Safety from predators or competitors? Interference competition leads to apparent predation risk.

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Abstract

Prey often react to predation risk by foraging preferentially in safe, rather than risky, patches. Yet prey also must deal with the negative effects of competition for the same patches. The pattern of patch use can mimic that created by predation risk if dominant competitors cause subordinates to increase their use of safe foraging patches. I develop a simple theory of this form of apparent predation risk that describes patch use by an optimal forager confronted with interference from individuals of a dominant, competing species. The theory predicts that predation risk for subordinate individuals increases with the density of nearby dominants. I tested the theory's prediction with meadow voles and southern red-backed voles foraging in pairs of safe and risky patches in four adjacent sub-grids in an old-field enclosure. I used dyadic encounters to confirm that meadow voles are dominant over red-backed voles. I estimated the density of meadow voles likely to be encountered by foraging red-backed voles as the number of uniquely marked meadow voles using at least one of a pair of safe and risky patches. Subordinate red-backed voles foraged indifferently between safe and risky patches when few meadow voles were encountered. Red-backed voles increased their use of both safe and risky patches as the number of nearby meadow voles increased. Giving-up densities were lower and harvesting efficiency higher in safe patches when the number of nearby meadow voles was high. These results document competition between the two species and suggest that competition increases the benefits of foraging more efficiently in safe than risky patches. Experiments using foraging behaviour to assess predation risk might misinterpret its effect unless they first account for competition among foraging individuals.

Lay Summary

Faculty and students in the Department of Biology are bound together by a common interest in explaining the diversity of life, the fit between form and function, and the distribution and abundance of organisms. The research reported here shows how predation and competition jointly affect the value of habitat to foraging rodents. I first develop theory that predicts how subordinate competitors foraging in safe and risky patches should react to predation risk and dominant competitors. I then describe two experiments with meadow voles and southern red-backed voles that test the predictions from the theory. The first experiment shows that meadow voles are dominant over red-backed voles. The second experiment shows that meadow voles cause red-backed voles to spend more time foraging in food patches, and to forage more efficiently in safe over risky patches. Competition from dominant voles made food patches more valuable for subordinate voles and magnified the risk of predation. The theory and experiments demonstrate that assessments of predation risk can be misinformed when prey compete for foraging patches. Ecological studies, as well as conservation and management strategies, that fail to account for competitive interactions are likely to misinterpret the role of predators in determining habitat quality.

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Introduction

Predators not only kill prey, they also modify a host of behaviours such as habitat choice (Brown 1999; Morris 2001), vigilance (Brown 1999; Altendorf et al. 2001; Dall et al. 2001), patch use (Brown and Kotler 2004; Orrock et al. 2004), and nest-site selection (Forstmeier and Weiss 2004), while also influencing growth rates of offspring (Coslovsky and Richner 2011) and causing indirect mortality (McCauley et al. 2011). Such effects are particularly interesting in modeling prey foraging games (Brown 1999, Brown and Kotler 2004) where prey typically optimize foraging by harvesting more resources from safe patches (those where predators are less likely to be encountered) than from risky ones.

Although predation risk is undoubtedly important to decisions made by foraging prey, prey foraging games in nature are played in arenas co-occupied by competitors. Under these conditions, avoidance of dominant competitors can mimic the effect of predation when dominants cause subordinates to forage more in safe than risky patches ('apparent predation risk', Morris 2009). Exploitation competition, on the other hand, can reduce the importance of predation risk when resource depression by competitors reduces the energetic state of competing foragers (Brown 1988; Mitchell et al. 1990; Davidson and Morris 2001); hungry individuals are more willing to forage in rich risky patches than are sated prey. The risk of predation in this case is real, but its magnitude revealed by prey behaviour depends on competitor abundance (Morris 2009). A third possibility is that dominant individuals exclude subordinates from safe patches, thereby making otherwise safe patches risky to subordinates. In each of these examples, competitors modify the role of the predator in the prey foraging game. It is thus possible that predators' influence on prey behaviour has been misinterpreted because competitors can produce foraging patterns normally attributed to predation risk.

Morris (2009) highlighted the role of competition in the prey foraging game using experiments assessing patch use by large meadow voles (*Microtus pennsylvanicus*) competing with smaller southern red-backed voles (*Myodes gapperi*). *Myodes* harvested more resources from safe patches in the presence of *Microtus* than in its absence. Although the experiment clearly documented that competitors modify predation risk, it did so through the outcome of differential foraging and did not rigorously test for the underlying competitive mechanism. Two options appear likely: 1) foraging *Microtus* spent more time in risky patches and caused *Myodes* to increase use of safe patches; 2) the presence and abundance of *Microtus* caused *Myodes* to forage more apprehensively. Increased apprehension toward competitors could have detracted from *Myodes'* ability to manage predation risk. Less time for anti-predator apprehension (Dall et al. 2001) could thereby cause *Myodes* to increase its foraging in safe patches.

Thus, I evaluate how interference between *Microtus* and *Myodes* induces competitor-modified predation risk. I begin by developing a model for dominant and subordinate individuals competing for safe and risky patches. I test the model's assumptions that voles compete aggressively, and that meadow voles are dominant over red-backed voles. I then use a controlled field experiment to understand the underlying mechanisms of apparent predation risk. I interpret the results in the light of theory and conclude by discussing the implications of competitively mediated foraging behaviour to our understanding of predation risk.

Theory

Optimally foraging individuals maximizing resource intake will quit harvesting resources from a patch when the benefits of foraging outweigh the costs. Thus, the quitting harvest rate (QHR) of a forager (*j*) in a patch (*i*) can be modelled as:

$$\mathrm{QHR}_{ij} = C_{ij} + \frac{\mu_{ij}F_{ij}}{\left(\frac{\partial F}{\partial e}\right)_{ij}} + \frac{\phi_{t_{ij}}}{p_{ij}\left(\frac{\partial F}{\partial e}\right)_{ij}} \tag{1}$$

where C is the metabolic cost of foraging, μ is the instantaneous predation rate, F is the fitness obtained from foraging in a patch, Φ_t is the marginal fitness associated with time engaged in other fitness-related activities (missed opportunities), p is the probability of surviving the foraging period, and $\left(\frac{\partial F}{\partial e}\right)$ is the marginal value of energy in the currency of fitness (Brown 1988, 1992).

The payoff from foraging in a patch with diminishing returns is inversely proportional to the QHR. Thus, foraging experiments that estimate QHR (or its correlate, giving up-density [GUD]) in otherwise identical patches, where μ is modified by protective cover, are used frequently to evaluate predation risk, and demonstrate that QHRs and GUDs are lower when μ is small than when μ is large (Brown 1988, 1992, 1999; Brown et al. 1992; Kotler and Blaustein 1995; Verdolin 2006).

The predictions change abruptly if one assumes that dominant foragers interfere with subordinates' access to patches. Interference competition can lead to apparent predation risk in two ways. First, if dominant individuals have lower preference for safe patches than putatively risky patches, then avoidance of dominants in the risky patches can lead subordinates to increase their relative use of safe patches. In order to appreciate this effect, assume that the subordinate's aversive cost of foraging is additional to predation risk. Modifying equation (1), the QHR of the subordinate species (*S*) in patch *i* then becomes

$$\mathrm{QHR}_{iS} = C_{iS} + \frac{[\mu_{iS} + f(N_{iD})]F_{iS}}{\left(\frac{\partial F}{\partial e}\right)_{iS}} + \frac{\phi t_{iS}}{p_{iS}\left(\frac{\partial F}{\partial e}\right)_{iS}} \qquad (2)$$

where $f(N_{iD})$ represents the density-dependent effect of dominant individuals using the same patch. This scenario is likely to be rare, however, unless the two species have different perceptions of danger (for example, if they vary in the effectiveness of their vigilance, susceptibility to different predators, or perception of predation risk).

It seems more likely that the effect of interference will be modulated through other differences in behaviour. Subordinate individuals frightened by possible encounters with dominant aggressors may increase apprehension and vigilance toward dominants at the expense of increasing vulnerability to attack from predators. The risk of predation would be exacerbated and cause subordinates to increase their use of safe patches (or reduce their use of risky patches). The magnifying effect of apprehension toward dominants on predation risk would thus be modeled as

$$\mathrm{QHR}_{iS} = C_{iS} + \frac{[\mu_{iS}(1 + g(N_D))]F_{iS}}{\left(\frac{\partial F}{\partial e}\right)_{iS}} + \frac{\phi t_{iS}}{p_{iS}\left(\frac{\partial F}{\partial e}\right)_{iS}} \qquad (3)$$

where $g(N_D)$ represents the density-dependent effect of increased apprehension towards dominant competitors on the susceptibility to predation.

Although an individual's QHR represents the appropriate payoff to foragers maximizing harvest rates (e.g., Brown 1988), it is difficult to measure in the field, and especially so if multiple foragers use the same patch. Fortunately, QHR is closely related to patch residence time (PRT) that can be estimated from Holling's (1959) disc equation

$$\mathrm{PRT} = \left(\frac{1}{\alpha}\right) * \ln\left(\frac{N_0}{N_f}\right) + h(N_0 - N_f) \tag{4}$$

where α is the instantaneous search rate, N_0 is initial food density, N_f is final food density after foraging (GUD), and *h* is the time required to handle and process each food item before resuming search for another (Kotler and Brown 1990). Assuming that all foragers are equally efficient, the derivative of the amount of food consumed with respect to PRT yields the quitting-harvest rate of the final forager visiting the patch (Fig. 1). More generally, one can use PRT as a reliable indicator of the payoff from foraging unless foraging efficiency (e.g., as revealed by the relationship between GUD and PRT, Kotler et al. 2010) differs between patches. Search rate in risky patches can be expected to decline, for example, if foragers are more apprehensive in those patches than in safe ones.

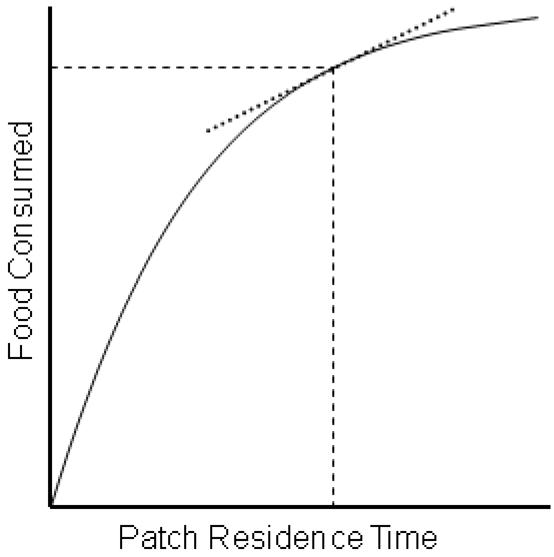
These considerations lead to the following general hypotheses:

H_1: If the dominant species excludes the subordinate species from patches of only one type, then the subordinate's PRT in that patch type should decline with increasing density and the total PRT in that patch by the dominant species.

H_2: If increasing abundance of the dominant species increases the subordinate species' apprehension while foraging, then the subordinate should either

H_{2A}: allocate proportionately more time to the safer patch or

Figure 1. A hypothetical harvest curve (solid line) for an individual foraging in a food patch with diminishing returns. As the amount of food consumed increases, the time taken to harvest one unit of food also increases. The point at which an individual quits harvesting (dashed lines) corresponds to the giving-up density (initial food minus food consumed) and the giving-up time (patch residence time). The derivative of the amount of food consumed with respect to foraging time is the quitting harvest rate (dotted line).


Food Consumed
Patch Residence Time

H_{2B}: forage more efficiently in the safer patch.

Materials and methods

Voles as a model system

Microtus is a field-dwelling herbivorous rodent, whereas *Myodes* is a smaller, forest-dwelling, omnivorous rodent. Both species are active during the day and night and defend nests against intruders (Merritt 1981; Reich 1981). Although each species prefers a different habitat (field *versus* forest), they co-occupy these habitats where they compete for resources (Grant 1969; Morris 1969; Morris 2009). *Microtus* is dominant over, and aggressive towards, *Myodes* (Cameron 1964; Grant 1969, 1972; Morris 1969; Iverson and Turner 1972; Turner et al. 1975; Morris 2009), and may even competitively exclude *Myodes* (Cameron 1964; Iverson and Turner 1972). Dominance by *Microtus* is an effect of its larger body size [*Microtus* adult weight range = 35 – 60 g (Reich 1981); *Myodes* adult weight range = 15 – 35 g (Merritt 1981)]; larger species are typically dominant over smaller species (Getz 1962; Parker 1974; Maynard Smith and Parker 1976).

Field protocol

I transplanted wild-caught male voles of both species to the Lakehead University Habitron [N 48°19’49”, W 89°47’27” (NAD83); Fig. A1.1, Fig. A1.2]. I used only male voles in order to eliminate complications associated with sex-related differences in behaviour such as courtship, reproduction, and inter-sexual competition for resources (Christian 1971; Madison 1980; Webster and Brooks 1981). All experimental animals were live-trapped in natural habitats within 10 km of the Habitron.

Assessing dominance

I conducted one-on-one behavioural encounters between voles in order to assess aggression as a component of competitive interference. Each set of seven weekly encounters (18 July to 31 August 2011) contrasted two male *Myodes* and four male *Microtus* of different weights (14 different *Myodes* and 28 different *Microtus*; Appendix 2). The range in body size for *Microtus* exceeded that of *Myodes*, so I used more *Microtus* than *Myodes* in order to capture the full variance in body size-related aggression of each species. This procedure also maximized interactions by the supposed subordinate (*Myodes*) with dominant competitors (*Microtus*).

Voles interacted in a neutral arena for five minutes during each trial. I structured encounters such that each vole competed in one intraspecific trial, each *Myodes* competed in four interspecific trials, and each *Microtus* competed in two interspecific trials. I assigned aggression and submission values (Table 1) to each vole for each interaction within each trial, then calculated the aggression score as the ratio of the sum of aggression values divided by the sum of aggression plus submission values (Matthews et al. 2005).

Patch residence times and giving up densities

I measured the foraging activity of nine male *Microtus* (mean weight [g] = 23.8 ± 2.4) and nine male *Myodes* (mean weight [g] = 18.9 ± 3.0; Fig. A1.3) in four 25 m × 25 m field enclosures from 15 August to 1 September 2010. Enclosures were made from rodent-proof galvanized fences (0.75 m high, buried 0.5 m in soil) surrounding old-field

Table 1. Behaviours recorded in competitive trials assessing dominance between male *Microtus pennsylvanicus* and *Myodes gapperi* in 2011 (after Matthews et al. 2005).

Behaviour	Aggression Value	Submission Value
Chasing or pinning the opponent without resistance	1	0
Wrestling/interacting with the opponent, after which the opponent runs away	0.75	0.25
Wrestling/interacting with the opponent where there is no clear winner	0.5	0.5
Wrestling/interacting with the opponent, then running away	0.25	0.75
Running away from the opponent when chased	0	1
Being pinned by the opponent without struggling	0	1
Indifferent to opponent	0.5	0.5

habitat that had been converted to a young red-pine (*Pinus resinosa*) plantation (tree-height ~ 3 m). I initiated the experiment by placing four individuals of each species into separate enclosures (control) with the intent to then introduce different numbers of competitors (treatment). Enclosures were open to predators and voles appeared to be especially vulnerable when restricted to a single enclosure (seven of eight *Myodes* disappeared within seven days of initiating this design).

I replaced the missing animals and allowed nine male voles of each species free movement amongst four enclosures via single 9.25 cm circular gates positioned midway along adjoining sides of each enclosure (Fig. A1.4). I implanted radio-frequency identification (RFID) transponders (Trovan 100) in each vole, and monitored movements of rodents between all gates with remote RFID antennae (Vantro Systems, Burnsville, MN, USA). The antennae recorded an animal's RFID identity as well as the exact time (1/100 second accuracy) when individually marked voles moved between enclosures. I added two additional male *Microtus* and two additional male *Myodes* to the enclosures on 22 August to replace one *Myodes* eaten by an ermine (*Mustela erminea*: transponder found in ermine faeces), and another *Myodes* and two *Microtus* that disappeared at the same time. I used only data collected from the period after these new animals were released into the enclosures (22 August to 1 September 2010).

I placed one pair of plastic "bell pot" foraging trays (diameter = 40 cm, depth = 3 cm) one meter apart in each enclosure, and filled each tray with 4.0 g of cleaned whole millet seed (0.2 mm diameter) mixed thoroughly into 1.5 L of sieved silica sand (60 – 90 grain). Each tray rested on top of a remote antenna that recorded the entry and exit time of each vole. I placed one tray under a 8.75 cm tall wooden frame covered with a 60 cm ×

60 cm piece of plywood (safe patch), and the other tray under a similar frame covered with a 60 cm × 60 cm transparent polycarbonate sheet (risky patch, Fig. A1.5). Voles entered the tray under each cover through a 3 cm gap between the cover and soil surface. I placed trays in each enclosure at 17h00 and removed them the next day at 14h30 (21.5 hr foraging period). I sifted the remaining millet seeds from each tray, cleaned the samples of debris and faeces, and weighed the seeds to the nearest 0.01 g (GUD). I recharged trays with new food and sand mixtures daily (Sunday to Friday). Every Sunday I collected and recharged trays that I placed in the enclosures on Friday to ensure that voles continued to forage over the weekend (but excluded weekends from my analyses).

Differential movement by voles amongst the enclosures allowed me to measure *Myodes*' patch use as the local abundance of voles varied. Although this design was unable to measure foraging by *Myodes* in the absence of *Microtus* (and vice versa; I was, however, able to assess *Myodes* foraging when no *Microtus* entered a patch), other studies document that *Myodes* forages more in safe than risky patches in the absence of *Microtus* (Morris and Mukherjee 2007a,b; Andruskiw et al. 2008; Lemaitre et al. 2010).

Statistical design

I conducted all analyses as repeated measures through time using the lme4 package in R (Bates et al. 2010). I used the lmer function for linear mixed effects models and the lmer function with family = binomial for logistic regressions. I compared competing models with bias-corrected Akaike's Information Criteria (AICc) [pkg: qpcR; fcn: AICc (Spiess and Ritz 2010)]. I considered the model with the lowest AICc as the "best" model describing the data as long as the difference in AICc (ΔAICc) between models was > 2. I chose the most parsimonious model whenever ΔAICc < 2 (Akaike 1973; Bozdogan 1987).

I used the dyadic encounters to evaluate whether *Microtus* was dominant over *Myodes.* I tested for differences in dominance between species by analysing the aggression score of each individual during each behavioural trial (n = 154) using a linear mixed effects analysis: fixed effects = species (*Microtus* or *Myodes*), competition (interspecific or intraspecific), and their interaction; random effect = trial (the temporal order of each trial; Appendix 2) nested within individual (identity of the focal individual; n= 42). If *Microtus* is dominant over *Myodes*, then only the species effect would be significant. If, however, dominance depended on the type of encounter, then the interaction term would be significant.

I used mean PRT [the total time that all individuals of one species spent in a patch during one foraging period (total PRT), divided by the total number of individuals of that species recorded in a patch during the same period] and GUD to evaluate the two hypotheses on apparent predation risk. The distributions of PRT and GUD were both right skewed, and could not readily be transformed for parametric analyses. I therefore created binary variables for mean PRT, *Myodes* mean PRT, *Myodes* total PRT, *Microtus* mean PRT, *Microtus* total PRT, number of *Microtus*, number of *Myodes*, and GUD using a median rule (=1 when the datum > than the median value; = 0 when the datum ≤ the median value). I used these binary variables in all analyses involving PRT or GUD.

I assessed patch preferences of each species by analysing the daily mean PRT (n = 128) of *Microtus* and *Myodes* with binary logistic regression; fixed effects = species, patch type, and the two-way interaction between species and patch type; random effect = station (location of the pair of safe and risky patches, n = 4) nested within day (daily foraging period, n = 8).

I used a similar model to test whether the daily mean PRT of *Myodes* (n = 64) increased in safe patches when the number of *Microtus* recorded at a station was high or low; fixed effects = number of *Microtus*, patch type, and the interaction between number of *Microtus* and patch type; random effect = station nested within day. I compared this model to an alternative model that substituted *Microtus* total PRT in a patch for number of *Microtus*. I also included a third model that included both the PRT and number of *Microtus* in a saturated model. These competing models tested whether *Myodes* reacted to direct interference from *Microtus* in the patches (*Microtus* total PRT = test of H_1) or to competition outside of the patches (number of *Microtus* = test of H_2).

Myodes foraged in the absence of *Microtus* at one station for seven of the eight days during the experiment. I used these data to represent a ‘control’ on *Myodes* patch preference in the absence of *Microtus* {paired Mann-Whitney U test in R [pkg: stats; fcn: wilcox.test; paired=TRUE (R Development Core Team 2010)]}.

I used binary logistic regression to test for differences in GUD between safe and risky stations, and for the possibility that GUDs corresponded with different foraging efficiencies (different GUDs but similar PRT in safe and risky patches); fixed effects = *Microtus* total PRT in a patch, *Myodes* total PRT in a patch, patch type, and the two-way interactions between *Myodes* total PRT and patch type, and between *Microtus* total PRT and patch type; random effects = station nested within day. I compared this model with two alternative models, the first of which substituted *Myodes* mean PRT and *Microtus* mean PRT for *Myodes* total PRT and *Microtus* total PRT, respectively, and the second of which substituted number of *Myodes* and number of *Microtus* for *Myodes* total PRT and *Microtus* total PRT, respectively. If GUDs varied only with total PRT in a patch, then foraging efficiency would be similar between patches (accept $H_{2A)}$; but if GUDs varied with the number of voles and not PRT, then foraging efficiency varied between patches (accept $H_{2B)}$.

Results

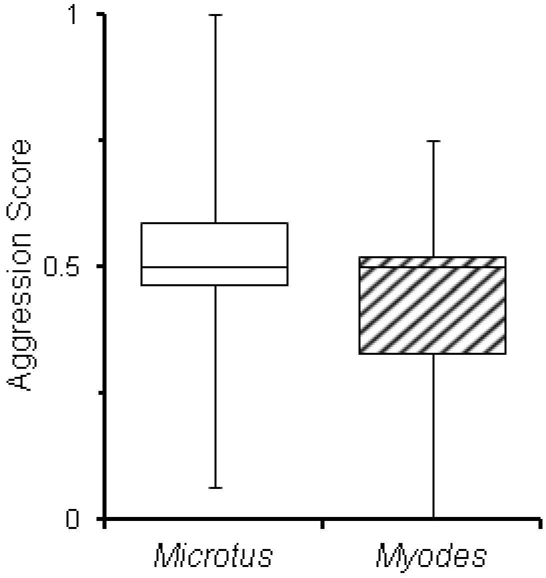
Throughout the experiment, nine *Microtus* and seven *Myodes* used the foraging trays. All nine *Microtus* were active (used gates or foraging patches) throughout the experiment. The number of *Myodes* known to be active decreased from seven on 22 August to four on 1 September (the last day of the experiment). A minimum of five *Microtus* and three *Myodes* used the foraging trays on any given day of the experiment, and on the final day of foraging, seven *Microtus* and four *Myodes* used the foraging trays (Fig. A1.7).

The best model of aggression score included only species (Table A3.1); *Microtus* was dominant over *Myodes* (mean aggression score of *Microtus* = 0.53 ± 0.04; mean aggression score of *Myodes* = 0.43 ± 0.04; $t_{1,40} = 2.91$, $p = 0.0058$; Table 2, Fig. 2). *Myodes* tended to avoid *Microtus* and rarely engaged in jointly aggressive interactions. The majority of interactions between *Myodes* and *Microtus* involved sniffing and *Myodes* being chased by *Microtus*. *Myodes* typically occupied the opposite side of the arena from *Microtus* and moved to maintain the maximum distance possible whenever *Microtus*

Table 2. Parameter values of the ‘best’ model (Table A4.1) describing aggression scores of voles competing in dyadic encounters at the Lakehead University Habitron in Northern Ontario, Canada. Species was coded as an indicator variable, where *Microtus* = 0 and *Myodes* = 1.

Parameter	Estimate (S. E.)	df	*t*	*p*
Intercept	0.53 (0.02)	112	24.26	<0.0001
Species (*Myodes*)	-0.10 (0.03)	40	-2.91	0.0058

Figure 2. Aggression scores of *Microtus* and *Myodes* in dyadic encounters recorded at the Lakehead University Habitron in Northern Ontario, Canada. Aggression scores were higher for *Microtus* than for *Myodes*. Aggression score was unaffected by the type of competition (intraspecific or interspecific; Appendix 3, Table A3.1). Boxes represent the interquartile range, lines within boxes represent the median values, and whiskers represent the minimum and maximum values.


1
0.5
0
Aggression Score
Microtus
Myodes

advanced. *Myodes* also had many non-aggressive interactions with conspecifics, whereas *Microtus* was always aggressive, regardless of the identity of the competitor. Occasionally *Myodes* was dominant over *Microtus*, but this occurred only when *Myodes* was of similar body size to *Microtus*.

Although the two rodent species differed in their allocation of foraging time to the two types of resource patches (species × patch type: log odds ratio = 1.89, $p = 0.04$; Fig. 3), *Microtus* allocated more foraging time to safe than risky patches, while *Myodes* allocated similar time to each patch type. *Myodes* also allocated more time to foraging than did *Microtus* (species: log odds ratio = 3.47, $p < 0.0001$; Table 3). The majority of individuals were more likely to allocate more foraging time to safe patches (patch type: log odds ratio = 1.53, $p = 0.02$).

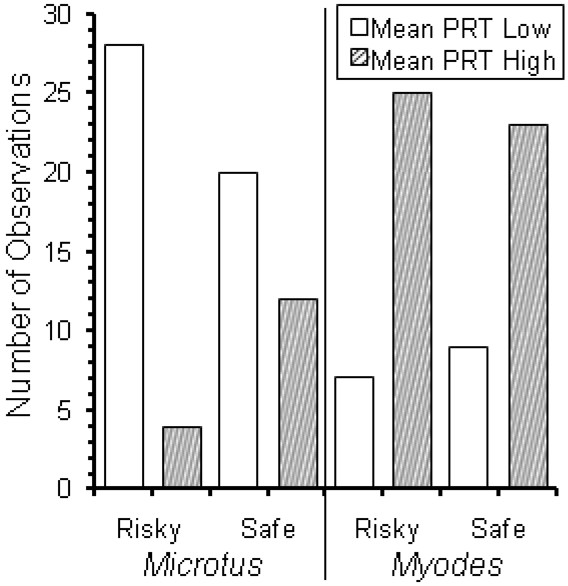
The selected model for *Myodes* mean PRT included only the number of *Microtus* (Table A3.2). *Myodes* spent more time foraging when *Microtus* abundance was high than when *Microtus* abundance was low (number of *Microtus*: log odds ratio = 1.27, $p = 0.02$; Table 4, Fig. 4). This effect was reinforced by the results from those instances where *Microtus* did not enter resource patches (the seven day 'control'). *Myodes*, in the absence of *Microtus*, spent more time in safe than risky patches on six of the seven days. These data are suggestive of *Myodes* preference for safe patches in the absence of interspecific competition, but the analysis was non-significant (*Myodes* mean PRT [s] in safe = 131.39 ± 85.02; risky = 81.96 ± 90.33; $V = 5$, $p = 0.16$).

The selected model for GUD also included the number of voles (Table A3.3). On average, GUDs were more likely to be high in safe patches than in risky patches (patch type: log odds ratio = 1.82, $p = 0.04$), but when *Microtus* abundance was high, GUDs

Table 3. Parameter values for the binary logistic regression of mean patch residence times (n = 128) of meadow voles (*Microtus pennsylvanicus*) and red-backed voles (*Myodes gapperi*) foraging in safe and risky patches at the Lakehead University Habitron. Estimates are log ratios. Species (*Microtus* = 0, *Myodes* = 1) and Patch Type (risky = 0, safe = 1) included as indicator variables.

Parameter	Estimate (S. E.)	*z*	*P*
Intercept	-2.09 (0.64)	-3.27	<0.001
Species	3.47 (0.72)	4.85	<0.0001
Patch Type	1.53 (0.67)	2.29	0.02
Species × Patch Type	-1.89 (0.90)	-2.10	0.04

Figure 3. Counts of the number of times that the mean PRT of *Microtus* and *Myodes* was either higher or lower than the median value in safe and risky patches at the Lakehead University Habitron in Northern Ontario, Canada.

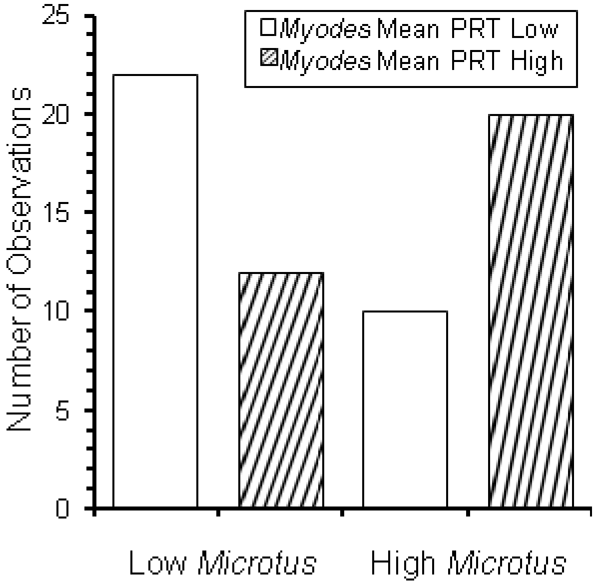


30
25
20
15
10
5
0
Number of Observations
☐ Mean PRT Low
▨ Mean PRT High
Risky
Safe
Microtus
Risky
Safe
Myodes

Table 4. Parameter values for the binary logistic regression of *Myodes gapperi* mean patch residence time (n = 64) when foraging in safe and risky patches in Northern Ontario, Canada. Number of *Microtus* is the number of different *Microtus* using a station during one foraging period (recoded as a binary variable; =1 when the datum > than the median value, = 0 when the datum ≤ the median value). Estimates are log ratios.

Parameter	Estimate (Std. Err.)	*Z*	*p*
Intercept	-0.59 (0.37)	-1.61	0.11
Number of *Microtus*	1.27 (0.54)	2.37	0.02

Figure 4. Counts of the number of times that *Myodes'* mean PRT as high or low in foraging in patches at the Lakehead University Habitron in Northern Ontario, Canada. Values greater than the median were high, and values less than or equal to the median were low.



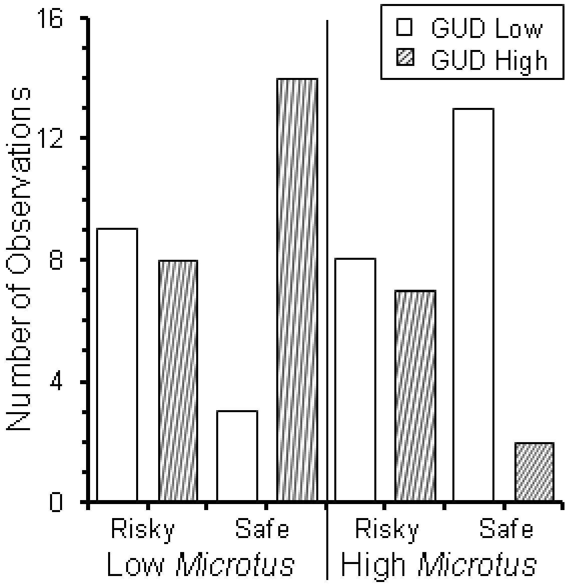
25
20
15
10
5
0
Number of Observations
☐ *Myodes* Mean PRT Low
▨ *Myodes* Mean PRT High
Low *Microtus*
High *Microtus*

Table 5. Parameter values for the ‘best’ binary logistic regression model (Table A4.3) of giving up densities (GUD, n = 128) for red-backed voles (*Myodes gapperi*) and meadow voles (*Microtus pennsylvanicus*) foraging in safe and risky patches in Northern Ontario, Canada. Estimates are log ratios.

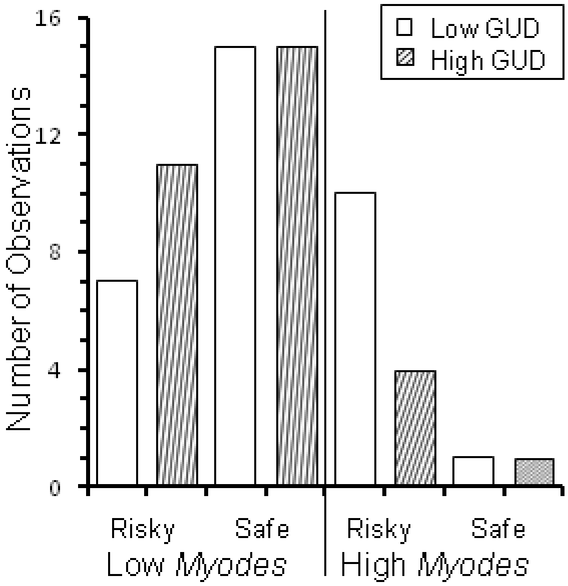
Parameter	Estimate (Std. Err.)	*Z*	*p*
Intercept	0.15 (0.57)	0.25	0.80
Patch Type	1.82 (0.88)	2.08	0.04
Number of *Myodes*	-2.24 (0.97)	-2.30	0.02
Number of *Microtus*	1.44 (1.08)	1.33	0.18
Patch Type × Number of *Microtus*	-5.31 (1.60)	-3.32	< 0.001

Figure 5. Counts of the number of times that the giving-up density (GUD) of safe and risky patches was high or low when there were many (high) or few (low) *Microtus* (A) or *Myodes* (B) using foraging patches at the Lakehead University Habitron in Northern Ontario, Canada. GUDs greater than the median were high and all other values were low.

A)


16
12
8
4
0
Number of Observations
□ GUD Low
▨ GUD High
Risky
Safe
Low *Microtus*
Risky
Safe
High *Microtus*

B)


16
12
8
4
0
Number of Observations
□ Low GUD
▨ High GUD
Risky
Safe
Low *Myodes*
Risky
Safe
High *Myodes*

were more likely to be low in safe patches (number of *Microtus* × patch type: log odds ratio = 5.31, $p < 0.001$; Table 5, Fig. 5A). As expected from the assumption of density-dependent foraging, GUD in both patches was more likely to be low when the number of *Myodes* using a patch was high, rather than low (number of *Myodes*: log odds ratio = 2.24, $p = 0.02$; Fig. 5B).

Discussion

Predation risk reduces foragers' patch use (Brown 1988, 1992, 1999; Thorson et al. 1998; Altendorf et al. 2001) and foraging efficiency (Lima et al. 1985; Werner and Hall 1988; Cooper 2000; Dall et al. 2001), and thereby modifies their time allocation (Brown 1999; Lima and Bednekoff 1999; Kotler et al. 2004, 2010). These indirect effects profoundly influence prey distribution and abundance, usually leading to more individuals using safe than risky habitats in both terrestrial (Ferguson et al. 1988; Abramsky et al. 1997; Fontaine and Martin 2006; Thomson et al. 2006; Valeix et al. 2009) and aquatic systems (e.g. Gilliam and Fraser 1987; Jordan et al. 1997; Linehan et al. 2001; Dupuch et al. 2009), and also cause individuals to significantly increase their foraging in safe relative to risky patches (Brown 1992, 1999; Grand and Dill 1999; Altendorf et al. 2001; Kotler et al. 2004). Yet this study, and that by Morris (2009) using the same vole system, suggest that predation risk may often be over-estimated in field experiments because it can include an apparent component associated with competitive interactions.

Although *Myodes'* PRT revealed only a slight preference for safe over risky patches in this study, *Myodes* clearly altered its patch use when confronted with different numbers of *Microtus*. *Myodes* increased its residence time in patches as the number of nearby *Microtus* increased. GUDs were also lower in safe patches when *Microtus* was more abundant, which suggests that *Myodes* foraged more apprehensively and less efficiently with increased *Microtus* abundance (equation 3). Under low *Microtus* abundance, GUDs were more often high in safe patches, whereas under high *Microtus* abundance, GUDs were more often low in safe patches. The relative safety of safe patches increased as competition increased. Reduced GUD and increased mean PRT by *Myodes w*ere both caused by *Microtus* abundance, which implies that *Microtus*' affect on *Myodes* PRT was reflected in GUDs. However, both *Microtus* and *Myodes* were foraging in the patches and were responsible for GUDs, so patterns in GUD were not solely caused by *Myodes*. Regardless, it is likely that apprehension toward *Microtus* interacted with predation risk as suggested by Morris (2009). Lower GUD is consistent with apprehension because PRT increased in both patches for *Myodes*, yet GUD decreased only in safe patches. This suggests that foraging efficiency was highest in safe patches, and that despite spending additional time in risky patches, there was no reduction in GUD.

The combination of higher aggression, lower mean PRT by *Microtus*, changes in *Myodes* mean PRT with the number of *Microtus*, and lower GUDs in safe than risky patches provides a plausible explanation for apparent predation risk. If *Microtus* forage to a higher GUD than *Myodes* (due to higher habitat quality and reduced marginal value of energy, as implied by lower mean PRT of *Microtus*), and if direct interference competition with *Microtus* causes *Myodes* to forage more apprehensively (*Microtus* was more aggressive), then *Myodes* should forage longer and less efficiently in patches when there is increased competition for food (increased PRT of *Myodes* as the number of *Microtus* increases). And if *Myodes* also forage more apprehensively under increased predation risk, then *Myodes* will forage more efficiently in safe than risky patches and obtain a lower GUD in safe than risky patches, especially when apprehensive of dominant competitors (hypothesis 2B). Thus, it appears that potential for interference, as well as competition for resources, intensifies with local variation in *Microtus* abundance (equation 3). Both effects reduce habitat quality for *Myodes* thereby increasing the marginal value of energy (equation 1). Apprehension towards dominant *Microtus* increases the risk of predation (equation 3) with the result that *Myodes* harvest more from safe than risky patches.

The response of *Myodes* to variation in the local abundance of *Microtus* also suggests an unappreciated effect of scale. If *Myodes*' patch use depended on total *Microtus* density, then patch use should have been constant through time. The significant effect of local *Microtus* abundance suggests a sophisticated small-scale assessment of risk by *Myodes* that varied with *Microtus*' use of different foraging stations during the experiment. Increased apprehension towards *Microtus* caused *Myodes* to forage longer and to a lower giving-up density in safe patches.

If *Myodes* reacted to direct interference over patch selection, then its patch use should have changed with that of *Microtus*. Since *Myodes* mean PRT did not vary with *Microtus*' total PRT, we can reject this hypothesis. *Microtus*' preference for safe patches similarly rejects the hypothesis that *Myodes*' patch choice was caused by direct interference with *Microtus* in risky patches. Both patterns reinforce the perspective that the consequences of interference are mediated indirectly through patch use by *Myodes*. Yet the theory presented here also suggests that *Myodes* should be increasingly apprehensive as competition increases. It will thus be important for future research to assess the prediction that *Myodes*' foraging efficiency and predator vigilance decline with increased *Microtus* density.

It remains, nevertheless, somewhat unclear how effectively *Myodes* can manage predation risk through differential patch use. Predation risk was real in the enclosures (at least one red-backed vole was eaten by an ermine), but *Myodes*, under decreased competition from *Microtus*, expressed only marginal preference, if any, for 'covered' versus 'open' patches [Morris (2009) reported a similar pattern). Other studies on the same species, however, documented more foraging from patches under natural cover than from putatively risky patches placed in the open (Morris and Mukherjee 2007a,b; Andruskiw et al. 2008; Lemaitre et al. 2010). I suspect that these apparently divergent results might reflect unknown cues of predation risk in addition to those associated with covered and open patches. It is possible, for example, that predation risk, or at least its assessment by *Myodes*, has declined with the growth of red pine in the Habitron since Morris and Muhkerjee (2007a,b) conducted their experiments (in 2005 and 2006 respectively).

Apparent predation risk has rather serious implications for the assessment of factors influencing community structure. The cost of predation, for example, is deemed greater than that of interspecific competition in determining habitat use by gerbils in the Negev desert (Abramsky et al. 1998, 2001, 2002). It seems clear, however, that the effects of competition can often be misconstrued as predation risk. It may not even make sense to contemplate the relative roles of competition versus predation risk because my experiments, and those by Morris (2009), demonstrate that competition and predation risk act synergistically to influence patch use. With these complexities in mind, astute ecologists would do well to control for competition in experiments focussed on predation risk, control for predation risk in experiments focussed on competition, and examine both processes simultaneously when attempting to infer factors structuring ecological communities.

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Appendix 1: Images of the Lakehead University Habitron, the Habitron’s location in Northwestern Ontario, equipment used at the Habitron, and comparisons of voles used in experiments.

Figure A1.1. A representative photo of some of the 24 rodent enclosures at the Lakehead University Habitron. Photo credit: Jody T. MacEachern, 2008.

Figure A1.2. A map of Northwestern Ontario, highlighting the location of the Lakehead University Habitron and sites used to capture male voles for experiments (map of Ontario from http://geography.about.com/library/blank/blxont.htm, accessed 5 March 2012).

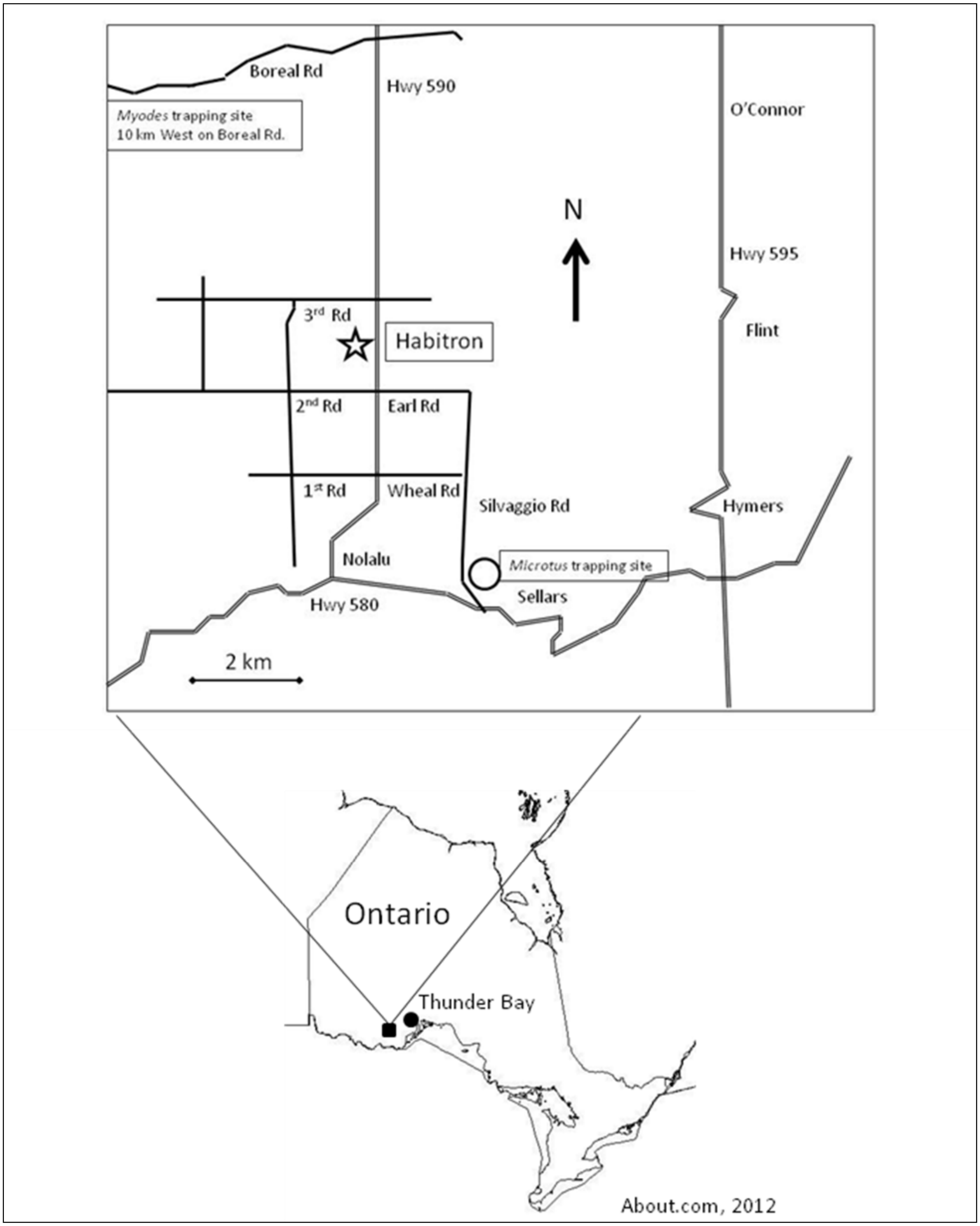

Boreal Rd
Hwy 590
Myodes trapping site
10 km West on Boreal Rd.
O'Connor
N
Hwy 595
3rd Rd
Habitron
Flint
2nd Rd
Earl Rd
1st Rd
Wheal Rd
Silvaggio Rd
Hymers
Nolalu
Microtus trapping site
Sellars
Hwy 580
2 km
Ontario
Thunder Bay
About.com, 2012

Figure A1.3. A boxplot of the body weights of *Microtus* and *Myodes* used in experiments at the Lakehead University Habitron, in Northern Ontario, Canada. The boxes represent the interquartile range, the line within the box represents the median value, and the whiskers represent the minimum and maximum values.

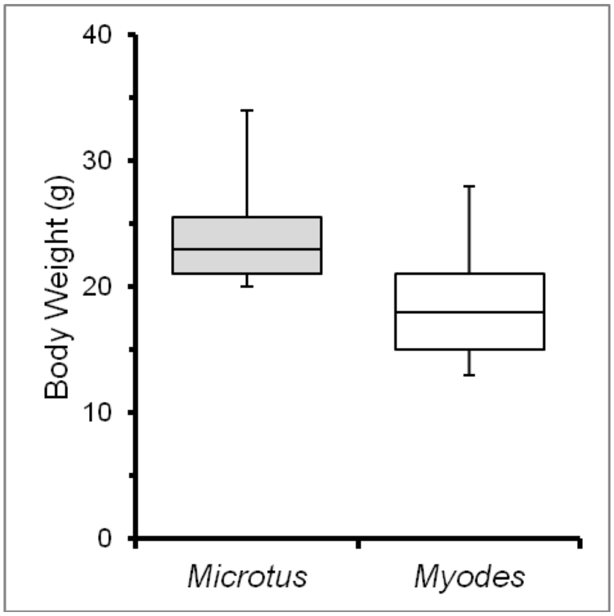

40
30
20
10
0
Body Weight (g)
Microtus
Myodes

Figure A1.4. Photographs of gates (diameter = 9.25 cm) connecting enclosures within the Lakehead University Habitron (Northern Ontario, Canada). Gates were opened during the experiment so that rodents could move between enclosures. Remote antennae recorded the time when a vole passed through each gate (seen embedded in wooden ‘cradles’ on the opposite side of the gate). Photo credit: William D. Halliday.

Figure A1.5. Safe (top) and risky (middle) patches used to obtain patch residence times and giving-up densities of male voles foraging within four interconnected enclosures at the Lakehead University Habitron, Northern Ontario, Canada. Each patch contained a foraging tray (bottom) with 4.0 g of whole millet mixed in 1.5 L of sieved silica sand (60 $\leq$ 90 grain). Patches were monitored with remote antennae connected to data loggers (top photos), in order to obtain the patch residence time of RFID-tagged voles. Photo credit: William D. Halliday.

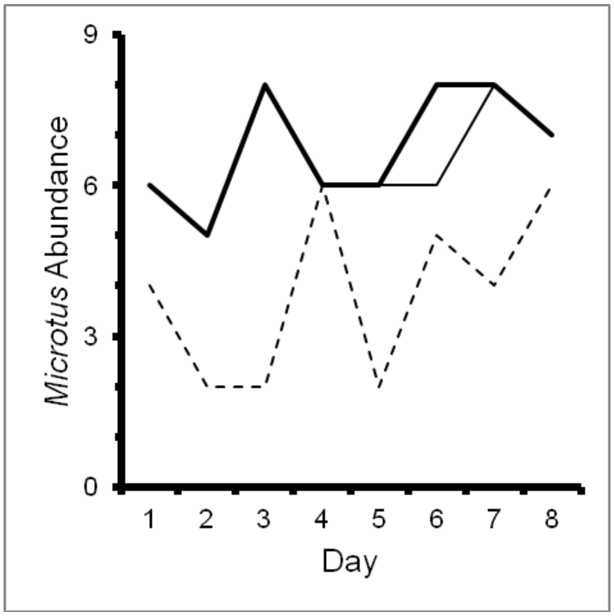
Figure A1.6. Photos of the cages used to house male meadow voles (*Microtus pennsylvanicus*) and male red-backed voles (*Myodes gapperi*) for behavioural trials at the Lakehead University Habitron in Northern Ontario, Canada. Each cage contained a nest box, food (rodent chow and alfalfa wafers), water, and PVC tubing for enrichment. Photo credit: William D. Halliday.

B
C

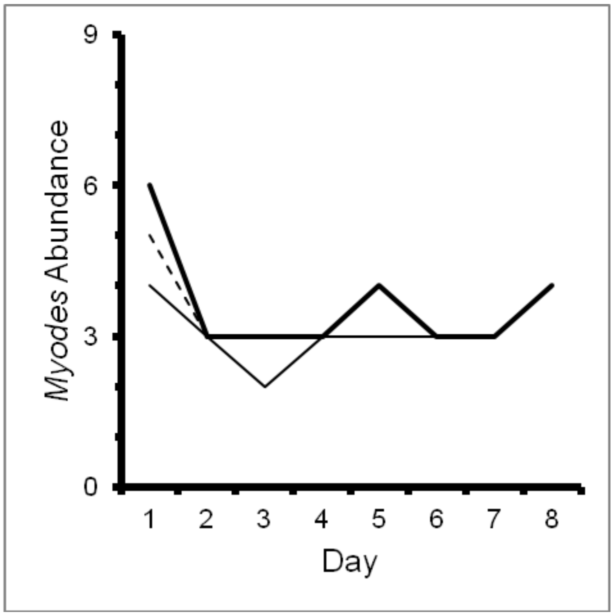
E
G
B

Figure A1.7. Patch use by *Microtus* (A) and *Myodes* (B) at the Lakehead University Habitron in Northern Ontario, Canada. More *Microtus* visited safe than risky patches, while most *Myodes* visited both patches. Bold solid lines represent the total number of individuals visiting patches during one day, the lighter solid lines represent the number of individuals visiting safe patches during one day, and the dashed lines represent the number of individuals visiting risky patches during one day.

A)


9
6
3
0
Microtus Abundance
1
2
3
4
5
6
7
8
Day

B)


9
6
3
0
Myodes Abundance
1
2
3
4
5
6
7
8
Day

Appendix 2: Description of the test for a dominance hierarchy between *Microtus* and *Myodes*.

I housed two wild caught male *Myodes* and four wild caught male *Microtus* under ambient temperatures in separate cages (Appendix 1, Fig. A1.6) at the Lakehead University Habitron each week between 18 July and 31 August 2011. The walls and floor of each cage were made of plywood (60 cm × 60 cm × 30 cm), covered by a hardware cloth lid. Each cage contained a nest box with cotton bedding, food (rodent chow and alfalfa wafers) and water *ad libitum*, as well as PVC tubing providing behavioural enrichment. The floor of each cage was covered in wood chips, and the pens were protected from wind and rain. I allowed the voles to acclimate to captivity for 24 to 48 hours.

All voles competed in trials within a neutral arena (20 litre white plastic pail, diameter ≈ 30 cm). I placed each vole on opposite sides of a clear polycarbonate partition bisecting the arena, removed the partition after voles acclimated to separate sides of the arena for two minutes, then allowed the voles to interact for five minutes. I recorded each trial with an infrared video camera while viewing the trials on a remote monitor. I returned the voles to their cages after the trial, sanitized the arena with dilute bleach, and replaced the wood chips with unused ones. All voles competed in one intraspecific trial at 08h00, and each *Myodes* then competed in an interspecific trial at two hour intervals until 16h00. Individual *Microtus* never competed in two consecutive interspecific trials. Each *Myodes* competed with each *Microtus*, and each *Microtus* competed with each *Myodes*. I released each animal at its point of capture after all trials were completed.

Carry-over effect

Each vole competed in multiple trials, and each *Myodes* competed every two hours over an eight-hour period. Behaviour in previous trials may have influenced the outcome of subsequent trial(s). I included the order of each trial in my analysis as a random variable to control for this carry-over effect.

Appendix 3: Akaike's information criteria for analyses of aggression scores, *Myodes* patch residence times, and giving up densities from experiments with two species of voles in Northern Ontario, Canada

Table A3.1. Selection of models describing how species and competition affect aggression score using bias-corrected Akaike's information criteria (AICc). All models included order of trial nested within individuals as a random effect. Bold text indicates the selected model. K = number of parameters.

Model	K	AICc	ΔAICc
Aggression Score = Species	**5**	**-84.54**	**0**
Aggression Score = Species + Competition	6	-77.43	7.11
Aggression Score = Species + Competition + Species × Competition	7	-77.20	7.34

-

Table A3.2. Model selection for the 'best' model (bold) of *Myodes*' mean PRT using the bias-corrected Akaike's information criterion (AICc). *Myodes* mean PRT was analysed with a binary logistic analysis, and the independent variables (all binary) were Patch Type, number of *Microtus*, and *Microtus* total PRT. * represents a competing, but less parsimonious, model. K = number of parameters.

Model	K	AICc	ΔAICc
Myodes* mean PRT = number of *Microtus	**4**	**90.73**	**0**
Myodes mean PRT = number of *Microtus* + patch type	5	91.62	0.89*
Myodes mean PRT = number of *Microtus* + patch type + number of *Microtus* × patch type	6	93.61	2.88
Myodes mean PRT = *Microtus* total PRT + patch type + *Microtus* total PRT × patch type	6	95.67	5.94
Myodes mean PRT = *Microtus* total PRT + number of *Microtus* + patch type + *Microtus* total PRT × patch type + number of *Microtus* × patch type + *Microtus* total PRT × number of *Microtus* × patch type	10	98.91	8.18

Table A3.3. Model selection for the ‘best’ model (bold) of giving up density (GUD) using Akaike’s bias-corrected information criterion (AICc). GUD was analysed using binary logistic analysis with patch type and three metrics of *Myodes* and *Microtus* patch use as fixed effects. * represents a competing model. The ‘best’ model has the lowest AICc and fewest parameters (K).

Model	K	AICc	ΔAICc
GUD = patch type + number of *Microtus* + number of *Myodes* + patch type × number of *Microtus*	**7**	**79.64**	**0**
GUD = patch type + number of *Microtus* + number of *Myodes* + patch type × number of *Microtus* + patch type × number of *Myodes*	8	81.62	1.98*
GUD = patch type + number of *Microtus* + patch type × number of *Microtus*	6	83.40	2.76
GUD = patch type + *Microtus* mean PRT + *Myodes* mean PRT + patch type × *Microtus* mean PRT + patch type × *Myodes* mean PRT	8	85.46	5.82
GUD = patch type + *Microtus* total PRT + *Myodes* total PRT + patch type × *Microtus* total PRT + patch type × *Myodes* total PRT	8	88.63	8.99