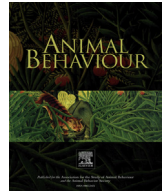




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## Special Issue: Breeding Aggregations

## Dispatches from the field: sociality and reproductive success in prairie voles

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One way to characterize sociality is by the type and variability of social organization exhibited by individuals within populations. Social unit size and composition can result in costs and benefits to female group members, which may affect their reproductive success. We tested this hypothesis using data from two natural populations of prairie voles, *Microtus ochrogaster*, that live in habitats differing in the distribution of vegetation and in population density. During short-term investigations of populations in Indiana and Kansas (4–8 weeks), we detected significant differences between populations in the type of social units in which adult females resided, with most adult females in Kansas living as single females, whereas in Indiana most females resided in groups. However, neither social unit size nor composition was related to female reproductive success in either population. When we studied the same Indiana population for 15 weeks, the length of time that females were detected on the study grid or were residents at a nest predicted the number of offspring they produced. In addition, the number of offspring produced by females tended to decrease with group size, although this relationship was not statistically significant. Finally, social unit size was not significantly related to the amount of time females were detected in the population. Our results suggest that females do not obtain increased direct or indirect fitness by living in larger groups. Rather, persistence and residency status of females in the population are the best predictors of female reproductive success.

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Understanding the evolutionary significance of intraspecific variation in sociality is a topic of great interest in behavioural ecology (Blumstein et al., 2010; Hofmann et al., 2014) because increased insight into group living may help to explain selective factors favouring it. Numerous hypotheses have been proposed to explain mammalian sociality and the intraspecific variation observed (Kappeler, Barrett, Blumstein, & Clutton-Brock, 2013; Silk, 2007). Because intraspecific variation in factors such as group size and composition can result in costs and benefits to group members, we expect to see differences in survival and reproductive success related to variation in group size (Clutton-Brock, 2016).

Adaptive hypotheses often assume an optimal size and type of social unit in which individuals can maximize their net direct and indirect fitness benefits. For example, in socially monogamous species, females living in male–female pairs may experience greater reproductive success relative to solitary females, due to the

benefits of paternal care (Kleiman & Malcolm, 1981). In other species, females may live in a group with more than two adults because they gain more fitness benefits compared to living alone or with a male social partner (Koenig, Pitelka, Carmen, Mumme, & Stanbuck, 1992; Lewis & Pusey, 1997; Silk, 2007; Stacey & Ligon, 1987, 1991). Fitness benefits may include increased female survival due to increased foraging and decreased risk of predation (Clutton-Brock et al., 1999; Ebensperger & Wallem, 2002) and increased production and survival of offspring (Clutton-Brock et al., 2001; Hayes & Solomon, 2004; Hayes, 2000; Packer, Lewis, & Pusey, 1992). There are also potential costs of living in a group if fecundity and survival decrease in larger groups due to increased competition for resources or breeding opportunities (Clutton-Brock, Albon, & Guinness, 1982; Ebensperger et al., 2011; van Schaik, 1983). For example, in colonial tuco-tucos, *Ctenomys sociabilis*, yearling females that bred in their natal group had significantly lower reproductive success than those that dispersed from their natal nest and bred alone as yearlings. Also, per capita direct fitness of females decreased with increasing number of females per group (Lacey, 2004). In other species, intermediate group sizes may be the most beneficial for females (Krause & Ruxton, 2002). For example,

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in yellow-bellied marmots, *Marmota flaviventris*, female reproductive success (pup survival to weaning) initially increased with increasing group size and then decreased when group size increased beyond an optimal size (Armitage & Schwartz, 2000). In addition, all females in a group did not obtain equal direct fitness, which may have been due to competition among female group members in larger groups (Armitage & Schwartz, 2000). The relative magnitude of the benefits and costs of sociality are expected to vary across populations due to numerous extrinsic (e.g. population density) and intrinsic (e.g. age of female) factors, so the size and composition of the social unit that maximizes a female's fitness is unlikely to be constant throughout the range of a species.

### Study Species

Prairie voles, *Microtus ochrogaster*, are herbivorous rodents that inhabit grasslands of north central North America ranging from relatively low-quality prairie habitats, to brome grass habitats in Kansas (Rose & Gaines, 1978) to habitats in Illinois, with a greater percentage of forbs, which are critical in the diet of prairie voles (Getz, 1985). Although survival varies with a number of factors (e.g. season of birth and population density), prairie voles have relatively short reproductive life spans, and most voles do not survive for longer than one breeding season (Getz, Simms, McGuire, & Snarski, 1997).

Although this species is typically described as socially monogamous, in natural populations, adult females reside and breed in one of three different types of social units. In addition to socially monogamous male–female pairs, some females reside at a nest without any other adults, while other females live in groups (referred to as communal groups by Getz, McGuire, Pizzuto, Hofmann, & Frase, 1993). All three types of social units have been commonly observed within the same natural population, and the frequency of these three social units varies temporally within populations as well as geographically among populations (Getz et al., 1993; Streatfeild, Mabry, Keane, Crist, & Solomon, 2011). Some variation in social structure within or between populations is known to be affected by extrinsic factors such as population density (Cochran & Solomon, 2000) and the distribution and abundance of vegetation (Streatfeild et al., 2011).

Laboratory studies reveal that male prairie voles exhibit high levels of paternal care (Oliveras & Novak, 1986; Solomon, 1993; Thomas & Birney, 1979), and pups reared communally receive alloparental care, i.e. from group members other than the parents, including offspring from a previous litter or other lactating females (Hayes & Solomon, 2004; Solomon, 1991). Because parental or alloparental care can affect offspring growth, development and subsequent behaviour (Ahern & Young, 2009; Solomon, 1991, 1994), the size or composition of the social unit in which a female prairie vole resides could influence her reproductive success in field populations.

The relationship between the social unit in which a female resides and her survival and reproductive success was examined by Getz and McGuire (1993) and McGuire, Getz, and Oli (2002) using 7 years of live-trapping data from a natural population of prairie voles in east-central Illinois. They assumed that all juveniles (individuals  $\leq 20$  g) were offspring of the adult female(s) living at the nest where a juvenile was first captured. Within social units with more than one female, reproductive success could only be estimated on a per capita basis because maternity could not be assigned based on genetic data. In this population, the mean number of offspring surviving to 30 days did not differ significantly between paired females (0.47 offspring) versus single females (0.56 offspring). When considering all social units, the mean number of

offspring surviving to 30 days (1.68 offspring) produced during their lifetime by females living in social units with three adults was significantly greater than females living in social units with more or less than three adults (0.84 offspring). There was no relationship between group size and adult survival, so reproductive success of females in groups of three was not related to their increased survival. The authors concluded that this social unit size may be optimal for female reproductive success, at least in this population.

In another study, the relationship between group size, food availability and lifetime reproductive success (LRS) was examined using data from seminatural populations of prairie voles living in 0.1 ha enclosures. Solomon and Crist (2008) estimated the per capita LRS of females in social units with only one breeding female or with multiple breeding females. The estimated LRS for females in male–female pairs was four times greater compared to larger social units containing only one breeding female. Food supplementation had no effect on production of offspring in social units with only one breeding female. In groups with multiple breeding females, Solomon and Crist (2008) estimated that LRS almost doubled with increased social unit size in populations where food was supplemented but not in unsupplemented populations. In contrast, in groups with six or more adult members, LRS decreased by approximately two pups compared to smaller social units (2–5 individuals) in unsupplemented populations. Thus, per capita LRS can be affected by group size and composition (i.e. the number of breeding females), as well as food availability.

In the current study, we analysed data on social organization and genetic parentage in two free-living populations of prairie voles (Indiana and Kansas) that differed in population density and the spatial structuring of vegetation, two factors that can affect social organization and reproductive behaviour in prairie voles (Streatfeild et al., 2011). The primary objectives of our study were to test the hypotheses (1) that a female prairie vole's survival and reproductive success are related to the number and sex of other adults residing with her at a nest, (2) that a female's reproductive success is related to the amount of time that she is a resident at a nest, (3) that the relationship between social unit size or composition and female reproductive success differs between populations that exhibit differences in ecological factors such as population density and habitat quality (Streatfeild et al., 2011) and (4) that we would be more likely to find a relationship between female survival, reproductive success and social unit size or composition in a long-term study than in a short-term study.

Based on the findings of Getz and McGuire (1993) and McGuire et al. (2002) from a natural population in Illinois, we predicted that female reproductive success would be highest in social units containing about three adults and decline in larger or smaller social units. We did not expect to find a relationship between size of social units and female survival, nor did we expect to find a relationship between female survival and reproductive success based on the results from Getz and McGuire (1993). In the Indiana (IN) population we studied, high-quality vegetation was more spatially structured and population density was higher than in the Kansas (KS) population we studied (for details, see Keane, Ross, Crist, & Solomon, 2015; Streatfeild et al., 2011). Since a previous study of prairie voles found that the number of groups and group size increased as adult density increased (Cochran & Solomon, 2000), we expected to find a greater frequency of groups and larger groups in IN than KS because population density was higher in IN on average and the vegetation was more clumped. Based on Solomon and Crist (2008), we expected that we would find population differences in female survival and reproductive success related to the size and the number of breeding females per social unit due to differences in the distribution and abundance of food resources. We also predicted that females in both populations that resided at a

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