

Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis

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Natal philopatry, or delayed dispersal of sexually mature offspring, may be due to ecological constraints on dispersal. In this study, we manipulated the population density of prairie voles (*Microtus ochrogaster*) living in experimental outdoor enclosures to test a prediction from the habitat saturation hypothesis that philopatry and subsequent group formation in this cooperatively breeding mammal is affected by the availability of suitable territories. We detected a significant, positive relationship between the proportion of offspring remaining philopatric and density, with females being more philopatric than males at all densities. This increase in philopatry led to a significant increase in the proportion of social units that were groups as well as a significant increase in group size. These results provide the strongest evidence of a causal effect of density on dispersal and group formation in a mammal. Our findings suggest that habitat saturation is at least a partial explanation for philopatry in prairie voles. However, we cannot eliminate the possibility that other variables, such as benefits accrued from remaining philopatric, may also be factors contributing to philopatry. Nonetheless, these results show that changes in ecological conditions can influence social structure within a population, leading to group formation and a social milieu conducive to the evolution of cooperative breeding. *Key words:* dispersal, ecological constraints, habitat saturation, philopatry, prairie voles. [*Behav Ecol* 19:774–783 (2008)]

Natal philopatry, also referred to as delayed dispersal of offspring, is one of the key tenets of cooperative breeding because it can result in multiple adults living together in a group and contributing to the care of offspring (Koenig et al. 1992; Solomon 2003). In singular cooperative breeders, reproductive suppression typically occurs and only a single male–female pair reproduces within a group (Brown 1978). Cooperative breeding in these species appears to pose a challenge to the Darwinian explanation for the evolution of philopatry because philopatric individuals typically forgo reproduction while remaining in the natal group past sexual maturity (Emlen 1982; Brown 1987). Because cooperative breeding often arises when offspring remain philopatric, understanding the basis of philopatry is the first step toward understanding cooperative breeding in many species (Gaston 1978; Emlen 1982; Mumme 1997; Lacey and Sherman 2007).

Three hypotheses have been commonly proposed to explain philopatry. The benefits of philopatry hypothesis emphasize the fitness benefits that accrue to offspring that remain at the natal nest as opposed to the costs of dispersal (Stacey and Ligon 1987, 1991). The life-history hypothesis predicts that philopatry is a consequence of certain life-history traits, like longevity, that reduce the likelihood of breeding vacancies arising and create a surplus of individuals within a population (Arnold and Owens 1998; Hatchwell and Komdeur 2000). Third, the ecological constraints hypothesis stresses that if there are constraints on natal dispersal, such as an absence of vacant breeding territories, the direct fitness cost

of remaining philopatric may be small compared with the costs associated with natal dispersal, such as increased predation risk (Emlen 1982, 1995). These 3 hypotheses are not mutually exclusive, and the relative importance of each has been widely debated (Stacey and Ligon 1991; Koenig et al. 1992; Emlen 1994; Jennions and Macdonald 1994; Arnold and Owens 1998; Solomon 2003; Doerr and Doerr 2006).

The ecological constraints hypothesis is the only one of the 3 hypotheses that proposes that the decision to remain philopatric or disperse is predominantly a function of some environmental limitation (e.g., available breeding territories or mates). One of the best-studied ecological constraints has been the availability of adequate breeding habitat, which directly affects the probability that a disperser will successfully find a suitable breeding territory (Koenig and Pitelka 1981; Komdeur 1992; Walters et al. 1992). The habitat saturation hypothesis posits that individuals remain philopatric when all suitable breeding territories are occupied (Koenig and Pitelka 1981). Although support for the habitat saturation hypothesis has been found in a cooperatively breeding cichlid (*Neolamprologus pulcher*—Bergmüller et al. 2005), the majority of support comes from avian studies (e.g., Kinnaird and Grant 1982; Pruett-Jones and Lewis 1990; Walters et al. 1992; Yáber and Rabenold 2002; Carrete et al. 2006; Moreira 2006). The most common type of supporting evidence comes from observational studies detecting a negative correlation between habitat availability and philopatry or group size (e.g., Woolfenden and Fitzpatrick 1984; Carrete et al. 2006; Moreira 2006). Whereas such correlations are consistent with the predictions of the habitat saturation hypothesis, these observational studies cannot determine causation. Much stronger support for the habitat saturation hypothesis comes from studies that have manipulated the availability of suitable breeding habitat. For example, Walters et al. (1992) showed that red-cockaded woodpeckers (*Picoides borealis*) remain philopatric at high densities when nest cavities become limiting but disperse when new nest cavities are created. Likewise, when Seychelles

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warblers (*Acrocephalus sechellensis*) were transferred to an unoccupied island, philopatry was not observed until after all high-quality areas were occupied (Komdeur 1992).

Although avian studies have been critical in advancing our understanding of the factors that influence philopatry, some investigators have questioned the generality of these conclusions as applied to mammals (Jennions and Macdonald 1994; Mumme 1997; Hayes 2000; Russell 2004). Viviparity and lactation in mammals skew the balance of parental care toward the female and can prevent the male social partner and offspring from previous litter(s) from providing an energetic investment in the young similar to that provided by females (Jennions and Macdonald 1994; Mumme 1997). For this reason, it is important that we more thoroughly examine the importance of habitat saturation as a factor underlying philopatry in mammals. Several observational studies have detected positive associations between population density and philopatry, data consistent with the predictions of the habitat saturation hypothesis (Wolff 1994; Cochran and Solomon 2000). Studies in which the removal of one or all adults from their territory resulted in philopatric individuals moving and filling the vacancies have provided stronger support for the habitat saturation hypothesis (Wolff 1992; Solomon et al. 1998; Jacquot and Solomon 2004). However, experimental manipulations of population densities to examine the effect of density on philopatry and group formation have yet to be conducted.

The socially monogamous prairie vole (*Microtus ochrogaster*) is an excellent species with which to test predictions of the habitat saturation hypothesis for several reasons. They are facultative, singular cooperative breeders. Alloparental care includes retrieving, grooming, and brooding pups (Solomon 1991b; Wang and Novak 1992; Hayes and Solomon 2007) as well as constructing and maintaining nests and runways (Solomon and Getz 1997). Getz et al. (1993) have described 3 different types of social units for prairie voles in a natural population in east central Illinois: 1) male–female pairs with or without offspring, 2) single females with or without offspring, and 3) groups containing at least 2 adults of the same sex with or without offspring. Individuals that are not residents of a single nest, called wanderers, also occurred within this population (Getz et al. 1993). Individuals that belong to all 3 types of social units and wanderers have also been observed within seminatural populations (Cochran and Solomon 2000). The relative proportions of the 3 types of social units within populations vary temporally within these studies, perhaps in response to ecological conditions (Getz et al. 1993; Cochran and Solomon 2000). Populations vary widely in density, with free-living populations ranging in density from 10 voles/ha to as many as 624 voles/ha (Getz et al. 1979; McGuire et al. 1990; Getz and McGuire 1997).

Although there is some evidence that dispersal rates in prairie voles are positively associated with density (Gaines et al. 1979), other data indicate that dispersal in prairie voles is negatively correlated with population density (Getz et al. 1993; McGuire et al. 1993; Cochran and Solomon 2000; Lin and Batzli 2001). Thus, there may be ecological constraints on dispersal. In addition, dispersal in prairie voles has been reported to be male biased in some studies (Cochran and Solomon 2000; Lin et al. 2006), whereas other studies report that males and females dispersed with equal probability (McGuire et al. 1993; Lin and Batzli 2004). Prairie voles are territorial with little spatial overlap between adjacent social units, and adult males and females defend their joint territory (Getz et al. 1993; McGuire and Getz 1998). Finally, prairie voles are easily maintained in outdoor enclosures (Desy and Batzli 1989) providing seminatural conditions for experimental manipulations, which cannot be performed with most

mammalian cooperative breeders such as mongooses, canids, and callitrichids.

The aim of this study is to manipulate the population density of prairie voles living in outdoor enclosures to examine predictions of the habitat saturation hypothesis. According to the habitat saturation hypothesis, higher population densities should limit available territories and thus increase the proportion of offspring remaining philopatric. Furthermore, sex differences in philopatry may occur if males and females respond differently to changing ecological conditions. If philopatry is female biased, we predict that males should display a greater proportional increase in philopatry from low to high densities compared with females. Conversely, if males and females disperse at equal rates, we would not expect to see any sex difference in the proportion of offspring remaining philopatric with increasing population density. Finally, an increase in philopatry should result in increased group size and the proportion of social units that are groups.

METHODS

Study area

This study was conducted in 2 fields, each containing 8 small mammal enclosures from June through September 2004 and 2005 at the Miami University Ecology Research Center (ERC) in Oxford, OH (39°30'N, 84°44'W). The 2 fields (North Field and South Field) were approximately 225 m apart. During each year, we used 4 of the 8 enclosures in the South Field and 6 of the 8 enclosures in the North Field. The 0.1-ha enclosures (~32 × 32 m) were constructed of 20-gauge galvanized steel panels, which extended 45 cm below the ground's surface and 75 cm above the surface to prevent movement of voles among enclosures (Cochran and Solomon 2000). Vegetation in the enclosures consisted primarily of goldenrod (*Solidago* spp. L.), bluegrass (*Poa pratensis* L.), clover (*Trifolium* spp. L.), fescue (*Festuca* spp. L.), timothy (*Phleum* spp. L.), and ryegrass (*Elymus* spp. L.). Each enclosure had a 1-m border, mowed to 5–10 cm in height, adjacent to the walls of each enclosure to help prevent voles from digging near the walls (Cochran and Solomon 2000). There was an electric fence around the outside perimeter of each set of enclosures to prevent some mammalian predators, primarily raccoons (*Procyon lotor*), from entering enclosures and disturbing traps. Aside from the exclusion of species that would disturb traps, all other predators (e.g., raptors, snakes, shrews) had access to enclosures, helping to maintain seminatural conditions for this study. Northern short-tailed shrews (*Blarina brevicauda*) were commonly observed in the enclosures; black rat snakes (*Elaphe obsoleta*) were observed both in the enclosures and climbing the enclosure walls.

Because the enclosures had been used in previous years for studies involving both *M. ochrogaster* and *M. pennsylvanicus*, all enclosures were live trapped for 2 weeks prior to the start of the study to remove all *Microtus* spp. This was done to ensure that all enclosures contained solely the founding individuals that we released at the start of our study.

Experimental design

F₁-generation prairie voles, descended from wild-caught animals collected in east central Illinois, were paired and bred in Miami University's wild animal facilities each year between January and May. Animals were housed in polycarbonate cages (17 × 28 × 13 cm) containing processed paper bedding (Cell Sorb Plus, A & W Products, Inc., New Philadelphia, OH), dried alfalfa, and a cotton Nestlet (Ancare Corp., North Bellmore, NY) for nesting material. The animal room was

maintained at 25 ± 3 °C with a 14:10 h light:dark period (lights on at 0600). Rodent chow (Rodent Breeder Diet No. 5013, PMI Nutritional International, Brentwood, MO) and water were provided ad libitum. All offspring (F_2) were separated from their parents at 21 days of age and were toe clipped for identification, removing no more than one toe per foot.

In June of 2004 and 2005, F_2 individuals were released into enclosures, with the 2 years serving as temporal replicates. Four of the 10 enclosures used each year of the study were established at a low density (4 founding males and 4 founding females per 0.1-ha enclosure), and the other 6 were established at a high density (12 founding males and 12 founding females per 0.1-ha enclosure). These densities were designated as low or high based on previous studies of natural populations, in which densities and home range sizes of prairie voles were determined (Getz et al. 1979; Desy et al. 1990). Our low- and high-density designations are also in accordance with McGuire and Getz (1998), who defined low density for prairie voles as less than 100 voles/ha and high density as greater than 100 voles/ha. Moreover, we considered a density of 80 voles/ha to be low because the average home range size for male and female prairie voles is approximately 100 m². Therefore, 4 pairs of voles should not occupy the entire 0.1-ha enclosure (Hofmann et al. 1984, Jike et al. 1988). Conversely, a starting density of 240 voles/ha should lead to increased competition for space due to saturation of the habitat.

Each year, treatments were randomly assigned to the enclosures (low density = 4, high density = 6). We established 2 high-density and 2 low-density enclosures within each set of enclosures. The North Field contained the 2 additional high-density enclosures in both years. Individuals were randomly assigned to enclosures, although steps were taken to minimize the number of related individuals within each enclosure. When siblings were assigned to the same enclosure, they were never from the same litter and were always of the same sex to prevent inbreeding. None of the founding voles placed in the low-density enclosures were half or full siblings, but each of the high-density enclosures ($n = 12$ enclosures) contained 5–10 pairs or trios of full siblings among the founders. Founding voles were between the ages of 35 and 117 days at the time of release. Because the minimum age for breeding under laboratory conditions is 31 days of age (Solomon 1991a), all founders should have been old enough to initiate breeding after release. Due to early mortality of founding individuals or escape of animals through previously undetected holes in enclosure walls, an additional release took place in 5 enclosures in 2004 (4 high density, 1 low density) after the first week of grid trapping to maintain starting densities (35 replacement individuals released, ca. 85% of replacements due to disappearance of individuals). Selection of replacement individuals followed the same protocol as selection of founders to limit relatedness and inbreeding within the enclosures.

Populations were monitored by live trapping using Ugglan multiple-capture traps (Grahnb, Hillerstorp, Sweden) baited with cracked corn, a low-quality food item (Desy and Batzli 1989). Cotton batting was added to traps when temperatures were predicted to be below 10 °C (Cochran and Solomon 2000). For each individual captured, the location of capture, ID, sex, reproductive status (males—scrotal or nonscrotal; females—pregnant, lactating, formerly lactating, or non-reproductive), age class, any injuries or other unique characteristics, and individuals with which they were captured were recorded. Offspring were toe clipped for identification at their first capture. Additionally, all individuals were weighed to the nearest gram using a spring scale (Pesola micro-line spring scale, Forestry Suppliers Inc., Jackson, MS). During the first year, founding adults were weighed once per week.

However, during the second year adult males were weighed weekly, whereas adult females were weighed every day that they were captured to help track pregnancy and births. In both years, offspring were weighed every time they were captured until they reached adulthood (≥ 30 g) and then were weighed as described for founding adult males and females. Age classes used were juveniles (≤ 19 g), subadults (20–29 g), and adults (≥ 30 g) as defined by Getz et al. (1993).

Live trapping during each temporal replicate (2004 and 2005) lasted 14 weeks, beginning 1.5 weeks after the initial release of animals. During those 14 weeks, a combination of grid and nest trapping was used to monitor populations. Grid trapping was conducted to monitor population density and to trap founding females in order to locate their nests. Nest trapping functioned to identify nest residents and capture offspring when they emerged. During grid trapping, traps were located in a 5×5 grid pattern with 5 m spacing between traps (25 traps per enclosure). Five trap checks occurred during every grid trapping week, with traps open from 2000 on Sunday until the 0700 trap check on Monday. Traps were reset at 1800 on Monday and Tuesday nights with trap checks taking place at 2100 those nights and 0700 the next mornings (Tuesday and Wednesday mornings).

Ultraviolet-reflective powder was used in combination with radio tracking to locate the nests of all founding females beginning the first week of trapping (Jike et al. 1988). We powdered females with uniquely colored UV-reflective powder (Radiant Color, Richmond, CA) during the morning trap check by dusting them up to their neck with UV-reflective powder. Females were then released at their points of capture immediately after powdering. The powder trails of females were followed after dark using an ultraviolet lamp (ML-49; UVP, Inc., San Gabriel, CA) to locate females' nests (as described by Lemen and Freeman 1985). Females to be radio tracked were also collected during the morning trap check, anesthetized using isoflurane (Phoenix Pharmaceutical, Inc., St. Joseph, MO), and radio collared with a small mammal radio collar (model PD-2C, Holohil Systems Ltd., Ontario, Canada). The radio collars weighed approximately 3 g and were always less than 10% of a collared female's body mass, so they did not influence females' daily energy expenditure (Berteaux et al. 1996). Females were given several hours to recover from anesthesia in a temperature-controlled animal room at the ERC, and then each vole was rereleased at her site of capture. The locations of collared individuals were identified via triangulation of transmitter signals with 2 receivers (Fieldmaster 16 channel receiver, Johnson's Telemetry, El Dorado Springs, MO) and 3-element Yagi antennas (Johnson's Telemetry, El Dorado Spring, MO) between 1100 and 1500. Fixes were taken at least 3 times per day, at 30- to 60-min intervals, for 3 consecutive days. We assumed that during this time period, females were likely to be in their nests to avoid the heat. We searched the areas to which individuals were tracked for surface nests or entrances to underground nests. Once nests were located by either powder tracking or radio tracking, 3 Ugglan traps were placed in surface runways less than 1 m from the nest entrance.

After 3 consecutive weeks of grid trapping (trapping weeks 1–3), nest trapping and grid trapping were alternated on a weekly basis for 8 weeks (trapping weeks 4–11). Each nest trapping week had 10 trap checks, divided into 2 periods, each with 5 trap checks. During the first period, traps were set at 1800 and checked at 2100 Sunday, Monday, and Tuesday as well as at 0700 on Monday and Tuesday. This schedule was then repeated Wednesday night through Friday night. We only conducted nest trapping during the final 3 weeks of the study (trapping weeks 12–14, referred to as the residency period) to determine the individuals residing at each nest, the

proportion of offspring that remained philopatric, and the composition of social units. At the end of each field season, all surviving voles were live trapped and removed from enclosures.

One high-density enclosure from 2004 and 2 high-density enclosures from 2005 were removed from all analyses due to predation by raccoons in 2004 and a long-tailed weasel (*Mustela frenata*) in 2005. All research procedures involving live animals followed the guidelines of the American Society of Mammalogists for the use of wild animals in research (Gannon et al. 2007) and were approved by the Miami University Institutional Animal Care and Use Committee.

Vegetation sampling

Vegetation sampling was conducted in June of each year in all enclosures to determine if there were differences between the 2 sets of enclosures (South and North Fields), between years, or between treatments. Square quadrats (0.36 m²) were randomly sampled within each 5 × 5 m section of the grid ($n = 36$ samples/enclosure). Within each quadrat, the proportion of vegetation from class Liliopsida (monocots) and class Magnoliopsida (dicots) was estimated. The proportion of monocots and dicots provided an index of habitat quality. Dicots were indicative of high-quality habitat because they comprise the majority of summer diet for prairie voles (Batzli 1985). Because the proportions of monocots and dicots were based only on the area within a quadrat that had vegetative cover, the total percentage of monocots and dicots in each quadrat always equaled 100%. We also measured the maximum height of vegetation within each quadrat to evaluate the amount of cover. Variation in the amount of cover among enclosures could influence the fitness of individuals within those enclosures because prairie vole survival and reproduction is positively correlated with the amount of cover available (Lin and Batzli 2001).

Demography

At the beginning of the study, enclosures could be categorically divided into those with low or high densities. Later in the study, however, the population densities had increased more quickly in some enclosures than in others, and density estimates for some low-density enclosures overlapped estimates for some of the high-density enclosures. To avoid the potential bias generated by using the minimum number known alive to calculate population density (Slade and Blair 2000; Pocock et al. 2004), we used a robust design model (Huggins closed capture estimator—see Huggins 1989, 1991) within the computer program MARK (White and Burnham 1999) to estimate population density based on data from the 7 grid trapping weeks. The Huggins closed capture estimator was chosen because it is more stable when sample sizes are small. The derived population estimate for each enclosure from week 11 was used as the density estimate for the analyses of philopatry and social structure because week 11 is the final grid trapping week before the start of the 3-week residency period. Therefore, density was used as a continuous variable in all analyses except the vegetation analyses, which were performed to ensure that there were no vegetative differences between high- and low-density treatments.

Trappability, the probability of capturing an individual at least once during a grid trapping week, and survival of all individuals (founders and offspring) between grid trapping weeks were also calculated for each enclosure based on data from grid trapping weeks using MARK (Kendall 2001). Offspring survival was calculated as the proportion of offspring that survived from first capture to the 3-week residency period. Only off-

spring that could have potentially reached sexually maturity, 30 days of age as estimated from date of first capture and body mass, by the 3-week residency period, were included in this analysis.

Social structure and philopatry

For subadults and adults, residency at a nest site was defined as having $\geq 75\%$ of all captures at one nest site for all individuals captured at least once per week (Cochran and Solomon 2000) during the 3-week residency period (trapping weeks 12–14). Individuals that were captured at least once per week but did not have $\geq 75\%$ of their captures at one nest site were termed wanderers (Cochran and Solomon 2000). Individuals with less than one capture per week were not classified and were excluded from analyses of philopatry and social structure.

The natal nest of each offspring was considered to be the nest at which it was first captured as a juvenile because prairie voles typically do not leave the natal nest prior to reaching 20 g (McGuire et al. 1993). Any offspring that weighed 20 g or more and was still a resident of its natal nest during the 3-week residency period was considered philopatric. Conversely, all offspring that weighed 20 g or more and were classified as residents of a nest other than their natal nest or that were classified as wanderers during the 3-week residency period were considered dispersers. Furthermore, only offspring that were at least 30 days old, the age of sexual maturity, during the 3-week residency period were included in the analysis of philopatry (McGuire et al. 1993). Of 17 enclosures included in the data analysis, 15 (low density = 6, high density = 9) contained individuals that met the requirements for the analysis of philopatry.

Composition of social units was determined based on the number of adults and subadults of each sex that were residents at the same nest site. Social units were defined as single male with or without offspring, single female with or without offspring, male–female pair with or without offspring, or group, at least 2 adults or subadults of the same sex, with or without offspring (sensu Getz et al. 1993). Group size was defined as the number of adult and subadult residents at a nest. One low-density enclosure in 2004 had no groups, so analysis of mean group size within enclosures is based on 8 enclosures for each year. The proportion of social units that were groups in each enclosure was determined by dividing the number of social units that were groups by the total number of social units within the enclosure.

Statistical analysis

Vegetative data were examined using 3-way analyses of variance (ANOVAs) to determine if there were effects of initial population density (high and low), field (South and North), and year. Bonferroni post hoc analyses using least squares means were used to investigate significant interactions. Based on the results of the vegetation analyses, year, field, and their interaction were included as blocks in all subsequent models to account for any variation in the analyses due to these factors.

A chi-square analysis was used to investigate potential differences in the numbers of males and females that were categorized as residents and wanderers. A 2-way ANOVA was used to determine if there were effects of sex or age class (adult and subadult) on group structure.

Logistic regression was used to determine if population density predicted the proportion of surviving offspring that were philopatric. Sex was also used as a factor in the logistic regression model for the analysis of philopatry to see if the proportion of offspring remaining philopatric differed between females and males. Analysis of covariance (ANCOVA) was used

to determine if population density (estimate determined at week 11) predicted differences in group size. Group sizes within an enclosure were averaged prior to analysis because groups within enclosures were not independent. Logistic regression was also used to determine if the probability that social units were groups was predicted by density. We used Pearson's correlation analyses to determine relationships between group size, the proportion of social units that were groups, and the proportion of offspring remaining philopatric.

For all regression analyses, the initial model included main effects as well as all possible interactions. For parsimony, the nonsignificant interactions and main effects were removed from the models through backward elimination. Therefore, only statistically significant differences are presented. The ANOVA and ANCOVA were checked for normality, and homogeneity of variance and data presented met the assumptions of the analyses. Nonparallelism was investigated in the ANCOVA by the inclusion of the interactions between the covariate (density) and blocking factors (year and field) in the model. All means and least squares means are presented ± 1 standard error. Statistical significance was set at $P < 0.05$.

RESULTS

Vegetation sampling

There were significant main effects of year ($F_{1,605} = 12.44$, $P = 0.0005$) and field ($F_{1,605} = 704.03$, $P < 0.0001$) on the percentage of dicots. The overall percentage of dicots was significantly less in 2004 than in 2005 (Table 1a). Furthermore, the percentage of dicots in the North Field was approximately 15 times greater than the percentage of dicots in the South Field (Table 1b). There was a significant year \times density interaction with regard to the maximum height of vegetation ($F_{1,605} = 9.57$, $P = 0.0021$). Although maximum vegetation height was not significantly different between low- and high-density enclosures in 2004, vegetation in the low-density enclosures was significantly taller than the vegetation in the high-density enclosures in 2005 (Table 2a). In addition, the maximum vegetation height in the low-density enclosures in 2005 was significantly taller than the vegetation in the low-density enclosures in 2004, although the maximum vegetation height in high-density enclosures did not differ significantly between years (Table 2a). There was also a significant year \times field interaction with regard to the maximum height of vegetation ($F_{1,605} = 24.77$, $P < 0.0001$). In 2004, the maximum height of the vegetation in the South Field was significantly greater than the maximum height of the vegetation in the North Field, but the maximum height of the vegetation did not differ significantly between fields in 2005 (Table 2b). The maximum height of the vegetation in the North Field in 2005

Table 1

The mean (\pm standard error) percentage of vegetation within an enclosure that was comprised of dicots presented (a) by year and (b) by field

	<i>n</i>	% dicot
(a) Year		
2004	9	40.4 \pm 11.7 ^a
2005	8	44.8 \pm 10.0 ^b
(b) Field		
South	6	4.1 \pm 1.4 ^a
North	11	63.4 \pm 4.2 ^b

Different letters within subsections indicate statistically significant differences. *n* = number of enclosures; 36 samples/enclosure.

Table 2

The least squares mean (\pm standard error) maximum height of vegetation in meters by year and by (a) density or (b) field

(a) Year	Initial density	<i>n</i>	Vegetation height (m)
2004	Low	4	0.84 \pm 0.02 ^{a,a}
	High	5	0.85 \pm 0.02 ^{a,a}
2005	Low	4	1.01 \pm 0.02 ^{a,b}
	High	4	0.89 \pm 0.03 ^{b,a}
(b) Year	Field	<i>n</i>	Vegetation height (m)
2004	South	4	0.93 \pm 0.02 ^{a,a}
	North	5	0.76 \pm 0.02 ^{b,a}
2005	South	2	0.92 \pm 0.04 ^{a,a}
	North	6	0.98 \pm 0.01 ^{a,b}

Different letters indicate statistically significant differences within year followed by statistically significant differences within (a) initial density or (b) field (Bonferroni test, $P < 0.05$). *n* = number of enclosures; 36 samples/enclosure. Low-density enclosures had an initial density of 8 voles/0.1 ha, and high-density enclosures had an initial density of 24 voles/0.1 ha.

was significantly taller than the vegetation in the North Field in 2004. The maximum height of the vegetation in the South Field did not differ significantly between years (Table 2b).

Demography

Although initial densities were either 8 or 24 voles/0.1 ha, by the final week of grid trapping (trapping week 11), density ranged from 6 to 77 voles/0.1 ha. The trappability of voles was high throughout the experiment, averaging 80% \pm 2% for the 17 enclosures. Survival of individuals from one grid trapping week to the next was also high (95% \pm 1%). Offspring survival, based on those that could have been at least 30 days old during the residency period (trapping weeks 12–14), was estimated to be 65% \pm 6%. Of the 584 subadults and adults in the enclosures during the residency period during the 2 years of the study, 359 (62%) were classified as residents, 106 (18%) were classified as wanderers, and 119 (20%) could not be classified because they did not have at least one capture per week. Of the 359 residents, 168 (47%) were male and 191 (53%) were female. In the case of the 106 wanderers, 67 (63%) were male and 39 (37%) were female. When the number of residents and wanderers of each sex were compared, females were significantly less likely to be wanderers than males ($\chi^2 = 8.817$, degrees of freedom [df] = 1, $P = 0.0030$). Overall, the mean proportion of adult and subadult females in each enclosure was 0.48 \pm 0.02.

Social structure and philopatry

In the first model with density, year, and field as independent variables, density was the only predictor that affected the proportion of offspring that remained philopatric ($\chi^2 = 15.77$, df = 1, $P < 0.0001$), with the proportion of philopatric individuals increasing as density increased (Figure 1). There were no statistically significant interactions among these factors.

Sex was a significant predictor of the proportion of offspring remaining philopatric ($\chi^2 = 4.86$, df = 1, $P = 0.0275$), with females being more philopatric than males at all densities (Figure 2). However, density had significantly different effects on the proportion of offspring remaining philopatric between years when sex was included in the model (density \times year, $\chi^2 = 5.07$, df = 1, $P = 0.0244$), with individuals from 2005

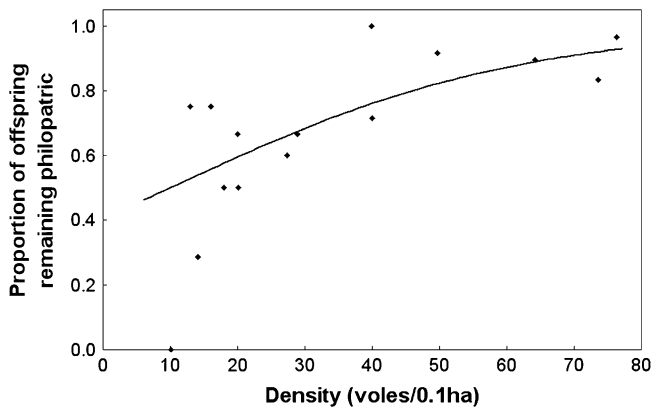


Figure 1

Proportion of prairie vole offspring within each enclosure that were classified as philopatric during the 3-week residency period (trapping weeks 12–14) as a function of density ($n = 15$ enclosures because 2 enclosures had no offspring meeting requirements for inclusion in the analysis). The line is the predicted logistic equation.

being less philopatric at low densities and more philopatric at high densities than individuals from 2004. Field was not a significant predictor of philopatry when analyzed by sex.

Groups ranged in size from 2 to 19 voles, with an overall group size of 4.2 ± 0.4 . Density had significantly different effects on group size between years (density \times year, $F_{1,12} = 6.58$, $P = 0.0248$). Although there was a positive relationship between group size and density in both years, group size showed a greater response to increasing density in 2005 than in 2004 (Figure 3). Field was not a significant predictor of group size.

On average, groups contained 1.4 ± 0.1 adult females, 1.3 ± 0.2 adult males, 0.7 ± 0.2 subadult females, and 0.8 ± 0.1 subadult males. The average number of adults was significantly greater than the average number of subadults in each group ($F_{1,57} = 14.29$, $P = 0.0004$). There was no significant difference in the mean number of males and females in each group ($F_{1,57} = 0.01$, $P = 0.9424$), with a mean proportion of adult and subadult females in groups equal to 0.51 ± 0.05 . This indicated that groups tended to have an approximately equal sex ratio, with 84% of the 63 groups having at least one male and one female. When considering only mature offspring within groups, the mean proportion of females was 0.50 ± 0.08 , similar to the overall sex ratio within groups. Most groups (86%) contained at least one founding individual, and 40% of the groups contained both a male and female founder.

Each enclosure contained 5.6 ± 0.6 social units with a range from 3 to 9 social units (Table 3). Density and year were both significant predictors of the proportion of social units that were groups ($\chi^2 = 10.16$, $df = 1$, $P = 0.0014$, and $\chi^2 = 7.14$, $df = 1$, $P = 0.0075$, respectively). The proportion of groups increased as density increased in both years, but at a given density the proportion of groups was significantly greater in 2005 than in 2004 (Figure 4). Field was not a significant predictor of the proportion of social units that were groups, and there were no statistically significant interactions.

Group size was significantly correlated with the proportion of social units that were groups (Pearson's correlation: $r = 0.63$, $P = 0.0087$, $n = 16$) and the proportion of offspring remaining philopatric (Pearson's correlation: $r = 0.54$, $P = 0.0447$, $n = 14$). The proportion of social units that were groups was significantly correlated with the proportion of offspring remaining philopatric (Pearson's correlation: $r = 0.67$, $P = 0.0095$, $n = 14$).

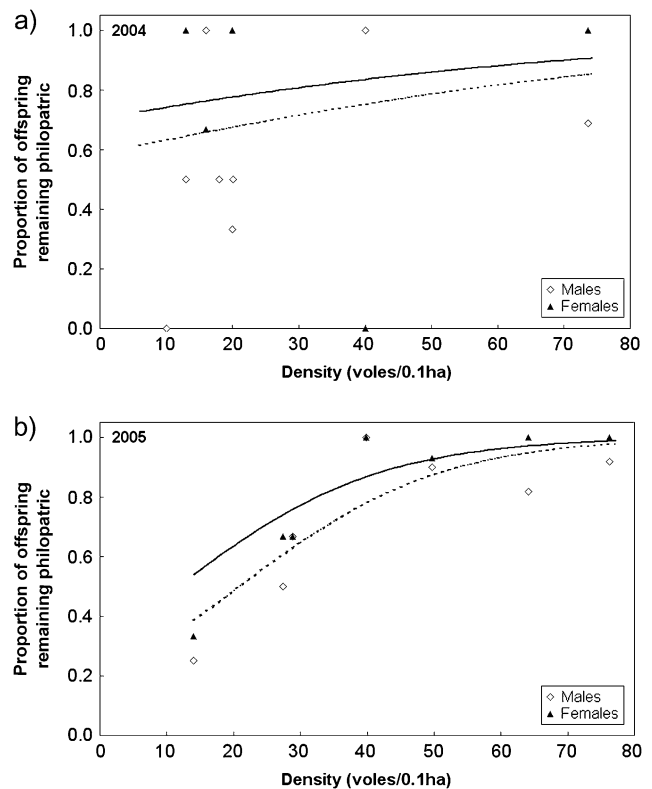


Figure 2

Proportion of male and female prairie vole offspring within each enclosure that were classified as philopatric during the 3-week residency period (trapping weeks 12–14) as a function of density. (a) $n = 8$ enclosures for males; $n = 5$ enclosures for females that met the requirements for inclusion in the analysis. (b) $n = 7$ enclosures for males; $n = 7$ enclosures for females that met the requirements for inclusion in the analysis. The solid line is the predicted logistic relationship between density and the proportion of females remaining philopatric from the logistic model. The dashed line is the predicted logistic relationship between density and the proportion of males remaining philopatric.

DISCUSSION

The results of our experiment provide strong evidence for a causal effect of population density on natal dispersal and group formation and are consistent with the predictions of the habitat saturation hypothesis. These predictions are based on the assumption that as population density increases the amount of available breeding habitat should decrease. Although we did not directly measure habitat use, because prairie voles are territorial (Getz et al. 1993; McGuire and Getz 1998), we assumed that the amount of available breeding habitat would decrease at higher densities as a result of increased intraspecific competition. This assumption was supported by the finding that the home range size of prairie voles in the lowest density enclosure ($45 \pm 16 \text{ m}^2$) was more than twice the home range size of animals in the highest density enclosure ($19 \pm 4 \text{ m}^2$) (Richmond 2007). However, when we examined the home range sizes for a subset of the adult male and female wanderers during the 2 grid trapping weeks just prior to the 3-week residency period, their home range sizes were not related to density ($r^2 = 0.05$). Thus, there was no evidence that density affected the exploratory excursions of wanderers. Furthermore, the wanderers in the high-density populations should have encountered more conspecifics within a similar sized area as voles at low density. Thus, wanderers should have

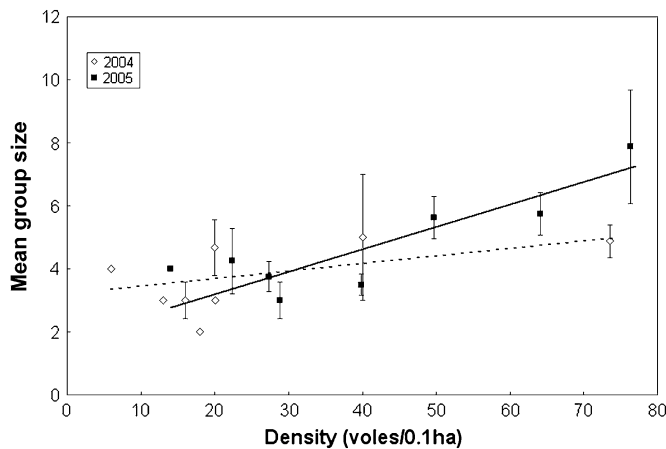


Figure 3

Mean (\pm standard error) prairie vole group size within enclosures during the 3-week residency period as a function of density and year. For 2004, $n = 8$ enclosures because one enclosure had no groups. In 2005, $n = 8$ enclosures. The dotted line is the predicted effect from the 2004 ANCOVA model, and the solid line is the predicted effect for the 2005 ANCOVA model.

been able to assess population density and presumably territory availability.

The finding that the proportion of offspring remaining philopatric within an enclosure increased as population density increased provides the strongest support of the habitat saturation hypothesis. In addition, the retention of offspring at the natal nests led to an increase in the proportion of social units that were classified as groups as well as an increase in group size. Taken together, these results suggest that as suitable breeding

habitat became occupied due to the increase in population density, mature offspring, especially females, were more likely to remain at the natal nest rather than dispersing and establishing their own territory or wandering within the population (*sensu* Getz et al. 1993; Solomon and Jacquot 2002).

A positive association between philopatry and population density has also been detected in prior studies of prairie voles. Cochran and Solomon (2000) observed that population density was positively correlated with the number of groups as well as group size within enclosed populations, a result they attributed to constraints on dispersal at high densities due to habitat saturation. Getz and colleagues found a positive correlation between population density and group formation in natural populations of prairie voles in Illinois (Getz et al. 1990, 1993; McGuire et al. 1993; Getz and McGuire 1997; Getz, McGuire, et al. 2005) where free-ranging prairie vole populations typically undergo large-scale temporal fluctuations in density (Getz et al. 2001, 2006; Getz, Oli, et al. 2005). A 25-year study of prairie voles in east central Illinois indicated that increased survival was the most important factor associated with the initiation of population fluctuations (Getz et al. 2006). Although the amplitude of the fluctuations was correlated with site-specific food availability, the occurrence of the fluctuations appeared to result from changes in predation rates by generalist predators (Getz et al. 2001, 2006). Thus, a relaxation of predation rates, particularly in habitats with high food quality, may result in ecological conditions that favor delayed dispersal and group formation in prairie voles.

In our study, the effect of predation should be similar among enclosures, but more offspring are produced (and survived) in the high-density enclosures because these enclosures contained more founding females. Thus, our results are consistent

Table 3

Prairie vole social structure presented as the number of each type of social unit within enclosures

Year	Enclosure	Density ^a	Groups ^b	M-F pairs ^c	Single F ^d	Single M ^e	Total social units ^f
2004	OE5	6.0	1	1	1	0	3
2004	NE6	10.1	0	0	2	1	3
2004	OE7	13.0	1	2	0	0	3
2005	OE5	14.0	2	2	0	0	4
2004	NE2	16.0	3	1	0	0	4
2004	OE3	18.0	1	2	5	0	8
2004	NE4	20.0	3	1	1	0	5
2004	OE1	20.1	1	0	1	1	3
2005	NE1	22.3	4	0	0	0	4
2005	OE7	27.3	4	1	0	0	5
2005	NE5	28.8	3	1	1	0	5
2005	NE6	39.9	6	2	0	0	8
2004	NE5	40.0	2	4	0	0	6
2005	NE2	49.7	8	0	0	0	8
2005	NE4	64.2	8	1	0	0	9
2004	NE3	73.6	8	1	0	0	9
2005	NE3	76.3	8	0	0	0	8
	Mean (\pm standard error)		3.7 \pm 0.7	1.1 \pm 0.3	0.7 \pm 0.3	0.1 \pm 0.1	5.6 \pm 0.6

Social units may or may not contain offspring. M, male; F, female.

^a In voles/0.1 ha.

^b At least 2 adults or subadults of the same sex.

^c Male-female pairs.

^d Single females.

^e Single males.

^f The total number of social units within each enclosure.

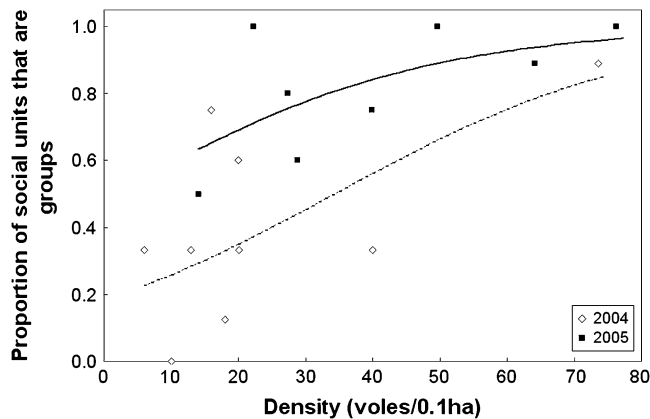


Figure 4
Proportion of prairie vole social units within an enclosure that were groups (≥ 2 adults or subadults of the same sex) during the 3-week residency period as a function of density and year. The dotted line is the predicted relationship from the 2004 logistic model, and the solid line is the predicted relationship for the 2005 logistic model.

with the hypothesis of Getz et al. (2006) that increased survival led to increased density, an increase that resulted in group formation.

It is typical for philopatry to occur in both sexes among singular breeding cooperative mammals (Solomon 2003; Russell 2004; Lacey and Sherman 2007). In our study, some male and female prairie voles were philopatric across the entire range of densities observed, but more females were philopatric than males at all densities. We had predicted that if philopatry was female biased, habitat saturation would have a disproportionate effect on male dispersal as population density increased. However, dispersal in both sexes was affected equally by density as evidenced by the lack of a statistical interaction between sex and density in our analysis of philopatry. The female-biased philopatry observed at all densities and the failure to detect a greater proportional increase in philopatry in males as density increased may be due to males being more likely to adopt a wandering strategy at all densities (Getz et al. 1993). In our study, 29% of the subadult and adult males trapped at least once per week during the residency period were classified as wanderers, whereas only 17% of females wandered among nests. Even at the highest densities when it might be expected that the proportion of philopatric voles should approach 1 for both sexes due to a lack of breeding vacancies, as it does for females in our study, some males still became wanderers instead of remaining at their natal nests. Other researchers have shown that the percentage of wandering males did not vary with density (Getz et al. 1993; Solomon and Jacquot 2002), a finding consistent with our data showing that a proportion of male offspring disperse even at high densities.

Philopatry in several cooperatively breeding mammals has been attributed, at least in part, to habitat saturation. Although some of the evidence supporting habitat saturation as the basis of philopatry comes from observational studies that have detected associations between density and group formation (Cochran and Solomon 2000; Randall et al. 2005), more rigorous support is provided by field studies in which adults were removed from their territories. In these experimental manipulations, animals rapidly immigrated into vacancies (Wolff 1992; Jacquot and Solomon 2004) and became reproductive (Solomon et al. 1998), suggesting that availability of a suitable territory is critical in stimulating dispersal. Our results add to the available experimental evidence supporting habitat saturation

by demonstrating that high population densities not only cause an increase in philopatry but also cause an increase in group formation and group size. These results provide one of the strongest empirical tests to date of the habitat saturation hypothesis.

The hypotheses proposed to explain the occurrence of philopatry are not mutually exclusive, and the emerging viewpoint is that both constraints and benefits are likely to affect dispersal in cooperative breeders (Koenig et al. 1992; Emlen 1994; Solomon 2003). Given the mean home range size of prairie voles, it was unlikely that individuals occupied the entire habitat in the lowest density enclosures. Therefore, the presence of philopatric individuals within these enclosures suggests that factors other than habitat saturation may affect whether or not prairie voles delay dispersal. Currently, there is little evidence to suggest that philopatric prairie voles gain direct benefits (e.g., survival—Getz et al. 1994, inherit natal territory—McGuire et al. 1993). However, philopatric prairie voles may accrue indirect benefits by helping to rear close relatives. A few studies provide evidence of benefits to pups born into singular breeding groups (Solomon 1991b; Getz et al. 1997; Solomon and Crist forthcoming). Future studies using genetic data to resolve parentage and relatedness should make it possible to more accurately assess some of the direct and indirect benefits that may accrue to philopatric prairie voles.

Habitat saturation has been proposed to be a factor influencing philopatry in numerous species of cooperatively breeding birds and mammals. However, most of the studies purporting to support the habitat saturation hypothesis, particularly in mammals, do not directly demonstrate that variation in the availability of suitable breeding habitat causes changes in philopatry. By manipulating population density, the results presented here provide strong empirical support of the habitat saturation hypothesis for a mammalian species by revealing a causal effect of density on philopatry, group size, and the proportion of social units that are groups. Therefore, ecological constraints, at least partially, result in philopatry in prairie voles. Furthermore, these results show that changes in ecological conditions, such as increasing population density, can influence social structure within a population, leading to group formation and a social milieu conducive to the evolution of cooperative breeding.

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