

Apparent predation risk: tests of habitat selection theory reveal unexpected effects of competition

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ABSTRACT

Questions: Does reducing density of one species increase habitat use by its competitor? If so, can the competitive effect mimic predation risk?

Hypotheses: A competing species should increase its use of secondary habitat as the density of its competitor in that habitat declines. And it should forage in safe sites more readily when its competitor is abundant than when it is sparse.

Organisms: Two co-existing species of northern voles (*Myodes gapperi* and *Microtus pennsylvanicus*) known to have distinct habitat preferences.

Field site: Two pairs of interconnected rodent-proof enclosures in field and forest habitat at the Lakehead University Habitron near Thunder Bay, Ontario, Canada.

Methods: I predicted density-dependent habitat use from first principles, then measured the density of *Myodes* in the two habitats as well as its quitting-harvest rate in artificial food patches. I tested the predictions by contrasting treatments where I reduced the density of *Microtus* in the presence of *Myodes*, versus controls where I reduced an equal density of *Myodes* existing alone.

Results: *Myodes* used its preferred forest habitat more at high *Microtus* density than at low *Microtus* density. But *Microtus* occupied both habitats at all densities. *Myodes* used safe foraging sites more intensely in the treatment where *Microtus* was present than in the control where it was absent.

Conclusions: Competition between these two vole species is reduced by density-dependent habitat selection. But *Myodes* also trades off food for safety to avoid competition with larger *Microtus*. Ecologists must first eliminate competition if they are to accurately estimate the effects of predation risk on species co-existence.

Keywords: apparent competition, density dependence, habitat, habitat selection, optimal foraging, predation risk, vole.

INTRODUCTION

Non-lethal trait-mediated interactions, where prey alter their phenotype in response to predators, are likely to influence prey distribution, abundance, and food-web dynamics at least as much as does direct mortality (e.g. Sinclair and Arcese, 1995; Lima, 1998; Werner and Peacor, 2003;

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Schmitz *et al.*, 2004; Pangle *et al.*, 2007). But few field experiments have examined non-lethal effects at a scale appropriate for assessing population dynamics, and especially so for terrestrial systems (Lima 1998). Such experiments are sorely needed because: (1) trait-mediated interactions may often depend on the density of other prey (Peacor, 2003); (2) trait-mediated effects, such as reduced prey activity in the presence of predators (Peacor and Werner, 1997), may themselves ‘cascade’ across trophic levels [examples include reduced consumption of lower trophic levels as well as differential responses of alternative prey species that modify their interactions with one another, and thus their effects on resource species (Werner, 1991; Werner and Peacor, 2003)]; and (3) the metrics that we use to assess non-lethal effects, such as harvest rates, are intrinsically density dependent (Mitchell *et al.*, 1990).

Non-lethal effects associated with predation also modify competitive interactions among prey. For example, when two or more prey species occupy similar patches, optimally foraging predators may aggregate in patches with the greatest total prey density, and harvest those patches more intensely than if the two prey species lived separately. Even if the prey do not compete with one another, the presence of an alternative prey species increases predation rates, and yields a local (—, —) interaction between them [short-term apparent competition (Holt and Kotler, 1987)].

Current theory does not easily allow us to evaluate the alternative possibility that interactions between competitors might modify our interpretation of predation risk. If two competing prey species choose separate patches normally associated with differences in predation risk [such as the ‘open’ and ‘shrub’ contrasts commonly employed in studies on rodents (Brown and Kotler, 2004)], avoidance of a competitor preferring open habitat could yield the same indirect effect as avoidance of predation risk. A similar effect can occur if both species prefer open patches, as might occur if these patches provide a more favourable thermal environment for foraging. Harvest rates of both species will decline as the species deplete resource levels in the shared patches. Individuals of each species will receive less energy from their foraging effort. Depleting harvest rates will thus increase the marginal value of energy and cause individuals to allocate more foraging effort to the ‘safe’ patch located under cover. It is thus crucially important to evaluate, in a single manipulative experiment, the joint effects of inter-specific competition and predation risk on prey behaviour.

There is at least one other important reason to conduct such studies. Many models of habitat selection assume implicitly that competing species with distinct habitat preferences will occupy only their preferred habitat when competitors are present (Rosenzweig, 1974, 1979, 1981; Morris, 1988). Specialists occupying their preferred habitat reduce the fitness expectations of competitors living there, and thereby alter the competing species’ proportional abundance across the different habitats that it occupies. So, when two species have a distinct habitat preference, their stable competitive co-existence will be resolved around a joint density where each lives in a separate habitat ‘independent’ of its competitor [the ghost of competition past (Rosenzweig, 1974)]. Competition between the species forces each one into its preferred habitat where it can no longer interact, directly, with its competitor. Computer simulations (Morris, 2003a, 2004) of ideal habitat selection by two species with distinct habitat preferences suggest instead that, for any given population size, such species can attain multiple equilibria of abundance. A variety of different possible mixtures of the two species can equalize each species’ fitness in the two habitats. Competition can still be resolved through habitat selection, but habitat use is dominated by partial preferences that illuminate the otherwise invisible competitive ghost (Morris, 1999; Wasserberg *et al.*, 2006, 2007).

To understand how partial preferences reveal competition, consider the case of two species living at equilibrium in two different habitats. An individual's expectation of fitness is equal in both habitats because inter-specific competition across habitats is balanced against intra-specific competition in its preferred habitat. But if the relative abundances of the species change, then the balance of intra- versus inter-specific competition will also change, and one or the other species may begin to occupy its competitor's preferred habitat (partial habitat preference). Since the species now overlap in habitat use, their competitive ghost is no longer invisible, and their true competitive interaction can be measured through careful assessments of population density (Morris, 1999).

Thus I describe a habitat selection experiment where I simultaneously assessed competition between two rodent species with distinct habitat preferences while documenting putative differences in predation risk. My assistants and I manipulated densities in a two-habitat system with the aim of answering two key questions: (1) When tested experimentally, do competitors with distinct habitat preferences segregate completely into their preferred habitats, or mix with one another? (2) Does a competing species alter our perception of predation risk?

I begin with a brief review of habitat selection theory as it applies to designing appropriate experiments to assess competition. I also review foraging theory to assess how competitors influence patch use. I then describe the model system and experimental design. The results of the experiment might surprise you. Despite their distinct habitat preferences, both species occupied both habitats at all population sizes. But at a smaller scale, habitat-mediated competition between the species altered harvest rates in a way that would normally be ascribed to predation risk.

Theoretical context

Habitat selection and convergence of species densities

Imagine two species that encounter patches of two different habitats in proportion to the habitats' abundance [fine-grained (Brown and Rosenzweig, 1986)]. The same sets of limiting resources exist in both habitats. Each species is more efficient at harvesting resources from a different habitat. Thus they possess distinct habitat preferences. Individuals will forage in only their preferred habitat as long as their quitting-harvest rate in patches of that habitat exceeds their harvest rate in patches of the alternative habitat. Harvest rates will decline as population density increases. Each species will thus possess a critical density above which it will forage in both habitats. Below this critical density, each species will occupy only its preferred habitat (zero habitat overlap produces a ghost of competition). But when the density of both species exceeds their respective thresholds, each occupies patches in both habitats (Brown and Rosenzweig, 1986). An experiment that manipulates densities when the species are sparse would be unable to detect the competition that is expressed only at higher population densities.

Does the same type of competitive ghost exist in a coarse-grained environment where individuals can allocate their entire home range to a single habitat? To answer the question let us assume that the population growth of each species can be modelled as Lotka-Volterra-Gause dynamics such that

$$\frac{dN_{1j}}{dt} = r_{1j}N_{1j}\left(1 - \frac{N_{1j} + \alpha_{12j}N_{2j}}{K_{1j}}\right), \quad (1)$$

where subscripts denote species 1 and 2 in habitat j , N is population density, r is the maximum instantaneous rate of population growth, α is the habitat-specific competition coefficient, and K is carrying capacity. Now assume further that each species obeys an ideal-free distribution (Fretwell and Lucas, 1969), and that per capita population growth rate is an accurate estimate of an individual's fitness. The density in each habitat that equalizes fitness represents a Nash equilibrium (Pulliam and Caraco, 1984) revealed by the habitat isodar (Morris, 1987, 1988). Thus, for species 1 with a preference to occupy habitat B,

$$N_{1B} = (C + b\alpha_{(1,2)A}N_{2A} - \alpha_{(1,2)B}N_{2B}) + bN_{1A}, \quad (2)$$

where the term in brackets represents the straight-line isodar intercept and where

$$C = \frac{(r_{1B} - r_{1A})}{r_{1B}} K_{1B},$$

$$b = \frac{r_{1A} K_{1B}}{r_{1B} K_{1A}}$$

(Morris, 2003b). Equation (2) reveals, for constant competition coefficients, that despite our assumption of distinct preferences, each species can occupy the other's preferred habitat. And when it does, we can use regression to measure the competitive effect (e.g. Rodríguez, 1995; Morris *et al.*, 2000).

But we obtain a very different prediction when we model the same pair of species using consumer–resource dynamics. In a consumer–resource system, species compete indirectly through consumption of resources, and similar species should compete for the same limiting resources. If such species occupy habitats in a coarse-grained manner, the species that persists in each habitat will be the one that is most efficient at harvesting resources in that habitat and can thus maintain a stable population size at the lowest resource density [the R^* rule (Tilman, 1976)]. Moreover, if the two species have similar carrying capacities and are equally abundant, each will obtain a lower resource density in its preferred habitat. Thus, if population dynamics are similar for the two species, each should occupy only its preferred and separate habitat.

But if species densities are not in equilibrium, such as could occur if species 2 is sparse and species 1 is abundant, species 1 will crop resource concentrations in its preferred habitat B below those maintained by species 2 in its preferred habitat A. Species 1 would then deplete resources in habitat B below the level profitable for species 2 (e.g. $R_{1B} < R_{2B}$, where R = resource concentration). But because species 2 is sparse, $R_{2A} \geq R_{1A}$, and species 1 can occupy both habitats while species 2 occupies only one. Imagine that we conduct an experiment on these species that sequentially removes individuals of species 2 while keeping the total number of individuals of species 1 constant. Each serial reduction in the density of species 2 provides opportunities for increased density in habitat A by species 1. To see this we remove the competitive effect of species 2 on species 1 in habitat B and re-write the isodar equation as

$$N_{1B} = C + b(N_{1A} + \alpha_{(1,2)A}N_{2A}). \quad (3)$$

If the equation is to remain valid as we reduce the density of species 2, individuals of species 1 must move to habitat A. Moreover, since the total number of species 1 is constant, any movement to increase density in habitat A must be accompanied by an equal reduction of

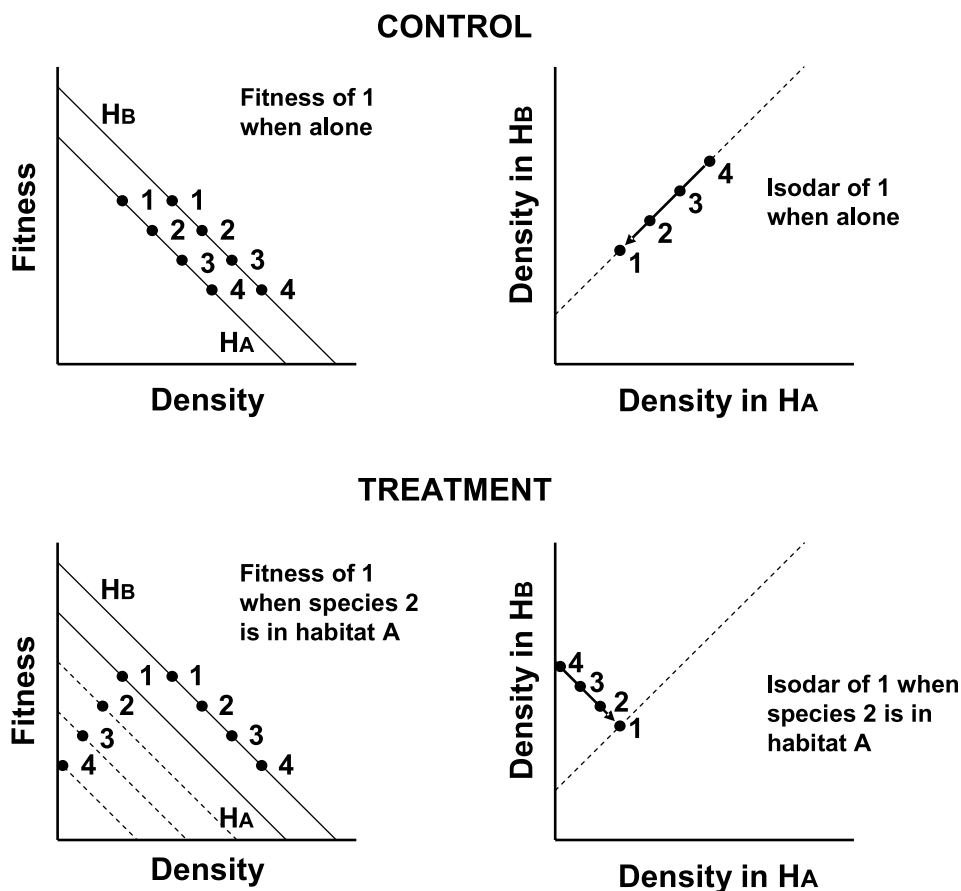


Fig. 1. Experimental removals of competing and target species cause convergence of their respective habitat isodars. Panels on the left illustrate the ideal-free fitness exhibited by species 1 when living alone at different densities (upper) versus living at a constant density in the presence of a competitor occupying only habitat A. Paired numbers represent ideal-free distributions at different population sizes (target species in the top panels; competitor in the bottom panels). Panels on the right illustrate the resulting isodars in a removal experiment. The arrow pointing south-west represents the isodar calculated from a control where the target species' density is reduced. The arrow pointing south-east (negative slope) represents the isodar calculated from a treatment where the competitor's density is reduced. The two arrows converge on the same point.

density in habitat B. Thus, across the range of densities represented by the removal experiment, the isodar will have a slope of -1 (Fig. 1).

Now imagine that, in addition to our two-species experiment, we also assess habitat selection in a replicated pair of the same habitats by species 1 alone (control). We begin with the density of species 1 equivalent to the combined density of the two species in the removal treatment. Then, as we sequentially reduce the density of species 2 in the removal experiment, we also reduce the density of species 1 in the control by the same amount. Treatment and control should, when all removals are completed, converge on the same pair of densities (Fig. 1).

Patch use and predation risk

Brown (1988, 1992) developed a novel method to measure the cost of predation in free-living organisms. If individuals forage optimally to maximize their reproductive value, then

$$QHR = C + \frac{\mu F}{\left(\frac{\partial F}{\partial e}\right)} + \frac{\phi_t}{p \left(\frac{\partial F}{\partial e}\right)}, \quad (4)$$

where QHR is the individual's quitting-harvest rate, C is the metabolic cost of foraging, μ is the instantaneous predation rate, F is the fitness obtained from foraging in the patch, ϕ is the marginal fitness associated with time engaged in alternative activities, p is the probability of surviving the foraging period, and $\partial F/\partial e$ is the marginal value of energy in the currency of fitness (Brown, 1988, 1992). The foraging cost of predation (second right-hand term in equation 4) increases directly with predation rate and is inversely correlated with the marginal value of energy. For our purposes, we note that as competing consumers reduce resource abundance, individuals will compete more intensely for energy of increasing marginal value and, assuming that the fitness value of energy is constant, the cost of predation is less (as are the missed opportunities of engaging in non-foraging activities, third term on the right-hand side), and quitting-harvest rate will decline. If patches reward consumers with diminishing returns, then quitting-harvest rate is negatively correlated with time spent in the patch. An optimal forager will thereby spend more time harvesting resources in risky patches. An experiment that monitored use of risky and safe patches while reducing competition would reveal less use of the risky patch with every reduction in the density of competitors. The increased cost of predation in the presence of competitors is real, but could not be attributed to either an increase in predator numbers or predator behaviour. I refer to such cases as 'apparent predation risk'.

Competitive effects associated with direct interference can also produce apparent predation risk. Interference from a competitor in its favoured patch will reduce use of that patch by subordinates. If the competitive dominant is abundant or most active in safe habitat, the subordinate may be forced to forage more intensely in risky areas than it otherwise would have. The foraging pattern in our experiment would mimic a reduced cost of predation. But if the dominant is more abundant or active in habitat that is risky for the subordinate species, avoidance of the dominant would yield increased foraging in safe patches. In both cases avoidance of one type of patch in favour of another is properly attributed to the direct effects of interference. The reduction or increase in the cost of predation that a foraging experiment would reveal may very well be more apparent than real.

Interference can have other effects including a reduction in resource encounter rate. A consumer that encounters resources less frequently will receive less marginal benefit from foraging and will thus reduce the time it allocates to harvesting resources (Mitchell *et al.*, 1990). Such a forager will leave all patches at a higher quitting-harvest rate. But if interference causes subordinates to avoid only rich patches, it will reduce their assessment of habitat quality. So individuals matching the perceived lower marginal value of the habitat (Charnov, 1976) will, on average, forage more intensely. And they will forage any rich patches they do encounter to a lower resource density than if their assessment of habitat quality was higher. If those patches tend to be in 'safe' habitat, the competitor's foraging behaviour would reveal an increased cost of predation without any change in predation risk. So it is naïve, or at least premature, to suggest that the structure of communities is determined primarily

by predation and predation risk because both are modulated by population density and inter-specific competition [for a similar caution related to the manifold effects of predators on competition, see Kotler and Holt (1989)].

METHODS

Study system

My assistants and I tested the theory by manipulating densities of captive meadow vole (*Microtus pennsylvanicus*) and red-backed vole (*Myodes gapperi*) populations. Although their diets vary, the two herbivores consume a wide array of shared food items. Meadow voles prefer old-field habitats whereas red-backed voles prefer woodlands. Classic experiments where both species co-occur demonstrate that these voles segregate by, and compete for, habitat (Grant, 1972; Morris and Grant, 1972). Red-backed voles living in hornbeam-maple forest in Quebec readily moved into adjacent grassland when meadow voles were absent (Grant, 1969, 1972). In reciprocal experiments where red-backed voles were absent, meadow voles occupied only grassland (Grant, 1969). But meadow voles did occupy aspen woodland (with a well-developed grass/sedge layer) following red-backed vole removals in Saskatchewan (Morris and Grant, 1972). So experiments that assess red-backed vole habitat use, while removing meadow voles from their preferred field habitat, represent an appropriate model system to address whether habitat selection can reveal competition.

Field experiments

We conducted control and meadow-vole removal treatments in a lattice of four 50 × 50 m enclosures at the Lakehead University Habitron (located near the northwest corner of Lake Superior, Ontario, Canada). Galvanized metal fences 0.75 m tall are buried to a depth of 0.5 m. Each 50-m run of fencing has two 9.25-cm diameter gates that can be opened to allow voles access to the adjacent enclosure. We used two enclosures representing field habitat [a mixture of old-field forbs and grasses with interspersed 2-m tall red pine (*Pinus resinosa*) and a few invading alder shrubs (*Alnus incana* ssp. *rugosa*)], adjacent to two others composed of dense 5-m tall alder (forest habitat).

Our protocol established a control of 24 red-backed voles in one pair of enclosures and a treatment of 12 red-backed voles living with 12 meadow voles in the other pair (Appendix A). After the animals had become accustomed to the enclosures, we removed one individual (*Myodes* from control, *Microtus* from treatment) every 3 days. We monitored habitat use of the remaining voles by live trapping and measured giving-up densities (GUD) in artificial food trays located in open (safe) and shrub (risky) microhabitats (Appendix B).

I log-transformed the giving-up densities ($\text{Log}_{10}[\text{GUD} + 1]$) to estimate quitting-harvest rates of the final red-backed vole using each tray. The logarithmic transformation linearizes the relationship between giving-up density and quitting-harvest rate whenever animals forage in patches with diminishing returns (Brown and Kotler, 2004). Northern small mammals foraging in similar trays do so with diminishing harvest rates (Morris and Davidson, 2000; Davidson and Morris, 2001; Morris, 2001). I estimated population density in a trapping rotation as the number of adult voles captured in each enclosure.

I used the replicated estimates of density in the two habitats to draw the red-backed vole isodar via geometric-mean regression for both control and treatment populations.

I reasoned that the control isodar would confirm density-dependent habitat selection by *Myodes*. And I predicted that the treatment isodar should be negative with a slope of -1 as it converged on the control. Then I used the log-transformed giving-up densities to assess whether the presence of meadow voles altered the foraging behaviour of red-backed voles [saturated repeated-measures GLM: within-subjects effects = cover vs. open trays and between-subjects effects = treatment vs. control enclosures, field vs. forest, and time period (representing the different density-reduction treatments)]. I used SPSS (Versions 15 and 16; SPSS, Inc., Chicago, IL, USA) and MINITAB (Version 13; Minitab Inc., State College, PA, USA) for all statistical analyses.

RESULTS

Treatment densities coincided with targeted values, but control densities did not

Only one meadow vole disappeared during the 5-day acclimation period before we began to reduce rodent densities. Otherwise, we reduced meadow-vole density as planned during each trapping rotation. Four of the red-backed voles targeted for removal from the control enclosures disappeared during the 5 days of acclimation. Others learned how to climb vegetation (*Solidago*) or support posts along the fences and escaped to adjacent enclosures. These animals were returned on capture. We removed targeted red-backed voles only until 20 August. None of the 'additional' red-backed voles was captured after that date.

Despite these setbacks there was a reasonable range of adult red-backed voles across trapping intervals to calculate the isodars (10–24 voles in the control, 13–18 voles in the treatment). Targeted densities varied because 13 young adult voles (between 15 and 17 g) entered the population during the experiment. Most of these animals were nursing during the set-up and acclimation periods and were unavailable for capture until we started removals on 8 August. We trapped 55 juvenile red-backed voles (<15 g) produced by the original cohort of adult females during the experiment and immediately removed them. We captured these juveniles while they were becoming independent of their mothers (mean weight = 11.3 g). As they were unlikely to influence density-dependent habitat choices by adults (mean weight = 23.3 g), I did not include them in the isodar analyses.

The control isodar was significant and positive

Red-backed voles adjusted their habitat occupancy as we reduced the number of animals living in the control enclosures. These red-backed voles exhibited a distinct preference (Morris, 1988) for forest habitat over the field [significant isodar, $F_{1,6} = 16.95$, $P = 0.006$, $R^2 = 0.74$; intercept not significantly different from zero, $P = 0.36$; slope greater than 1.0 (95% CI = 1.04–3.20)] (Fig. 2A). I was concerned that the small range of densities in the two habitats might not reflect red-backed vole habitat preference at other population sizes. So I superimposed onto the isodar the number of adult red-backed voles that were living in the two habitats before we reduced density to 12 animals to start the experiment. This data point lies almost on top of the geometric-mean regression ($F_{1,7} = 31.47$, $P = 0.001$, $R^2 = 0.79$) (Fig. 2A) and supports our conclusion that *Myodes* prefers forest over field.

The treatment isodar was not significant

There was no relationship, in the treatment enclosures containing meadow voles, between the density of red-backed voles living in the two habitats ($F_{1,6} = 0.27$, $P = 0.62$) (Fig. 2B).

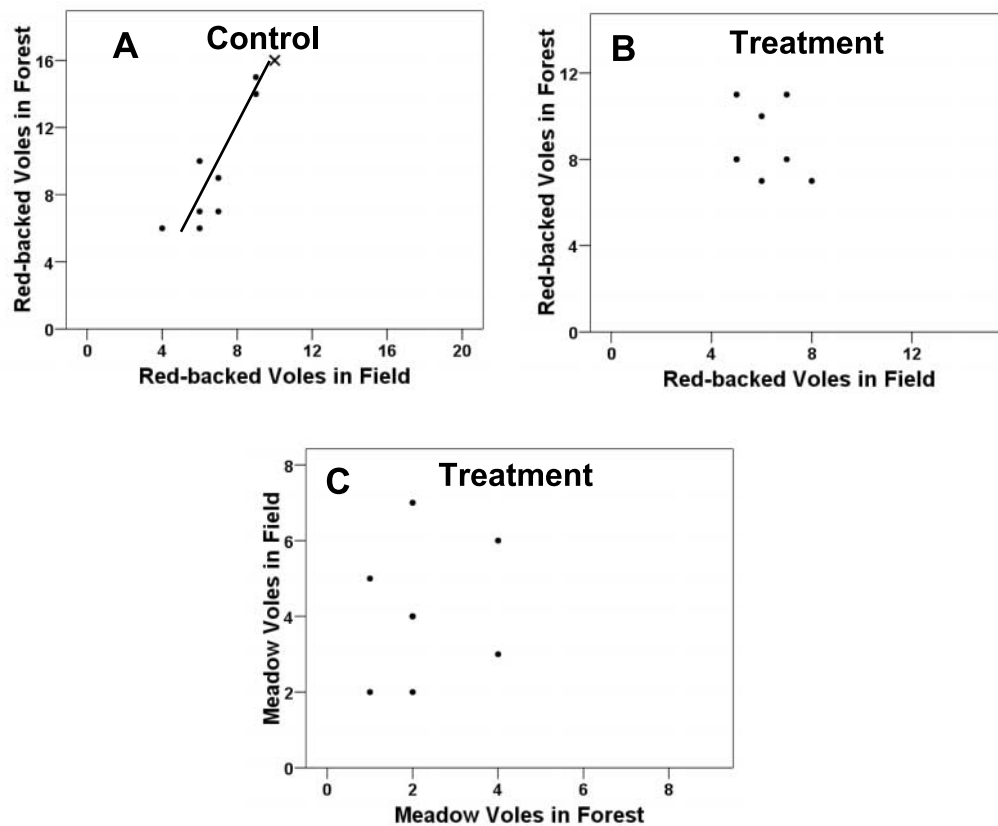


Fig. 2. The densities of red-backed and meadow voles living in paired forest and field enclosures at the Lakehead University Habitron. (A) The significant isodar from the control enclosures. The data point represented by the symbol \times corresponds to the initial density of voles living in the two enclosures just before starting the experiment. (B) There was no relationship between density of voles in forest and field enclosures in the meadow-vole treatment. (C) Meadow voles occupied both habitats throughout the experiment.

Thus, I reject the prediction that, in the presence of meadow voles, the red-backed vole isodar should have negative slope even though the overall pattern is in that direction (Fig. 2B).

Meadow voles occupied both habitats

Meadow voles did not remain solely in field habitat. Instead, they occupied both habitats across a wide range of population densities (Fig. 2C). This observation explains the deviation of red-backed voles from their predicted negative isodar. The isodar would always be negative only if meadow voles restricted their activity to the field habitat.

Estimated quitting-harvest rates were lower under cover than in the open

The log-transformed giving-up densities (our estimate of quitting-harvest rate) was less under the protection of cover than it was in the open (mean [cover] = 0.625, mean

Table 1. GLM summary of differences in log-transformed giving-up densities of red-backed voles foraging in artificial food trays

Source	d.f.	<i>F</i>	<i>P</i>
Cover	1,96	12.29	0.001
Habitat	1,96	59.17	< 0.001
Treatment	1,96	43.26	< 0.001
Period	7,96	9.06	< 0.001
Cover × Habitat	1,96	3.12	0.081
Cover × Treatment	1,96	8.56	0.004
Cover × Period	7,96	1.32	0.25
Habitat × Treatment	1,96	4.41	0.04
Habitat × Period	7,96	0.48	0.85
Treatment × Period	7,96	2.73	0.01
Cover × Habitat × Treatment	7,96	0.60	0.44
Cover × Habitat × Period	7,96	0.52	0.82
Cover × Period × Treatment	7,96	0.77	0.61
Habitat × Treatment × Period	7,96	1.39	0.22
4-way interaction	7,96	0.55	0.79

Note: Trays were located in the open and under cover in field and forest habitats nested within control and treatment enclosures associated with eight different density-reduction periods. **Bold** font indicates statistically significant outcomes.

[open] = 0.645) (Table 1). The estimate also differed significantly across time periods, but this difference was caused entirely by lower giving-up densities following the final density reduction when all remaining ‘introduced’ animals were removed from the enclosures [period 8 < periods 1, 3, 4, 5, 6 ($P \leq 0.005$ in all comparisons) and marginally so for periods 2 and 7 ($P = 0.058$ and 0.052 respectively), *post-hoc* Bonferroni multiple comparisons]. Estimated quitting-harvest rate was also less in the meadow-vole treatment enclosures than it was in the controls (mean [treatment] = 0.61, mean [control] = 0.66) (Table 1).

Estimated quitting-harvest rates were lower in forest than in field

Log-transformed giving-up density was less in forest than in field (mean [forest] = 0.606, mean [field] = 0.664) (Table 1). The giving-up density is reduced as foragers deplete a patch through time. Voles thus foraged longer in the forest than in the field habitat.

The difference in quitting-harvest rates varied between treatment and control

Although estimated quitting-harvest rate was less under cover than in the open, this difference was much greater in the meadow-vole treatment enclosures than it was in the control (mean difference in treatment = 0.04, mean difference in control = 0.008) (Table 1, Fig. 3). The difference was nearly twice as great in forest than in field (mean difference between control and treatment in forest = 0.0735, mean difference between control and treatment in field = 0.042) (Table 1). No other interactions were statistically significant.

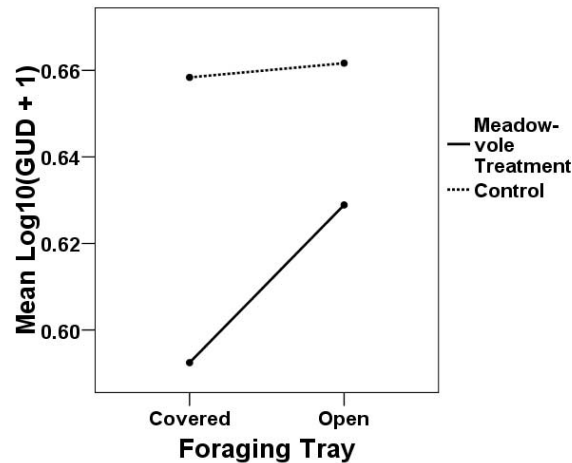


Fig. 3. Profile plots illustrating that the difference in estimates of quitting-harvest rates ($\text{Log}_{10}[\text{GUD} + 1]$) between open and covered microsites was greater in treatment enclosures containing meadow voles than in control enclosures containing only red-backed voles at the same target density.

DISCUSSION

Meadow voles compete with red-backed voles for habitat. When living alone, red-backed voles occupied forest and field, but with a clear forest preference. The preference disappeared in the presence of meadow voles. Meadow voles, despite a clearly documented preference for cover associated with field and grassland habitats (e.g. Grant, 1969; Morris and Grant, 1972; Basquill and Bondrup-Nielsen, 1999; Getz *et al.*, 2001, 2005; Lin and Batzli, 2001a, 2001b; Pusenius and Schmidt, 2002), also lived in the alder forest. These results are in contrast to classical coarse-grained theory where distinct habitat preferences should be reinforced by competition that causes each species to occupy a separate habitat [the ghost of competition (Rosenzweig, 1974, 1979, 1981)]. So it would appear, at the scale of my experiments, that the two species perceive fine-grained similarities in patch quality that allow them to occupy both habitats.

The joint occupancy of two habitats in our experiments has three crucially important and interconnected consequences. First, the prediction of a negative isodar depends critically on the competitor occupying a single habitat. If it does so across a range of densities, then the fitness expectations of the target species are reduced only in that habitat. The isodar, at a constant density of the target species, will have a slope of -1 (equation 2). But if the competitor occupies both habitats, and does so at variable densities, then the fitness of the target species is reduced to differing degrees in each habitat depending on how many competitors occupy those habitats. With ideal habitat selection the isodar will still exist, but it cannot be defined by a simple single-species relationship with density (Morris, 1999). Second, in the absence of a clearly defined negative isodar, the two species will not segregate into their distinct and separate habitats. Rather than displaying a transparent ghost of competition, they will co-exist in a translucent partial ghost region where the proportions of each species in the two habitats vary with population density. Although such ghosts have been best documented in three habitats (Wasserberg *et al.*, 2006), they necessarily exist in any state space where partial habitat preferences are caused by inter-specific competition (e.g. Morris,

1999). Third, the partial ghost illustrates that habitat-selecting competitors can co-exist at multiple equilibria of their joint densities in the two habitats. In this habitat-selecting game, the proportion of individuals living in a habitat thus appears to be constantly readjusted depending on the species identity of the first individual to move, and on the subsequent sequence of moves during dispersal (Morris, 2003a, 2004).

Perhaps an even more intriguing result is that, in the presence of meadow voles, red-backed voles forage more intensely in safe covered microhabitat than they do in open areas. Such a pattern is normally attributed to predation risk (e.g. Brown, 1988; Brown *et al.*, 1992). We have known for 30 years that the effect of predators can mimic competitive interactions [apparent competition (Holt, 1977; Holt and Kotler, 1987)]. But we have ignored the antagonist of apparent predation risk that emerged between meadow voles and red-backed voles in our experiments. Apparent predation risk inflates the importance of predation, but not fear, in our assessment of factors structuring ecological communities. And it may be ubiquitous in communities where competition is resolved by habitat selection.

You may suspect that both species foraged in our seed trays. If so, differences in estimated quitting-harvest rates could reflect joint consumption of seeds by both species in trays under shrubs and saplings rather than avoidance of nearby open trays by red-backed voles. At these small scales, meadow voles typically occupy areas of dense herbaceous cover and avoid habitats dominated by shrubs and trees (M'Closkey, 1975; M'Closkey and Fieldwick, 1975; Morris, 1979, 1984a, 1984b). My results suggest that when these 'open' microhabitats are occupied by meadow voles, red-backed voles forage more intensely under cover. But I cannot, at this time, exclude the possibility that meadow voles were also foraging in the bottles. Even if some of the microhabitat differences in giving-up density were caused by direct consumption of seeds by both species, it simply alters the mechanism responsible for apparent predation risk. Instead of the indirect cause of reduced use of sites occupied by meadow voles, apparent predation risk would emerge as a direct effect. When both vole species are present, they forage more intensely under cover than when red-backed voles exist alone at the same density.

Could exploitation competition cause red-backed voles to increase their use of covered trays? Exploitation increases the marginal value of energy and thereby reduces the cost of predation. As the density of a competitor increases, for example, it will reduce average resource abundance. Lower resource abundance reduces the energetic state of all foragers, increases the marginal value of energy, and thereby reduces the cost of predation. Avoidance of rich patches, or reduced resource encounter rates, should also reduce the energetic state of competing consumers and cause them to forage more intensely (lower giving-up densities). The giving-up densities of red-backed voles were lower in the presence of *Microtus*, and lower still in foraging trays under cover, which implies longer foraging times. The low giving-up densities in covered forest trays can thereby be interpreted as an example of apparent predation risk where the mere presence of *Microtus* inflates *Myodes*' use of safe patches.

Assuming that *Microtus* do interfere with foraging red-backed voles, what form does it take? One possibility is that meadow voles simply capitalize on their size advantage and interfere with patch use by smaller red-backed voles in all microhabitats. It is difficult to reconcile this mechanism with the observation that the difference in giving-up densities between covered and open trays was greater in the treatment enclosures than in the controls. It would thus appear that dominance by *Microtus* is linked to open habitat. This mechanism could be reinforced if meadow voles are also more efficient at harvesting out-of-tray

resources in open patches than they are under cover. The marginal value of the open patches would be reduced, as would the mean value of the habitat, and red-backed voles would forage longer in the trays to equalize their marginal return. The marginal return to red-backed voles in the open would be reduced further by the threat of interference, so red-backed voles would preferentially forage in areas with denser cover. As they do so, they deplete resources in those areas, and match their marginal value by foraging longer in the covered trays.

When *Microtus* move into red-backed vole habitat under natural conditions, it is quite likely that they do so because *Microtus* densities elsewhere are high. Dense populations of *Microtus* could attract predators and increase predation on other small mammals (apparent competition). So it is also possible that red-backed voles are cued to anticipate increased predation risk simply by the presence of meadow voles. I cannot exclude this possibility. Yet if predation risk was inflated by the few *Microtus* in our treatment enclosures, then I should have observed a similar shift in red-backed voles foraging in our adjacent control enclosures. I did not.

Apparent predation risk in our experiments was short term and caused by the increased use of a safe habitat by members of one prey species in the presence of another. Apparent predation risk may also be long term. Some species, whose life history and behaviour can tolerate higher predation rates, or that otherwise possess a fitness advantage in places of danger to their competitors, may reduce competing species' population growth rates in those places. The abundance of competing species would thus be relatively higher in safe habitat. The increased preference for safe habitat in both of these examples would typically be attributed to the direct or indirect effects of predators, even though the dominant interaction influencing space use is competition. It is likely that such effects can be disentangled only by carefully conceived manipulation experiments. These experiments should receive high priority so that we can begin to assess how often effects caused by competitors have been misappropriated to predation.

The dangers of misinterpreting the relative roles of predation and competition may be especially high with foraging studies that use differences in harvest rates to titrate trade-offs between safety and food. Although numerous studies on single species have repeatedly documented the influences of fear on foraging behaviour in a wide variety of organisms (e.g. Brown and Alkon, 1990; Brown *et al.*, 1992; Kotler *et al.*, 1999; Morris, 2005; Hochman and Kotler, 2006), studies involving two or more prey species may have inadvertently included avoidance of competitors in the titration. And if they have done so, then we might very well have mis-identified the factors causing non-lethal trait mediated effects. Such studies, especially when used for conservation or management, should receive extra scrutiny to ensure that they have properly identified cause and effect. Otherwise our interpretations of processes structuring ecological communities and food webs may have been flawed, and our recommendations and prescriptions for management and conservation could fail.

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APPENDIX A

We used descendants of voles used in other experiments (e.g. Morris and Mukherjee, 2007) to establish a control and treatment population of red-backed voles in the Lakehead University Habitron. Gates between pairs of enclosures were open so that each population could occupy a field enclosure and an adjacent equal-sized forest enclosure. Gates were open for 6 weeks before the experiment. From 31 July until 2 August 2007, we reduced densities with the aim of leaving only six adult red-backed voles in each of these four enclosures. We did not want to remove lactating females from their litters (two extra females), and two males targeted for retention were not captured subsequently, so we were unable to achieve an equal sex ratio. Simultaneously, we added 6 adult male and 6 adult female voles to the paired field enclosures (12 meadow voles added to the treatment, 12 red-backed voles added to the control, for a total of 24 adult voles in each pair of enclosures). We allowed the animals to familiarize themselves with the enclosures and each other for 5 days. Densities of meadow voles in enclosures can exceed those of red-backed voles by an order of magnitude [up to 300 per hectare in Illinois (Lin and Batzli, 2001a) and up to 800 per hectare in New York (Pusenius and Schmidt, 2002) compared with about 30–40 per hectare for red-backed voles (Morris and Mukherjee, 2007)]. So our densities should have corresponded to those that would have allowed *Microtus* to occupy only their preferred field habitat while *Myodes* exploited both field and forest.

On 7 August, we initiated the first of eight consecutive 3-day experimental 'replications'. We closed the gates between enclosures at noon, set two live-traps at each station in the evening (64 traps in each pair of enclosures), and checked them the next morning. We removed one 'experimental animal' (chosen at random) from each pair of enclosures (one meadow vole from the treatment enclosures and one red-backed vole from the control enclosures), plus any unmarked animals (mostly first-capture juveniles leaving the nest

for the first time), and a small number of ‘fence-jumpers’ that entered the enclosures from those nearby.

We maintained a sex ratio near 1:1 by never removing more than one ‘extra’ individual of the same sex. We repeated this protocol until 29 August when we removed all remaining ‘supplemental’ rodents. We thus aimed, with the exception of mortalities or escapes, to return red-backed vole densities in the treatment and control pairs of enclosures to their original value (12 adults) at the start of the experiment. The experiment ended on 31 August when we processed the final set of giving-up densities.

I included animals missing from one or two capture intervals whenever they were captured in the same enclosure immediately before and after their ‘disappearance’. High re-capture rates of both species minimized bias in population estimates. Twenty-three of the 24 voles originally targeted for retention over the entire experiment were subsequently recaptured after the experiment began. We recaptured 16 of these during each trapping occasion and two others on seven out of eight opportunities. The remaining five animals were captured during all opportunities that they were known to be alive (all disappeared after either the first or second trapping rotation). Re-capture rates for meadow voles were similar (11 of 12 treatment animals recaptured, 10 removed). Disappearance of a few animals in our experiment is not unusual because all enclosures are subject to predation from avian and meso-carnivores.

APPENDIX B

At noon on 8 August, we placed four pairs of foraging trays (opaque 9-litre water bottles with a single 3-cm opening) in each enclosure’s 4 × 4 trap-station matrix by randomly choosing stations in a Latin-square design. We placed one tray of each pair under the protective cover of an alder shrub or pine sapling and placed the other in the ‘open’ approximately 2 m away. Each bottle contained 4.0 g of sized millet seed (0.2 mm diameter), which we mixed thoroughly into 1.5 litres of screened (60–90 grain) silica sand.

Then we opened the gates between adjacent enclosures and allowed the voles to forage and move between enclosures for 46 h before re-closing the gates and collecting the bottles for processing. Bottles at each station were foraged by red-backed voles that had been trained to use them in the same enclosures from 20 to 30 July. Meadow voles could also enter the bottles, but although they will forage for whole oats in sand (e.g. Pusenius and Schmidt, 2002), they typically do not forage for millet during summer when natural resources are available (personal observation), and they were not trained to use the bottles.

We separated the sand from residual millet with soil sieves and weighed the cleaned millet with an electronic balance to the nearest 0.01 g (the giving-up density). We recharged the bottles with millet and stored them outside of the enclosures, before setting live-traps in the evening for the next 3-day replicate.

