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EFFECTS OF FOOD SUPPLEMENTATION ON THE SOCIAL ORGANIZATION OF PRAIRIE VOLES (*MICROTUS OCHROGASTER*)

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Mammalian social organization can vary over ecological time. We experimentally manipulated food resources in enclosed populations of prairie voles (*Microtus ochrogaster*) to test the hypothesis that food quality influences the potential for group formation. During each field season, populations were started by releasing 5 pairs of prairie voles into each of 8 0.1-ha enclosures. Populations were monitored for 18–19 weeks during each field season. One-half of the enclosures received supplemental food, and the other one-half were unsupplemented controls. Density of voles increased throughout each field season. There were significant increases through time in philopatry and number of groups in both the food-supplemented and unsupplemented treatments, but there were no differences between treatments. Groups formed early in the season, apparently before the need for thermoregulatory benefits. Results are consistent with the hypothesis that the social organization of prairie voles is not flexible in response to changes in food quality but that formation of groups might be a density-dependent response.

Key words: food supplementation, *Microtus,* rodents, social organization, vole

Lott (1991) compiled considerable evidence showing that social organization can vary over ecological time. These observations suggest that intraspecific variation in social organization is a result of variation in behavior of individuals in response to ecological circumstances. Some ecological factors that individuals may be able to assess include weather, predation pressure, density, nest-site availability, and quality, quantity, or distribution of food (Erlinge et al. 1990; Jeppsson 1990; Lott 1991; Madison 1990; Ostfeld 1985; Stacey and Ligon 1987; Ylonen et al. 1988).

One type of social system, cooperative breeding, occurs when mature offspring remain at their natal nest beyond weaning and assist in the care of young, hence the name ''helpers-at-the-nest.'' Because cooperatively breeding rodents have been studied primarily in habitats with high food quality and high densities (Agren et al. 1989; FitzGerald and Madison 1983), it is unclear which of these factors causes group formation. Even with experimental approaches, it is difficult to clearly distinguish which factor may be causal because manipulating 1 variable may have direct or indirect effects on the dependent measure. For example, increasing food may lead to increases in density and changes in social behavior; thus, food could have direct effects on behavior and indirect effects through density.

The prairie vole (*Microtus ochrogaster*), an arvicoline rodent, has been described as a cooperative breeder (Solomon and Getz 1997). In a habitat with high availability and quality of food (alfalfa field) in east-central Illinois, prairie voles are found in groups of a breeding pair, their offspring,

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and ≥1 additional adult of either sex (Getz et al. 1990a, 1992). Additional adults may be offspring that have reached maturity at the natal nest or unrelated adults. In these same environments, prairie voles also are found living as male–female pairs (with or without 1 litter of offspring) and single females (1 adult female with or without her offspring), which may be the remnant of male–female pairs (Getz et al. 1990a, 1993). Prairie voles can be found in other habitats, including bluegrass (*Poa*) and tallgrass prairie (Getz 1985). Food quality and densities of voles can differ dramatically among these habitats (Batzli and Cole 1979); prairie voles showed peak densities in alfalfa (200–620 animals/ha), which were about 5 times more than those occurring in bluegrass (75–128 animals/ha) and 8 times as high as those in tallgrass prairie (38–75 animals/ha—Getz et al. 1993).

In a short-term study of prairie voles in 3 types of habitats, groups were found with the same frequency, and group sizes were similar regardless of habitat quality (Getz et al. 1992). Thus, Getz et al. (1992) hypothesized that social organization of prairie voles is fixed; the conclusion that prairie voles are phenotypically inflexible in their social organization may have been premature because their study was observational rather than an experimental investigation of the role of habitat quality in group formation. A recent laboratory study also suggests that there are intraspecific differences between prairie voles obtained from a population in Illinois compared with those from Kansas (Roberts et al. 1998), where habitat quality differs. Although these behavioral differences are found in animals from habitats of differing quality, we do not know whether these differences are genetically determined or environmentally induced. Thus, our objective was to experimentally evaluate hypotheses concerning effects of food quality on social organization of the prairie vole.

If social organization of the prairie vole is phenotypically inflexible, variation in food quality should not lead to differences in the degree of juvenile philopatry. Thus, there would be no changes in group size and composition or in the proportion of each type of breeding unit regardless of experimental manipulation. Previous studies with arvicoline rodents have shown that an increase in food quality or density is associated with a decrease in female home range and an increase in the degree of space sharing (Ims 1987; Ostfeld 1986; cf. Slade et al. 1997). Pusenius et al. (1998) and Lambin and Yoccoz (1998) also showed that when food quality was sufficient, nest sharing by kin was probable.

Furthermore, Desy et al. (1990) found that male prairie voles in populations with supplemental food showed less aggression toward conspecifics. Their study on prairie voles, in conjunction with those on other arvicoline rodents (Ims 1987; Ostfeld 1986), suggests that changes in behavior in response to supplemental food would lead to an increased tolerance of conspecifics and an increased sharing of space. Thus, an alternative hypothesis is that if prairie voles respond to food quality, we should observe increased philopatry and tolerance of unrelated individuals with the addition of supplemental food. Support for this alternative hypothesis would include increases in group size and the proportion of groups during the breeding season with the addition of high-quality food.

Materials and Methods

Study site and experimental design.—Our experiment was conducted in June–November 1994 and March–July 1995 at Miami University's Ecology Research Center near Oxford, Ohio (39°30′N, 88°44′W). Those time periods were selected to represent mid- to late 1994 breeding season (referred to as late season) and early to mid-1995 breeding season (referred to as early season); we did not monitor populations during the nonbreeding season. We did not compare early and late breeding season but selected those 2 time periods to examine changes over an entire breeding season.

During each field season, populations of prai-

rie voles were established in eight 0.1-ha experimental enclosures. Enclosures were constructed of 20-gauge galvanized steel extending 75 cm above and 45 cm below ground. Those walls were sufficient to prevent movement of rodents among enclosures. We intended that the baseline habitat resemble a field of moderate quality; thus, in all enclosures we planted a mixture of 75% bluegrass (*Poa pratensis*), 10% clover (*Trifolium*), and 5% each of fescue (*Festuca*), timothy (*Phleum*), and ryegrass (*Elymus*) in April 1994. A 1-m-wide strip of vegetation was mowed periodically around the inside of each enclosure wall to discourage voles from digging around walls. To ensure that all voles were removed prior to each field season, we livetrapped enclosures for 2 weeks prior to release of founders. Throughout the study, in the few instances when mammals other than prairie voles were captured (e.g., short-tailed shrews, *Blarina brevicauda*, and meadow voles, *Microtus pennsylvanicus*), they were removed from enclosures.

The 8 enclosures were divided into 2 treatments (food supplemented and unsupplemented) with 4 replicates per treatment. Food quality was manipulated by supplementing one-half of the enclosures with rabbit chow (rabbit diet HF #5326, PMI Feeds Inc., St. Louis, Missouri) to alter food quality without changing vegetative cover—often a confounding variable in previous studies (Getz et al. 1992; Lott 1991). Rabbit chow was selected as a high-quality food because prairie voles grew and reproduced well when fed rabbit chow in previous studies (Cole and Batzli 1978; Desy and Batzli 1989). Food was evenly distributed using feeding stations placed near each grid trapping station (25 feeding stations/enclosure). Feeding stations, quart glass jars placed on their sides, were filled as necessary to ensure that food was fresh and available ad libitum. Food also was broadcast, 1 handful per station, each week. Even distribution of feeding stations and broadcasting of food each week minimized the likelihood that social interactions prevented subordinate individuals from access to food (Desy and Thompson 1983). Presence of scat around feeding stations and disappearance of food indicated that voles were using feeding stations. Empty feeding stations were placed in the other 4 enclosures to control for their presence.

Vegetative sampling was conducted each field season in July to compare cover and composition between treatments. Twelve samples were taken from each enclosure. Three random samples were taken from each quadrant within each enclosure. For each sample, a 0.25-m^2 circular patch of vegetation was clipped at ground level. Vegetation was grouped into total biomass (standing biomass and litter), monocots, high-quality dicots (clover and alfalfa), and other dicots. Samples were sorted by category, oven-dried at 80°C for 48 h, and weighed to the nearest 0.1 g.

Monitoring vole populations.—At the beginning of each field season, 5 pairs of adult voles from a laboratory colony were released into each enclosure. That number was selected because 10 voles per enclosure (100 voles/ha) was a moderate to high density for the species (Getz et al. 1987). Additional voles were released between the 1st and 2nd weeks of grid trapping to replace any that died in traps. All founder voles were born in the laboratory to animals 4 generations from wild-caught voles collected near Lawrence, Kansas. Founder voles were separated from parents at 30–60 days of age and housed in sibling groups until 45–90 days of age. Two days prior to release, unrelated animals were toe-clipped for individual identification and paired with an opposite-sex conspecific to enable formation of pair bonds. No more than 2 siblings were introduced into each enclosure.

Trapping began 1 week following release. Traps were baited with cracked corn, a low-quality food that does not support growth or reproduction in the laboratory (Desy and Batzli 1989). To reduce mortality, traps were covered with white shingles to lower daytime temperatures of traps. Cotton batting was added to traps when temperatures were predicted to be <10°C. On 1st capture, individuals were toe-clipped for identification. Body mass, sex, age class, reproductive status, and trap location of all captures were recorded. We classified each individual as a juvenile ($\leq$20 g), subadult (21–29 g), or adult ($\geq$30 g—Getz et al. 1987). Males were classified as reproductive or nonreproductive when testes were scrotal or abdominal, respectively. Females were classified as reproductive when they were pregnant, were lactating, or had an open vulva and nonreproductive if the vulva was closed.

A trapping regime similar to that used by Getz et al. (1990a) was followed that included grid trapping and burrow trapping (trapping near pu-

tative nests). Grid trapping was conducted 1 week out of 4 and was followed by 3 consecutive weeks of burrow trapping. Because that method of trapping has been conducted by L. L. Getz and colleagues for years, we presumed that the intensive level of trapping we used did not have a negative effect on animals.

Grid trapping provided data on densities of voles. Trap stations were arranged in a grid with 25 Sherman traps (5.3 m apart in a 5-by-5 array) within each enclosure. Traps were set for a 3-day session each month; traps were positioned in runways of voles ≤1 m of each grid stake. Traps were opened Tuesday evening between 1900 and 2000 h and checked at 0800, 1500, and 2100 h through Friday morning (0800 h) for a total of 7 trap checks. Throughout our study, underground nests were located by visually searching for burrow entrances and, during grid trapping sessions, by dusting adult females with ultraviolet reflective powder (Radiant Color, Richmond, California—Lemen and Freeman 1985). After dark, we followed trails of females to their burrow entrances using a battery-operated UV light (UVP, Inc., Upland, California). After locating a nest, 4–8 Sherman live traps were placed in runways near burrow entrances.

The objective of burrow trapping was to identify residents and monitor groups. During weeks of burrow trapping, traps were set on Monday morning between 0630 and 0700 h and checked every 3–4 h until 2300 h. On Tuesday, traps were checked between 0630 and 0700 h and again 3–4 h later. Thus, during each 2-day trapping period, traps were checked 7 times. The same 2-day trapping schedule was followed again starting Thursday morning. Nests were monitored twice weekly throughout the study except during grid-trapping weeks. Thus, 3 weeks of burrow trapping was conducted for a total of 12 days and 42 trap checks each month. At the end of each field season, all animals within the enclosures were removed.

Statistical analyses.—A nested analysis of variance was used to test for vegetation differences between treatments with enclosures, nested within treatments. Densities of voles in each enclosure were estimated using the minimum number known alive (MNKA = number of animals captured at time t + individuals captured both before and after time t). Because estimates of trapabilities (proportion of animals known alive at time t captured at time t) were high in our study (late season, 82% ± 3 *SE*; early season, 81% ± 3 *SE*), the minimum number known alive should be an accurate reflection of population density (Boonstra 1985). Densities of voles were compared between treatments throughout each field season using repeated-measures analysis of variance. Data on density were log transformed prior to analysis. Recruitment was defined as the cumulative number of unmarked animals. Cumulative recruitment of males and females was compared between treatments during the entire study in each field season, late season, and early season using 2-tailed unpaired t-tests.

For the analysis of social organization, we selected weeks 8, 12, 16, and 19 in the late season and weeks 6, 10, 14, and 17 during the early season (representing the last week of each 3-week burrow trapping period) for comparison of treatments. To be considered residents of a nest during each of the 3 weeks of burrow trapping, adults and subadults had to be captured during ≥1 trapping session per week and 75% of the time at 1 nest. Those criteria were similar to those used by Getz et al. (1992), who assigned residency to individuals that were trapped primarily at a given nest for 10 consecutive days. Juveniles were classified as residents if they were caught at a nest when ≤20 g. Adults and subadults captured frequently but at several different nests were classified as wanderers (Getz et al. 1993). Based on number of recaptures at a nest and proportion of captures at 1 nest, size and composition of groups were determined. After assigning residency, breeding units were classified as single female, male–female pair, or group (Getz et al. 1993). Proportion of each type of breeding unit was compared between treatments using repeated-measures analysis of variance.

Juvenile survival was quantified so that we could determine proportion of juveniles that remained philopatric. Number of juveniles that survived was compared between treatments using chi-square analysis with the 4 replicates pooled within each treatment. We defined philopatry as remaining at the natal nest until disappearance or removal at the end of the study (McGuire et al. 1993), in contrast to dispersal, which was defined as a permanent movement to another burrow within the enclosure. Only individuals caught at a nest as juveniles and surviving beyond 30 days, the age at which most

TABLE 1.—Mean (±*SE*) biomass (g dry weight per 0.25 m^2) of vegetation in supplemented and unsupplemented enclosures from 12 samples collected from each of 4 replicates (48 replicates/treatment). A nested analysis of variance (ANOVA) was used to compare each vegetative category.

	Cover	Monocots	Clover-alfalfa	Other dicots
Mid- to late breeding season (1994)				
Unsupplemented	149.3 ± 7.8	43.4 ± 2.6	4.2 ± 1.4	37.5 ± 7.3
Supplemented	157.0 ± 14.1	74.6 ± 14.4	2.3 ± 0.9	24.6 ± 3.2
	$P = 0.65$	$P = 0.08$	$P = 0.29$	$P = 0.16$
Early to mid-breeding season (1995)				
Unsupplemented	163.3 ± 4.6	90.4 ± 5.1	2.7 ± 2.0	11.7 ± 3.8
Supplemented	163.6 ± 4.8	92.9 ± 5.3	17.6 ± 3.1	5.2 ± 2.5
	$P = 0.98$	$P = 0.83$	$P = 0.14$	$P = 0.44$

animals are capable of reproducing (McGuire et al. 1993), were included in that analysis. To examine philopatry, the study period was divided into 2 periods chosen to represent the 1st and 2nd one-half of each field season. Degree of philopatry (proportion of individuals captured while ≤20 g and surviving to ≥30 g that remained at the natal nest until disappearance or dispersal to another nest) was compared using analysis of variance for late-season data. For the early season, juveniles were caught in only 3 of 8 enclosures during the 1st one-half of our study; thus, analysis of the proportion of juveniles remaining philopatric could not be conducted. During the 2nd one-half of the study, juveniles were captured in 7 of 8 enclosures, and thus we examined proportion of philopatric individuals between treatments only during the 2nd one-half of the study period using an unpaired *t*-test. Arcsine transformation was used on the proportion of each type of breeding unit and degree of philopatry (Sokal and Rohlf 1981). Results are reported as means ± 1 *SE*. For all repeated-measures analyses of variance, interactions between treatment and time are reported only if they are significant ($P < 0.05$).

RESULTS

Vegetation and demography.—Although enclosures differed in vegetative composition, no differences were significant during the late or early breeding seasons (all $P > 0.08$; Table 1). For each field season, repeated-measures analysis of variance showed that population density changed over time (late season, $F = 118.80$, *d.f.* = 18, 108, $P < 0.001$; early season, $F = 125.21$, *d.f.* = 17, 102, $P < 0.001$). Densities of voles tended to increase during the mid- to late breeding season at a higher rate in enclosures with supplemental food ($F = 1.68$, *d.f.* = 18, 108, $P = 0.054$). During that time, densities increased to 63.7 ± 6.5 voles/enclosure in the supplemented treatment and 44.7 ± 7.3 voles/enclosure in the unsupplemented treatment (Fig. 1a). The treatment × time interaction resulted from an increase in density at a higher rate in the enclosures with supplemental food than in the unsupplemented enclosures for female ($F = 1.83$, *d.f.* = 18, 108, $P = 0.031$) but not male prairie voles. During the early to mid-breeding season, densities increased to 75.7 ± 16.0 voles/enclosure in the supplemented treatment and 64.5 ± 8.7 voles/enclosure in the unsupplemented treatment (Fig. 1b). During that time, there was no significant difference between treatments ($P = 0.5545$) and no treatment × time interaction.

In the late season, 69.0 ± 10.5 and 51.5 ± 11.6 new recruits per enclosure were marked in the supplemented and unsupplemented populations, respectively. In the supplemented enclosures, 33.5 ± 6.7 males were marked and 27.0 ± 7.3 males were marked in the unsupplemented enclosures, and 38.3 ± 3.8 and 24.5 ± 4.8 females were marked in the supplemented and unsupplemented enclosures, respectively. During the entire field season, there was no

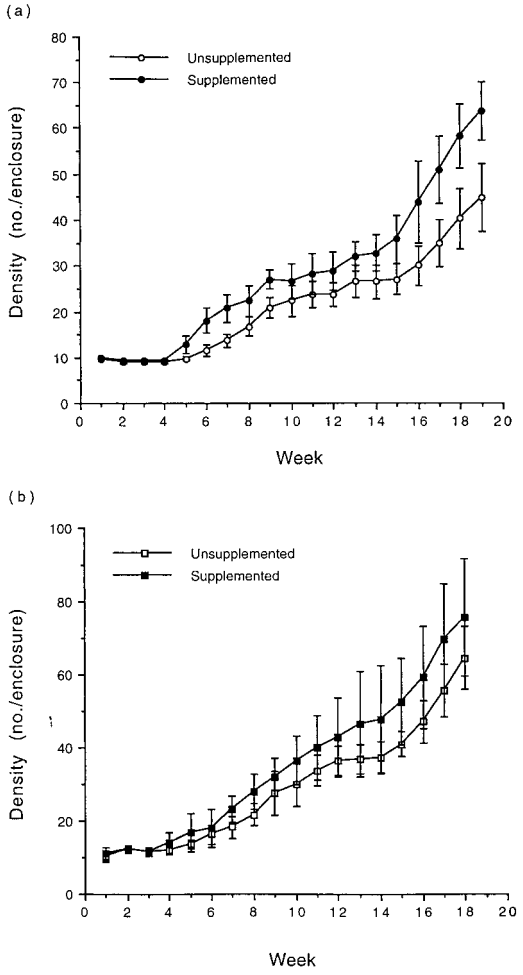

FIG. 1.—Densities (minimum number alive per 0.1 ha) of prairie voles in the unsupplemented and supplemented enclosures for a) mid- to late breeding season (1994) and b) early to mid-breeding season (1995); means ± 1 *SE* for 4 replicates/treatment.

difference in recruitment for males (P = 0.537), but there was a tendency toward higher recruitment of females in supplemented compared with unsupplemented enclosures (t = 2.246, *d.f.* = 6, P = 0.066). In the early season, there were 81.7 ± 17.2 and 64.0 ± 11.0 new recruits/enclosure in the supplemented and unsupplemented treatments, respectively. In the supplemented treatment, 39.2 ± 7.4 males were marked and 32.0 ± 5.6 males were marked in the unsupplemented treatment, and 42.5 ± 10.0 females were marked in the supplemented and 32.0 ± 5.8 females were marked in the unsupplemented enclosures. In the early season, there were no differences in recruitment for males (P = 0.465) or females (P = 0.397).

Social organization.—All 3 types of breeding units (single females, male–female pairs, and groups) were present in both treatments. During the first 3 weeks of burrow trapping, most breeding units were either single females or male–female pairs. In the unsupplemented treatment during the late season, 54 breeding units were monitored, and 20.4% 13.0%, and 66.7% were single females, male–female pairs, and groups, respectively. During this time, 50 breeding units were monitored in the supplemented treatment; 20.0%, 24.0%, and 54.0% of the breeding units were single female, male–female pairs, and groups, respectively. During the early season, 81 breeding units were monitored in the unsupplemented treatment; 18.5%, 16.0%, and 65.4% were single females, male–female pairs, and groups, respectively. In the supplemented treatment during the early season, 80 breeding units were monitored; 21.2%, 23.7%, and 55.0% were single females, male–female pairs, and groups, respectively. During each field season, there was an increase in the proportion of groups (proportion of the total number of breeding units that were categorized as groups) over time (late season, F = 17.28, *d.f.* = 3, 18, $P < 0.001$; early season, F = 4.94, *d.f.* = 3, 18, P = 0.011) but no treatment effect (late season, P = 0.342; early season, P = 0.370; Fig. 2).

Group size (total number of residents) throughout the entire study was variable over time but was similar between treatments (late season, supplemented 5.7 ± 0.8; unsupplemented 5.2 ± 0.5; early season, supplemented 5.9 ± 0.5, unsupplemented 4.7 ± 0.3). Repeated-measures analysis of variance showed a change in group size over time during the mid- to late breeding

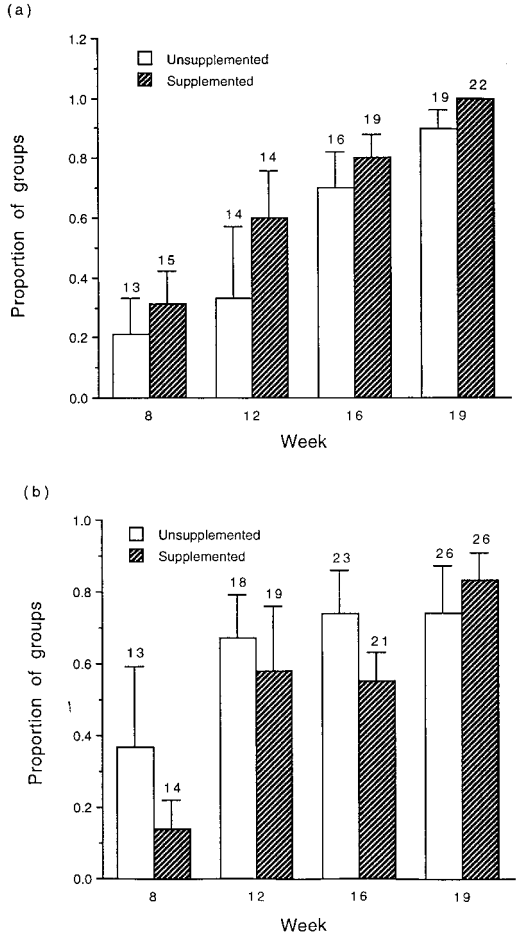

FIG. 2.—Proportion of groups, defined as having >1 adult of the same sex, during a) the mid- to late breeding season (1994) and b) the early to mid-breeding season (1995) in unsupplemented and food-supplemented treatments. Each time period consists of 3 weeks of burrow trapping and 1 week of grid trapping. Values are means ± 1 *SE* for 4 replicates/treatment; numbers of breeding units above bars; breeding units could be single females, male–female pairs, or groups with or without juveniles.

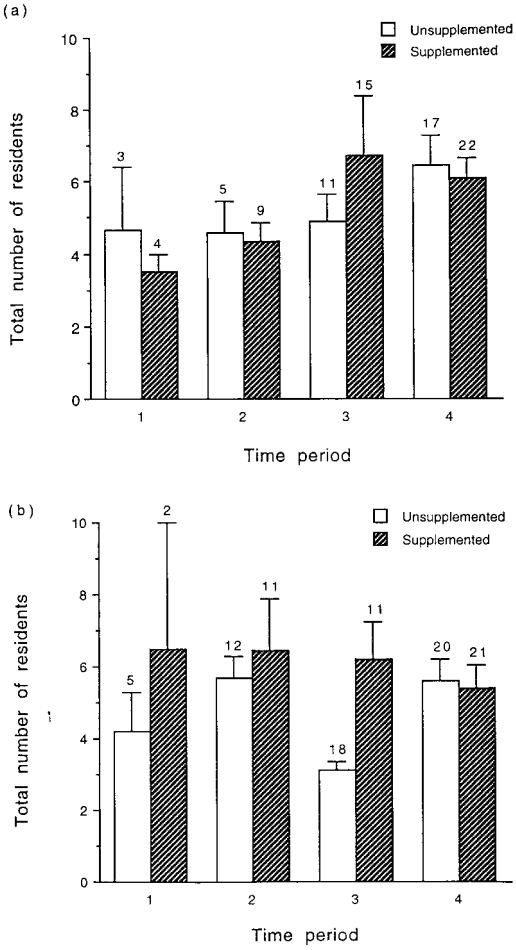

FIG. 3.—Size of prairie vole groups in unsupplemented and food-supplemented treatments during a) mid- to late breeding season (1994) and b) early to mid-breeding season (1995). Each time period consists of 3 weeks of burrow trapping and 1 week of grid trapping. Values are means ± 1 *SE* for 4 replicates/treatment; numbers of breeding units above the bars; breeding units could be single females, male–female pairs, or groups with or without juveniles.

season ($F = 2.84$, $d.f. = 3, 71$, $P = 0.044$) but no treatment effect ($P = 0.961$; Fig. 3a). During the early to mid-breeding season, the treatment × time interaction was nearly significant ($F = 2.62$, $d.f. = 3, 86$, $P = 0.056$; Fig. 3b). There was no change in group size over time during the early to mid-breeding season ($P = 0.142$) because group size by week 8 was as high as the highest level during the previous field season. In general, group size was higher in the supplemented treatment during the majority of the study during early season but did not differ from the unsupplemented treatment during the last time period.

Most groups formed when juveniles re-

mained at the natal nest beyond maturity. However, some groups formed when breeding females disappeared and their daughters began reproducing or when unrelated individuals joined breeding units. During the mid- to late breeding season, total number of animals captured as juveniles and recaptured as adults was 55 in the supplemented treatment and 29 in the unsupplemented treatment. Of those individuals, the percentage that remained philopatric was 18.2 ± 13.3% males, 49.0 ± 17.7% females, and 42.5 ± 12.0% of both sexes in the supplemented treatments and 42.9 ± 15.1% males, 62.5 ± 13.1% females, and 53.1 ± 6.2% of both sexes in the unsupplemented treatments. During the early to mid-breeding season, total number of animals captured as juveniles and recaptured as adults was 17 in the supplemented treatment and 30 in the unsupplemented treatment. Of those individuals, 58.3 ± 25.0% of males, 66.7 ± 23.6% of females, and 66.7 ± 11.8% of both sexes in the supplemented treatments and 50.0 ± 17.3% of males, 75.7 ± 13.0% of females, and 64.3 ± 10.7% of both sexes in the unsupplemented treatments remained philopatric.

Survival of juvenile males was 85.4% in the supplemented treatment and 83.3% in the unsupplemented treatment in the late season but was lower during the early season (58.9% and 41.7% in the supplemented and unsupplemented enclosures, respectively). A similar pattern was seen in female juveniles. During the late season, survival of juvenile females was 86.3% and 88.5% in the supplemented and unsupplemented enclosures, respectively. Again, survival of female juveniles in the early season was lower: 46.3% and 39.4% in the supplemented and unsupplemented enclosures, respectively. There were no differences between treatments in survival of male (late season, $P = 0.815$; early season, $P = 0.902$) or female (late season, $P = 0.787$; early season, $P = 0.565$) juveniles in either field season.

During the late season (1994) for both sexes combined, there was an increase in philopatry over time ($F = 9.94$, $d.f. = 1, 5$, $P = 0.025$) but not an effect of treatment ($P = 0.594$). We did find a significant treatment × time interaction ($F = 10.47$, $d.f. = 1, 5$, $P = 0.023$) showing that philopatry increased in the unsupplemented treatment compared with the supplemented treatment. The percentage of animals that remained philopatric was 24 ± 16% and 37 ± 16% in the unsupplemented and supplemented enclosures, respectively, during the 1st one-half of the mid- to late field season. During the 2nd one-half of the mid- to late field season, 87 ± 13% of the juveniles in the unsupplemented and 41 ± 16% of the juveniles in the supplemented enclosures remained philopatric. During the 2nd one-half of the early to mid- field season (1995), the percentage of philopatric juveniles in the unsupplemented treatment was 66 ± 5% and 79 ± 12% in the supplemented treatment, which did not differ ($P = 0.310$).

Discussion

Our results are consistent with the hypothesis that social organization of prairie voles is not flexible in response to changes in food quality. Most aspects of social organization were similar in the food-supplemented and unsupplemented enclosures. Under the conditions of our study, there were no differences between treatments in the proportion of each type of breeding unit or group size. In the mid- to late breeding season, density of voles tended to increase in the food-supplemented treatment compared with the unsupplemented treatment, but that difference was not reflected in differences in social organization between treatments. During the early to mid-breeding season, there were no differences between treatments for those variables. Because no demographic effects were found during the early to mid-season, it is surprising that group size was slightly higher during 3 quarters of the study in the supplemented treatment than in the unsupplemented treatment (Fig. 3b). There were no

other effects on social organization, although the percentage of groups showed a similar pattern to that found for group size.

The patterns late in the breeding season differed to some extent from those in the early to mid-breeding season. As mentioned previously, we were not attempting to compare early to late breeding season but just selected those 2 periods so that we would be examining changes over the course of an entire breeding season. Some of the differences between field seasons also might have resulted from a change in vegetation between them. Enclosures were planted in April 1994, and during that 1st field season, foxtail, *Setaria faberii*, was extremely prevalent but was absent during the 2nd field season. Overall, however, there was a greater percentage of monocots in the 2nd than in the 1st field season. There was a much greater percentage of high-quality dicots (clover and alfalfa) in the supplemented treatment during the 2nd field season compared with the unsupplemented treatment or to both treatments during the 1st field season. Additionally, there was a smaller percentage of other dicots during the 2nd field season than in the 1st season, especially in the supplemented treatment. These vegetational differences may have influenced demography and social organization in the 2 field seasons. A study replicating seasons would be needed to distinguish these 2 factors (vegetation and season).

The lack of a difference in social organization as a function of habitat quality supports the findings of Getz et al. (1992), which showed similar proportions of each type of breeding unit and similarities in group sizes in different quality habitats in east-central Illinois. Getz et al. (1992) found that 76.5%, 71.0%, and 81.2% of the breeding units monitored in alfalfa, bluegrass, and tallgrass prairie, respectively, were groups. In our study, 74–100% of breeding units were groups by the end of the field season, but these 2 studies are not directly comparable because we used enclosures and monitored social organization during summer and fall, whereas Getz et al. (1992) studied unenclosed populations of prairie voles during winter. Nevertheless, results of our experimental manipulation are consistent with those of Getz et al. (1992).

In our study, high densities in both treatments and the fact that the populations in enclosures still appeared to be growing at the end of each field season suggest that food was not a major limiting factor in the unsupplemented enclosures. Changes in social organization in response to food resources might only occur when food is severely limited; the unsupplemented treatment may not have been of low enough food quality or quantity to yield changes in individual behavior and consequently differences in social organization between treatments. It is important to consider that about 25% of previous food-supplementation studies have shown a lack of response in the dependent variable, which has usually been population density (Boutin 1990). Boutin (1990) also concluded that populations respond to additions of food more frequently when conditions are poor compared with those with fair to good baseline conditions. The relative response also is greater when the baseline habitat is poor (Boutin 1990). Alternatively, distribution of food might be an important factor that affects social organization. Other studies that showed differences in social organization supplied food in a patchy manner (Ims 1987; Ostfeld 1986). Because female territoriality is predicted to be most pronounced in arvicoline populations when food is low in quality and patchily distributed (Ostfeld 1985), it may be that changes in distribution of food also are important.

There are a number of other variables (e.g., population density, seasonality, or predation) that can affect social organization (Lott 1991). Our results are consistent with an alternative hypothesis that groups form when dispersal is constrained due to habitat saturation (Koenig and Pitelka 1981) and density is high. Increase in number of animals relative to suitable territory

may be an important factor leading to formation of extended family groups in rodents (Solomon and Getz 1997; Wolff 1994, 1997) because dispersal at higher densities may not be an option for subadults because of a lack of suitable breeding territories (Solomon and Getz 1997). Territoriality, especially at high densities, may prevent immigration into neighboring groups because of a ''social fence'' of territorial, aggressive adult males and females (Hestbeck 1982). For this reason, cost of emigration would be increased, and young would tend to remain philopatric. If this hypothesis explains changes in social organization in prairie voles, we would expect to see an increase in philopatry and thus in the proportion of groups as population density increases. During both field seasons, changes in social organization were seen over time in both treatments. The proportion of groups, size of groups, and density increased in both field seasons. The degree of philopatry also showed an increase that seemed to be correlated with increasing density in the late season. Too few juveniles were caught early in the 2nd field season to determine whether philopatry increased during that time, although the proportion of juveniles that remained philopatric also was very high and within the range seen during the late breeding season in 1994.

Population densities can get very high in natural, unenclosed populations of prairie voles, ranging from 30 to >600/ha, and reach the latter during the peak of population cycles (Getz et al. 1993). At the end of both field seasons, densities of voles were as high as those in peak populations. In unenclosed populations of prairie voles, a greater proportion of groups occurs at high density (>100 voles/ha) than at low density (<100 voles/ha—Getz et al. 1993), which is consistent with the hypothesis that high density may restrict individual options and lead to group formation. The data of Getz et al. (1993) also suggest that our results are not an artifact of using enclosures. Proportions of groups and group size were correlated with density in summer and winter in an unenclosed population of prairie voles (Getz et al. 1993).

It is possible that the formation of groups that are characteristic of cooperative breeders may be an indirect effect of high-quality food, which increases density. Previous studies on effects of supplemental food on arvicoline populations indicate that general effects on demography are increases in population density, reproductive activity, and recruitment with supplemental food (prairie vole—Cole and Batzli 1978; meadow vole, *M. pennsylvanicus*—Desy and Thompson 1983; Townsend's vole, *M. townsendii*—Taitt and Krebs 1981; California vole, *M. californicus*—Ostfeld 1986). In some cases, supplemental food also increased apparent survivorship (Cole and Batzli 1978; Desy and Thompson 1983). Thus, habitats with high-quality food are typically characterized by high densities, which in turn can lead to an absence of suitable breeding territories (Solomon and Getz 1997) and formation of groups.

Based on previous studies of prairie voles, the high proportion of groups in both treatments toward the end of the late field season (1994) could have been influenced by either high population densities or seasonal factors. One hypothesis, that prairie voles form groups for thermoregulatory benefits like other rodent species (Madison 1984; West and Dublin 1984; cf. Getz and McGuire 1997), predicts that we would see groups in the late autumn but not spring and summer in food-supplemented and unsupplemented populations. During the mid- to late season, most of our data on social organization came from the latter part of the breeding season, so we could not separate effects of density from those of season. However, in the 2nd field season (1995), all data on social organization came from summer; thus, results during that field season are more consistent with the hypothesis that group formation occurs at high density. Nonetheless, density is still confounded with time to some degree, and we would

need to manipulate density (Ostfeld and Canham 1995) to separate density from seasonal effects. Further increases in the proportion of groups in the population or group size may occur in winter, but seasonal changes do not appear to be necessary to induce group formation.

Finally, Getz et al. (1990b) have proposed a different causal pathway to explain the increase in the proportion of groups as a result of increased survival of young, which ultimately results in higher densities. Increased survival occurs, according to their hypothesis, later in the breeding season because of a decrease in predation by snakes on young voles. We did not see any snakes in our enclosures, so we cannot be sure that we had not excluded them from our populations, but Lin and Batzli (1995) have argued that snakes are not important predators in populations of prairie voles. Thus, although our results are most consistent with the hypothesis that formation of family groups might be a density-dependent response, studies of cooperative breeders in which population densities are manipulated are needed to test that hypothesis.

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