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Animal Ecology

Rapid ideal habitat selection in a homogeneous environment

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Abstract

Studies of density-dependent habitat selection typically assess choices between two or more distinctly different habitat opportunities. Although such studies can clearly document habitat choice, they cannot unambiguously differentiate the effects of density from underlying differences in habitat and their associated cues for choosing some habitats over others. I resolve the ambiguity by assessing habitat selection between natural enclosures differing only in population density of meadow voles. Voles added weekly and cumulatively to one enclosure were allowed to disperse to a second. I maintained identical per capita food abundances in both enclosures. Student interns and I monitored vole numbers with live trapping, measured the amount of food eaten, and assessed foraging with giving-up densities in safe versus risky foraging patches. The number of voles and giving-up densities in the enclosures equilibrated weekly through dispersal. Resource consumption increased and giving-up densities declined with increasing vole density. Giving-up densities were lower in safe than in risky foraging trays, and the difference between trays declined with increasing vole density. The results document that the voles equilibrated densities and foraging gains with respect only to population density and did so without other obvious cues or mechanisms underlying habitat choice. Those cues and mechanisms may be sufficient to account for habitat choice, but it is only density that is necessary for density-dependent habitat selection.

KEYWORDS

density dependence, dispersal, foraging, giving-up density, habitat, habitat selection, ideal free distribution, meadow vole, predation risk

INTRODUCTION

Patterns in the distribution and abundance of species emerge through a combination of current and past population dynamics, dispersal, and stochastic contingencies in time and space. One way to visualize their interactive effects is to imagine a heterogeneous environment exploited by habitat-selecting consumers. Choices of which habitats to occupy, and the opportunities and constraints of doing so, determine reproduction, survival, the movements of organisms through space, and thus the local growth and decline of populations.

Underlying expectations of fitness and abundance are encapsulated in theories of ideal habitat selection (e.g., ideal free distribution, Cressman & Křivan, 2006; Fretwell, 1972; Fretwell & Lucas, 1969; Rosenzweig, 1981; ideal despotic distribution, Fretwell, 1972; Fretwell & Lucas, 1969; ideal pre-emptive distribution, McPeek et al., 2001; Morris & MacEachern, 2013; Pulliam, 1988; Pulliam & Danielson, 1991; Rodenhouse et al., 1997). Whether the expectations hold depends on our abilities to sort through competing versions of the theory (e.g., Tregenza, 1995) that relax assumptions of equal competitors (e.g., DiNuzzo & Griffen, 2020; Humphries et al., 2001; Sutherland & Parker, 1985), cost-free movement (e.g., Åström, 1994; Kennedy & Gray, 1993; Křivan & Cressman, 2024; Morris, 1987), perfect information (Abrahams, 1986), free choice (e.g., interference; Sutherland, 1983), differences in resource-holding power (Kokko et al., 2006), and the ability of individuals to match their phenotype with differences in habitat characteristics (Camacho & Hendry, 2020; Edelaar et al., 2008; Maynard Smith, 1966; Ravigné et al., 2004 and references therein). In each case, it is also crucial to recognize differences between direct density dependence including social attraction (Fletcher, 2007; Stamps, 2001; Swift et al., 2023) and Allee effects associated with mating opportunities, versus indirect effects such as those associated with public information (Doligez et al., 2002; Valone, 1989), safety, and resource depression.

Tests of habitat selection theory typically use experiments that enable the choice of alternative patches either expected or manipulated to yield different fitness outcomes (e.g., Kennedy & Gray, 1993; Milinski, 1979; Morris, 2003; Tregenza, 1995 and many others). Such studies, when densities differ between alternatives, definitively reject a null expectation of passive diffusion. They also clearly document the "stopping rule" of ideal density-dependent habitat selection: "do not disperse when density equalizes the expectation of fitness in each habitat." The experiments are less reliable at revealing the assumption of a density-dependent starting rule "disperse when density elsewhere corresponds with an expectation of higher fitness" because fitness expectations might also depend on innate or manipulated differences among habitats. It is thus necessary to devise experiments enabling movement between identical habitats that differ only in density.

Controlling density dependence is relatively straightforward in small-scale studies that vary resource ratios available to foragers choosing among identical patches (e.g., Sirovnik et al., 2021 and references therein). Controls varying only density can also be implemented in laboratory studies using organisms with short generation times such as unicellular algae (Moses et al., 2013) and asexual hexapods (Bajina et al., 2019). Similar experiments are far more difficult at larger scales where wild animals must disperse from one habitat to another under natural conditions. Field-scale experiments are nevertheless crucial to eliminate confounding influences on habitat choice, to explore the speed and spatial scale of habitat selection, and to evaluate additional influences associated with differences among individuals including sex (e.g., Bowers & Smith, 1979; Fortin et al., 2022; Morris, 1984), age (e.g., Anders et al., 1998), and personality (Edelaar et al., 2008).

Successful experiments, whether between different or identical options, require assessments of fitness or suitable proxies associated with individuals' choice. Quitting-harvest rates, estimated with giving-up densities (GUDs, Brown, 1988, 1989), represent an appropriate fitness surrogate for energy-limited foragers. GUDs accurately reflect habitat-dependent differences in fitness (Morris & Davidson, 2000) and are reliable metrics for assessments of habitat selection theory in field experiments with small mammals (e.g., Morris, 2011, 2014, 2020, 2024 and references therein).

I thus outline an experiment that standardized habitat quality in two connected habitats while sequentially increasing the population density of meadow voles (*Microtus pennsylvanicus*, a common and widely distributed 30-g North American herbivore) in only one. I describe how I use and analyze GUDs from safe and risky patches to test the theory. I conclude by evaluating the importance of the results to habitat-selection theory and our understanding of the importance of habitat selection in determining patterns of distribution and abundance.

METHODS

Field experiments

Three undergraduate assistants and I conducted the experiment in August 2023 in two adjacent and identical 25 m × 25 m outdoor vole-proof enclosures in northwestern Ontario, Canada (48°19′49″ N, 89°47′27″ W [North American Datum 83]). Each enclosure was surrounded by a solid galvanized metal fence (1.25 m tall buried to a depth of 50 cm). When open, voles could move between enclosures through a single circular ground-level gate (diameter = 9.25 cm). The release enclosure (15) had previously been used in a different experiment in which mulched straw had been added to two of its four census stations. Most of that straw was fully decomposed and had no influence on the results. Complete field methods are detailed in Appendix S1.

We sequentially added equal numbers of adult male and female voles to the release enclosure weekly (Thursday, day 1) when we also provisioned each enclosure with rabbit chow equal to the combined energetic needs of all voles in the experiment. We opened the gate for six consecutive days and nights during which the voles could disperse between enclosures. We placed pairs of plastic trays containing 8 g of whole oats mixed thoroughly in 1.5 L of sieved silica sand at eight equally spaced foraging and live-trap stations to measure GUDs twice during each treatment period (day 2 and day 7, respectively, available for 22 h from 15:00 to 13:00 the following day). Voles could choose a safe tray (under a plywood cover) or a risky one (under a clear polyethylene cover) nearby. We collected trays, re-sieved the contents to collect, clean, and weigh residual oats (GUD), then recharged each one with new oats for the next foraging period. We divided the weekly allotment of rabbit chow equally among 32 small wooden feeders in each enclosure and placed two under each enclosure's eight safe and eight risky covers used for measuring GUDs. We closed the gate on Wednesday afternoon, live-trapped the voles overnight, weighed any leftover rabbit chow, added four more voles to the experiment, and adjusted the allotment of chow to the new number of voles ($N = 20$ voles and 128 GUDs). We completed our fieldwork by live-trapping during two consecutive nights and days with the intent to capture all voles used in the experiment.

Statistical analyses

I began by evaluating the number and sexes of voles captured in each enclosure during the four treatment periods (= density treatments). I then used a repeated-measures general linear model (GLM) to assess whether GUDs varied through time, between safe and risky patches, and between the previously straw-covered versus no-straw stations in enclosure 15 (patch type and presence/absence of straw treated as between-subjects effects, within subjects factor = foraging bout). The purpose of this analysis was twofold. 1. To search for any residual differences between enclosures that voles might have perceived related to the 2021 experiment. 2. To evaluate whether differences between the two station types might be consistent with territorial behavior (assumption: territorial voles should prefer the added cover of potentially protective straw). I repeated this analysis on the amount of chow eaten. I assumed that the sphericity assumption was violated and applied the Greenhouse–Geisser (G–G) correction to all tests involving time.

The GLMs detected no significant differences between straw-covered versus no-straw treatments, so I used repeated-measures mixed models (random effect = station, method = Restricted Maximum Likelihood, covariance structure for random effects = variance components and diagonal for repeated effects, df adjusted with Satterthwaite's approximation) to assess time-dependent differences in GUDs and the amount of chow eaten between enclosures and between safe versus risky patches. I used separate analyses for each dependent variable because there were large differences in the magnitudes of the variables and because the underlying number of samples varied between the GUD and chow estimates (8 samples across 4 treatment periods for GUDs, 4 samples for amount of chow eaten). All analyses were conducted using IBM SPSS V 29 software.

RESULTS

There was no difference in density between enclosures

The number of captured voles increased through time (Figure 1A). The number of voles in each enclosure was either identical (even numbers of voles) or differed by only one animal (odd numbers of voles). Target densities were met, however, only during the first treatment period, likely because there was no attempt to restrict predators (Canada jays [*Perisoreus candadensis*] were observed chasing newly released

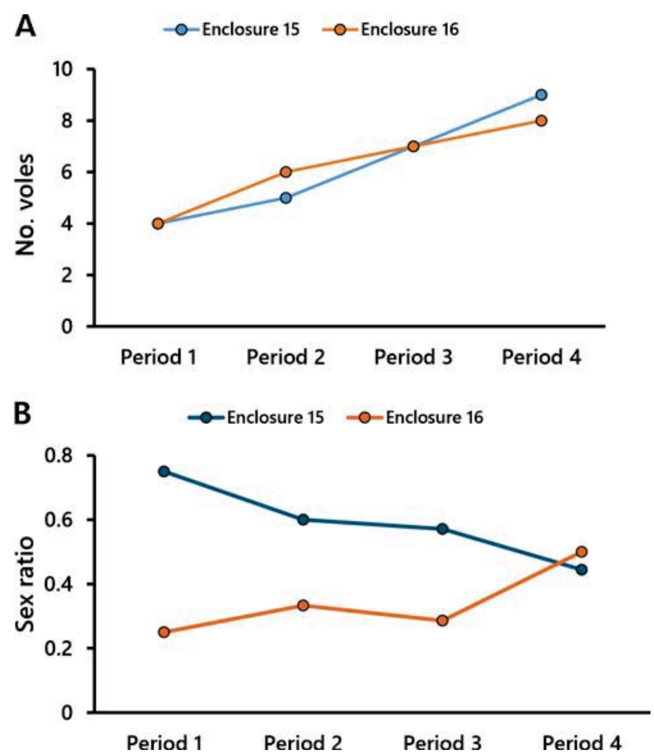

FIGURE 1 (A) The number of meadow voles captured during four census periods in two connected enclosures at the Lakehead University Habitron in northern Ontario, Canada. (B) The sex ratio of meadow voles (males/total) during the same four census periods. All voles were released in enclosure 15. All voles in enclosure 16 immigrated from 15.

voles). Even so, the number of voles increased as designed throughout the experiment and thus enabled valid assessments of habitat selection and foraging with changes in population size (corresponding to population densities ranging from 128 to 320 ha^{-1} roughly encompassing the maximum densities of meadow voles observed in long-term studies in southern Manitoba [~200 ha^{-1}, Mihok et al., 1985] and in enclosed old pasture habitat in Illinois [338 ha^{-1}, Lin & Batzli, 2001]). There were two unusual captures. One juvenile deer mouse was captured and removed from enclosure 15 during treatment period 1. One young (25 g) untagged female vole first appeared in enclosure 16 during period 2, was captured during both periods thereafter, and contributed to our live-trap measures of population size. We captured no animals that moved between enclosures other than those intended, so it is likely that this animal was a surviving juvenile from a litter produced by female voles living in that enclosure during 2022.

Sex ratios converged during the experiment

Sex ratios favored males in enclosure 15, and females in enclosure 16, during the first three treatment periods, but converged towards 1:1 in the fourth and final density treatment (Figure 1B; an odd number of animals [9] made a perfect 1:1 ratio in enclosure 15 impossible).

GUDs declined with density and were lower in safe foraging patches than in risky ones

Mean GUDs in enclosure 15 declined across foraging bouts as the number of voles increased ($F_{2.27,10.67} = 32.43$, $p_{G\text{–}G} < 0.001$, $\eta^2 = 0.89$; Figure 2). No interaction using the G-G correction was statistically significant at the 0.05 level. GUDs were lower in safe patches in the enclosure 15 analysis ($F_{1,4} = 19.22$, $p = 0.12$, $\eta^2 = 0.83$, marginal mean in safe patches = 3.18 g, 95% CI 2.82–3.54; marginal mean in risky patches = 3.98 g, 95% CI = 3.62–4.34; Table 1), and also in the analyses comparing enclosures (below). GUDs were not different between controls and two stations treated with straw in 2021 (enclosure 15; Appendix S1), nor did that treatment affect differences between cover and open trays (Table 1).

Resource consumption in enclosure 15 was not influenced by the previous straw treatment

Voles ate more chow from safe foraging patches (66.67 g, 95% CI 52.4–80.95) than they did from risky ones (41.47 g, 95% CI = 27.29–55.84; $F_{1,4} = 11.92$, $p = 0.026$, $\eta^2 = 0.75$; Table 1). The main effect of the 2021 straw treatment and its interaction with safe versus risky patches was not significant (Table 1).

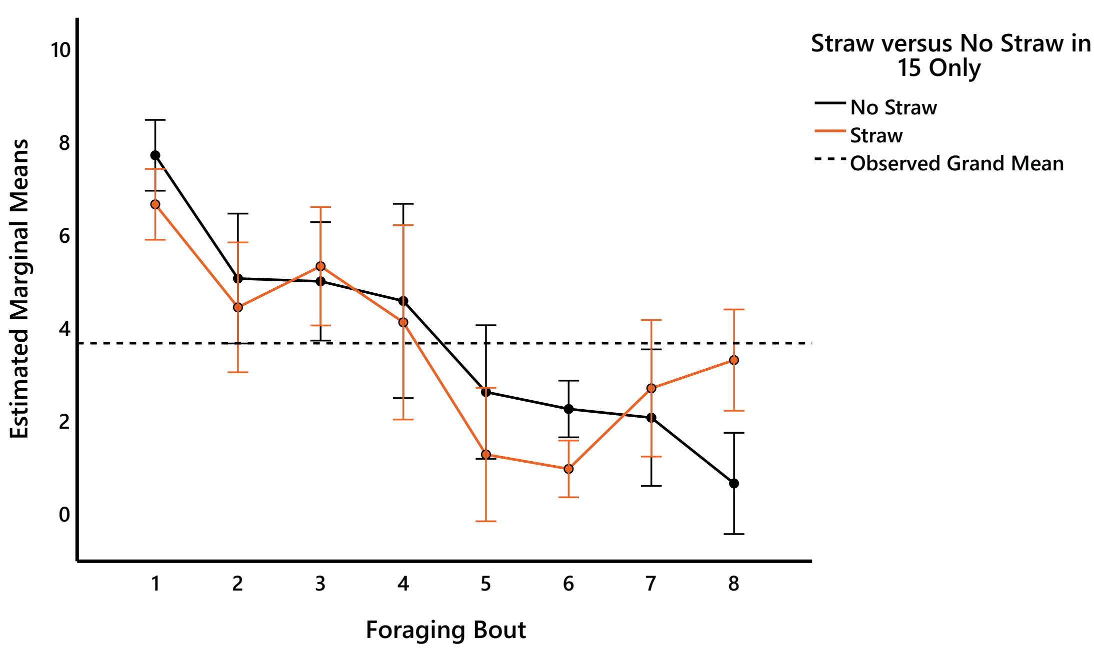

FIGURE 2 The decline through eight foraging bouts of mean giving-up densities (in grams) of meadow voles foraging at stations paired by previous treatments of additional cover (straw) or control (no straw) in release enclosure 15 at the Lakehead University Habitron in northern Ontario, Canada. Vertical lines with horizontal bars are 95% CIs.

TABLE 1 Results of repeated-measures general linear models assessing between-subjects effects for giving-up densities and chow eaten in enclosure 15 at the Lakehead University Habitron in northern Ontario, Canada.

Source	df	*F*	*p*	Partial η^2
Giving-up densities				
Intercept	1	1544.88	<0.001	0.997
Safe versus risky patch	1	19.22	0.012	0.828
Straw versus no straw	1	0.63	0.472	0.136
Two-way interaction	1	4.25	0.108	0.515
Error	4			
Chow eaten				
Intercept	1	221.66	<0.001	0.982
Safe versus risky patch	1	11.92	0.026	0.749
Straw versus no straw	1	0.34	0.592	0.078
Two-way interaction	1	1.00	0.374	0.200
Error	4			

Differences in consumption between safe and risky patches decreased with increased vole density

The total amount of chow eaten by voles increased through treatment periods ($F_{1,4.58} = 20.40$, $p = 0.004$; Table 2, Figure 3), but the amount did not vary between enclosures (Table 2). The difference in the amount of chow eaten in safe minus risky patches decreased through treatment periods ($F_{1,5.08} = 6.96$, $p = 0.03$) and did not depend on ($p = 0.87$), or interact with, enclosure ($p = 0.16$; Table 2).

The difference in GUDs, as that for chow consumption, varied through treatment periods ($F_{1,21.85} = 3.24$, $p = 0.04$; Table 2). The difference in GUDs was much smaller in the fourth treatment period (marginal mean GUD = 0.108, 95% CI = −0.903–2.119) than in either period 1 (marginal mean = 1.926, 95% CI 1.122–2.729) or period 3 (marginal mean = 1.369, 95% CI = 0.689–2.049), but was not significantly different from that in period 2 (marginal mean = 1.116, 95% CI = 0.224–1.784). Voles had lower GUDs in safe patches during periods 3 and 4 (marginal means and 95% CIs = 2.16, 1.07–3.25 and 2.33, 1.30–3.36, respectively) than in periods 1 and 2 (marginal means and 95% CIs = 4.33, 3.24–5.43 and 4.03, 3.29–4.77; $F_{3,18.32} = 10.58$, $p < 0.001$; Table 2).

Mean GUDs were lower in enclosure 15 (emigrants) than in enclosure 16 (immigrants)

Mean GUDs declined through foraging bouts ($F_{3.92,47.04} = 30.40$, $p_{G\text{–}G} < 0.001$, $\eta^2 = 0.717$) with a temporal trend that differed weakly between enclosures ($F_{3.92,47.04} = 2.69$, $p_{G\text{–}G} = 0.043$, $\eta^2 = 0.183$; Figure 4). Mean GUDs were less in safe patches (marginal mean = 3.41, 95% CI = 2.87–3.95) than in risky patches (marginal mean = 4.54, 95% CI = 4.00–5.08; $F_{1,12} = 10.38$, $p = 0.007$, $\eta^2 = 0.464$; Table 3) and less in enclosure 15 (marginal mean = 3.58, 95% CI = 3.04–4.12) than in enclosure 16 (marginal mean = 4.37, 95% CI = 3.83–4.91; $F_{1,12} = 5.09$, $p = 0.044$, $\eta^2 = 0.298$; Table 3). Neither effect depended on the other (no patch × enclosure interaction; Table 3).

TABLE 2 Results of repeated-measures mixed models assessing fixed effects for the total chow eaten, differences in chow eaten between paired safe minus risky foraging patches, and differences in giving-up densities between risky minus safe foraging patches at the Lakehead University Habitron in northern Ontario, Canada.

Source	df	*F*	*p*
Total chow eaten			
Intercept	1, 3.522	77.701	0.002
Treatment period	3, 4.585	20.395	0.004
Enclosure	1, 3.522	0.551	0.504
Two-way interaction	3, 4.585	0.952	0.487
Difference in chow eaten between paired safe minus risky foraging patches			
Intercept	1, 5.854	19.184	0.005
Treatment period	3, 5.080	6.956	0.030
Enclosure	1, 5.854	0.029	0.871
Two-way interaction	3, 5.080	2.631	0.160
Difference in giving-up densities between paired risky minus safe foraging patches			
Intercept	1, 6.325	35.532	<0.001
Treatment period	3, 21.848	3.240	0.042
Giving-up density in safe patches			
Intercept	1, 7.209	95.815	<0.001
Treatment period	3, 18.325	10.575	<0.001

There was no difference in mean GUDs between enclosures after dispersal

I wondered whether data collected on the day following release (foraging from 15:00 Thursday through 13:00 Friday; day 2) may not have provided sufficient time for newly released animals to move to the other enclosure. If so, then the difference in mean GUDs between enclosures should disappear from dispersed voles foraging on

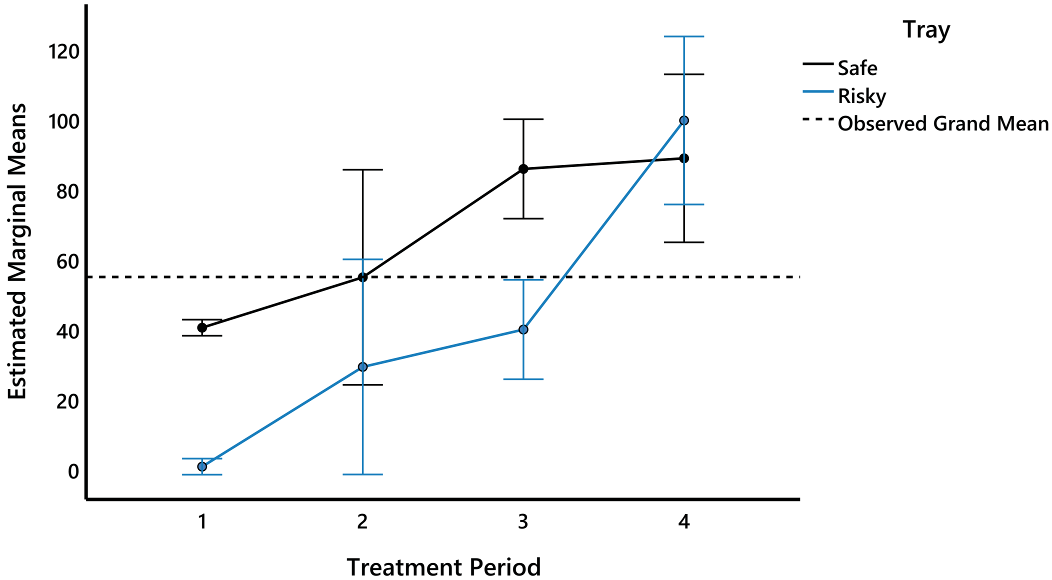

FIGURE 3 The increase in the mean amount (in grams) of rabbit chow eaten by meadow voles during four census periods in safe versus risky foraging sites at the Lakehead University Habitron in northern Ontario, Canada. Vertical lines with horizontal bars are 95% CIs.

the day that we closed the gates for live trapping (from 15:00 Tuesday through 13:00 Wednesday; day 7). I assessed this possibility using only the "day seven" data.

Mean GUDs declined as population density increased during treatment periods of the experiment ($F_{2.28,27.29} = 19.41$, $p_{G–G} < 0.001$, $\eta^2 = 0.618$). This effect differed between safe and risky patches ($F_{2.28,27.29} = 3.50$, $p_{G–G} = 0.039$, $\eta^2 = 0.226$), but not between enclosures ($F_{2.28,27.29} = 0.96$, $p_{G–G} = 0.406$, $\eta^2 = 0.074$). Mean GUDs were marginally less in safe patches (marginal mean = 2.99, 95% CI = 2.26–3.72) than in risky patches (marginal mean = 3.97, 95% CI = 3.24–4.70; $F_{1,12} = 4.28$, $p = 0.0.061$, $\eta^2 = 0.263$; Table 4) and were not significantly different between enclosures (enclosure 15 marginal mean = 3.08, 95% CI = 2.36–3.81; enclosure 16 marginal mean = 3.88, 95% CI = 3.15–4.61; $F_{1,12} = 2.82$, $p = 0.12$, $\eta^2 = 0.191$; Table 4). Neither effect depended on the other (no patch × enclosure interaction; Table 4).

DISCUSSION

Vole abundances and foraging were consistent with quick adjustments to density expected from ideal habitat selection. The number of voles occupying each identical enclosure was either equal (when the number of enumerated voles was an even number) or varied by a single individual (when the number enumerated was an odd number). Sex ratios in the two enclosures were more volatile through time, but converged towards equal proportions at the end of the experiment.

Lin and Batzli (2001) reported similarly rapid ideal-free habitat selection by meadow voles in Illinois. The more monogamous and social (e.g., Getz et al., 1981; Thomas & Birney, 1979) prairie vole (*Microtus ochrogaster*) in that study also achieved ideal-free distributions, but only near the end of the 22-week experiment. It thus appears that mating and social systems can delay, but not forever forestall, ideal habitat selection.

The voles consumed similar amounts of supplemental food from each enclosure, ate more oats (lower GUDs), and accepted more foraging risk (a smaller difference between chow consumption in safe vs. risky patches) as resources and density increased. Several non-exclusive mechanisms can account for this pattern including foragers in a reduced energetic state (Brown, 1988), safety in numbers (Rosenzweig et al., 1987), intraspecific competition (e.g., Menezes et al., 2018), and learned behaviors such as altering time schedules to forage during periods of low risk, increasing vigilance or its effectiveness, and increasing foraging efficiency and tenacity (Brown & Kotler, 2004). Whatever the cause, the result supports an expanding literature demonstrating that risk from competitors often yields patterns of foraging and vigilance that might otherwise be ascribed to predation (Dupuch et al., 2014; Halliday & Morris, 2013; Morris, 2009, 2019; Shalev et al., 2025). The key point to be resolved is not which mechanisms or combinations apply to voles, but instead whether the animals' foraging truly exposed them to reduced schedules of survival and reproduction. The answer remains moot except that there was no obvious trend towards increased mortality during the experiment.

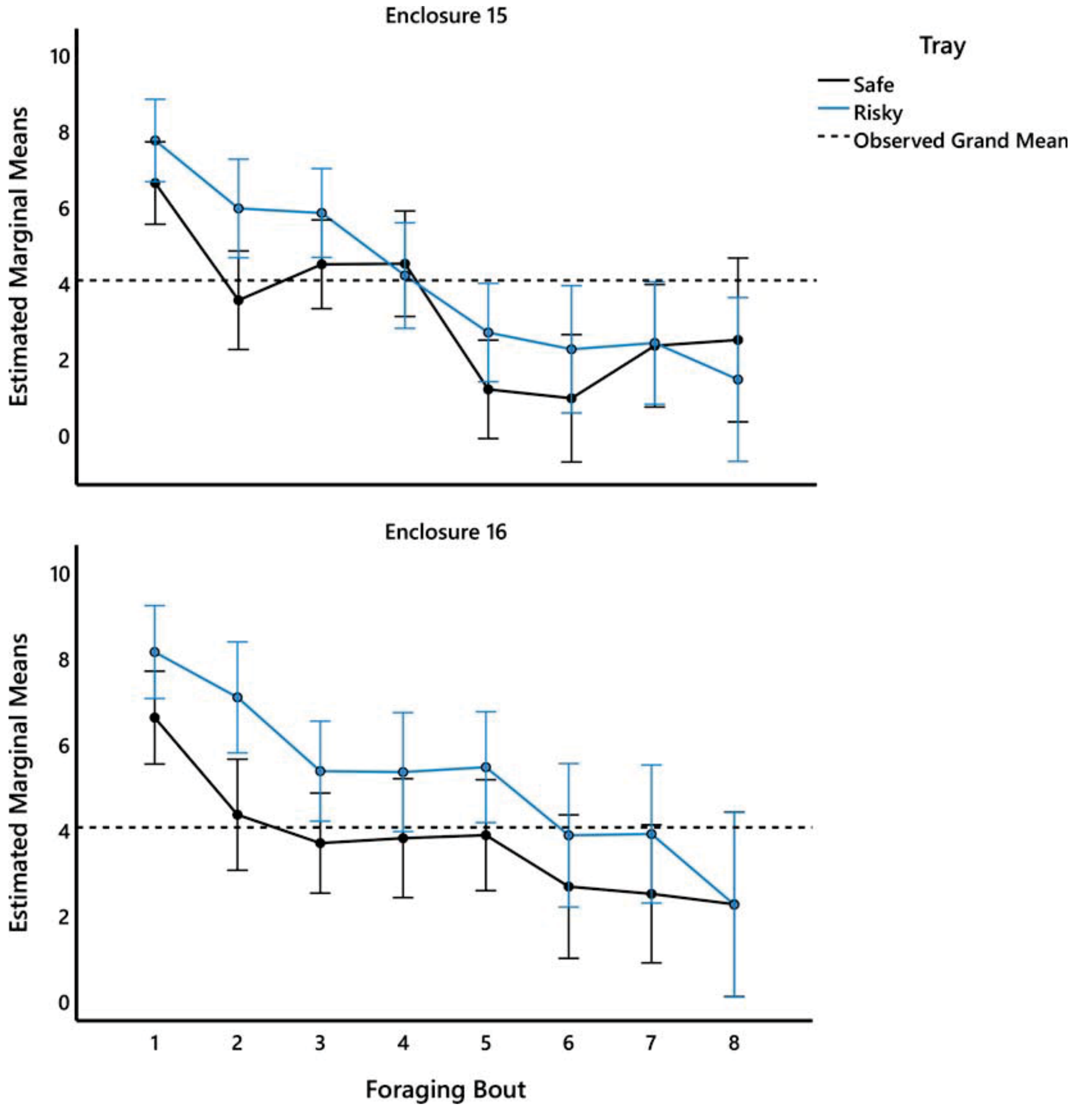

FIGURE 4 The decline through eight foraging bouts of mean giving-up densities (in grams) of meadow voles foraging at stations in two connected enclosures at the Lakehead University Habitron in northern Ontario, Canada. All voles were released in enclosure 15. All voles in enclosure 16 immigrated from enclosure 15. Vertical lines with horizontal bars are 95% CIs.

GUDs tended to be lower in the emigrant enclosure (15) than in the immigrant enclosure (16). This difference disappeared when GUDs were restricted to the seventh day after release. GUDs in safe foraging patches were strikingly lower than those observed in risky patches. None of these results appeared influenced by a previous treatment that added additional straw cover at two of the four stations in enclosure 15.

The experimental design eliminated possible confounding effects of innate or manipulated differences between enclosures, as well as systematic differences in phenotypes such as those related to age, mass, body size, and previous habitat exposure. It is thus clear that the voles, given a choice between two otherwise identical habitats, quickly harmonized densities and foraging to reflect the habitats' equal opportunities. This does not necessarily mean that the rodents cued their choices directly on density, only that whatever cues they may have used were reliable representations of the effects of density on resource harvest.

The experiment's clear indication of density dependence does not eliminate the likelihood that habitat choice can be influenced by experience (e.g., Davis & Stamps, 2004; Stamps, 2001, and many others), public information (e.g., Doligez et al., 2002; Valone, 1989), sex (e.g., Bowers & Smith, 1979; Fortin et al., 2022; Morris, 1984), age (e.g., Anders et al., 1998), and social attraction (Fletcher, 2007; Stamps, 2001; Swift et al., 2023). Nor does it eliminate the possibility that habitat selection can be thwarted by social fences

TABLE 3 Results of repeated-measures general linear models assessing between-subjects effects for meadow vole giving-up densities between safe and risky foraging patches in two enclosures at the Lakehead University Habitron in northern Ontario, Canada (8 foraging bouts).

Source	df	*F*	*p*	Partial η^2
Intercept	1	515.57	<0.001	0.977
Safe versus risky patch	1	10.38	0.007	0.464
Enclosure 15 versus enclosure 16	1	5.09	0.044	0.298
Two-way interaction	1	0.88	0.365	0.069
Error	12			

TABLE 4 Results of repeated-measures general linear models assessing between-subjects effects for meadow vole giving-up densities between safe and risky foraging patches in two enclosures at the Lakehead University Habitron in northern Ontario, Canada (four foraging bouts; day 7 only).

Source	df	*F*	*p*	Partial η^2
Intercept	1	216.82	<0.001	0.948
Safe versus risky patch	1	4.282	0.061	0.263
Enclosure 15 versus enclosure 16	1	2.824	0.119	0.191
Two-way interaction	1	0.678	0.426	0.054
Error	12			

(Hestbeck, 1982), or that different processes might underlie habitat selection at different population sizes. For example, safety from predators drives habitat choice by elk in Yellowstone at low density, whereas access to food dominates habitat choice at high density (Smith et al., 2023). The design of the experiment reported here eliminates such effects, as well as habitat area or volume, that while sufficient to cause or modify habitat choice are not necessary for ideal density-dependent habitat selection, at least by meadow voles living in northwestern Ontario.

Most proposed mechanisms that might influence habitat choice are, in one way or another, linked to the ability of individuals to choose habitats that match their phenotype with the habitat yielding the best prospects for fitness (Camacho & Hendry, 2020; Edelaar et al., 2008; Turku & Rossi, 2022). The ability of organisms to match phenotypes with habitat has numerous ecological and evolutionary effects involving gene flow (Edelaar et al., 2008), dispersal dynamics and niche conservatism (Holt & Barfield, 2008, 2015), maintenance of polymorphisms (Ravigné et al., 2004), sympatric speciation (Maynard Smith, 1966), species diversity (Ravigné et al., 2009), and many more (see Ravigné et al., 2009 for an early list). The consequences of matching habitat choice (not to be confused with "habitat matching rules" [Fagen, 1987; Morris, 1994; Pulliam & Curaco, 1984] that are explicitly density dependent) can nevertheless be expected to not only vary with density but to influence evolution through their interaction with demography and life history (Morris, 2025). The clear density-dependent choice of habitat by meadow voles alerts us that we must work towards better understanding the interactions between processes of habitat choice and the dynamics of populations in space and time. It is density dependence, after all, that acts to regulate populations and organize ecological communities (Morris, 1988; Rosenzweig, 1981).

Even so, if phenotypes are sufficiently variable, then individuals capable of matching their phenotype with habitat should often reap higher fitness than individuals that fail to do so. The existence of effective phenotype matching depends on the likelihood that different phenotypes can choose between readily available alternative habitats. Examples include the choices made between pools and riffles by phenotypically plastic salamanders (Lowe & Addis, 2019) and adaptive choices of thermal microhabitats by pygmy grasshoppers (*Tetrix subulate*) painted either black or white (Karpestam et al., 2012). Yet, phenotype matching does not always correlate with fitness prospects. Large male pied flycatchers (*Ficedula hypoleuca*) prefer deciduous forests while smaller males prefer to breed in coniferous forests, but recruitment success from nest boxes does not correspond with size-dependent habitat preference (Camacho et al., 2015). Organisms that abandon a formerly suitable habitat when its quality is compromised, as in amphibious fishes seeking hypoxic terrestrial habitats when their aquatic habitat dries out (Turku & Rossi, 2022), document strong phenotype × environment interactions, but the interaction does not bear directly on density-dependent habitat selection.

Whether phenotypic matching occurs, whether it is adaptive or not, and whether experience also influences habitat selection has minimal influence on the habitat selection by voles reported here. The use of naïve voles of similar size and age eliminated all obvious cues related to phenotype and experience. The weekly addition of naïve adult animals, however, departs substantially from the recruitment of juvenile animals expected under natural patterns of population growth. The treatment is appropriate for the purpose of assessing voles' abilities at density-dependent habitat selection. It is not a valid predictor of patterns or dynamics that one would observe in a free-living population of voles subject to various forms of phenotypic and temporal matching. Priority effects, for example, are much more likely when large and dominant adult residents compete for habitat against smaller subordinate juveniles than when they are exposed to the pulsed onslaughts of immigrants of similar ages and body sizes in field experiments. These concerns aside, it remains clear that voles in northwestern Ontario can select habitats that balance density and resource harvest. These abilities can no doubt be augmented by past experience, phenotype matching, public information, and other characteristics that modify habitat choice. It is worth repeating that those abilities, while sufficient for habitat choice, are nevertheless unnecessary to produce density-dependent patterns of habitat use in agreement with simple models of habitat selection.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Morris, 2026a, 2026b, 2026c) are available from Borealis: https://doi.org/10.5683/SP3/SHPZOX, https://doi.org/10.5683/SP3/PFKTB6, https://doi.org/10.5683/SP3/NKRB3I.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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