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EFFECTS OF PATCH QUALITY ON DISPERSAL AND SOCIAL ORGANIZATION OF PRAIRIE VOLES: AN EXPERIMENTAL APPROACH

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The quality of the habitat patch in which individuals reside may influence demographic processes, thus affecting social organization. We manipulated the risk of predation and food availability to test the hypothesis that high patch quality decreased the propensity to disperse, increased the likelihood of social units becoming groups, and increased overall group size in prairie voles (*Microtus ochrogaster*). Prairie voles are socially monogamous, at least in part of their range, and they display varied social organization within a population, including groups (containing a breeding pair and at least 1 additional adult of either sex), male–female pairs, and single females. Our results indicated that the likelihood of dispersal from high-quality patches was significantly less than from low-quality patches. Dispersers also were significantly more likely to settle in similar or higher quality patches than the ones in which they were originally released. These patterns were primarily due to the dispersal of young males. Although the proportion of social units that were groups appeared to decrease with lower patch quality, the difference in social organization among patch types was not statistically significant. The total number of founding voles and founding males per social unit residing in the highest quality patches at the end of the study were significantly greater than in the lowest quality patches. Thus, under the conditions of our experiment, patch quality affected dispersal and group size but not the tendency to form groups.

Key words: dispersal, *Microtus*, patch quality, risk of predation, social organization, supplemental food

The spatial heterogeneity seen in many habitats may result in variation in the suitability of different habitat patches for survival and reproduction for a particular species. Differences in the quality of habitat patches, resulting from such factors as predation risk, food availability, and population density, have been demonstrated to modify demographic processes (e.g., birth, death, immigration, and emigration) within animal populations (Covas et al. 2004; Heg et al. 2004; Komdeur and Edelaar 2001; Krebs et al. 1995). In particular, variation in the quality of habitat patches has been proposed to explain the evolution of delayed dispersal in many cooperatively breeding species (e.g., Solomon and French 1997; Stacey and Koenig 1990).

Cooperative breeding occurs when offspring delay dispersal and remain on a territory or habitat patch with their parent(s) beyond weaning (Ebensperger 2001; Emlen 1995; Hayes 2000; Koenig et al. 1992; Pen and Weissing 2000; Solomon 2003). The occurrence of delayed dispersal is influenced by the benefits and costs of dispersal versus those of philopatry (Koenig et al. 1992; Solomon 2003; Stacey and Ligon 1987, 1991). When the net benefit of philopatry is greater than dispersal, weaned offspring should delay dispersal.

Koenig and colleagues suggested that the fitness benefit from philopatry is likely to be greater for young residing in high- than in low-quality patches because the quality of the latter are less likely to be above the dispersal threshold (dispersal threshold model—Koenig and Pitelka 1981; Koenig et al. 1992). Therefore, young residing in high-quality patches are more likely to remain philopatric than those in low-quality patches.

However, the results from empirical studies are contradictory. In acorn woodpeckers (*Melanerpes formicivorus*—Stacey and Ligon 1987) and Seychelles warblers (*Acrocephalus sechellensis*—Komdeur 1992; Komdeur and Edelaar 2001) the likelihood that offspring delay dispersal increased with quality of the natal territory. In contrast, in sociable weavers (*Philetairus socius*), Covas et al. (2004) found that food supplementation decreased the age of 1st reproduction and

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caused a greater proportion of colony members to disperse and engage in independent breeding. Furthermore, Cochran and Solomon (2000) found that food supplementation had no effect on the dispersal of offspring in prairie vole (*Microtus ochrogaster*) populations relative to populations without supplemental food. Lin and Batzli (2001) found that increasing the perceived risk of predation by manipulating vegetative cover increased the dispersal rate of prairie voles within a population, whereas Heg et al. (2004) found that dispersal decreased in the presence of high predation risk for a cooperatively breeding cichlid (*Neolamprologus pulcher*). Finally, Ebensperger and Cofré (2001) found no effect of predation risk among hystricognath rodents, because group size was not influenced by differences in the amount of vegetative cover in the habitat.

The previously mentioned studies have employed various methodologies at varying spatial scales, which may have contributed to the conflicting results. In addition, previous empirical studies have been unable to control for the initial size and composition of social units, a variable that may affect dispersal in addition to habitat quality. In the current study, we used an experimental approach that controlled the physical features of patches (size, distance, and juxtaposition) and the initial size and composition of social units to investigate how patch quality affects dispersal and social organization of a cooperatively breeding rodent, the prairie vole. Patch quality was varied by manipulating the amount of food and cover present. Previous studies of prairie voles have found that increased availability of high-quality food and greater vegetative cover are associated with improved habitat quality. The former resulted in greater growth rates and reproductive success (Desy and Batzli 1989; Lin and Batzli 2001), whereas the latter led to increased density, apparently because of improved protection from predation (Lin and Batzli 2001). In this study, we tested the hypothesis that high patch quality reduces dispersal, thus increasing the likelihood of social units becoming groups and increasing overall group size through the retention of offspring at their natal site.

Prairie voles can be found in various habitats, including alfalfa fields, bluegrass, and tallgrass prairie (Klatt and Getz 1987), that vary in quality (e.g., food quality—Cole and Batzli 1979; vegetative structure—Klatt and Getz 1987), and the reproduction and survivorship of voles can differ dramatically among these habitats (Getz et al. 1987). Getz and colleagues (Getz et al. 1993; Getz and McGuire 1997) have documented variation in social units within prairie vole populations. These social units may be groups (containing a breeding pair and one additional adult of either sex), male–female pairs, or single females, the latter of which may be the remnant of male–female pairs (Getz et al. 1990, 1993; Getz and Carter 1980; Solomon and Getz 1997).

MATERIALS AND METHODS

Study area.—The study was conducted from June through August of 2002 at Miami University's Ecology Research Center located outside Oxford, Ohio (3930′N, 84°44′W). The study area was an old field with vegetation dominated by perennial grasses and forbs, and consisted of four 0.1-ha enclosures. The walls of the enclosures were constructed of sheets of galvanized steel that were 75 cm in height aboveground and buried 45 cm into the ground to prevent movement of voles among enclosures. An electric wire prevented most mammalian predators (primarily raccoons) from gaining access to the enclosures and disturbing the traps. Although avian as well as some terrestrial predators (e.g., snakes) were able to enter the enclosures, the voles could not leave.

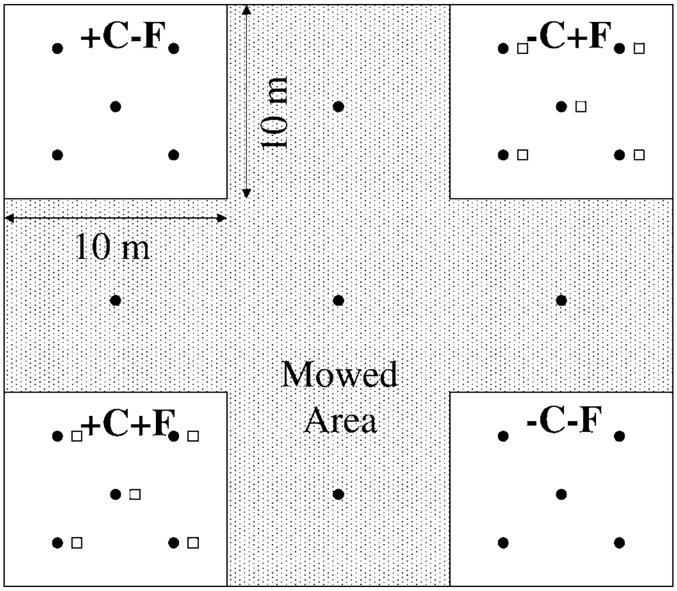

FIG. 1.—Diagram of habitat patches within each of the four 0.1-ha enclosures. Locations of habitat types were randomly assigned within each enclosure. The 4 habitat types are coded as (+C+F) supplemental cover, supplemental food; (−C+F) no supplemental cover, supplemental food; (+C−F) supplemental cover, no supplemental food; and (−C−F) no supplemental cover, no supplemental food. Locations of trapping stations (●) and feeding stations (□) are indicated.

Experimental design.—We created four 10 × 10-m discrete habitat patches in each enclosure by manipulating the amount of food and cover (Fig. 1). Within each enclosure, 2 patches were provided with supplemental cover and 2 with supplemental food, in a factorial design. The 2 × 2 design generated 4 patch types (Fig. 1): supplemental cover, supplemental food (+C+F); no supplemental cover, supplemental food (−C+F); supplemental cover, no supplemental food (+C−F); and no supplemental cover, no supplemental food (−C−F). Thus, there were 4 patches in each of the 4 enclosures, resulting in 16 patches studied in each temporal replicate. Habitat patches were separated by a 10-m-wide, low-cover matrix. The matrix was mowed to 5–10 cm in height and raked clean to create an inhospitable habitat for prairie voles. The mowed matrix delineated the edges of the 100-m^2 patches, which were similar in size to home ranges measured in enclosed populations of prairie voles (Jike et al. 1988). Habitat patches within enclosures were randomly assigned to treatments. Habitat patches with supplemental cover were created by evenly spreading approximately 5 m^3 of dry vegetation collected from mowed matrix areas throughout each patch. The added dead vegetation increased the amount of litter in these patches. Lin and Batzli (2001) found vole population density was associated with the amount of litter. Increased density likely occurred because thick litter provided better protection from predators. Habitat patches with supplemental food contained 5 evenly spaced feeding stations, each of which consisted of a 250-ml glass jar lying on its side with ad libitum commercial rabbit chow (Purina Mills LLC, St. Louis, Missouri). We selected rabbit chow because it is a high-quality food that increases body growth and reproductive success of prairie voles in the laboratory (Desy and Batzli 1989). The quality of the 4 habitat types was ranked as follows: +C+F > +C−F = −C+F > −C−F. Each habitat patch contained 5 evenly spaced trapping stations, with 1 Ugglan multiple-capture live trap (Ugglan Special No. 2, GRAHNAB, Marieholm, Sweden) at each station. The mowed area between patches also contained 5 trapping stations, each with 1 Ugglan multiple-capture live trap (Fig. 1).

A male–female pair of prairie voles along with 2 or 3 of their offspring of weaning age (approximately 21 days) were released into the center of each patch within each enclosure. All animals used in this experiment were laboratory-born individuals from an outbred colony maintained at Miami University and were descendents of wild prairie voles captured in southern Illinois. None of the adults released into an enclosure were siblings and all individuals were uniquely toe-clipped for identification. Fourteen days after the vole families were released into their respective patches, livetrapping was initiated to locate the nest sites of the founding adult females. Traps were baited with cracked corn and shielded from the weather by aluminum flashing and vegetation. Traps were set after 1700 h and checked the following day between 0700 and 0800 h. This livetrapping schedule was followed for a 5-day period. Date, location, identification number, body weight, sex, and reproductive condition were recorded for each capture. Males were classified as reproductive when their testes were scrotal, and nonreproductive when testes were abdominal. Females were classified as reproductive when they were pregnant or lactating.

We used radiotelemetry to locate the underground nests of the founding adult females. Each founding adult female that was trapped during this period was fitted with a collar containing a PD-2C radio transmitter (Holohil Systems Ltd., Carp, Ontario, Canada). After locating an underground nest, 4 Ugglan multiple-capture traps were placed near nest entrances. During the 4th week after release of the founding voles, we trapped at the nests for 4 consecutive days with 1 trap-check the 1st day, 5 trap-checks during the 2nd and 3rd days, and 2 trap-checks on the 4th day, for a total of 13 trap-checks. At the end of the 4th week, all prairie voles were removed from the enclosures. The length of this experiment should have allowed time for dispersal of young males and females because McGuire et al. (1993) reported that the average age of dispersal during the breeding season was 42 days of age.

The experiment was temporally replicated twice during summer 2002 for a total of 8 replicate enclosures. The dates on which the families were released into the patches were 17 June and 29 July for the 1st and 2nd replicates, respectively. Each family was randomly assigned to an enclosure and a patch within the enclosure. Because of mortality of young and variance in litter size at birth, it was not possible for all of the families released into the enclosures to have the same number of young. For the 1st temporal replicate, 15 of the 16 families contained 3 young each. The remaining family had 2 young. For the 2nd replicate, 13 of the 16 families released contained 3 young each, whereas the other 3 families each contained 2 young. Across all families and replicates we recorded 48 male and 44 female offspring (ratio 1:0.92). The procedures used in this experiment, both in the animal colony and in the field enclosures, were performed in a humane manner that followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998), and were approved by the Miami University's Institute of Animal Care and Use Committee.

Data analysis.—Livetrapping data from the 4th week of the study (13 trap checks) were used to assess the patch residency of individuals as well as the composition of social units. For animals trapped more than once, if more than 75% of their captures were at the same nest, they were categorized as a member of the social unit associated with that nest and a resident of the patch where the nest was located (Cochran and Solomon 2000; Jacquot and Solomon 2004). Voles trapped more than once, but with less than 75% of their captures at 1 nest, were classified as wanderers (Solomon and Jacquot 2002).

An individual was considered to have dispersed if in the 4th week of the experiment it was a resident in a different patch than the one into which it was initially released. Individuals that dispersed could become resident in a higher quality patch (upgrade), a lower quality patch (downgrade), or traded food for cover or cover for food (same-grade) relative to the type of habitat patch into which they were originally released. Because the type of habitat patch into which dispersers were originally released differed, the probability of an upgrade, same-grade, or downgrade for dispersers differed, for example, a disperser originally released into +C+F patch could only downgrade, whereas a disperser originally released into +C−F patch had a 33% chance of upgrade, same-grade, or downgrade. Therefore, we calculated the expected values for random settlement in each patch type by dispersers based on where the dispersers were originally released and their initial number in each patch type. We examined the influence of age, sex, and patch type on dispersal using logistic regression, chi-square, and Fisher exact tests. Throughout our analyses, the adult voles originally released in each patch are referred to as adults, whereas their offspring at the time of release are referred to as young voles. Founders refer to the animals originally released into the enclosures at the start of the experiment regardless of age.

The composition of each social unit was defined on the basis of the number and sex of adult voles determined to be residing at a particular nest regardless of whether or not offspring were present. Nests with more than 2 resident adults were classified as groups, whereas pairs referred to nests at which only an adult male and female resided (Cochran and Solomon 2000; Getz et al. 1993). We also recognized single adult male or female social units. To test for the effect of patch type on the number of founders, founding males, and founding females per patch during the 4th week of the study, as well as the number of founding individuals still residing in their patch of release, we used a 1-way analysis of variance (ANOVA) with a post hoc Tukey test. Data were logarithmically transformed to meet the assumptions of ANOVA.

RESULTS

We compared data between the 2 temporal replicates and found no significant difference between them in total number of voles that survived until the 4th week of the study ($\chi^2 = 0.07$, $d.f. = 1$, $P = 0.79$), the total number of voles for which we were able to assign residency ($\chi^2 = 0.353$, $d.f. = 1$, $P = 0.55$), or the total number of voles that remained residents in the original patch into which they were released ($\chi^2 = 0.65$, $d.f. = 1$, $P = 0.42$). Therefore, all subsequent analyses were based on combined data from the 2 temporal replicates.

Of the 156 prairie voles released into the enclosures at the start of experiment, 133 (86%) survived until the 4th and final week of the study (Table 1). The patch type into which an individual was originally released had no significant effect on the likelihood of survival until the end of 4 weeks when considering either all individuals ($\chi^2 = 1.27$, $d.f. = 3$, $P = 0.74$) or just the founding offspring ($\chi^2 = 2.39$, $d.f. = 3$, $P = 0.50$). Also, no significant difference was found in the likelihood of survival by sex ($\chi^2 = 0.43$, $d.f. = 1$, $P = 0.51$).

We were able to assign residency to a patch during the 4th week for 102 (77%) of the 133 surviving voles. The remaining

Table 1.—The number of prairie voles released into each patch type, number of voles released into each patch type that survived until week 4 of study, number of voles released into each patch type with known residency during week 4 of study, and number of voles that dispersed from each patch type. The patch types are coded as supplemental cover, supplemental food (+C+F); no supplemental cover, supplemental food (−C+F); supplemental cover, no supplemental food (+C−F); and no supplemental cover, no supplemental food (−C−F).

Patch type of release	Sex	+C+F	+C−F	−C+F	−C−F
Number of voles released into patch	Males	21	18	22	19
	Females	17	21	17	21
Number of voles released in each patch type that survived until week 4	Males	18 (86%)	17 (94%)	21 (96%)	16 (84%)
	Females	16 (94%)	16 (76%)	16 (94%)	13 (62%)
Number of voles released in each patch type with known residency during week 4	Males	14 (78%)	13 (77%)	14 (67%)	12 (75%)
	Females	11 (69%)	13 (81%)	14 (88%)	11 (85%)
Number of dispersers	Males	0	5 (39%)	8 (57%)	9 (75%)
	Females	0	3 (23%)	0	2 (18%)

Table 2.—The number of adult and young male and female prairie voles that still resided in the same patch into which they were released and that dispersed to a new patch by the 4th week of the study. Expected values based on the age and sex structure of the 102 individuals with known residency are given in parentheses.

Age and sex	Remained in patch of release	Dispersed to new patch
Adult males	16	7 (6.09)
Adult females	25	2 (7.05)
Young males	15	15 (7.94)
Young females	19	3 (5.82)

31 surviving voles were either caught only once ($n = 19$, males = 11, females = 8) or were classified as wanderers ($n = 12$) because they did not meet the criteria for being considered a resident (Cochran and Solomon 2000). Neither sex (males = 8, females = 4, $\chi^2 = 0.83$, *d.f.* = 1, $P = 0.35$) nor age (adult = 4, young = 8, $\chi^2 = 0.47$, *d.f.* = 1, $P = 0.49$) affected the number of voles classified as wanderers. The patch type into which an individual was released also did not seem to influence whether an individual became a wanderer (+C+F = 3, +C−F = 2, −C+F = 4, −C−F = 3).

The 102 voles for which we could establish residency were not significantly affected by the patch type into which they were originally released when considering either all founders ($\chi^2 = 0.51$, *d.f.* = 3, $P = 0.92$) or just the founding offspring ($\chi^2 = 0.77$, *d.f.* = 3, $P = 0.86$). Nor did the number of males for which we could assign residency differ from that for females ($\chi^2 = 0.16$, *d.f.* = 1, $P = 0.69$). Among the voles for which we could assign residency, 75 (74%) were still residing in the patch into which they had been released, whereas the remaining 27 (26%) voles dispersed. Only 14 (19%) of the 75 voles that were still residing in the patch into which they had been released were trapped at least once in a patch other than their patch of residency at the end of the experiment. No sex (males = 7, females = 7, $\chi^2 = 0.16$, *d.f.* = 1, $P = 0.46$) or age (adult = 5, young = 9, $\chi^2 = 0.89$, *d.f.* = 1, $P = 0.35$) difference was found in the number of these resident voles that were trapped in more than 1 patch. The patch type these individuals resided in also did not seem to influence the likelihood that they would visit another patch (+C+F = 2, +C−F = 5, −C+F = 5, −C−F = 2).

Age and sex of dispersers.—Using logistic regression, the probability of dispersal was significantly influenced by sex ($\chi^2 = 9.94$, *d.f.* = 1, $P = 0.002$) but not age ($\chi^2 = 1.80$, *d.f.* = 1, $P = 0.18$). The interaction between sex and age also was not statistically significant ($\chi^2 = 0.017$, *d.f.* = 1, $P = 0.90$). Males (42%) were significantly more likely to disperse than females (10%). The probability of adult males dispersing to new patches was significantly higher than for adult females ($\chi^2 = 4.46$, *d.f.* = 1, $P = 0.04$; Table 2). This held true for young animals as well ($\chi^2 = 7.42$, *d.f.* = 1, $P = 0.006$; Table 2).

Dispersal and patch quality.—Logistic regression indicated that neither cover ($\chi^2 = 0.006$, *d.f.* = 1, $P = 0.94$) nor food ($\chi^2 = 0.006$, *d.f.* = 1, $P = 0.94$) by itself influenced the probability of dispersal from a patch. No dispersal occurred from +C+F patches (Table 1) and prairie voles were significantly less likely to disperse from +C+F patches than from +C-F, −C+F, and −C−F patches combined ($\chi^2 = 9.0$, *d.f.* = 1, $P = 0.003$). No significant difference was observed in the likelihood of dispersal among +C−F, −C+F, and −C−F patches ($\chi^2 = 1.54$, *d.f.* = 2, $P = 0.46$). Furthermore, dispersing prairie voles did not settle randomly. Relative to the patch in which they were originally released, more dispersing animals settled in similar or better quality patches than expected, whereas fewer dispersing animals settled in worse quality patches than expected ($\chi^2 = 8.22$, *d.f.* = 2, $P = 0.02$; Fig. 2). Considering each age–sex class separately, only young males ($n = 15$) were significantly more likely to become residents in a higher quality patch relative to the ones in which they were originally released ($\chi^2 = 8.12$, *d.f.* = 2, $P = 0.02$; Fig. 3). The sample sizes were too small to resolve the

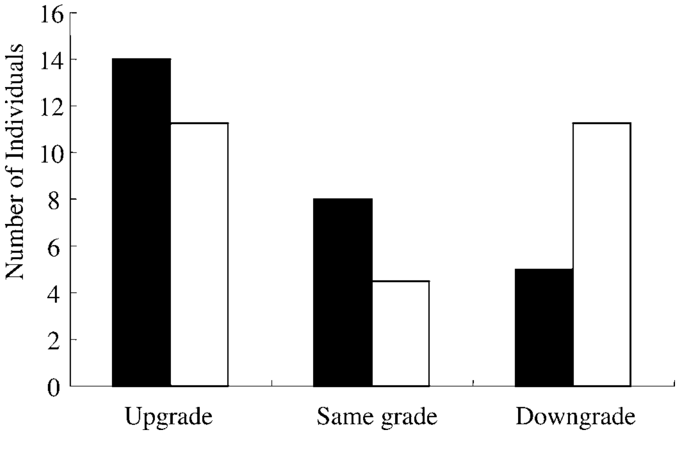

Fig. 2.—The number of individuals (filled bars) that dispersed and became resident in a higher quality patch (upgrade), a lower quality patch (downgrade), or traded food for cover or cover for food (same-grade) relative to the type of habitat patch into which they were originally released. Open bars give expected values for random settlement.

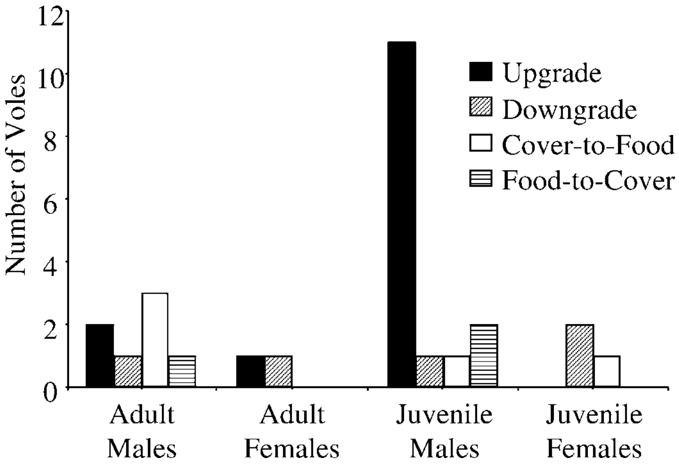

FIG. 3.—The number of individual prairie voles that dispersed and became resident in a higher quality patch (upgrade), a lower quality patch (downgrade) or, in a same-grade change, traded food for cover (food-to-cover) or cover for food (cover-to-food) relative to habitat patch they were originally released into as a function of age and sex.

effects of patch quality on the dispersal and settlement of other age–sex classes (Fig. 3).

Because the sex ratio among the litters we released ranged from 0% to 100% males, it is possible that the tendency of young males to immigrate into higher quality habitat patches was because the sex ratio among young voles was male-biased or that young males were disproportionately released into lower quality patches. This does not appear to be the case. The overall sex ratio of young voles (48 males : 44 females) across the 8 replicates at the start of the experiment did not differ significantly from 50:50 ($\chi^2 = 0.174$, *d.f.* = 1, $P = 0.68$). Nor did the number of young males released in each patch type differ significantly (+C+F = 13, +C−F = 10, −C+F = 14, −C−F = 11, $\chi^2 = 0.83$, *d.f.* = 3, $P = 0.84$).

Social organization and patch quality.—The most common social unit detected at the end of this study was groups (containing a breeding pair and at least 1 additional adult of either sex; $\chi^2 = 17.03$, *d.f.* = 2, $P = 0.0002$). All groups contained at least 1 adult male and 1 adult female vole. There were no groups of only 1 sex. The +C+F patches were the only patch type in which all social units were groups, and the proportion of social units that were groups appeared to decrease with patch quality (Fig. 4), although this difference was not statistically significant ($\chi^2 = 3.6$, *d.f.* = 3, $P = 0.31$). The mean number of founding individuals ($F = 3.42$, *d.f.* = 3, 28, $P = 0.03$) and number of founding males ($F = 5.27$, *d.f.* = 3, 28, $P = 0.005$) per social unit during the 4th week of the study was significantly greater in the +C+F than the −C−F patches (Table 3). No other differences in the mean number of founders or founding males per social unit were detected among patch types. Patch type had no significant effect on the mean number of founding females ($F = 1.00$, *d.f.* = 3, 28, $P = 0.40$) in each social unit, but the number of founding individuals that remained residents in the patch in which they were released approached statistical significance ($F = 2.92$, *d.f.* = 3, 28, $P = 0.052$). More founders remained in the patch in which they were released when patches were of higher quality. At the end of the study 100% of the +C+F and +C−F patches contained resident voles, whereas 12.5% and 25% of −C+F and −C−F patches, respectively, did not contain any resident voles (Fig. 4).

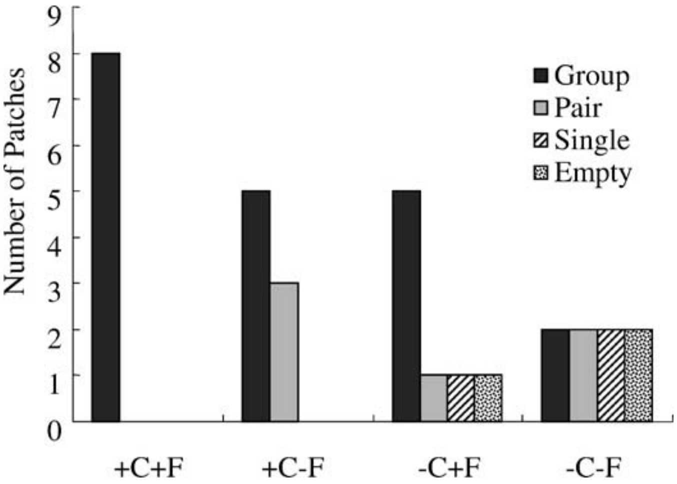

FIG. 4.—The number of patches of each habitat type that contained a group, a male–female pair, a single adult prairie vole or no adult residents (empty) at the end of the experiment. The 4 patch types are coded as (+C+F) supplemental cover, supplemental food; (−C+F) no supplemental cover, supplemental food; (+C−F) supplemental cover, no supplemental food; and (−C−F) no supplemental cover, no supplemental food.

DISCUSSION

Our results indicated that variation in patch quality due to differences in the availability of high-quality food and amount of vegetative cover affected the dispersal and social organization of prairie voles. First, the rate of dispersal from low-quality patches was greater than that from high-quality patches. Second, no individuals remained in some of the low-quality patches (e.g., −C+F and −C−F), whereas 100% of both other patch types were occupied by voles. Third, dispersing voles were more likely to settle in patches of similar or higher quality than the patches into which they were originally released. Finally, the sizes of social units were greater in high- than low-quality patches. Thus, the hypothesis that individuals living in high-quality patches are less likely to disperse, resulting in group size becoming larger and a greater proportion of social units becoming groups, is partially supported. Only the proportion of social units that were groups was not significantly affected by patch quality.

The overall dispersal rate in this study was 27%. No dispersal occurred from the highest quality patches. All founding individuals of +C+F patches that had survived until the 4th week remained in situ. The dispersal rates in other patches were 29% in −C+F patches, 31% in +C−F patches, and 48% in −C−F patches. The rates of dispersal we observed were similar to those from previous studies of prairie voles. In an unenclosed population, approximately 33% of individuals dispersed to different nests during the breeding season (i.e., spring–autumn—McGuire et al. 1993). Additionally, we found

Table 3.—Mean (±1 *SE*) number of founders per patch, founding males per patch, founding females per patch, and number of founding individuals still residing in their patch of release for each habitat type during week 4 of the experiment. The patch types are coded as supplemental cover, supplemental food (+C+F); no supplemental cover, supplemental food (−C+F); supplemental cover, no supplemental food (+C−F); and no supplemental cover, no supplemental food (−C−F). Patches with same lowercase letters were not significantly different (post hoc Tukey tests).

Habitat type	+C+F	+C−F	−C+F	−C−F
Mean number of founders per patch	4.13 ± 0.44a	2.88 ± 0.61ab	3.50 ± 0.63ab	1.75 ± 0.49b
Mean number of founding males per patch	2.50 ± 0.35a	1.63 ± 0.38ab	1.75 ± 0.37ab	0.63 ± 0.26b
Mean number of founding females per patch	1.63 ± 0.26a	1.25 ± 0.31a	1.75 ± 0.31a	1.13 ± 0.30a
Mean number of founding individuals still residing in their patch of release	3.25 ± 0.41a	2.38 ± 0.60a	2.38 ± 0.38a	1.38 ± 0.38a

dispersing voles moved from patches of low quality to patches of higher quality. Although our study examined movements between patches, the findings were comparable to a study that examined movement between habitats (populations—Lin and Batzli 2004).

We also found that dispersal was more likely to occur in males (42%) than in females (10%); this was true for adult voles (30% versus 7%) as well as young animals (50% versus 14%). Evolutionary theory predicts a lack of a sex bias in dispersal for species with a monogamous mating system (Greenwood 1980) and prairie voles are socially monogamous, at least in Illinois where the voles used in this study were collected (Getz et al. 1981). Thus, we expected no sex bias in the tendency to disperse, as was found in previous studies of prairie voles (Lin and Batzli 2004; McGuire et al. 1993). However, a recent study reported genetic evidence of multiple paternity in a population of prairie voles from Illinois (Solomon et al. 2004); if prairie voles are not genetically monogamous, than the male-biased dispersal patterns we observed in our study are consistent with theoretical predictions. Furthermore, although no significant sex bias in dispersal has been reported in vole populations from east-central Illinois (Lin and Batzli 2004; McGuire et al. 1993) and Indiana (Boonstra et al. 1987), male-biased dispersal has been described from populations in Kansas (Boonstra et al. 1987).

Our results are partially consistent with the hypothesis that the social organization of voles changed in response to patch quality (Ostfeld 1986; Tamarin et al. 1990; Ylonen et al. 1988; also see Lott 1991). Although the proportion of social units that were groups was not significantly different among patch type, the sizes of social units during week 4 of the study, including the average number of founding adults and number of founding males per social unit, were significantly greater in the +C+F than the −C−F patches. One of the reasons why we detected no difference in the propensity toward group formation between patch types was that young animals tended to remain in their natal sites regardless of patch quality. Because many more young females than males delayed dispersal, it is possible that the delayed dispersal of young animals, particularly among young females, could be a default tendency. In central Illinois, Getz et al. (1992) found similar proportions of social units that were groups and similarities in group sizes in prairie vole populations occupying habitats of varying overall quality. They found that 76.5%, 71.0%, and 81.2% of breeding units monitored in alfalfa, bluegrass, and tallgrass prairie, respectively, were groups, and suggested the hypothesis that social organization of prairie voles is not very flexible in response to ecological conditions (Getz et al. 1992). An alternative explanation was that the habitats were saturated, so that most young were forced to delay dispersal and form groups. Indeed, our study provided only 4 habitable patches, and all were initially occupied by founding social units.

Because dispersal occurred primarily in males, particularly young males, and dispersers tended to move to a higher quality patch, dispersal of young males contributed to the larger sizes of social units in the highest quality patches. Consequently, we found that the mean number of founding males per social unit was significantly greater in the +C+F than the −C−F patches. Generally, high patch quality is correlated with greater reproductive success. Nevertheless, it is often difficult to differentiate the effects of increased natal philopatry versus immigration on the sizes of social units in the field (e.g., Macedo and Bianchi 1997; Reed and Walters 1996; Russell et al. 2004). However, our experimental results indicated that patch quality can affect group size through differential dispersal.

Variation in patch quality created the potential for individuals to select a particular patch type in which to reside. Although males and females responded differently to heterogeneity in patch quality under the conditions of our experiment in which patches were occupied, the results from this study demonstrate that at least some individuals seem to respond to variation in patch quality in their environment. In our study, dispersal was influenced by the quality of both the patch of release and the colonizing patch, because individual voles were more likely to disperse from low-quality patches and settle in high-quality patches than expected by chance. This finding suggests that individuals were moving into habitats that would increase their future direct fitness.

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LITERATURE CITED

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

BOONSTRA, R., C. J. KREBS, M. S. GAINES, M. L. JOHNSON, AND I. T. M. CRAINE. 1987. Natal philopatry and breeding systems in voles (*Microtus* spp.). Journal of Animal Ecology 56:655–673.

COCHRAN, G. R., AND N. G. SOLOMON. 2000. Effects of food supplementation on the social organization of prairie voles (*Microtus ochrogaster*). Journal of Mammalogy 81:746–757.

COLE, F. R., AND G. O. BATZLI. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. Journal of Animal Ecology 48:455–470.

COVAS, R., C. DOUTRELANT, AND M. A. DU PLESSIS. 2004. Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. Proceedings of the Royal Society of London Series, B. Biological Sciences 271:827–832.

DESY, E. A., AND G. O. BATZLI. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. Ecology 70:411–421.

EBENSPERGER, L. A. 2001. A review of the evolutionary causes of rodent group-living. Acta Theriologica 46:115–144.

EBENSPERGER, L. A., AND H. COFRÉ. 2001. On the evolution of group-living in the New World cursorial hystricognath rodents. Behavioral Ecology 12:227–236.

EMLEN, S. T. 1995. An evolutionary theory of the family. Proceedings of the National Academy of Sciences 92:8092–8099.

GETZ, L. L., AND C. S. CARTER. 1980. Social organization in *Microtus ochrogaster* populations. Biologist 62:56–69.

GETZ, L. L., C. S. CARTER, AND L. GAVISH. 1981. The mating system of the prairie vole, *Microtus ochrogaster*—field and laboratory evidence for pair-bonding. Behavioral Ecology and Sociobiology 8:189–194.

GETZ, L. L., D. F. GUDERMUTH, AND S. M. BENSON. 1992. Pattern of nest occupancy of the prairie vole *Microtus ochrogaster* in different habitats. American Midland Naturalist 128:197–202.

GETZ, L. L., J. HOFFMANN, B. J. KLATT, L. VERNER, F. R. COLE, AND R. L. LINDROTH. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in east-central Illinois. Canadian Journal of Zoology 65:1317–1325.

GETZ, L. L., AND B. MCGUIRE. 1997. Communal nesting in prairie voles (*Microtus ochrogaster*): formation, composition, and persistence of communal groups. Canadian Journal of Zoology 75:525–534.

GETZ, L. L., B. MCGUIRE, J. HOFMANN, T. PIZZUTO, AND B. FRASE. 1990. Social organization and mating system of the prairie vole, *Microtus ochragaster*. Pp. 69–80 in Social systems and population cycles in voles (R. H. Tamarin, R. S. Ostfeld, S. R. Pugh, and G. Bujalska, eds.). Advances in Life Sciences. Birkhaeuser Verlag, Basel, Switzerland.

GETZ, L. L., B. MCGUIRE, J. HOFMANN, T. PIZZUTO, AND B. FRASE. 1993. Social organization of the prairie vole, *Microtus ochrogaster*. Journal of Mammalogy 74:44–58.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

HAYES, L. D. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. Animal Behaviour 59:677–688.

HEG, D., Z. BACHAR, L. BROUWER, AND M. TABORSKY. 2004. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. Proceedings of the Royal Society of London, B. Biological Sciences 271:2367–2374.

JACQUOT, J. J., AND N. G. SOLOMON. 2004. Experimental manipulation of territory occupancy: effects on immigration of female prairie voles. Journal of Mammalogy 85:1009–1014.

JIKE, L., G. O. BATZLI, AND L. L. GETZ. 1988. Home ranges of prairie voles as determined by radiotracking and by powdertracking. Journal of Mammalogy 69:183–186.

KLATT, B. J., AND L. L. GETZ. 1987. Vegetation characteristics of *Microtus ochrogaster* and *M. pennsylvanicus* habitats in east-central Illinois. Journal of Mammalogy 68:569–577.

KOENIG, W. D., AND F. A. PITELKA (EDS.). 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Chiron Press Inc., New York.

KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology 67:111–148.

KOMDEUR, J. 1992. Importance of habitat saturation and territory quality for the evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495.

KOMDEUR, J., AND P. EDELAAR. 2001. Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment. Behavioral Ecology 12:706–715.

KREBS, J. R., ET AL. 1995. Impact of food and predation on the snowshoe hare cycles. Science 269:1112–1115.

LIN, Y. K., AND G. O. BATZLI. 2001. The influence of habitat quality on dispersal and population densities of voles. Ecological Monographs 71:245–275.

LIN, Y. K., AND G. O. BATZLI. 2004. Movements of voles across habitat boundaries: effects of food and cover. Journal of Mammalogy 85:216–224.

LOTT, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge, United Kingdom.

MACEDO, R. H., AND C. A. BIANCHI. 1997. Communal breeding in tropical Guira cuckoos *Guira guira*: sociality in the absence of a saturated habitat. Journal of Avian Biology 28:207–215.

MCGUIRE, B., L. L. GETZ, J. E. HOFMANN, T. PIZZUTO, AND B. FRASE. 1993. Natal dispersal and philopatry in prairie voles (*Microtus ochrogaster*) in relation to population density, season and natal social environment. Behavioral Ecology and Sociobiology 32:293–302.

OSTFELD, R. S. 1986. Territoriality and mating system of California voles. Journal of Animal Ecology 55:691–706.

PEN, I., AND F. J. WEISSING. 2000. Towards a unified theory of cooperative breeding: the role of ecology and life history reexamined. Proceedings of National Academy of Sciences 267:2411–2418.

REED, J. M., AND J. R. WALTERS. 1996. Helper effects on variance components of fitness in the cooperatively breeding red-cockaded woodpecker. Auk 113:608–616.

RUSSELL, E. M., R. J. BROWN, AND M. N. BROWN. 2004. Life history of the white-breasted robin, *Eopsaltria georgiana* (Petroicidae), in south-western Australia. Australian Journal of Zoology 52:111–145.

SOLOMON, N. G. 2003. A reexamination of factors influencing philopatry in rodents. Journal of Mammalogy 84:1182–1197.

SOLOMON, N. G., AND J. A. FRENCH (EDS.). 1997. Cooperative breeding in mammals. Cambridge University Press, New York.

SOLOMON, N. G., AND L. L. GETZ. 1997. Examination of alternative hypotheses for cooperative breeding in rodents. Pp. 199–230 in Cooperative breeding in mammals (N. G. Solomon and J. A. French, eds.). Cambridge University Press, New York.

SOLOMON, N. G., AND J. J. JACQUOT. 2002. Testing functional hypotheses for wandering in prairie voles, *Microtus ochrogaster*. Canadian Journal of Zoology 80:951–955.

SOLOMON, N. G., B. KEANE, L. R. KNOCH, AND P. J. HOGAN. 2004. Multiple paternity in socially monogamous prairie voles (*Microtus ochrogaster*). Canadian Journal of Zoology 82:1667–1671.

STACEY, P. B., AND W. D. KOENIG. 1990. Cooperative breeding in birds. Cambridge University Press, New York.

STACEY, P. B., AND J. D. LIGON. 1987. Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. American Naturalist 130: 654–676.

STACEY, P. B., AND J. D. LIGON. 1991. The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. American Naturalist 137:831–846.

TAMARIN, R. H., R. S. OSTELD, S. R. PUGH, AND G. BUJALSKA (EDS.). 1990. Social systems and population cycles in voles. Advances in life sciences. Birkhaeuser Verlag, Basel, Switzerland.

YLONEN, H., T. KOJOLA, AND J. VIITALA. 1988. Changing female behavior and demography in an enclosed breeding population of *Clethrionomys glareolus*. Holarctic Ecology 11:286–292.

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