate great flexibility in the degree to which prairie voles engage in (social) monogamy and further indicate how their behavior adapts to the local ecological contexts. Ideally a large-scale field study employing a true common-garden design comparing populations from geographically and ecologically distinct original sources could best address the extent to which variation in mating system is rooted in ecological, geographic, and/or genetic differences.

Some environmental and social parameters that might affect reproductive strategies can be simulated in the laboratory (e.g., photoperiod, social cohabitation, and/or mating). Thus, it is possible to test captive animals for the *capacity* to exhibit affiliative and paternal behaviors under varied socioecological conditions. However, studying whether socioecological conditions (e.g., population density, predation intensity) induce variation in reproductive tactics is best executed under naturalistic conditions, rather than under captivity (Blondel et al., 2016; Keane et al., 2007; Ophir et al., 2007; Shuster et al., 2019; Solomon et al., 2009).

It is worth a brief note that most field studies that have focused on vole species have used either radio-telemetry or repeated live trapping on grids to determine whether males and females are typically monogamous or not. Mating system status is thus inferred as the degree to which male-female pairs occupy highly overlapping home ranges and nest sites, or else maintained separate territories/ranges and nest sites (Getz, Gudermuth, & Benson, 1992; Getz, McGuire, Hofmann, Pizzuto, & Frase, 1990). However, it has been difficult to directly relate patterns of space use (and spatial variation therein) with measurable differences in specific reproductive decisions under free-living naturalistic conditions. Laboratory experiments that have focused on differences in partner preferences, stranger-directed aggression, mate-guarding, and paternal care (see below) have facilitated the ability to assess such behavior, and have aided in building bridges among these profoundly different experimental contexts. However, caution should be taken when presuming the equivalency of a pair bond assessed by spatial overlap in the field and a pair bond assessed with a partner preference test in the laboratory. Although they are designed to assess similar things, these experimental outcomes might not equate directly with each other.

4. Alternative mating tactics in prairie voles

As reviewed above, both laboratory and field studies clearly indicate significant capacity for flexibility in reproductive decision-making within species and among populations. The potential for population differences in mating decisions raises questions about the actual prevalence of individual differences in reproductive decisions within natural populations. Efforts to address these questions have focused on the observation that prairie voles studied in the field (both free-living or in outdoor enclosures) demonstrate different behavioral motifs that are consistent with behaviorally-based alternative mating tactics. Although paternal and affiliative behaviors have received substantial attention in laboratory studies (Hartung & Dewsbury, 1979; Salo et al., 1993; Williams et al., 1992), few laboratory studies have been conducted under specific circumstances in which captive animals would most likely engage in alternative mating tactics (see Blocker & Ophir, 2016; Wolff, Mech, Dunlap, & Hodges, 2002 for exceptions). Moreover, the existing comparative studies have centered on characterizing differences in social behaviors (e.g., presence or absence of partner preferences, stranger-directed aggression, paternal care) found *between*, rather than *within*, species. Yet, within species (and within-population) comparisons hold the potential to capture a much more nuanced and comprehensive characterization of the behaviors, decisions, and mating tactics that prairie voles demonstrate. In the following section, we provide a more in-depth review of the variation in tactics found in this socially monogamous species.

4.1 A tale of two tactics: Residents and wanderers

In the field, prairie vole males and females adopt either a socially monogamous tactic known as "residency" or a non-monogamous tactic known as "wandering" (Getz et al., 1993; McGuire & Getz, 2010; Ophir, Phelps, et al., 2008; Ophir, Wolff, et al., 2008). These categories are based largely on measures of space use collected using grid trapping or radio telemetry in free-living animals housed in semi-natural field enclosures. Substantial evidence from independent laboratories has demonstrated that the majority of adult prairie voles (both males and females) become residents, whereby they form territories that they defend with an opposite-sex partner, presumably the pair-bonded mate. Between 60% and 75% of males (and females) adopt residency (Getz et al., 1993; McGuire & Getz, 2010; Ophir et al., 2007; Ophir, Phelps, et al., 2008; Solomon & Jacquot, 2002; Streatfeild, Mabry,

Keane, Crist, & Solomon, 2011; Zheng, Larsson, Phelps, & Ophir, 2013),
which is one reason why prairie voles are considered monogamous (Getz
et al., 1993). These studies were conducted in Illinois, Indiana, Ohio, or
Tennessee on animals originally trapped in (or descended from) populations
from Kansas, Illinois, Indiana, and/or Tennessee, and the patterns detected
probably represent the typical proportion of residency across the prairie vole
distribution. At the same time, a significant (but minority) proportion of
adult prairie voles become *wanderers*. These individuals live alone, do not
appear to establish or defend a territory, and frequently intrude into the
territories of residents (Getz et al., 1993; McGuire & Getz, 2010; Ophir,
Phelps, et al., 2008; Ophir, Wolff, et al., 2008; Shuster et al., 2019;
Solomon & Jacquot, 2002).

Prairie voles have long been known to show the variation in mating tac-
tics represented by residency and wandering. Getz and Hofmann (1986)
reported that only half of sampled nest sites in a population of free-living
prairie voles consisted of resident adult male and female pairs. The remaining
half of the nests consisted of non-monogamous configurations of adult res-
idents, and were divided approximately evenly between nests consisting of a
single adult female and nests with multiple sexually mature males and/or
females (Getz & Hofmann, 1986). However, Getz and Hofmann (1986)
acknowledge that their account of monogamous breeding pairs was likely
based on conservative estimates and that they were unable to eliminate
the possibilities that (1) single-female nests consisted of pair-bonded females
with recently deceased male partners, or that (2) the nests containing mul-
tiple sexually mature males/females consisted of a bonded adult pair with
adult offspring (Getz et al., 1987).

Still, these initial studies suggested the existence of variation in reproduc-
tive decisions within a predominantly monogamous mating system.
Subsequent studies in prairie voles living in semi–naturalistic environments
have provided a systematic approach to confirming, identifying, and defin-
ing their potential alternative mating tactics. Studies suggest that between
20% and 35% of prairie voles may adopt a wandering mating tactic (Getz
et al., 1993; Ophir, Campbell, et al., 2008; Ophir, Phelps, et al., 2008;
Ophir, Wolff, et al., 2008; Solomon & Jacquot, 2002). Although both adult
males and females can display the non-bonded, non-territorial wandering
mating tactic, approximately 70% of wandering individuals are males
(Getz et al., 1993; Ophir, Campbell, et al., 2008; Ophir, Phelps, et al.,
2008; Ophir, Wolff, et al., 2008; Solomon & Jacquot, 2002; Zheng
et al., 2013).

The distinction between these two mating tactics (pair-bonded and territorial residents; non–pair-bonded and non–territorial wanderers) has been the traditional focus of most work on alternative mating tactics in prairie voles (McGuire & Getz, 2010; Ophir, Phelps, et al., 2008; Ophir, Wolff, et al., 2008; Solomon & Jacquot, 2002). Research assessing the relative fitness of each tactic has yielded results that are seemingly, although not necessarily, contradictory. Ophir, Campbell, et al. (2008), Ophir, Phelps, et al. (2008), and Ophir, Wolff, et al. (2008) found that male residents have higher success rates in siring offspring than do male wanderers. Specifically, 72% of all resident males sired offspring, but only 27% of wanderer males mated successfully (Ophir, Phelps, et al., 2008). It is important to note that this study focused on a single breeding cycle and captured females before giving birth, which increased confidence in assigning paternity but did not account for differences in offspring survivability or whether biparental care had any effect on potential survivability. Another study, using longitudinal data on free-living populations of prairie voles, has similarly concluded that male residents hold a relative advantage in reproductive success, estimating that resident males sired between 62% and 96% of all pups over a period spanning 5 years (McGuire & Getz, 2010). The extrapolated estimates, however, were based on assumptions of assortative mating preferences between wandering males and wandering females (i.e., assumed that pups born to wandering females were sired by wandering males and pups born to resident females were sired by resident males). However, a recent study that compiled over 3 years of parentage data from prairie voles living in Indiana and Kansas found no such assortative mating preference between wandering males and wandering females (Shuster et al., 2019). This lead Shuster et al. (2019) to conclude that the previously extrapolated success estimates for resident males, which assumed that pups born of resident females are sired by resident males, was an overestimate.

In contrast to these results, other studies spanning multiple breeding cycles have shown that wandering males obtain high measures of indirect fitness. For example, wandering males tended to outlive resident males (McGuire & Getz, 2010) and display healthier body condition than resident males (Solomon & Jacquot, 2002). Then again, McGuire and Getz (2010) and Ophir, Wolff, et al. (2008) found that male residents and wanderers did not differ statistically in measures of body mass or weight. By contrast, using procedures as described by Ophir, Wolff, et al. (2008), we have also found that resident males weighed more than wandering males (unpublished data; Resident and Wander mean (±SE) weight in

grams: 38.8 g ($\pm$1.147) and 34.3 g ($\pm$1.184), respectively; Mann-Whitney U$=$74, $n_1=30$, $n_2=10$, $P=0.02$).

In order to address this seeming contradiction, a recent investigation provided an exhaustive analysis of multigenerational fitness dynamics between resident and wandering mating tactics in semi-natural populations. By determining parentage of juveniles across 3 years, Shuster et al. (2019) concluded that average fitness did not differ between resident and wandering tactics in prairie voles of either sex. Importantly, the authors also highlighted that selection seems to be strongest within male mating tactics themselves (i.e., within residents or within wanderers) rather than between them (Shuster et al., 2019). Therefore, differences within respective mating tactics in male prairie voles may make very important contributions to variation in reproductive fitness.

Consistent with this conclusion is the emerging view that resident male prairie voles might be best broken down into two "sub-types" of males, based on sexual fidelity (Ophir, 2017; Rice, Restrepo, & Ophir, 2018). The increased ease of using molecular techniques in the field to study monogamous mating systems has revealed that extra-pair copulations are common within monogamous species and that extra-pair fertilizations are common and prevalent (Gowaty & Karlin, 1984; Hughes, 1998; Klug, 2018). It is now widely accepted that sexual monogamy (i.e., mating exclusively between pair-bonded partners) is actually rare, and that most individuals in a monogamous mating system participate in social monogamy (i.e., form a pair bond, defend a territory, and engage in biparental care, but also engage in extra-pair copulations) (Carter & Perkeybile, 2018; Solomon et al., 2004). Indeed, reports of multiple sired litters by females and hints of extra-pair copulations long suggested social monogamy in prairie voles (e.g., Carter Porges, Williams, & Witt, 1990; Solomon & Jacquot, 2002), and Ophir, Campbell, et al. (2008), Ophir, Phelps, et al. (2008), and Ophir, Wolff, et al. (2008) demonstrated that prairie voles are indeed best described as being socially monogamous (Ophir, Phelps, et al., 2008). Furthermore, we know from laboratory studies that pair-bonded prairie vole females readily mate multiply when given simultaneous access to novel adult males (Wolff et al., 2002).

Extra-pair copulations offer resident males additional opportunities to increase their fitness outside of their pair bonds (Solomon et al., 2004). However, the benefits to resident males in seeking extra-pair copulations may be offset by corresponding decreases in mate-guarding of their own pair bond partner. Indeed, we have noticed that some resident males respond to

the trade-off decision by foregoing extra-pair copulations, and instead mate-guarding intensely and produce offspring exclusively through in-pair fertilizations (Ophir, Phelps, et al., 2008). Neurobiological differences (see below) support the idea that differences in neural phenotypes might enable a proportion of wanderers to mate successfully (Okhovat, Berrio, Wallace, Ophir, & Phelps, 2015; Ophir, Phelps, et al., 2008; Zheng et al., 2013). Thus, neural variation appears to account for differences in reproductive success among residents and wanderers. Moreover, a deeper examination of such variation appears also to identify that among residents, some males are predisposed to mate faithfully and mate-guard, whereas others seem predisposed to seek extra-pair matings at the cost of potential cuckoldry (Phelps & Ophir, 2009). Based on these results, we have hypothesized that residents would be best sub-divided into two sub-categories: the reproductively faithful former (i.e., "true residents"), and residents who seek extra-pair copulations, loosely mate-guard, and produce offspring through both in-pair and extra-pair fertilizations (i.e., "roving residents," or simply "rovers") (Ophir, 2017). Rice et al. (2018) suggests through theoretical modeling, that true residents and roving residents could be stable strategies depending on the composition of tactics adopted by other males within a population. Interestingly, the probability of being a successful rover is predicted to increase as the proportion of other rovers in the population increases, credited to the overall population-level reduction in mate-guarding. This study also showed that a higher proportion of wanderers reduced the potential reproductive pay offs associated with roving (Rice et al., 2018). The added depth of understanding of the forms of reproductive decisions that males (and females) demonstrate has enriched this already interesting example of variable reproductive decision-making, and has revealed the extent to which social context is a crucial factor in shaping individual mating decisions.

4.2 Neurobiological differences underlying laboratory measures of monogamy

In addition to enabling a systematic study of components that shape monogamous behavior (i.e., partner preference, selective aggression, and parental behavior), laboratory studies on voles have also provided a powerful opportunity for exploring the underlying neurobiological basis of these behaviors and others, such as social attachment, that influence monogamy (Carter & Perkeybile, 2018; Ross & Young, 2009; Wang & Insel, 1996; Young & Wang, 2004). Nonapeptides (oxytocin [OT] and arginine vasopressin

[AVP] and their non–mammalian homologs) are a specific class of neuropeptide hormones that have been implicated in numerous aspects of social behavior (both affiliative and aggressive; Goodson, 2013; Goodson & Thompson, 2010). Despite their broad roles in modulating social behavior, these neuropeptides are perhaps best recognized for their functional roles in forming and maintaining monogamous behaviors among voles. The general understanding that has emerged over the last three decades is that affiliative bonds are facilitated by nonapeptide agonists, and eliminated by receptor antagonists (Carter, Grippo, Pournajafi-Nazarloo, Ruscio, & Porges, 2008; Cho, Devries, Williams, & Carter, 1999; Gobrogge & Wang, 2016; Johnson & Young, 2017; Lim & Young, 2004; Liu, Curtis, & Wang, 2001; Tickerhoof & Smith, 2017; Winslow et al., 1993). We will provide only a brief discussion of this aspect of the literature because detailed reviews exist for the roles of OT and AVP (and their receptors) in the formation of partner preferences, on the expression of parental behavior, and selective aggression to non–mate conspecifics (see references above). We restrict our discussion primarily to OT and AVP because these are the systems that have received the majority of attention as regulators of prairie vole monogamy, but we also acknowledge the important point that other neural (and peripheral) signaling systems are also critical for the expression of these behaviors.

As mentioned above, 24 h cohabitation with or without mating is sufficient to induce selective partner preferences and rejection of intruding conspecifics in prairie voles (Insel & Hulihan, 1995). Both AVP and OT are necessary and sufficient to facilitate these behaviors. Central administration of AVP induces selective partner preference in male prairie voles even in the absence of mated cohabitation, whereas AVP receptor subtype 1a (V1aR) antagonists block partner preference formation when delivered prior to mated cohabitation (Winslow et al., 1993). Similarly, central administration of OT agonists and OT receptor (OTR) antagonists induce and inhibit (respectively) the formation of selective partner preferences in females (Carter Porges et al., 1990; Insel & Hulihan, 1995). The role of these hormones was initially proposed to be sexually dimorphic, with AVP inducing pair bonding in males and OT doing so in females. Although there is evidence for sex-biases in the relative importance of AVP and OT (Dumais & Veenema, 2015), recent research has also shown that each nonapeptide plays an important role in both sexes, and for bonding in particular. For example, central administration of OT facilitates partner preference in males with the same efficacy as central AVP and, conversely, AVP is

involved in the formation of partner preference in females (Cho et al., 1999). To some degree, similar outcomes of some studies administering relatively high levels of exogenous OT or AVP can be attributed to the increasingly appreciated fact that OT and AVP are cross-reactive with each other's receptors (Anacker, Christensen, LaFlamme, Grunberg, & Beery, 2016; Bales, Kim, Lewis-Reese, & Carter, 2004; Manning et al., 2012; Schorscher-Petcu et al., 2010; Song & Albers, 2017; Song, Larkin, Malley, & Albers, 2016; Song et al., 2014). Indeed, OT and AVP have a high degree of homology and share deep evolutionary roots (Grimmelikhuijzen & Hauser, 2012).

Exploring mechanisms that govern monogamy in voles requires attention to how signaling peptides function. Synthesis and release rates of peptides best reflect the moment to moment activational roles of signaling molecules, whereas receptors for neuromodulators best represent evolutionary pressures on the mechanisms that govern behaviors under their control (Ketterson & Nolan, 1999). This perspective has greatly influenced the approach taken to compare nonapeptide receptor profiles among monogamous and non-monogamous species of voles. Indeed, differences in the location and density of OTR and V1aR in the brain align well with both within and between species variation in monogamous behaviors (Hammock & Young, 2005; King, Walum, Inoue, Eyrich, & Young, 2016; Okhovat et al., 2015; Ophir, Wolff, et al., 2008). For example, when comparing across species, the density and distribution patterns of OTRs and V1aRs differ in accordance with mating system (Insel et al., 1994; Insel & Shapiro, 1992; Young, Winslow, Nilsen, & Insel, 1997). Comparative studies have revealed that socially monogamous prairie voles have higher receptor density in the medial prefrontal cortex (mPFC; OTR), nucleus accumbens (NAcc; OTR), bed nucleus of stria terminalis (BNST; OTR), and ventral pallidum (VPall; V1aR), but lower receptor density in the lateral septum (LS; V1aR) than their non-monogamous congeners (Insel et al., 1994; Insel & Shapiro, 1992; Lim & Young, 2004; Smeltzer, Curtis, Aragona, & Wang, 2006; Wang et al., 1997; Young et al., 1997). In general, these brain regions are known for their influence in processing social recognition, motivation, and bonding. In a truly elegant study, Lim et al. (2004) virally transferred the prairie vole vasopressin receptor gene, avpr1a, into the VPall of meadow voles and found that this not only caused a prairie vole-like overexpression of V1aR, but that it induced a typically monogamous partner preference formation in this otherwise non-monogamous species (Lim et al., 2004). Similar experiments have also found

that overexpression of OTR in the NAcc of female meadow voles is not sufficient to promote a partner preference (Ross et al., 2009).

Subsequent research on prairie voles has cultivated a deeper understanding of these neural structures, and led to the idea that they form a circuit important for the modulation of pair bonding (e.g., Johnson & Young, 2017; Young & Wang, 2004). Central to this circuit are two neural areas closely associated with modulating valence and reward, the VPall, and the NAcc. For instance, whereas overexpression of V1aR in the VPall of male prairie voles facilitates the formation of partner preferences, its downregulation eliminates pair bond formation (Barrett et al., 2013; Pitkow et al., 2001). Similarly, in female prairie voles, OT administration in the NAcc induces a partner preference in the absence of mating, whereas pharmacological blockade prevents the formation of a mating-induced partner preference (Gobrogge & Wang, 2016; Liu & Wang, 2003).

The lateral septum (LS) is a brain region most often associated with facilitating social recognition, approach, play, and aggression in rodents, but it can also mediate the formation of a partner preference in prairie voles (Ferguson, Young, & Insel, 2002; Gabor, Phan, Clipperton-Allen, Kavaliers, & Choleris, 2012; Liu et al., 2001; Tickerhoof & Smith, 2017). The LS contains both OTRs and V1aRs, and AVP administration into the LS of male prairie voles can induce a partner preference even in the absence of mating during a short cohabitation period with a female (Liu et al., 2001). Conversely, administration of an AVP or OT antagonist into the LS blocks the formation of a partner preference, even if it involves an extended period of cohabitation with mating (Liu et al., 2001). Interestingly, the AVP circuitry in the LS of male prairie voles exhibits some contextual dependency. The LS receives vasopressinergic inputs from the AVP-producing neurons in the BNST (Wang, 1995). Shortly after cohabitation with a female, males show an increase in AVP gene expression in the BNST, however, this also corresponds with a decrease in AVP innervating fibers in the LS (Bamshad, Novak, & de Vries, 1994; Wang, Ferris, et al., 1994; Wang, Smith, et al., 1994).

Although it is not central to the so-called "pair bonding neural circuit," the anterior hypothalamus (AH) facilitates selective aggression against non-mate conspecifics by pair-bonded males (Gobrogge, Liu, Young, & Wang, 2009). Pair-bonded males also exhibit higher density in V1aR binding in the AH than do sexually naïve males. Furthermore, administration of V1aR antagonist into the AH enhances affiliation toward stranger females, and eliminates selective aggression in pair-bonded males (Gobrogge, Jia,

Liu, & Wang, 2017). Likewise, administration of AVP or overexpression of V1aR in the AH of sexually naïve males induces selective aggression (Gobrogge et al., 2009; Winslow et al., 1993). Thus, V1aR activity in the AH appears to contribute to the selective aggression against stranger conspecifics in pair-bonded male prairie voles, a defining characteristic of their monogamous mating system.

4.3 Neurobiological differences underlying field-based measures of monogamy

Just as between species differences in receptor profiles predict differences in mating system, within species differences in receptor phenotypes might predict differences in mating tactics within prairie voles. Among resident and wandering prairie voles, evidence for differences in V1aR and OTR phenotypes has been found, however the kinds of differences that have been reported do not fully replicate the spectrum of species differences discussed above. Nevertheless, neural structures critical for pair bonding that differ between monogamous and non-monogamous vole species have also been observed to differ between monogamous (resident) and non-monogamous (wanderer) prairie voles. For example, VPall V1aR density has been found to be greater among female residents than female wanderers (Zheng et al., 2013), but this difference is not found in males (Ophir, Wolff, et al., 2008). We note that this difference in VPall V1aR could relate to the pregnancy status of females (which was more common among female residents than wanderers), based on the fact that newly pregnant females exhibit greater V1aR density in the VPall, compared to non-pregnant females or females in late pregnancy (Ophir, Sorochman, Evans, & Prounis, 2013). Similarly, although female residents and wanderers do not differ in OTR density, resident males (including both *roving* and *true residents* combined) exhibit greater OTR density in NAcc than do wandering males (Ophir, Gessel, Zheng, & Phelps, 2012). This result in males is consistent with other laboratory research showing that polymorphisms in non-coding regions in the prairie vole oxytocin gene, *oxtr*, predict OTR density in the NAcc and individual variation in laboratory pair bonding (King et al., 2016). It is also consistent with the observation that the formation of pair bonds is accompanied by an increase in OTR density in the NAcc (Ross et al., 2009), and that such OTR changes could be regulated epigenetically (Duclot et al., 2016; Wang, Duclot, Liu, Wang, & Kabbaj, 2013).

Contrary to expectations, no other brain region of the pair bonding circuit differed in OTR or V1aR density between male or female residents or

wanderers (Ophir, Wolff, et al., 2008). Particularly surprising was that, counter to predictions based on the literature, neither OTR nor V1aR density differed between residents and wanderers in the VPall of males, NAcc of females, or LS of either sex (Ophir et al., 2012; Ophir, Wolff, et al., 2008; Zheng et al., 2013). Importantly, the NAcc and VPall have traditionally been viewed as serving sex-specific roles in the formation of laboratory pair bonds, with male pair bonds depending on changes in AVP modulation in the VPall, and female pair bonds depending on changes in OT modulation in the NAcc (Francis, Young, Meaney, & Insel, 2002; Lim & Young, 2004). These results fit the emerging understanding that the roles of OT and AVP are not nearly as sex-specific as once thought. Rather, it might be that sex differences in neuroendocrine mechanisms compensate to diminish behavioral sex differences, as proposed by the dual function hypothesis for neural sex differences (De Vries, 2004; De Vries & Boyle, 1998).

Although between tactic differences were not found in many of the neural structures typically associated with bonding, important differences have been discovered in areas of the brain that are more closely associated with general social behavior, and with processing social and/or spatial memory. In females, OTR in the hippocampus (HPC), and V1aR in the BNST and AH were found to differ between reproductively successful and unsuccessful residents and wanderers (Zheng et al., 2013). Specifically, pregnant female residents and non-pregnant female wanderers had the highest density of OTR and V1aR in these brain areas, whereas non-pregnant female residents and pregnant female wanderers had the lowest densities. This suggests that high density in these brain regions facilitates the female resident mating tactic, and that low-density facilitates the female wandering mating tactic. The HPC is typically closely associated with context dependent memory (see immediately below), but the BNST and AH are important parts of a larger circuit that is thought to modulate social behavior, and specifically play important roles in regulating prosocial–antisocial behavior and social attraction (Goodson, 2005).

The demands on male and female behavior to maximize reproductive success are similar in some ways, but quite different in many others (Trivers, 1972). For this reason, it is not terribly surprising that a different picture has emerged in males. What is particularly striking is that the same interaction pattern just described for females is generally observed in males, however this pattern is not necessarily found in the same parts of the brain in males and females. For example, although males and females show the same pattern of OTR expression in the HPC, this pattern is not found in male

BNST or AH (Ophir et al., 2012). Instead, this pattern is found in the septo-hippocampal nucleus (SHi, OTR), the laterodorsal subdivision of the anterior thalamus (LDTh, V1aR), and the retrosplenial cortex (RSC, V1aR) of males (Ophir et al., 2012; Ophir, Wolff, et al., 2008). As has been reviewed elsewhere, these four structures represent a highly interconnected network of brain areas that are deeply involved in context dependent social and spatial memory (Ophir, 2017). Moreover, Okhovat et al. (2015) found that a polymorphism in the non-coding regions of the prairie vole *avpr1a* predicts differences in V1aR density in the RSC, and is associated with differences in sexual fidelity in male prairie voles (Okhovat et al., 2015). This work has led to the hypothesis that nonapeptides are critical not only for the formation of pair bonds, but also for neural processing underlying decision-making that occurs upstream of bond formation.

Ophir (2017) argued that natural selection might have worked to reduce variation in the circuit that governs pair bond formation, in essence predisposing males to form bonds when the opportunity arises. Modest support for this hypothesis comes from the data mentioned above suggesting that bonded males have potentially higher reproductive success than do single males. Nonapeptides may very well operate on this "socio-spatial memory neural circuit" to enable males to assess the social context and determine when forming bonds could be maximally beneficial, or to determine when remaining single is best. In this way, assessing the social landscape could better enable males to determine how to best maximize their reproductive success via adoption of one of the possible mating tactics discussed above (wandering, roving residents, or true residents).

As discussed previously, modeling experiments suggest that social context can influence the potential fitness payoffs associated with different reproductive tactics (Rice et al., 2018). Moreover, Rice, Sanin, and Ophir (2019) demonstrated that spatial memory is enhanced by the social context experienced in semi-natural enclosures. More precisely, males that lived under a male-biased sex ratio in semi-natural outdoor enclosures demonstrated better performance in the HPC-dependent and spatial memory-dependent Morris water maze, when compared to males that lived under a female biased sex ratio. This is an important point, revealing a direct link between *social* context and *spatial* cognition. Unfortunately, this experiment did not track whether differences in spatial memory performance related to differences between residents or wanders, but studies such as these are currently underway. Indeed, additional research is needed to assess whether males of different mating tactics differ in their ability to navigate social

landscapes. More research is also needed to determine whether RSC, HPC or other socio-spatial memory processing regions mediate the formation of socio-spatial memories and shape reproductive success among various mating tactics. Nevertheless, these studies underscore that socio-spatial cognitive processes could play an important role in influencing social decisions such as mating success and mating tactics (Ophir, 2017).

To recap, lab studies alone have provided powerful insights into the neural control of bonding, but have also potentially masked the variation in the neural substrates that govern individual variation in behavior. Indeed, accounting for multiple mating decisions (i.e., whether to form a monogamous pair bond, or not, and whether to seek opportunities to mate outside of the pair bond) has revealed variation in mating tactics within this predominantly socially monogamous mating system. Comparing the neurobiological profiles of individuals employing alternative mating tactics has resulted in new insights into the neural mechanisms that impact monogamous mating tactics, with some surprising cases of unanticipated differences and lack of predicted differences. These results highlight how fundamental behaviors, such as forming pair bonds, are contextual and influenced by the socio-spatial landscape. Notably, this view reinforces and emphasizes the original importance of space use in defining mating systems and mating tactics, with a deeper appreciation for the potential neural mechanisms that govern them.

5. Mating tactics respond to social, ecological, and spatial contexts

By definition, alternative mating tactics consist of discrete variants in reproductive behaviors and feature individual flexibility (i.e., plasticity) (Oliveira et al., 2008; Shuster et al., 2019). This is in contrast to alternative mating strategies, which typically represent distinct evolutionary stable traits in populations that persist via balancing selection (Gross, 1996; Shuster et al., 2019; Shuster & Wade, 2003). Naturalistic studies spanning multiple breeding cycles have found that individual prairie vole males can switch between resident and wandering tactics within their own lifetimes, thus demonstrating that these are not fixed patterns of behavior (McGuire & Getz, 2010; Shuster et al., 2019; Solomon & Jacquot, 2002). Plastic behavioral phenotypes, such as alternative mating tactics, allow individuals (or genotypes) to respond to different environmental contexts. In prairie voles, we have a limited understanding as to which environmental contexts (e.g., social, ecological, spatial) are capable of producing non-monogamous mating tactics.

Below we outline prospects and potential future directions for research on how variation in the environment can influence the expression of alternative mating tactics in the socially monogamous prairie vole.

Behavioral plasticity is one popularly studied form of plasticity that accounts for the degree to which species respond to changes in the environment within a short, non-evolutionary, timescale (i.e., within the lifetime of an individual; Dingemanse & Wolf, 2013; Foster, 2013; Foster & Sih, 2013). Activational plasticity results in distinct and reversible behaviors based on differences in the immediate environment of the individual (Snell-Rood, 2013), and has been observed among prairie vole mating tactics. Specifically, males can switch between resident (true and rovers) and wandering tactics within their lifetime (McGuire & Getz, 2010; Shuster et al., 2019; Solomon & Jacquot, 2002).

Emlen and Oring (1977) propose the evolution of mating systems is influenced by the potential to monopolize multiple mates, which is in turn determined by ecological factors that impact the spatial and (reproductive) temporal distribution of mates. Under this framework, an inability to monopolize multiple reproductive mates combined with restrictive ecological conditions should encourage the evolution of monogamous behaviors (Kleiman, 1977; Komers & Brotherton, 1997; Shuster, 2009; Trivers, 1985). Thus, social factors such as the intensity of reproductive competition can also influence the mating system by limiting the ability to monopolize mates (Emlen & Oring, 1977; Weir et al., 2011). Social context is just one of the many possible factors that might influence tactic switching. As discussed above, theoretical work suggests that tactics of other males in the population, can—and should—influence the distribution of mating tactics in prairie voles (Rice et al., 2018). Moreover, the operational sex ratio, or the ratio of the reproductively available males to females, not only impacts reproductive competition in a population (Shuster & Wade, 2003), but should also alter the evolution of spatial cognition, which could contribute to reproductive success within a particular mating tactic (Ophir, 2017; Rice et al., 2018, 2019). A number of other socioecological factors likely also influence individual prairie voles to change between mating tactics. For example, low population densities in prairie voles have been associated with higher numbers of residents (Getz & Hofmann, 1986), and there is a decrease in the percentage of wandering females in the winter (Getz et al., 1993).

Another commonly studied form of plasticity, developmental plasticity, results from different environments, at specific life history phases for an individual, directing underlying biological networks to follow distinct

irreversible behavioral trajectories (Snell-Rood, 2013). Protracted periods of immaturity allow animals to integrate environmental cues across development, and to then follow different developmental trajectories that ultimately lead to distinct adult phenotypes (Snell-Rood, 2013). If environmental cues can predict the socioecological context that an individual will encounter at maturity, developmental plasticity may begin to form an adaptive phenotype in anticipation of that future environmental context (Kasumovic, 2013). Importantly, developmental plasticity often plays an important role in the formation of later mate choice preferences (Snell-Rood, 2013). For example, birds and mammals sexually imprint on songs or scents (respectively) they experienced early in life. As adults, passerine birds and rodents prefer to mate with partners displaying auditory or olfactory cues they recognize as familiar (Fillion & Blass, 1986; Holveck & Riebel, 2014).

Supporting the role of developmental plasticity here, captive studies on prairie voles have shown that pups' early life experiences influence their adult mating decisions. Manipulations of the early life social environment have included removing a father shortly after birth (i.e., rearing pups in a single parent environment, Bales & Saltzman, 2016) and/or housing post-weaning pups either singly or socially with their own littermates (Grippo, Wu, Hassan, & Carter, 2008). In one study, male and female adults raised only by mothers require a week of cohabitation with a mate before developing a partner preference (Ahern & Young, 2009). This contrasts with pups raised with both parents, which showed a partner preference after just 24 h of cohabitation with mating. Prounis and Ophir (2019) extended this result by again raising male prairie voles with mothers alone or with both parents, and then next housed the males either alone or with a sibling after weaning. This double hit of social deprivation appeared to produce the opposite effects of single parent rearing on the formation of adult pair bonds, whereby males that were both single parented as pups and singly housed after being weaned formed a partner preference after 24 h of cohabitation with a female. This was in contrast to "control" males (i.e., reared with both parents and housed socially post-weaning), which did not show a partner preference 24 h after cohabitation with a female (Prounis & Ophir, 2019). This result is an example of a case in which different phases of development, and early life experience therein, interact in complex ways to influence behavioral phenotypes such as the formation of pair bonds.

An additional line of evidence that links the early life social environment experienced by prairie vole pups to adult mating decisions comes from investigations into the neurobiological changes induced by single vs double

parenting. Early life social experiences have the profound ability to alter the neural phenotype of animals. For example, typical development under lab conditions alters the function of OT and AVP (Kelly, Hiura, & Ophir, 2018) and tyrosine hydroxylase (the rate-limiting enzyme in the biosynthesis of dopamine; Hiura, Kelly, & Ophir, 2018), and alters the density of OTR and V1aR (Hiura & Ophir, 2018; Prounis, Thomas, & Ophir, 2018). Furthermore, additional differences in OTR and V1aR density of adults that experience post-weaning environmental enrichment (i.e., social and spatial complexity) indicate that neural development extends beyond weaning age and into sub-adulthood. Thus, animals' neural development remains plastic over time. Notably, male prairie voles demonstrated many more differences across development, particularly with respect to V1aR, than did females. This could be seen as a biological indicator that males are more sensitive to environmental effects during development (see, Ahern & Young, 2009; Wang, Smith, et al., 1994; but also Bales et al., 2007).

Although most studies on prairie vole development have focused on how social experiences alter their bonding behavior or stress-responsiveness, few studies have attempted to tie any such effects to their behavioral ecology or the mating tactics they adopt. One exception to this was Prounis, Foley, Rehman, and Ophir (2015), which found that differences in the early life environments of male prairie voles not only altered V1aR density in the LS and social recognition behavior, but also that males raised by just mothers and then raised alone post-weaning differed in OTR and V1aR density in regions of the brain that process socio-spatial information (Prounis et al., 2015). Specifically, V1aR density in the RSC was sensitive to the presence or absence of fathers before weaning, and OTR density in the SHi was sensitive to grouped or single housing after weaning in male prairie voles. When combined, these results demonstrated that males that were raised in both socially reduced contexts partially recapitulated the nonapeptide neural patterns that Ophir, Campbell, et al. (2008), Ophir et al. (2012), Ophir, Phelps, et al. (2008), and Ophir, Wolff, et al. (2008) had shown to result in poor reproductive success in wanderers (i.e., high density of SHi OTR and RSC V1aR; see above).

In wild populations, approximately one third of voles (36.8%) are reared by single mothers (Getz & Hofmann, 1986; Getz et al., 1993; Thomas & Birney, 1979). Taken together, the results reviewed above suggest that this sub-population of mother-only raised males would be predisposed to become unsuccessful wanderers. However, Prounis et al. (2015) also demonstrated a potentially protective effect of being raised with others after

weaning. When male prairie voles disperse, they do so just after weaning (Arias del Razo & Bales, 2016). Thus, it is possible that males reared without fathers might delay the decision to leave the nest or not leave the nest at all, which could have protective effects on a portion of the neural phenotype that might otherwise handicap them if they were to leave the nest and adopt a wandering tactic (J.M. Powel, G.S. Prounis, & A.G. Ophir, unpublished data). Accumulating evidence, such as that which was just discussed, suggests that the type of social environment that prairie voles experience during development could impact their eventual reproductive decisions as adults. However, continued work in this area is needed if we are to ever determine whether these experiences alter developmental trajectories with the direct potential to influence their mating tactics and reproductive success.

6. Conclusions

Although mating systems are normally defined by species–typical suites of reproductive decisions, it has become increasingly clear that there can be significant variation in reproductive behaviors within species. A useful way of conceptualizing within species differences in mating system is not that they represent a unified fixed product of natural selection, but rather that they represent a flexible and variable set of adaptive responses that plastically react to various ecological and socio–spatial contexts at the individual level to maximize reproductive success. Comparative work on monogamous and non–monogamous species of voles has been fundamental to our understanding of the neurobiological basis of reproductive behaviors, and thus the biology of mating systems. However, this research has over–shadowed other work showing that mating decisions are profoundly variable and flexible.

The majority of captive studies on voles have focused primarily on the formation and expression of pair bonds. Studying mating tactics reveals a nuanced, and richer social phenotype that is currently profoundly underappreciated. By studying mating tactics, for example, we can make distinctions between neurobiological capacity to form a pair bond and active choice in forming pair bonds. The latter integrates information from multiple social, spatial, and ecological environments and is therefore more likely to provide a contextual understanding of the relationship between behavior and neural systems. For example, as reviewed above, current studies on alternative mating tactics have revealed a surprising lack of individual variation between mating tactics and OTR/V1aR densities in the "pair bonding neural

circuit." Instead these studies have suggested that this circuitry functionally interphases with upstream circuitry more often associated with spatial navigation and cognition.

Finally, appreciation of the intrinsic plasticity of alternative mating tactics opens up new and important avenues of research. Understanding how social contexts alter behavioral decisions and neural function will provide a deeper appreciation for the individual variation that collectively represents the larger mating system. Similarly, focus on early life social experiences during development will elucidate the sources of variation that bend developmental trajectories toward or away from particular reproductive decision-making that are observable at adulthood. Embracing these approaches and integrating them with behavioral and neurobiological efforts holds tremendous promise to advance our overarching understanding of the behavior of the intact animal (Tinbergen, 1951).

A rather overly simplistic view of prairie vole pair bonding and monogamy has emerged over the past few decades. However, a deeper dive into the behavioral ecology literature, particularly with an effort toward elucidating neurobiological and developmental studies, has provided a more complex characterization of this textbook example of mammalian social monogamy. Indeed, although prairie voles are clearly a socially monogamous species, this reproductive decision is simply the mode, and varies across individuals, is flexible within individuals, and stands open to influences from the developmental and adult environments. These principles generalize past prairie voles, to their closest relatives and beyond. Integrative studies that span levels of analysis and disciplines and that are built upon an evolutionary framework, provide a much richer understanding of, and lead toward an increasingly unified characterization of, the fundamental principles that govern behavior and the mechanisms that enable it.

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