Fitness consequences of sociality in prairie voles, *Microtus ochrogaster*: influence of group size and composition

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We used 7 years of live-trapping data from an Illinois population of prairie voles to examine how survival and reproductive success varied with size and composition of social groups. Specifically, we examined measures of fitness for residents of single female units, male–female pairs and communal groups. Reproductive success, measured as either the number of young that survived to 12 or 30 days of age per adult female in a group, was higher for groups of three adults than for smaller or larger groups. The ideal group composition with respect to reproductive success appeared to be one adult female and two adult males. Individuals born into groups with three adults survived longer than did those born into smaller or larger groups. There was no clear relationship, however, between group size and survival of adult members of groups. Sudden disappearance of a group, presumably to predation by weasels, was associated with relative group size such that the largest groups were more likely to disappear. Overall, our data indicate that prairie voles living in communal groups with three adult members have higher fitness than those living in smaller groups or in larger communal groups.

Group living has been documented in several mammalian taxa and questions regarding its adaptive significance have long been the focus of socioecological research (Alexander 1974; Packer et al. 1990; Solomon & Getz 1997; Hayes 2000). A frequently invoked hypothesis focuses on the costs and benefits of living in groups (Alexander 1974; Bertram 1978; Madison 1984; Pulliam & Caraco 1984). The benefits of group living include enhanced thermoregulation and care of young, improved ability to detect or defend against predators, and to detect, defend or exploit food resources. Common costs to group-living individuals include suppressed reproduction, increased conspicuousness to predators (or prey), competition with other group members for food or mates, and a greater likelihood of transmission of disease and parasites. Group living is predicted to evolve when the benefits exceed the costs (Alexander 1974; Hoogland & Sherman 1976; Bertram 1978; Madison 1984; Pulliam & Caraco 1984). Under these conditions, there may exist an optimal group size; the fitness of members of groups of optimal size should be higher than the fitness of those living in smaller or larger groups.

Prairie voles live in communal groups that typically consist of members of an extended family and a few apparently unrelated adults (Getz et al. 1993). Extended families form in this species because most offspring remain at their natal nest (McGuire & Getz 1995). Unrelated adults typically join extended families once philopatric offspring have reached adulthood (Getz & McGuire 1997). Communal groups, while present throughout the year, are most common in late autumn and winter (Getz et al. 1990). In a previous paper, we compared costs and benefits of communal nesting in prairie voles based on patterns of dispersal from communal groups (McGuire & Getz 1995). We identified lack of mating opportunity as a probable cost to individuals living in groups composed solely of family members (McGuire & Getz 1995). We have also presented evidence that neither conservation of energy nor enhanced exploitation of food resources is involved in the formation of communal groups in this species (Getz et al. 1993; McGuire & Getz 1995). In addition to communal groups, male–female pairs and single female units are present in natural populations of prairie voles (Getz et al. 1993). We have previously shown that adult females survived longer...
when living in a pair than when living singly, but that estimates of reproductive success were similar for paired and single females (Getz & McGuire 1993).

In this paper, we investigate the fitness consequences of communal nesting in prairie voles in contrast to living in smaller groups such as single female units and male–female pairs. Specifically, we examine the relationships between size of social group and survival and reproductive success of group members. Here, we present direct measures of reproductive success for all types of social groups rather than the estimates previously presented for single female units and male–female pairs (Getz & McGuire 1993). Furthermore, whereas our earlier analysis of costs and benefits of communal nesting in prairie voles was based on animals that dispersed from communal nests (McGuire & Getz 1995), the present paper is restricted to animals that remained as residents of nests. Many studies of the fitness consequences of group living have focused on group size and ignored group composition. However, sex and reproductive status of group members can have substantial fitness consequences, particularly in small mammals such as voles. For example, reproduction in young voles and other mammals may be suppressed through contact with family members or adult females or their urine (Vandenbergh 1987; Creel et al. 1992; Carter & Roberts 1997; Oli & Dobson 1999). Therefore, we also examined measures of fitness in relation to composition of social groups, specifically the number of adult male and adult female members.

**METHODS**

**Study Site**

Our study site was situated at the University of Illinois Biological Research Area, 6 km northeast of Urbana, Illinois. The site included two adjacent alfalfa (Medicago sativa) fields that also contained ragweed (Ambrosia spp.), goldenrod (Solidago spp.), wild parsnip (Pastinaca sativa) and bluegrass (Poa pratensis). We used one field during October 1980–July 1984, and the other during June 1983–May 1987. Getz et al. (1987) provide a more detailed description of the study site.

**Procedures**

We used three different trapping protocols to monitor our study population. Grid trapping provided demographic data and identified newly established social groups (Getz et al. 1987). Trapping directly at the nests of social groups provided detailed information on social organization (Getz et al. 1993) and trapping at the outskirts of home ranges of social groups assessed the potential for social interaction away from nests (McGuire et al. 1990). In all three trapping protocols we baited with cracked corn and used wooden multiple-capture live-traps designed after those described by Burt (1940). The traps were made of redwood (1.5 cm thickness), which provided ample protection from extremes of low temperature. We covered the traps with aluminium shields for protection from sun and rain.

We conducted grid trapping twice a month. Grid stations were located at 10-m intervals and each had a single trap. We set and checked all grid stations for 3 days each month. Traps were set Tuesday afternoon and first checked that evening at 2100 hours; daily checks at 0800 hours, 1500 hours and 2100 hours continued through Friday afternoon. Two weeks after the 3-day session we set and checked those grid traps more than 15 m from known nests; these traps were checked on the above schedule from Wednesday through to Friday afternoon.

We trapped directly at the nests of social groups for up to 28-h periods each week (Monday–Tuesday and Thursday–Friday); we checked traps seven times, approximately every 3–4 h, during each of these 2-day periods. The Thursday–Friday session did not occur during the week of grid trapping. Nests (underground nests and surface nests of woven grass) were located either by visual search of the study site or more commonly by following trails left by animals dusted with ultraviolet reflective powder (Lemen & Freeman 1985). Upon finding an underground nest, we placed four or five traps at the entrances of burrows leading to the underground nest chamber; for surface nests, we placed traps in runways leading to the nest. We considered an individual to be a resident of a particular nest once it had been captured primarily at that nest for at least 10 days. In the case of young animals, we considered individuals that weighed less than 20 g when first captured at a nest to be offspring of a resident female at that nest. We stopped trapping at a nest when 2 weeks passed without a capture.

Our third trapping regimen was designed to estimate potential for social interactions between resident and nonresident animals away from nests. We encircled the nests of social groups with five to eight traps; these traps were set in active runways about 5 m from the focal nest and were checked five times during one 34–h period each week except during the week of grid trapping each month. Such checks began on Tuesday afternoon and ended on Wednesday evening and were conducted during March 1986–April 1987.

We weighed animals at first capture and when captured in a grid trap, and identified them by toe-clip. At each capture we recorded location, sex and reproductive condition (reproductive males had scrotal testes and reproductive females had open vulva, or were pregnant or lactating). We classified animals as adult when they weighed at least 30 g; this classification was based on observations of the age and mass at which captive-born animals (descendants of individuals captured at our sites) became reproductive.

**Social Organization**

Our study population contained the following three types of social groups: (1) male–female pair (adult male and adult female, usually with young), (2) single female (adult female but no resident adult male, usually with young), and (3) communal group (typically pairs or single...
female units at which offspring remained until adulthood; apparently unrelated adults often joined these extended families or sometimes came together to form a communal group. Some animals in our population were classified as ‘wanderers’ because they made frequent visits to the nests of established social groups and did not meet the criterion for residency at any nest. For example, during the breeding period (April–November) about 45% of males and 24% of females were classified as wanderers. Getz et al. (1993) and Getz & McGuire (1997) provide further descriptions of social groups and wandering animals.

Data Analysis

We examined three components of fitness: reproductive success, juvenile survival and adult survival. We calculated two measures of reproductive success. First, we calculated the number of offspring that survived to 12 days of age per adult female in a group. Twelve days is the age at which young first emerge from underground nests and are trappable above ground. Second, we calculated reproductive success as the number of offspring that survived to 30 days of age per adult female in the group. Thirty days is the approximate age at which prairie voles reach reproductive maturity (Carter et al. 1980; Solomon 1991a). Because we did not determine genetic relationships among group members, including offspring produced by specific females, our measures of reproductive success were on a per adult female basis for each group. For example, if eight young survived to 30 days of age at a particular group and there were four adult females at that group, then reproductive success for that group would be two offspring per adult female; the value 2.0 would be assigned to that group and used in the analysis. Thus, our unit of analysis for reproductive success was the group and not individual females. In addition, we included only those groups that contained at least one reproductive female and remained in existence long enough that offspring had the opportunity to reach 30 days of age.

In our analyses of juvenile and adult survival we included only those animals that died while residents of groups. We did not include animals that either dispersed from groups or remained at the nest after the group changed to a different status (e.g. a communal group became a pair or single female unit through mortality of group members). Because we could not examine underground nests without destroying them, we did not have precise dates of birth for animals born at nests. We thus calculated juvenile survival (number of days) from the time an animal first emerged from its nest and entered a trap (about 12 days of age) to the time it disappeared from the nest. We considered it unlikely that such animals dispersed rather than died because all surrounding habitat suitable for voles was monitored by grid trapping and thus individuals that dispersed would probably have been captured (trappabilities of 92% were typical in our fields; Getz et al. 1987). Our measure of adult survival was number of days survived while living in a group.

We defined group size as total number of adult residents. However, the number of adult residents of communal groups often changed over time as members died or dispersed, new animals joined the group, and resident offspring reached adulthood; such groups could change in size and composition yet still retain their status as a communal group. Thus, for our analyses of reproductive success and adult survival, we used the most representative group size, defined as the size that characterized the group for most of its, or the adult’s, existence, respectively. Typically, the most representative group size characterized the group for about 85% of its or the adult’s existence. For our analysis of juvenile survival in relation to group size, we used the size of group into which the individual was born.

In our analyses of adult and juvenile survival, we used individuals and not groups as the unit of analysis. In this manner, we could assign a most representative group size to each individual living in a communal group. We recognized that this approach might raise questions regarding possible nonindependence of measurements within a group. However, we considered our approach to be more appropriate than assigning a ‘fixed’ group size and composition to each communal group and then considering all individuals within the group as the unit. Furthermore, we did not measure any individual more than once. The following group sizes corresponded to the different types of social groups in our population: (1) group size of 1= single female units, (2) group size of 2= mostly male–female pairs and a small number of two-female communal groups, and (3) group size of 3 or more = communal groups.

We plotted each of the four variables (two measures of reproductive success, juvenile survival and adult survival) against size of social group. We first identified extreme observations; we considered such observations outliers and excluded them from further analyses. The numbers of observations excluded from analyses of reproductive success, juvenile survival and adult survival and descriptions of the excluded observations are presented with the results for each of these variables. Next, if an optimal group size was apparent from a plot of the remaining data, we used two-sample t tests (two-tailed) to compare reproductive success or survival at groups of optimal size with that of groups smaller and larger than the optimum. We used polynomial regression to further explore nonlinear relationships between measures of fitness and size of group; we used stepwise procedures for variable selection. However, regression of fitness measures on the variables selected always explained 6% or less of the variation and thus we did not include the results of our regression analyses. In addition to examining reproductive success and survival in relation to total number of adult residents, we also examined these measures in relation to number of adult males and number of adult females. All means are presented ± 1 SE.

There were 19 instances in which all members of a group disappeared fairly suddenly from their nest (trapping data revealed that such disappearances typically occurred over a period of about 1–2 weeks). We did not capture individuals from these groups elsewhere in the
study site or in adjacent fields and thus we assumed they were lost to predation. We considered least weasels, *Mustela nivalis*, and long-tailed weasels, *M. frenata*, to be the most likely predators responsible for these disappearances because (1) they were captured at the study site when at least four of the 19 groups disappeared (four young weasels were captured together in a trap and 2 weeks later an adult was captured), (2) there was no digging or disturbance of traps at the 19 nests (skunks typically destroy underground nests through digging, and feral cats and raccoons usually disturb traps), (3) all such instances occurred from late November through early March when snakes are inactive in east-central Illinois, and (4) weasels are well-known predators of voles (Pearson 1985; Lin & Batzli 1995) that often kill all instances occurred from late November through early March when snakes are inactive in east-central Illinois, and (4) weasels are well-known predators of voles (Pearson 1985; Lin & Batzli 1995) that often kill all members of a social group (MacLean et al. 1974; Madison et al. 1984). We used chi-square tests of association to evaluate the relationship between relative group size (categorized as at or below the maximum size in the field at the time a group disappeared) and sudden loss of the entire group. More specifically, for the 19 instances we compared the size of the group that disappeared to the sizes of other groups present in the field at the time of the group’s disappearance. We also examined whether absolute group size influenced the likelihood of disappearance.

**Ethical note**

We used toe clipping to permanently mark voles in our study population. We clipped a maximum of two toes per foot; this made possible several thousand unique identifications and was necessary due to the long-term nature of the present study and the occurrence of several simultaneous studies in neighbouring fields. Our field protocol was approved by the University of Illinois Laboratory Animal Resource Committee.

Today, more benign marking methods are available (Schooley et al. 1993; Weyand 1998) and toe clipping of rodents is deemed a method of last resort to be performed only on altricial neonates (Guide for the Care and Use of Laboratory Animals, Institute of Laboratory Animals, Commission on Life Sciences, National Research Council 1996). At the time of our study (1980–1987), however, some alternatives, such as electronic identification using transponders, were not available, and toe clipping was considered an acceptable method for individual identification of rodents (Kumar 1979). We chose toe clipping over ear tagging because ear tags can be lost and toe-clips can be read more accurately than numbers on tags at night. In recent years, several studies have examined the effects of various marking methods on the health and survival of free-living rodents. Toe clipping has been found to have no deleterious effects on survival or body weight (Korn 1987; Wood & Slade 1990; Braude & Ciszek 1998). In contrast, ear tagging, while considered more humane, has been shown to increase infestation by ticks (Ostfeld et al. 1993) and tags are frequently lost (tag loss for prairie voles has been assessed at 10–16%; Wood & Slade 1990; Harper & Batzli 1996). This rate of tag loss would have seriously compromised our ability to monitor composition of social groups at our study site. To reiterate, however, while this 1980–1987 study relied on the then-acceptable practice of toe clipping to mark individuals, this practice should be avoided today as better, more ethical, alternatives are available.

**RESULTS**

Six hundred and forty-seven groups met our criteria for inclusion in the data set on reproductive success (i.e. groups contained at least one reproductive female and remained in existence long enough that offspring had the opportunity to reach 30 days of age). We identified eight of the 647 observations as outliers and excluded them from analyses. These eight observations involved groups with all of the following characteristics: (1) more than 10 adult residents, (2) more than four adult females and (3) more than seven offspring that survived to 30 days of age. The number of reproductive females in the remaining 639 groups ranged from one to four with a mean of 1.20 ± 0.02. The total number of adults ranged from one to nine, with groups of two adults being most common (Fig. 1a). The mean numbers of adult males, adult females, and total adults per group were 0.84 ± 0.03, 1.27 ± 0.03, and 2.11 ± 0.05, respectively.

Size and composition of communal group influenced reproductive success measured as the number of young that survived to 12 days of age per adult female in a group (Fig. 1b–d). On average, females living in groups of three adults had higher reproductive success (2.36 ± 0.30, N=70) than those living in smaller or larger groups (1.66 ± 0.08, N=569; unequal variances: $t_{70.8}=2.23$, $P=0.028$; Fig. 1b). Furthermore, females living in groups with two adult males had higher reproductive success (2.48 ± 0.36, N=53) than those living in groups with fewer or more males (1.67 ± 0.08, N=586; unequal variances: $t_{57.4}=2.20$, $P=0.031$; Fig. 1c). Finally, females living in groups in which they were the only adult female had higher reproductive success (1.85 ± 0.10, N=519) than females living in groups with other adult females (1.23 ± 0.11, N=120; unequal variances: $t_{32.3}=4.23$, $P<0.0001$; Fig. 1d).

Size and composition of communal group also influenced reproductive success measured as the number of young that survived to 30 days of age per adult female in a group (Fig. 2a–c). The pattern was similar to that for number of young that survived to 12 days of age. Females living in communal groups of three adults had significantly higher reproductive success (1.68 ± 0.26, N=70) than those living in smaller or larger groups (0.84 ± 0.06, N=569; unequal variances: $t_{75.8}=3.16$, $P=0.002$; Fig. 2a). In addition, females living in groups with two adult males had higher reproductive success (1.89 ± 0.32, N=53) than those living in groups with fewer or more males (0.84 ± 0.06, N=586; unequal variances: $t_{55.4}=3.25$, $P=0.002$; Fig. 2b). Finally, females living in groups in which they were the only adult female tended to have higher reproductive success (0.96 ± 0.07, N=519) than females living in groups with other adult females (0.78 ± 0.08, N=120) but this difference was not statistically significant (unequal variances: $t_{30.5}=1.61$, $P=0.108$; Fig. 2c).

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Eight hundred and five individuals met our criteria for inclusion in the data set on juvenile survival (i.e. individuals were born into a group and died while a

Figure 1. Reproductive success and size of social group in prairie voles. (a) Frequency distribution by size of 639 groups in the study population. Reproductive success, measured as the number of young that survived to 12 days of age per adult female in the group, in relation to total number of adults (b), number of adult males (c) and number of adult females (d). Points on scatter plots may represent more than one group.

Figure 2. Reproductive success and size of social group in prairie voles. Reproductive success, measured as the number of young that survived to 30 days of age per adult female in the group, in relation to total number of adults (a), number of adult males (b) and number of adult females (c). Points on scatter plots may represent more than one group.
We identified 21 of the 805 observations as outliers and excluded them from further analyses. The 21 excluded observations involved 15 individuals with survival times of more than 210 days and six individuals from groups with at least six adults and survival times of more than 120 days. The remaining 784 individuals were from 302 different groups that ranged in size from one to 15 adults (Fig. 3a). Survival of individuals was influenced by the size of the group into which they were born (Fig. 3b). On average, young born into groups of three adults survived longer ($47.73 \pm 3.10$ days, $N=140$) than did those born into smaller or larger groups ($39.05 \pm 1.30$ days, $N=644$; $t_{782}=2.76$, $P=0.006$). Inspection of the relationships between juvenile survival and number of adult males suggested that groups with one adult male were optimal for juvenile survival (Fig. 3c). However, young born into groups with one adult male did not survive longer on average ($41.51 \pm 1.70$ days, $N=411$) than those born into groups with no male or two or more males ($39.60 \pm 1.37$ days, $N=373$; $t_{782}=0.79$, $P=0.43$). Although young born into groups with two females tended to live longer ($43.52 \pm 2.48$ days, $N=207$) than those born into groups with one or three or more females ($39.55 \pm 1.38$ days, $N=577$), the difference was not statistically significant ($t_{782}=1.45$, $P=0.149$; Fig. 3d).

One thousand three hundred and seventy-five animals met our criteria for inclusion in the data set on adult survival (i.e. individuals weighed $\geq 30$ g and died while a resident of a group). These individuals were from 598 different groups that ranged in size from one to 18 adults (Fig. 4a). Group size appeared to have little effect on the survival of adults, and there was no clear optimal group size for adult survival (Fig. 4b).

The range of group sizes shown in plots of data on reproductive success (range 1–9; Fig. 1a, b) is smaller than the range of group sizes shown in plots of data on juvenile survival (range 1–15; Fig. 3a, b) and adult survival (range 1–18; Fig. 4a, b). In our population, the average group size was smaller in spring through early autumn (the time when most reproduction occurred seasonally) than in late autumn and winter (Getz et al. 1990, 1993). The smaller group sizes in spring through early autumn probably resulted from snake predation; snakes are inactive in Illinois during late autumn and winter and thus the increased survival of individuals at this time resulted in larger groups (Getz et al. 1990).

Although most groups of two adults in our population were male–female pairs, there were a few two-female communal groups. We compared fitness for members of male–female pairs with that of members of two-female groups. Reproductive success, measured as the number of young that survived to 12 days of age per adult female in a group, did not differ between pairs ($1.72 \pm 0.12$, $N=294$) and two-female groups ($1.25 \pm 0.32$, $N=12$; unequal variances: $t_{14.2}=1.39$, $P=0.18$). Similarly, reproductive

![Figure 3](image-url)

Figure 3. Juvenile survival and size of social group in prairie voles. (a) Frequency distribution showing sizes of groups into which 784 young were born in the study population. Groups with 10 or more adults were rare (<0.13%). Juvenile survival in relation to total number of adults (b), number of adult males (c) and number of adult females (d). Points on scatter plots may represent more than one individual.
success, measured as the number of young that survived to 30 days of age per adult female in a group, did not differ between groups of two-female (0.62 ± 0.21, N=12) and two-female groups (0.32 ± 0.08, N=294) and two-female groups (0.62 ± 0.21, N=12; unequal variances: t_{14.0}=0.88, P=0.40). Young born into male–female pairs did not differ with respect to survival (40.01 ± 0.20 days, N=283) from those born into two-female groups (40.22 ± 0.33 days, N=41; t_{22}=0.40, P=0.65). Finally, adult members of pairs survived longer (44.55 ± 1.72 days, N=216) than did adult members of two-female groups (27.73 ± 4.46, N=11; t_{22}=2.19, P=0.03).

Sudden disappearance of a group, presumably to predation by weasels, was associated with relative group size (chi-square test: \( \chi^2=40.71, P<0.0001 \)). During periods when entire groups suddenly disappeared from our study site, 24.1% (7/29) of groups that were at the maximum size in the field disappeared, compared with 1.9% (12/622) of groups that were less than the maximum size. With respect to absolute group size, the following proportions of groups disappeared: 1–2 individuals, 0.0% (0/249); 3–4 individuals, 5.7% (7/116); 5–7 individuals, 5.0% (7/132); ≥8 individuals, 3.6% (5/135; \( \chi^2=13.23, P<0.0005 \))

**DISCUSSION**

In general, prairie voles living in communal groups of three adults had higher fitness than those living in smaller groups (single female units, male–female pairs and two-female communal groups) or larger communal groups. More specifically, prairie voles living in groups of three adults had higher reproductive success, measured as the number of young that survived to 12 or 30 days of age per adult female in the group, than did those living in smaller or larger groups. Although there was no clear relationship between group size and survival of adult members, juveniles born into groups of three adults survived longer than did those born into groups of smaller or larger size.

Increased conspicuousness to predators may be a cost of sociality in prairie voles. We found that the likelihood of an entire group disappearing, presumably to predation by weasels, was associated with relative group size. Groups that were at the maximum size in the field at a particular time were more likely to disappear. Madison et al. (1984) reported that a group size of three individuals was ideal for meadow voles, *Microtus pennsylvanicus*, because individuals in larger groups appeared more susceptible to predation from species such as ermine, *Mustela erminea*, and fox, *Vulpes fulva*. These authors noticed greater concentrations of faeces, tunnels and tracks, and breathing holes in the snow at large groups and suggested that predators used these cues to locate nests of meadow voles. Greater activity in large communal groups and the resultant accumulation of cues might also explain why groups of prairie voles that were the largest in the field at a particular time were more likely to disappear. Similarly, the decline in reproductive success and juvenile survival at groups with four or more adult residents might reflect increased predation on large groups.

Reproductive suppression may be another cost of sociality in prairie voles. Reproductive success was highest in groups with only one adult female. This pattern reached statistical significance when reproductive success was measured as the number of offspring that survived to 12 days of age and near significance when the measure was number of offspring that survived to 30 days of age. Among cooperatively breeding rodents, prairie voles are considered ‘singular breeders’ because usually only one female produces young within a social group (Solomon & Getz 1997). Laboratory data indicate that interactions between related females (Bamshad & Novak 1992) and between unrelated females (Firestone et al. 1991) are often aggressive in the presence of an adult male or young. Social stress within groups appears to influence fitness of group members in prairie voles (Firestone et al. 1991) and in some larger mammals (van Noordwijk & van Schaik 1999). In addition, adult female prairie voles produce a urinary chemosignal that suppresses reproductive maturation in young females (Getz et al. 1983). However, frequent interactions with non-resident males may override the suppression of young females (McGuire & Getz 1991), and explain why some groups in our study population had more than one reproductive female. Nevertheless, the lower reproductive success in groups with more than one female may reflect reproductive suppression of some female members, especially females that were recruited as young born into the group, through behavioural or chemical means. A
similar situation has been described for yellow-bellied marmots, *Marmota flaviventris*, although fitness begins to decline in marmots when matriline size reaches four or five females (Armitage & Schwartz 2000).

We have previously identified lack of mating opportunity as a cost related to group composition for some prairie voles (McGuire & Getz 1995). Because prairie voles typically do not breed with family members (McGuire & Getz 1981; Carter et al. 1986; McGuire & Getz 1991), individuals living in communal groups in which all members are genetically related have no opportunity for mating within their group. Neither competition for food nor competition for mates appears to be an important cost of sociality for prairie voles (McGuire & Getz 1995).

We have no information on the relationships between group size and either parasite infestation or disease in our study population.

Using our live-trapping data and published data from direct observations of prairie voles under seminatural laboratory conditions, we can tentatively identify specific benefits of group living for individuals in natural populations. Getz et al. (1992), for example, found that prairie vole nestlings of single females are more likely to be killed by short-tailed shrews, *Blarina brevicauda*, in a seminatural environment than are nestlings of male-female pairs, suggesting an antipredator advantage to prairie voles of living at least in pairs. Shrews kill only young that are left unattended in the nest. Presence of adults other than parents at a nest would probably also deter shrews. Furthermore, although mother and father prairie voles typically coordinate visits to the natal nest, there are times during the preweaning period when pups of pairs are left unattended (McGuire & Novak 1984). Thus, the presence of additional group members would be expected to further reduce the time pups are left alone and susceptible to shrew predation.

Another benefit of sociality for prairie voles may be enhanced direct care of offspring. Older offspring of both sexes have been observed to care for their younger siblings under seminatural conditions. Such behaviour results in increased time spent by prairie vole mothers away from the natal nest in activities such as foraging (Wang & Novak 1992). In more standard laboratory caging, but under temperatures designed to simulate conditions in burrows of prairie voles in spring and late autumn, the presence of older offspring resulted in elevated weaning mass of younger pups and shorter interlitter intervals for parents (Solomon 1991b). Enhanced care and protection of young at the nest may be a benefit of group living for prairie voles, resulting in the higher reproductive success and survival of juveniles in groups with three adults as compared to those with one or two adults.

Reproductive success in our study population was influenced by group composition, in addition to group size. The optimal group appeared to be two adult males and one adult female. In some mammals, reproductive success and juvenile survival are positively associated with the number of adult males or a greater proportion of adult males in a social group (Koenig 1995; Treves 2001). The roles of males in care of young and defence against predators and conspecifics have been suggested as possible explanations for these patterns (Treves 2001). Adult male prairie voles provide substantial parental care to their offspring (Oliveres & Novak 1986) and actively protect them against shrews (Getz et al. 1992). In addition, the presence of resident adult males reduces intrusions by nonresident males into the group’s home range (McGuire et al. 1990). Philopatric male offspring care for younger siblings and their presence at the nest allows their mother to spend more time foraging (Wang & Novak 1992). Young male prairie voles tend to spend more time in contact with pups and respond to them more frequently than do young females (Roberts et al. 1998). Thus, having two males in a group may be particularly effective in enhancing maternal condition as well as care and protection of young in prairie voles; this may explain the higher reproductive success in these groups compared with those having no males or only one male. However, there was no clear optimal number of males with respect to survival of young born into communal groups.

For some species of voles, the benefits of sharing a nest with other individuals include enhanced thermoregulation (e.g. meadow vole, *M. pennsylvanicus*; Madison 1984; Madison et al. 1984; Madison & McShea 1987) and the collection and sharing of winter food stores (taiga vole, *M. xanthognathus*; Wolff & Lidicker 1980, 1981). Although prairie voles probably gain energetic benefits from group nesting in winter, we have previously shown that such benefits are incidental and not the main reason for formation and maintenance of communal groups in this species (McGuire & Getz 1995). Enhanced access to food caches also does not appear to be an important benefit of group living in prairie voles; excavation of recently vacated nests and burrows at our study sites revealed only two of 30 burrows with food caches (Mankin & Getz 1994).

In summary, prairie voles living in communal groups with three adult residents had higher fitness than those living in smaller groups (mostly single female units and male–female pairs) or larger communal groups. The optimal group size of three may represent a balance between higher mortality from predators at very small and very large groups. Some predators, such as shrews, appear to prey on pups left unattended in the nest (Getz et al. 1992), a condition that would occur most frequently in small groups such as single female units and groups with two adults. Other predators, such as weasels, appear to focus on larger groups (this study; Madison et al. 1984), perhaps due to the increased conspicuousness of such groups. The optimal group composition in our study population was one adult female and two adult males. This composition may limit the cost of reproductive suppression by adult females of young females and also maximize the benefits of enhanced care and protection of young.

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