

Active density-dependent habitat selection in a controlled population of small mammals

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Abstract. Density-dependent habitat selection has numerous and far-reaching implications to population dynamics and evolutionary processes. Although several studies suggest that organisms choose and occupy high-quality habitats over poorer ones, definitive experiments demonstrating active selection, by the same individuals at the appropriate population scale, are lacking. We conducted a reciprocal food supplementation experiment to assess whether voles would first occupy a habitat receiving extra food, then change their preference to track food supplements moved to another habitat. Meadow voles, as predicted, were more abundant in food-supplemented habitat than in others. Density declined when food supplements ceased because the voles moved to the new habitat receiving extra food. Although males and females appeared to follow different strategies, meadow-vole densities reflected habitat quality because voles actively selected the best habitat available. It is thus clear that behavioral decisions on habitat use can motivate patterns of abundance, frequency, and gene flow that have widespread effects on subsequent evolution.

Key words: adaptive movement; density dependence; dispersal; field experiment; food supplements; habitat selection; *Microtus pennsylvanicus*; small mammals.

INTRODUCTION

Theories of density-dependent habitat selection are central to our understanding of such apparently diverse phenomena as population and metapopulation dynamics, spatial distribution and dispersal, species interactions, niche evolution, patch use, and speciation (reviewed in Morris 2003a). The theory also has great promise to inform conservation and management (Rosenzweig 1987; reviews in Gillis [2003] and Morris [2003b]). Habitat-selection theory demands, therefore, rigorous and fool-proof tests, particularly in vertebrates where it is most often applied.

Field tests of the theory typically take one of two forms: correlations of density (and occasionally fitness) among habitats varying in quality, or assessments of density (and more rarely estimates of fitness) among manipulated patches of habitat. Correlation tests include Rosenzweig and Abramsky's (1985) creative graphical analyses of a transformed Simpson's index, isodars (Morris 1987, 1988), paraisodars (Shenbrot and Krasnov 2000), Emlen et al.'s (2003) interaction assessment, life history (Messier et al. 1990, Morris 1991), foraging behavior (Morris and Davidson 2000), and some resource selection functions (McLoughlin et al. 2006, Fortin et al. 2008). Experiments typically involve habitat manipulation such as removing vegetation (Moenting and Morris 2006), adding food supplements (often in concert with vegetation removal as by

Lin and Batzli [2001] and Pusenius and Schmidt [2002]) and reduction (Haugen et al. 2006) or enhancement (Knight et al. 2008) of animal density. Adaptive dispersal (e.g., Clobert et al. 2001), correlations of dispersal with either density (Morris and Diffendorfer 2004) or fitness (Doligez and Pärt 2008), and choice of habitats based on experience (e.g., Stamps et al. 2009) are also consistent with density-dependent habitat selection, but do not definitively demonstrate that individuals change their preference relative to habitat quality or population density.

Although the bulk of evidence weighs heavily in favor of density-dependent habitat selection, contrary evidence may seldom be published (Palmer 2000), experiments at the habitat scale are somewhat ambiguous, and none has altered treatments in a way that would cause a fixed density of animals to change their habitat choice in the field. We address these shortcomings with a simple manipulative experiment that yields five predictions, all of which must be true, in order to demonstrate density-dependent habitat selection. Our experiment on small herbivorous mammals confirmed each prediction. The rodents are active habitat selectors, and thereby demonstrate the potential for adaptive movement to influence a variety of ecological and evolutionary processes.

METHODS

We conducted the experiment on meadow voles (*Microtus pennsylvanicus*) living in old-field habitat surrounded by rodent-proof enclosures in northern Ontario, Canada (the Lakehead University Habitron,

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see Appendices A and B). These small (~35 g), native mammalian herbivores occupy old-field and grassland habitats throughout much of North America.

We marked 39 male and 39 female voles in July 2008 with radio-frequency identification tags. We allowed the voles to move freely among four small (25 × 25 m) enclosures arranged in a 2 × 2 grid (Appendix B) for several days. We monitored their use of control and experimental enclosures with remote antennae placed on opposing sides of ground-level exit gates between adjoining enclosures until 20 September 2008. During the experiment voles could move east and west between enclosures in each small pair, but not north and south from one pair into the other.

After voles had opportunity to choose enclosures (see Appendix A) we allowed the voles nine further days to equilibrate densities (phase 1) between each pair of the four small enclosures while we enriched one (enclosure 13) with sunflower seeds and alfalfa cubes every two days (the additional resource renewal rate was sufficient to meet the energetic needs of 624 lactating voles/ha, see Appendix A). We initiated the experiment (phase 2) on 9 August by opening two gates that linked each pair with a single large (50 × 50 m) enclosure. Voles using one small pair could access the other small pair only by traveling through the large enclosure. Unlike classical experiments (e.g., Milinski 1979) that manipulated feeding rates in foraging patches, voles acquired travel costs while moving between the treated enclosures, as well as additional costs associated with establishing and maintaining a new home range (males) or territory (female voles are territorial; e.g., Madison 1980). The 0.0625-ha area of our small enclosures exceeds the average daily home-range/territory sizes of male and female meadow voles revealed by radio telemetry in Virginia (males, ~0.02 ha; females, ~0.007 ha; Madison 1980) as well as that of multiple-day estimates of female voles in Pennsylvania (0.04 ha [Jones 1990]; male home ranges [0.24 ha] were larger). We confirmed our assumption that the experiment manipulated habitat quality, rather than patches used by the same voles, by demonstrating that the vast majority of voles used only one of the two treatment enclosures (Appendix C).

We reversed the feeding treatment on 19 August (phase 3) by curtailing supplementary feeding in enclosure 13, and added the same amount of food to enclosure 15 instead. We summarized the data as the number of marked animals using each of the enclosures each day. All field methods were approved and certified by Lakehead University's Animal Care Committee.

Predictions

If voles preferentially occupy enclosures with greater resource abundance, then

1) The number of voles recorded in enclosures containing food should be greater than the number recorded in other enclosures of similar size.

2a) The number of voles recorded in enclosure 13 should be consistently high or increasing during resource enrichment (phase 2).

2b) The number of voles in enclosure 13 should decline during phase 3 when supplemental feeding was curtailed.

3a) Density in enclosure 15 should remain low or decline during phase 2 (control).

3b) Density in enclosure 15 should increase during resource enrichment (phase 3).

Predictions 2a and 2b yield a concave downward relationship of density through time (high density while food is added, declining density as resources become depleted when supplemental food is moved elsewhere). The opposite pattern should prevail in enclosure 15 where predictions 3a and 3b yield a concave upward relationship of density through time. No mechanism other than density-dependent habitat selection can be expected to produce these clear and opposite effects.

Some readers might wonder how we can infer density-dependent habitat selection when the total population of marked voles was constant. Density-dependence emerges from the interactions among density, population dynamics, and resource renewal. It is thus possible to assess its implications by manipulating any of the three variables. Moreover, our choice of manipulating resource renewal yields two additional predictions for animals that maximize their rate of resource harvest while selecting habitat according to an ideal-free distribution (Fretwell and Lucas 1969).

4) Quitting-harvest rates in enclosure 13 (and its connected enclosure 14; Appendix B) should exceed those in enclosure 15 (and 16) early during phase 3 because animals had insufficient time to complete habitat selection.

5) Differences in quitting-harvest rates among enclosures should disappear toward the end of phase 3 after animals had completed their density-dependent habitat choice.

We tested prediction 1 with two analyses of variance (GLM, SPSS 16, SPSS Inc., Chicago, Illinois, USA) contrasting the number of voles recorded in each small enclosure (fixed factor) during the final eight days of food supplements (day was included as a covariate to assess changes in density through time). One analysis contrasted densities early in the experiment when resources were added to enclosure 13, the second analysis contrasted densities late in the experiment when resources were added to enclosure 15. We selected an eight-day interval because it corresponded with the number of days of valid data associated with phase 2. We tested the "concavity predictions" (2 and 3) with quadratic regression (SPSS 16; -ve quadratic term predicted in enclosure 13; +ve quadratic term predicted in enclosure 15). We assessed time-dependent differences in quitting-harvest rates with a repeated-measures ANOVA on the log-transformed giving-up resource

TABLE 1. Results of analyses of variance contrasting differences in the mean number of meadow voles using antennae located in two food-supplemented enclosures and three non-supplemented enclosures at the Lakehead University Habitron during summer, 2008.

Source	df	F	P
Comparisons when enclosure 13 was supplemented			
Model	4	48.68	<0.001
Intercept	1	513.92	<0.001
Enclosure	3	59.82	<0.001
Day	1	15.26	0.001
Error	27		
Comparisons when enclosure 15 was supplemented			
Model	4	71.35	<0.001
Intercept	1	23.38	<0.001
Enclosure	3	92.87	<0.001
Day	1	6.81	0.015
Error	27		

densities achieved in paired foraging patches placed in each enclosure (Appendix D; see also Plate 1).

RESULTS

Meadow voles preferentially occupied enriched habitats.—The voles yielded a total of 35 524 separate RFID records over the 43-day duration of the experiment. More voles used enclosure 13 than any other enclosure while that enclosure received food supplements (mean number of voles recorded in enclosure 13 = 30.25, mean in remaining three enclosures = 17.96; Table 1, Fig. 1A). The difference among enclosures varied through time as one would expect through habitat selection. The same was true for enclosure 15 during the final eight days while it received food supplements (mean in enclosure 15 = 25.25, mean in remaining three enclosures = 11.04; Table 1, Fig. 1B).

Meadow voles reduced habitat use when quality declined.—The number of voles using enclosure 13 declined after food supplements were moved to enclosure 15. As predicted, the relationship between the number of voles recorded and time was concave downward (quadratic regression, $F_{2,37} = 181.94$, $P < 0.001$, $R^2 = 0.91$, Fig. 2A).

Voles increased habitat use when quality increased.—The number of voles using enclosure 15 increased after food supplements were added. The relationship between the number of voles recorded and time, as predicted, was concave upward (quadratic regression, $F_{2,37} = 14.75$, $P < 0.001$, $R^2 = 0.44$, Fig. 2B).

But males and females differed in their response to habitat manipulation.—Both males and females reduced their use of enclosure 13 similarly (females $F_{2,37} = 45.44$, $P < 0.001$, $R^2 = 0.71$; males $F_{2,37} = 129.24$, $P < 0.001$, $R^2 = 0.88$, Fig. 2C, E). But only females increased use of habitat when quality improved (enclosure 15, females $F_{2,37} = 95.08$, $P < 0.001$, $R^2 = 0.84$, Fig. 2D; males $F_{2,37} = 0.18$, $P = 0.83$, Fig. 2F).

Significant differences in giving-up densities among enclosures were eliminated by habitat selection.—Log-

transformed giving-up densities in enclosures 13 and 14 were greater than those in enclosures 15 and 16 early in phase 3 before animals completed habitat selection. Differences in giving-up densities disappeared at the end of the experiment when animals had adjusted densities among habitats (time \times grouped enclosures interaction, $F_{1,14} = 5.21$, $P = 0.039$, Appendix D).

DISCUSSION

Density-dependent habitat selection has manifold effects on evolutionary processes because it constrains selection gradients and modifies the relative influences of gene flow and drift (Holt 1987). Many experimental tests of the underlying ideal-free distribution have, however, concentrated on the use of individual foraging patches (see reviews in Kacelnik et al. 1992, Kennedy and Gray 1993, Weber 1998, Krivan et al. 2008) rather

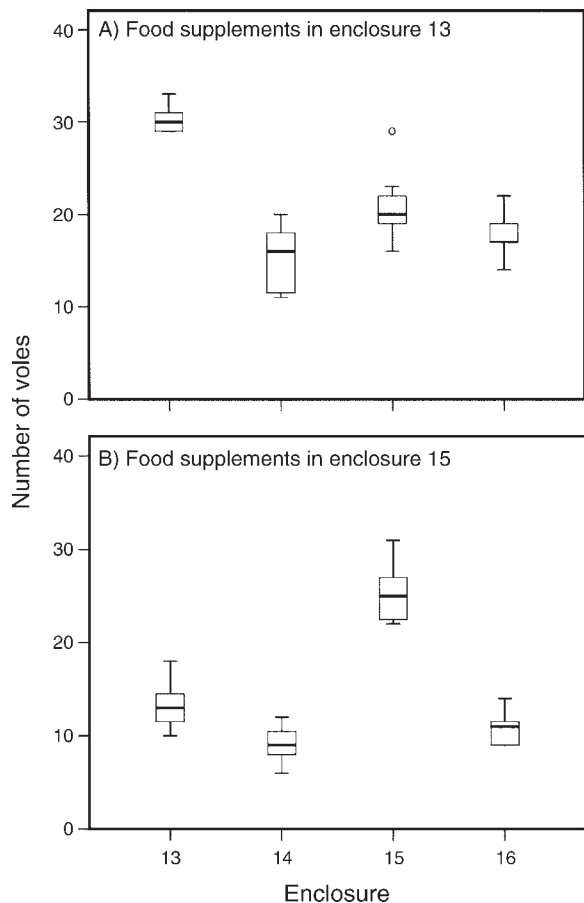


FIG. 1. Box plots illustrating significant differences in the mean number of voles recorded using food-supplemented vs. non-food-supplemented enclosures in the Lakehead University Habitron during summer 2008. (A) Food was added to enclosure 13 only. (B) Food was added to enclosure 15 only. The middle line of each box represents the median, the length of each box corresponds to the interquartile range (IQR), whiskers represent the range of values (excluding outliers), and the circle represents an outlier between 1.5 and 3 IQRs from the end of the box.

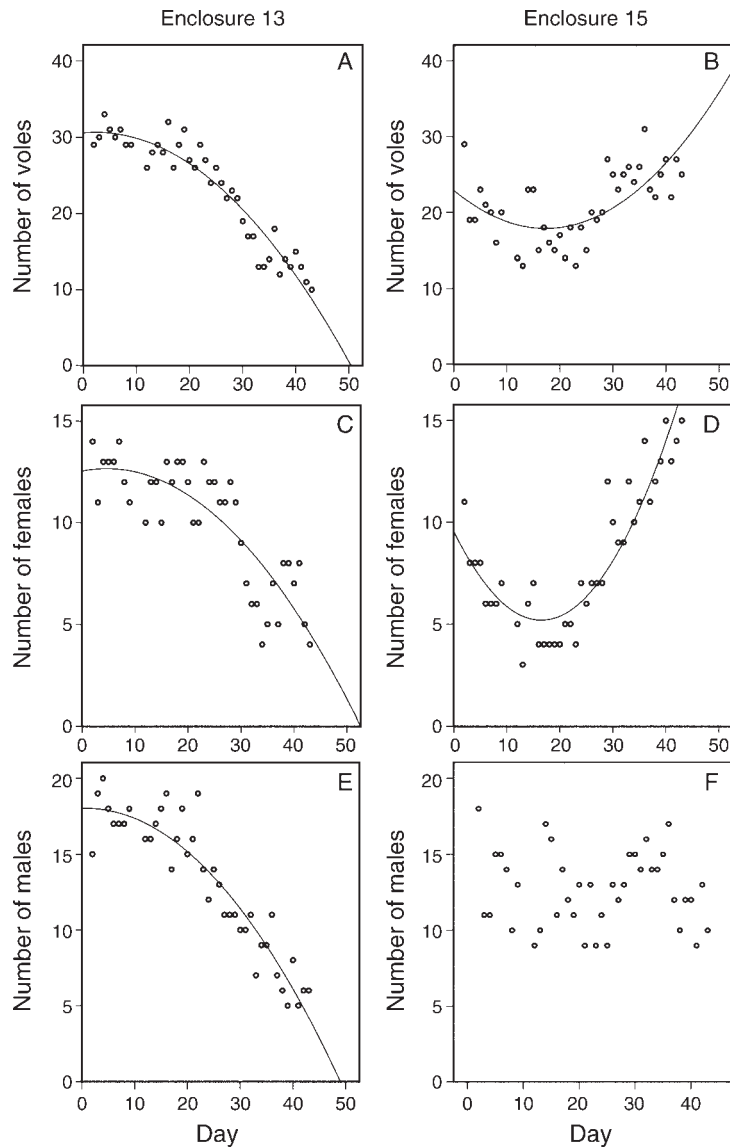


FIG. 2. Relationships between vole density and duration of supplemental feeding treatments in the Lakehead University Habitrion. Data represent the total number of voles as well as females and males considered separately. Lines correspond to best-fit quadratic regressions. Food was added to enclosure 13 during the early phase of the experiment, then moved to enclosure 15.

than on dispersal, and thus leave the question of habitat selection's potential influence on evolution mostly unresolved.

We aimed to enhance tests of the theory with definitive experiments evaluating whether meadow voles actively choose habitats of highest quality. We allowed voles to choose among pairs of four similar enclosures, added food to one of those enclosures, then moved the food to another. If free-ranging voles actively select habitat of the highest quality, then their density should have been higher in supplemented enclosures than elsewhere, they should have reduced their use of the first supplemented enclosure when food was moved elsewhere, and the same voles should have increased their use of the newly

supplemented enclosure. Early in the experiment, when habitat selection was improbable, voles in the high-quality supplemented enclosure (and its connected control) should have possessed higher giving-up densities than voles living in the non-supplemented enclosure (and its connected control). These differences should have disappeared by the end of the experiment after voles had adjusted densities to resource renewal. Voles in our experiment confirmed each prediction. Meadow voles actively selected the highest-quality habitat.

Curiously, habitat-enrichment tests of habitat selection appear to have been applied mainly to voles (see Shenbrot et al. 2006 for an exception). Although none of these



PLATE 1. One pair of replicated “covered” (left) and “open” foraging patches used to assess giving-up densities of foraging meadow voles in an enclosed old-field habitat during summer 2008. An antenna under each foraging tray identified voles injected with radio-frequency identification tags. Data were stored in field recorders (small white box), then downloaded to a laptop computer. Acrylic covers protected the trays from rain and wind. Photo credit: D. W. Morris.

previous vole experiments unambiguously documented active habitat selection, all bolster our conclusion.

Lin and Batzli (2001) manipulated cover and food availability in habitats used by enclosed populations of two *Microtus* species in southern Illinois. The density of each species at the end of the 22-week experiment was greater in subplots with high cover and abundant food than in subplots with low cover. Dispersal varied inversely with carrying capacity and densities in “poor” habitat remained low through emigration. Lin and Batzli concluded, tentatively, that prairie voles (*M. ochrogaster*) selected habitat according to an ideal-despotic distribution, and that meadow voles followed an ideal-free model. But they also emphasized that a declining proportion of prairie voles in low-quality habitat was inconsistent with the ideal-despotic model. Higher recruitment success by female meadow voles in high-cover habitats relative to low-cover treatments was similarly at odds with the equal fitness expectations arising through ideal-free habitat selection.

Pusenius and Schmidt (2002) used a similar design to assess autumn habitat selection by meadow voles in

central New York State. Vole distributions reflected differences in habitat quality. Vole density was consistently higher in mowed plots with supplemental food than in mowed plots without food supplements. But vole density was also consistently higher in unmowed control plots without supplemental food than in food-supplemented unmowed treatments. Pusenius and Schmidt (2002) attributed these divergent results to pre-emptive habitat choice. Large reproductive voles were deemed to usurp the highest-quality unmowed plots and forced smaller, subordinate individuals into controls and risky mowed plots. Voles occupying mowed plots, on the other hand, were deemed ideal-free habitat selectors.

Oatway and Morris (2007) also tested habitat-selection theory with enclosed populations of meadow voles by manipulating density and food resources, but not cover. Three of four experimental replicates were consistent with active habitat choice. Oatway and Morris (2007) attributed the single exception to density-vague dynamics at the relatively low population sizes used in their experiment.

Although each published experiment was consistent with habitat selection, each also included at least one "exceptional pattern." We interpret those exceptions to represent natural variation that cannot be controlled with restricted sample sizes imposed by field tests of habitat selection. In concert with the experiment we report here, however, the bulk of evidence is conclusively incontrovertible. Meadow voles are density-dependent habitat selectors.

Even so, females and males responded differently in our experiment. Female voles tracked changes in food availability by changing their use of habitat. Male voles reduced use of one enclosure through time as its quality declined, but maintained approximately constant use of another enclosure in which quality increased through time. Two other studies suggest that this pattern is general and adaptive.

Lin and Batzli (2004) also reported sexual differences in use of enriched habitat. Dispersing female voles were more likely than males to settle in food-supplemented habitats. Taitt and Krebs (1981, 1983) reported a similar pattern in the congener, *M. townsendii*. Females responded more strongly to food supplements than did males. Both studies suggested that energetic demands of gestation and lactation force female mammals to track resources more tightly than males.

We can gain further insight into sexual differences in energetic requirements by examining changes in habitat use in our experiment through time. Female voles congregated in food-supplemented enclosure 13 during phase 1 while reducing their use of enclosure 15 (compare Fig. 2C and D). Although food was switched to enclosure 15 to begin phase 2 after nine days, females continued to congregate in enclosure 13 for several additional days. We suspect that part of the explanation for this delayed response lies in the voles' inability to immediately deplete the surplus of sunflower seeds that had accumulated in enclosure 13. But males appeared to leave enclosure 13 earlier than females (compare Fig. 2E and C), and female use of enclosure 15 also lagged behind its increasing resource value (Fig. 2D). We thus suspect a second delayed response linked to the 5-wk time-course of gestation and lactation in female meadow voles. It would hardly be surprising if females postponed dispersal to new habitats until completing maternal care of current offspring.

Regardless of the differences between the sexes in density-dependent responses, it is clear that meadow voles alter their use of space in a way that reflects changes in habitat quality. Voles are active habitat selectors and vole density reflects the active choice of some habitats over others. Meadow voles demonstrably confirm the potential of density-dependent habitat selection to alter local patterns in distribution and demography, and to modify gene flow.

Although we have much to learn about sex- and state-dependent habitat choice, every naturalist knows that the vast majority of labile species occupy multiple

habitats in heterogeneous environments. Those organisms should also be capable of active density-dependent habitat selection. Rather than simply documenting active habitat selection by these species, future research will be most effective if it also explores habitat selection's far-reaching implications to the dynamics of populations and evolutionary processes.

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APPENDIX A

Description of the Lakehead University Habitron and experimental protocols used to assess active density-dependent habitat selection by meadow voles (*Microtus pennsylvanicus*) (*Ecological Archives* E091-218-A1).

APPENDIX B

An illustration of the experimental design used to test active density-dependent habitat selection by meadow voles (*Microtus pennsylvanicus*) in the Lakehead University Habitron (*Ecological Archives* E091-218-A2).

APPENDIX C

A test to confirm that resource enrichment of habitron enclosures corresponded to that of distinct habitats used by meadow voles (*Microtus pennsylvanicus*) (*Ecological Archives* E091-218-A3).

APPENDIX D

A test demonstrating that estimates of quitting-harvest rates (log-transformed giving-up densities) of meadow voles foraging in artificial resource patches confirmed predictions from theories of density-dependent habitat selection (*Ecological Archives* E091-218-A4).