

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

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Prey often react to predation risk by foraging preferentially in the safety of cover rather than in more risky open patches. Yet this pattern of patch use also can be caused by dominant interspecific competitors. We develop a simple theory of this form of apparent predation risk that describes the patch use of an optimal forager confronted with dominant individuals. The theory predicts that subordinate animals should increase their use of safe foraging patches as the density of nearby dominants increases. We tested the theory with meadow voles (*Microtus pennsylvanicus*) and southern red-backed voles (*Myodes gapperi*). We used dyadic encounters to confirm that meadow voles are dominant over red-backed voles. We then evaluated their respective foraging patterns in pairs of covered and open patches in 4 adjacent subgrids in an old-field enclosure. Subordinate red-backed voles foraged indifferently between covered and open patches when few meadow voles were present. Red-backed voles increased their use of both patches as the number of nearby meadow voles increased. Giving-up densities were lowest, and harvesting efficiency highest, in covered patches when the number of nearby meadow voles was high. These results document competition between the 2 species and suggest that vigilance toward dominant meadow voles magnifies the risk experienced by red-backed voles in open patches. Investigators assessing foraging behavior between “safe” and “risky” patches might misinterpret the competitive effect as predation risk unless they 1st account for competition among foraging individuals.

Key words: apparent predation risk, competition, giving-up density, *Microtus pennsylvanicus*, *Myodes gapperi*, patch use

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Predators not only kill prey, they also modify a host of behaviors 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 modelling prey foraging games (Brown 1999; Brown and Kotler 2004), where prey typically optimize foraging by harvesting more resources from “safe” covered patches (those where predators are less likely to be encountered) than from “risky” open 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 under cover than in open patches (“apparent predation risk”—Morris 2009). Dominant competitors can impose 2 main foraging costs on subordinate

competitors: interference while foraging (Kotler and Brown 1988; Bouskila 1995) and risk of injury (Berger-Tal et al. 2009). Interference lowers the efficiency of foragers in a patch, and can even make it more valuable for foragers to select patches without interference (e.g., Bouskila 1995), and especially so if there also is risk of injury. The cost of aggressive competition modulated through interference and injury modifies the role of the predator in the prey foraging game. It is thus possible that predators’ influence on prey behavior has been misinterpreted because competitors can produce foraging patterns normally attributed to predation risk.

Morris (2009) highlighted the importance of competition in the prey foraging game with experiments assessing patch use by large meadow voles (*Microtus pennsylvanicus*; hereafter *Microtus*) competing with smaller southern red-backed voles (*Myodes gapperi*; hereafter *Myodes*). *Myodes* harvested more



resources from patches located under cover in the presence of *Microtus* than when *Microtus* was absent. 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: foraging *Microtus* spent more time in open patches where interference caused *Myodes* to increase use of covered patches, or the presence and abundance of *Microtus* caused *Myodes* to forage more apprehensively in open patches. Increasing competition would thereby increase foraging by *Myodes* in covered patches.

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

THEORY

Optimally foraging individuals maximizing resource intake will quit harvesting resources from a patch when the costs of foraging outweigh the benefits (Brown 1988, 1992). The costs traditionally include the metabolic cost of foraging, the cost of predation, and the cost of missed opportunities to enhance fitness. The quitting-harvest rate of a forager is typically measured in patches that yield diminishing returns and that vary in one of the costs (Brown 1988, 1992). The payoff from such a foraging patch is inversely proportional to the quitting-harvest rate. Foraging experiments that estimate the quitting-harvest rate (or its correlate, giving-up density [GUD]) in otherwise identical patches, where predation risk is modified with protective cover, are used frequently to evaluate predation risk. Virtually all of these experiments reveal that quitting-harvest rates and GUDs are lower when predation risk is low than when predation risk is high (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. Three different hypotheses involving interference can account for preference of covered patches by subordinates. First, if dominant individuals have lower preference for covered patches than open patches, then avoidance of dominants in the open patches can cause subordinates to increase their use of cover. This scenario is unlikely unless the 2 species have different perceptions of danger (e.g., if they vary in the effectiveness of their vigilance, susceptibility to different predators, or perception of predation risk). This direct cost of competition coupled with different microhabitat preferences

has rarely been examined using the quitting-harvest rate (Brown 1988). It seems more likely that the effect of interference will be modulated through other differences in behavior.

Second, subordinate individuals frightened by possible encounters with dominant aggressors may increase 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 covered patches (or reduce their use of open patches). The 3rd hypothesis predicts that subordinates forage more efficiently in cover than in the open because they are more apprehensive to possible interference from dominants in open patches. When predation risk is low, subordinates may forage similarly between otherwise risky and safe patches in the absence of dominants, but increase their use of covered patches in the presence of dominants in an effort to reduce aggressive encounters (Morris 2009). In this scenario, dominant competitors are an additional risk, and subordinates perceive greater risk in patches where they can easily be detected by dominants, such as in the traditional open patches.

These 3 competing hypotheses for apparent predation risk rely on 3 different mechanisms: direct interference, risk of competition compounding the risk of predation, or risk of competition in addition to predation risk. All 3 hypotheses rely on interference competition as either a direct or indirect mechanism mimicking predation risk.

Although an individual's quitting-harvest rate 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, the quitting-harvest rate is closely related to patch-residence time (PRT), which can be estimated from Holling's (1959) disc equation:

$$\text{PRT} = \left(\frac{1}{\alpha}\right) \left[\ln\left(\frac{N_0}{N_f}\right) \right] + h(N_0 - N_f), \quad (1)$$

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 (GUD decreases at a similar rate as PRT increases), 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).

These considerations lead us to 3 formal hypotheses (H) and predictions (P) necessary to document apparent predation risk, and to reveal the mechanism causing it.

H₁—direct interference: The dominant species excludes the subordinate species from open patches.

P₁: The subordinate's PRTs will decline in the patch preferred by the dominant, and increase in the opposite patch, as the dominant competitor's PRT increases in its preferred patch. The preference of dominants will be revealed if the

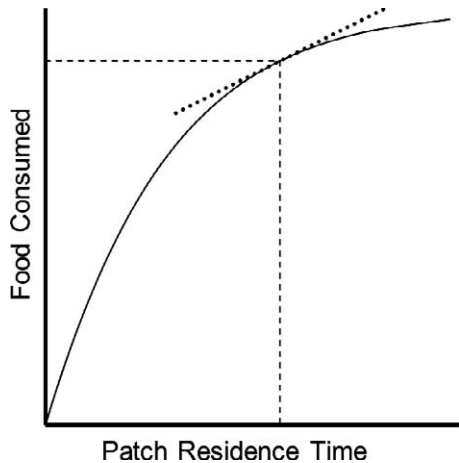


FIG. 1.—A hypothetical harvest curve (solid line) for an individual foraging in a food patch with diminishing returns. As the amount of food consumed increases, the time taken to harvest 1 unit of food also increases. The point at which an individual quits harvesting (dashed lines) corresponds to the 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 diagonal line).

residence time in one patch is greater than in another and GUD will decrease with increasing PRT.

H_2 —indirect competition interacting with predation risk: The dominant species magnifies the risk of predation and causes the subordinate species to forage more apprehensively in risky open patches.

P_2 : The subordinate species will forage less efficiently in open patches than in covered patches as the density of dominants increases. PRT of the subordinate will increase with the number of dominant competitors, and subordinates will spend more time foraging under cover than in open patches regardless of competition. GUD will depend more on competition (number of competitors) than on PRT.

H_3 —indirect competition in addition to predation risk: The likelihood of interference by the dominant species causes the subordinate species to forage more apprehensively in risky open patches.

P_3 : As in P_2 , the subordinate species will forage less efficiently in open patches than in covered patches as the density of dominants increases. The subordinates' PRT will increase with the number of dominant competitors, but contrary to P_2 , subordinates will not forage more in cover versus open patches in the absence of dominant competitors. GUD will depend more on competition (number of competitors) than PRT.

MATERIALS AND METHODS

Voles as a model system.—*Microtus* is a field-dwelling herbivorous rodent, whereas *Myodes* is a smaller, omnivorous species that prefers forest habitat. 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, they occasionally co-occupy forests or fields where they compete for resources (Grant 1969; Morris 1969; Morris 2009). *Microtus* is dominant over, and aggressive toward, *Myodes* (Cameron 1964; Grant 1969, 1972; Morris 1969; Iverson and Turner 1972; Turner et al. 1975; Morris 2009). Dominance by *Microtus* is associated with its larger body size (Merritt 1981; Reich 1981); larger voles are typically dominant over smaller ones (Getz 1962).

Field protocol.—We transplanted wild-caught male voles of both species to the Lakehead University Habitron in northern Ontario, Canada (48°19'49"N, 89°47'27"W [NAD83]). We used only male voles in order to eliminate complications associated with sex-related differences in behavior such as courtship, reproduction, and intersexual competition for resources (Christian 1971; Madison 1980; Webster and Brooks 1981). All experimental animals were livetrapped in natural habitats within 10 km of the Habitron. All experimental procedures were approved by Lakehead University's Animal Care Committee, which follows the guidelines of the Canadian Council on Animal Care and those of the American Society of Mammalogists (Sikes et al. 2011).

Assessing dominance.—We conducted one-on-one behavioral encounters between voles in order to assess dominance of *Microtus* over *Myodes*. Each set of 7 weekly encounters (18 July–31 August 2011) contrasted 2 male *Myodes* and 4 male *Microtus* of different masses (14 different *Myodes* and 28 different *Microtus*). The range in body size for *Microtus* exceeded that of *Myodes*, so we used more *Microtus* than *Myodes* 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*).

We captured voles from habitats surrounding the Habitron, and allowed voles to acclimate to captivity in solitary wooden cages with ad libitum food, water, and shelter for 24 h prior to interactions. We then placed 2 voles in a neutral arena (opaque polyethylene bucket: diameter = 26 cm, height = 36 cm; floor covered in fresh cedar chips) for a 1-min acclimation period (voles acclimated on either side of a transparent polyethylene divider) followed by 5 min of interaction (divider removed) for each trial. We structured encounters such that each vole competed in 1 intraspecific trial, each *Myodes* competed in 4 interspecific trials, and each *Microtus* competed in 2 interspecific trials, and we randomized the order of interactions. Voles of the same species could have been familiar with each other because they were trapped from the same site; however, interspecific competitors were unfamiliar with each other. We allowed voles to rest for at least 1 h in their cages between trials, and we cleaned the arena with dilute bleach and added fresh wood chips to the arena between trials.

We assigned aggression and submission values (Table 1) to each vole for each interaction within each trial, then determined dominance by calculating the aggression score as the sum of aggression values divided by the sum of aggression plus submission values (Matthews et al. 2005).

TABLE 1.—Behaviors recorded in competitive trials assessing dominance between male *Microtus* and *Myodes* in 2011 (after Matthews et al. 2005).

Behavior	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

We analyzed aggression scores for each individual in each trial ($n = 154$) using a linear mixed-effects model to confirm that *Microtus* was more aggressive than, and therefore dominant over, *Myodes*: fixed effects = species (*Microtus* or *Myodes*), competition (interspecific or intraspecific), and their interaction; random effect = trial (the temporal order of each trial) nested within individual (identity of the focal individual).

Assessing apparent predation risk.—We measured the foraging activity of 9 male *Microtus* (mass $\bar{X} = 23.8 \pm 2.4$ g [SE]) and 9 male *Myodes* (weight $\bar{X} = 18.9 \pm 3.0$ g) in one 50 × 50-m field enclosure with intersecting partitions (dissecting the enclosure into four 25 × 25-m quadrants) from 15 August to 1 September 2010. The enclosure and partition fences were made from rodent-proof galvanized metal (0.75-m high, buried 0.5 m in soil) surrounding old-field habitat that had been converted to a young red-pine (*Pinus resinosa*) plantation (tree height ~3 m). The vegetative cover in this enclosure also included a few jack pine (*Pinus banksiana*), many species of grass, and local forbs such as goldenrod (*Solidago spp.*), strawberry (*Fragaria virginiana*), red clover (*Trifolium pratense*), and raspberry (*Rubus idaeus*). Tree density ranged from 0.16 to 0.28 trees/m².

We allowed the voles of each species free movement among the 4 quadrants via single 9.25-cm circular gates positioned midway along adjoining sides of each quadrant. We implanted radiofrequency identification transponders (Trovan 100; Hessele, North Humberside, United Kingdom) in each vole, and monitored movements of rodents between all gates with remote radiofrequency identification antennae (Vantro Systems, Burnsville, Minnesota). The antennae recorded an animal's radiofrequency identification identity as well as the exact time (1/100-s time interval) when individually marked voles moved between quadrants. We added 2 additional male *Microtus* and 2 additional male *Myodes* to the enclosures on 22 August to replace 1 *Myodes* eaten by an ermine (*Mustela erminea*: transponder found in ermine feces within the enclosure), and another *Myodes* and 2 *Microtus* that disappeared at the same time. We used only data collected from the period after these new animals were released into the enclosure (22 August–1 September 2010).

We placed 1 pair of plastic bell-pot-saucer foraging trays (diameter = 40 cm, depth = 3 cm) 1 m apart in each quadrant, and filled each tray with 4.0 g of cleaned whole millet seed (0.2 mm diameter) mixed thoroughly into 1.5 liter of sieved silica sand (50–100 grain; 145–254 μ m). Each tray rested on top of a

remote antenna that recorded the entry and exit time of each vole. We placed 1 tray under a 8.75-cm-tall wooden frame covered with a 60 × 60-cm piece of plywood (safe covered patch), and the other tray under a similar frame covered with a 60 × 60-cm transparent polyethylene sheet (risky open patch). Our covered and open patches mimic the typical safe and risky patches often used in foraging studies. Other studies demonstrate that *Myodes* has a preference for cover in the absence of *Microtus* (Morris and Mukherjee 2007a, 2007b; Andruskiw et al. 2008; Lemaître et al. 2010). *Microtus* prefers covered over open patches (Morris and MacEachern 2010). Voles entered the tray under each cover through a 3-cm gap between the cover and soil surface. We placed trays in each quadrant at 1700 h and removed them the next day at 1430 h (21.5-h foraging period). We sifted the remaining millet seeds from each tray, cleaned the samples of debris and feces, and weighed the seeds to the nearest 0.01 g (GUD). We recharged trays with new food and sand mixtures daily (Sunday–Friday). Every Sunday we collected and recharged trays that we placed in the quadrants on Friday to ensure that voles continued to forage over the weekend (but excluded weekends from our analyses).

Differential movement by voles among the quadrants allowed us to measure patch use by *Myodes* as the local abundance of both vole species varied. To simplify our analyses, we calculated the number of individuals of each species that used either foraging patch in a quadrant during each foraging period, and did not examine movement behavior at a finer temporal scale. *Myodes* could compete with 0–9 *Microtus* in 1 quadrant on any given day. Nine *Microtus* in a quadrant is equivalent to a density of 144 *Microtus*/ha, which is considered close to carrying capacity (Lin and Batzli [2001] report carrying capacities of *M. pennsylvanicus* between 51 and 636 voles/ha, depending on habitat quality). Although this design was unable to measure foraging by *Myodes* in the complete absence of *Microtus*, please recall that several other studies document that *Myodes* forages more under cover than in open patches in the absence of *Microtus* (Morris and Mukherjee 2007a, 2007b; Andruskiw et al. 2008; Lemaître et al. 2010).

We used each species' mean PRT (the total time that all individuals of 1 species spent in a patch during one 21.5-h foraging period [total PRT], divided by the total number of individuals of that species recorded in that patch during the same period) and patch GUDs to evaluate the competing hypotheses on apparent predation risk. The distributions of

PRT and GUD were both right-skewed, and could not readily be transformed for parametric analyses. We therefore created high versus low binary variables for all continuous variables used in analyses of PRT and GUD using a median rule (= 1 when the datum > than the median value; = 0 when the datum \leq the median value). These variables include mean PRT, *Myodes* mean PRT, *Myodes* total PRT, *Microtus* mean PRT, *Microtus* total PRT, total PRT, number of *Microtus*, number of *Myodes*, and GUD.

Test of all hypotheses.—We assessed patch preferences of each species by analyzing high versus low daily PRT ($n = 128$) of *Microtus* and *Myodes* with binary logistic regression; fixed effects = species, patch type (covered versus open), and the 2-way interaction between species and patch type; random effect = station (location of the paired covered and open patches, $n = 4$) nested within day (daily foraging period, $n = 8$). If *Myodes* preferred covered over open patches, then H_2 (interference competition interacts with predation risk) is possible, whereas if *Myodes* exhibit no patch preference, then H_2 must be false. Similarly, if *Microtus* prefers covered patches, then direct competition cannot cause apparent predation risk and H_1 must be false.

Test of H_1 versus H_2 and H_3 .—We used binary logistic regression to assess if the frequency of high versus low PRT by *Myodes* ($n = 64$) increased in covered patches when the number of *Microtus* recorded at a station (number using either covered or open patches during the foraging period) 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. We compared this model to an alternate model that substituted *Microtus* total PRT in a patch for the number of *Microtus*. These competing models tested whether *Myodes* reacted to direct interference from *Microtus* in the patches (*Microtus* total PRT by patch-type interaction = test of H_1 [direct interference]) or to the combined effects of competition and predation or likelihood of interference (number of *Microtus* = test of H_2 [indirect interactive effect] and H_3 [indirect additive effect]).

We analyzed GUDs using binary logistic regression to examine the foraging efficiency of each species in both patches; fixed effects = *Microtus* total PRT in a patch, *Myodes* total PRT in a patch, patch type, and the 2-way interactions between *Myodes* total PRT and patch type, and between *Microtus* total PRT and patch type; random effects = station nested within day. High versus low GUDs for the same binary value of PRT represent a difference in foraging efficiency. We compared this model with an alternative model that substituted the number of *Myodes* and number of *Microtus* for *Myodes* total PRT and *Microtus* total PRT, respectively. If the frequency of high versus low GUDs varied only with total PRT of a species, regardless of the patch, then foraging efficiency would be similar between patches (reject H_2 and H_3 [indirect competition]); but if GUD varied with the number of voles and with patch type rather than with total PRT, then foraging efficiency would differ between patches and vary with the number of competitors (reject H_1 [direct interference]).

We also analyzed GUD using binary logistic regression to determine if one species foraged to a lower GUD than the other based on species identity of the final individual foraging in a tray (provides information about the cost a forager is willing to incur to obtain more food; a higher GUD infers greater foraging costs); fixed effects = species identity of the last forager, patch, and their interaction; random effects = station nested within day. We used radiofrequency identification data to determine which individual was the final forager in a patch and assigned that species' identity to the GUD.

Our 1st analysis of GUD detected a clear pattern of low GUD and high mean PRT of *Myodes* when nearby *Microtus* were abundant (the number of *Microtus* visiting either patch at a station). But a similar pattern in GUD could emerge if mean PRT of *Microtus* increased with its own abundance. We tested for this possibility with a binary logistic regression of mean PRT of *Microtus*: fixed effects = number of *Microtus*, patch type, and their interaction; random effects = station nested within day.

Statistical procedures.—We conducted all analyses as repeated measures through time using the lme4 package in R (Bates et al. 2010). We used the lmer function for linear mixed-effects models and the lmer function with family = binomial for logistic regressions.

We compared competing models with bias-corrected Akaike's information criteria (AIC_c ; pkg: qpcR; fcn: AIC_c —Spiess and Ritz 2010). We considered the model with the lowest AIC_c as the "best" model describing the data as long as the difference in AIC_c (ΔAIC_c) between models was > 2 . We chose the most-parsimonious model whenever $\Delta AIC_c < 2$ (Akaike 1973; Bozdogan 1987).

We used receiver-operator characteristic curves, and measured the area under the curve (AUC; pkg: ROCR; fcn: performance; measure: auc—Sing et al. 2009), to determine the fit of final models from binary logistic regression. We used $AUC \geq 0.7$ as our acceptance level for a reasonably accurate model (AUC values of 1.0 represent a perfect model, 0.5 represents no trend [Fielding and Bell 1997; Manel et al. 2001; Guenette and Villard 2005] and $AUC \geq 0.7$ represents fair to excellent [$AUC \geq 0.9$] accuracy [Hosmer and Lemeshow 2000]).

RESULTS

Assessing dominance.—As assumed by all competing hypotheses, *Microtus* was dominant over *Myodes* (mean aggression score of *Microtus* = 0.53 ± 0.02 [mean \pm SE]; mean aggression score of *Myodes* = 0.43 ± 0.02 ; $t_{1,40} = 2.91$, $P = 0.0058$; Table 2 in Appendix I; 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 in such a way as to maintain the maximum distance possible whenever *Microtus* advanced.

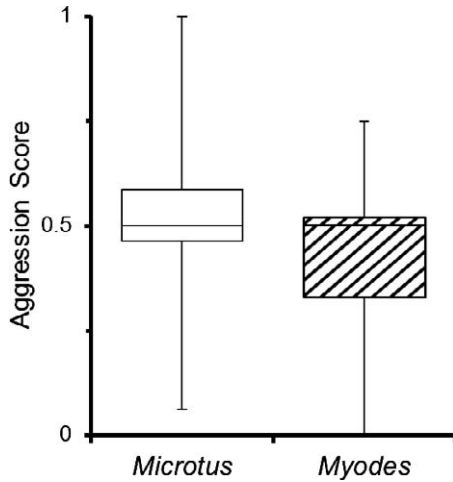


FIG. 2.—Aggression scores of *Microtus* and *Myodes* in dyadic encounters recorded at the Lakehead University Habitron in northern Ontario, Canada. Aggression scores were higher for *Microtus* than for *Myodes*. Aggression score was unaffected by the type of competition (intraspecific or interspecific;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

Assessing apparent predation risk.—All 9 *Microtus* were active (used gates or foraging patches) throughout the experiment. The number of *Myodes* known to be active decreased from 7 on 22 August to 4 on 1 September (the last day of the experiment). A minimum of 5 *Microtus* and 3 *Myodes* used the foraging trays on any given day of the

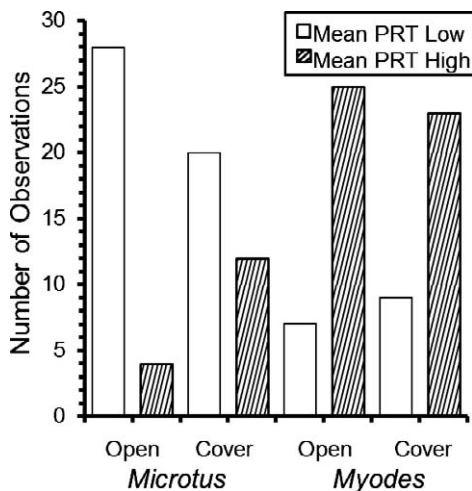


FIG. 3.—Counts of the number of times that the mean patch-residence time (PRT) of *Microtus* and *Myodes* was either higher (hashed bars) or lower (open bars) than the median value in covered and open patches at the Lakehead University Habitron in northern Ontario, Canada. Higher counts reflect a higher probability that mean PRT will be either high or low in a specific patch for a species. Mean PRT of *Microtus* had a higher probability of being high in covered than in open patches, whereas mean PRT of *Myodes* was not likely to be different between covered and open patches. Mean PRT of *Myodes* was more likely to be high than was mean PRT of *Microtus*.

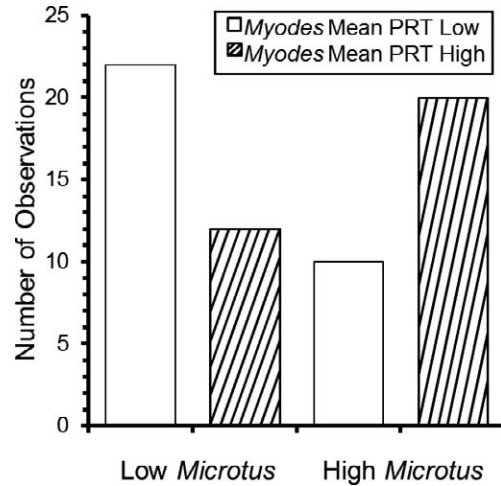


FIG. 4.—Counts of the number of times that mean patch-residence time (PRT) of *Myodes* was high (hashed bars) or low (open bars) in foraging patches at the Lakehead University Habitron in northern Ontario, Canada. Values greater than the median were high, and values less than or equal to the median were low. Higher counts reflect a higher probability that mean PRT of *Myodes* will be either high or low in response to the number of *Microtus*. *Myodes* had a higher probability of spending more time in patches when the number of *Microtus* in a quadrant was high.

experiment, and on the final day of foraging, 7 *Microtus* and 4 *Myodes* used the foraging trays (Fig. 6 in Appendix II details the daily distribution of voles between quadrants).

Test of all hypotheses.—Although the 2 rodent species differed in their allocation of foraging time to the 2 types of resource patches (species \times patch type: log odds ratio = 1.89, $P = 0.04$; AUC = 0.85; Fig. 3), *Microtus* allocated more foraging time to covered than open patches, whereas *Myodes* allocated similar time to each patch type. We therefore reject direct interference (H_1) because *Microtus* did not prefer open patches, and direct competition in open patches could not have caused *Myodes* to spend more time in covered patches. Similarly, we reject H_2 (indirect interactive effect) because *Myodes* did not show an innate preference for covered versus open patches (infers that predation risk and interference competition do not interact).

Test of H_1 versus H_3 .—Having rejected H_2 , we restricted our analysis to evaluating whether or not we could confirm H_3 . As predicted, *Myodes* spent more time foraging when abundance of *Microtus* was high than when abundance of *Microtus* was low (number of *Microtus*: log odds ratio = 1.27, $P = 0.02$; AUC = 0.77; Table 3 in Appendix I; Fig. 4). Indirect effects also were confirmed by our analysis of GUDs. Foraging efficiency differed between patches: the frequency of high versus low GUDs depended on an interaction between the number of *Microtus* and patch type, and differed with the risk of competition (number of competitors) rather than the amount of direct interference (PRT of competitors; Table 4 in Appendix I; AUC = 0.87; Fig. 7 in Appendix III details the relationships between GUD and total PRT of each species). The GUD was more likely to be high in covered than in open

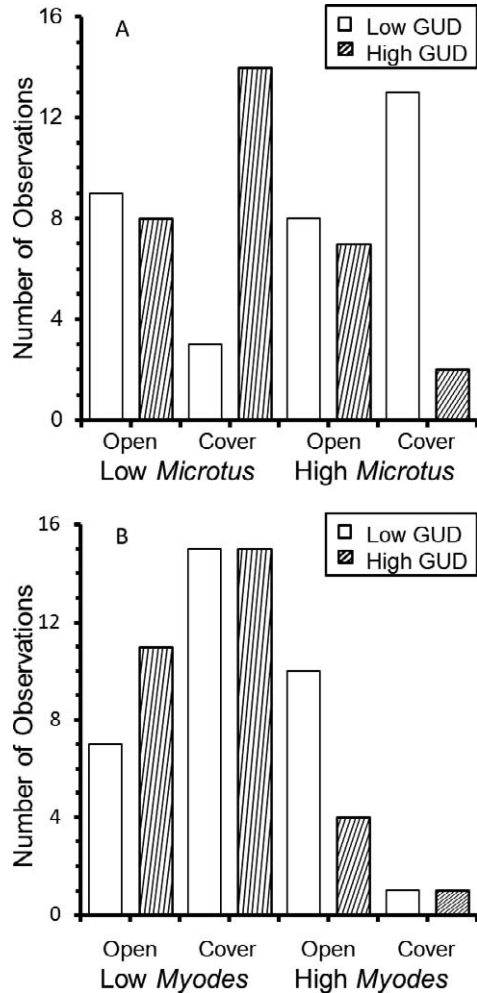


FIG. 5.—Counts of the number of times that the giving-up density (GUD) of covered and open patches was high (hashed bars) or low (open bars) when there were many (high) or few (low) A) *Microtus* or B) *Myodes* using foraging patches at the Lakehead University Habitatron in northern Ontario, Canada. GUDs greater than the median were high and all other values were low. Higher counts reflect a higher probability that mean patch-residence time (PRT) will be either high or low in a specific patch for a species. A) GUD was more likely to be low in covered patches when the number of *Microtus* was high, whereas GUD in open patches was relatively unaffected by the number of *Microtus*. B) GUD was more likely to be low when the number of *Myodes* was high.

patches (patch type: log odds ratio = 1.82, $P = 0.04$), but when abundance of *Microtus* was high, GUDs were more likely to be low in covered patches (number of *Microtus* \times patch type: log odds ratio = 5.31, $P < 0.001$; 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 (number of *Myodes*: log odds ratio = 2.24, $P = 0.02$; Fig. 5B).

Our analysis of GUD based on the final forager known to have visited the patch demonstrated that GUD was more likely to be low when *Microtus* was the final forager than when *Myodes* was the final forager, regardless of the patch type

(species identify: log odds ratio = -1.51 , $P = 0.027$). Our subsequent analysis of *Microtus* mean PRT confirmed that the patterns in GUDs were caused by foraging of *Myodes* rather than by negative density-dependence associated with *Microtus* (Table 5 in Appendix I; AUC = 0.76). *Microtus* was more likely to have a high mean PRT in covered patches than in open patches (patch type: log odds ratio = 1.56, $P = 0.01$), and this pattern was unaffected by the number of *Microtus* (number of *Microtus*: log odds ratio = 0.76, $P = 0.23$; AUC = 0.77). A closely competing model included the number of *Microtus*. This model was, however, less parsimonious and the effect of number of *Microtus* was not statistically significant. All results are consistent with H_3 : *Myodes* increased its use of covered patches because competition with *Microtus* was in addition to predation risk.

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 patches protected by cover than risky open patches 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 (e.g., Gilliam and Fraser 1987; Jordan et al. 1997; Linehan et al. 2001; Dupuch et al. 2009) systems. Predation risk also causes individuals to increase their foraging in cover relative to open 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 overestimated in field experiments because it can include an apparent component associated with competitive interactions. Our study and Morris's (2009) earlier study show that *Myodes* increased its use of safe covered patches when competition increased. Competitive effects can therefore mimic the effects of predation risk.

Although PRT of *Myodes* revealed no preference for covered versus open patches under low competition, *Myodes* clearly increased its residence time in patches as the number of nearby *Microtus* increased. GUDs also were lower in covered patches when *Microtus* was more abundant, suggesting that *Myodes* foraged less efficiently in open patches with increasing *Microtus* abundance. The relative safety, or at least the perceived relative benefits, of covered patches increased as interspecific competition increased. Under the conditions of our experiment, these results support our 3rd hypothesis: vigilance of *Myodes* toward dominant competitors caused them to increase their use of covered patches, relative to that of predation risk alone, when competition increased. A plausible explanation is that the risk of detection by dominant *Microtus* is higher in open than in covered patches, and that the risk increases with abundance of *Microtus*. Although an increased

presence of *Microtus* may actually increase the marginal value of energy (negative density-dependence), decrease the risk of predation (risk dilution), and thereby increase GUD for *Myodes* (more benefits from foraging caused by higher valuation of energy and lower risk), it also may increase vigilance directed against *Microtus* via horizontal sight lines (but not vigilance directed against aerial predators via vertical sight lines—see Embar et al. 2011). This vigilance against competitors comes at the expense of vigilance directed against predators, which increases predation risk, especially in open patches. In contrast to most situations where increased marginal value of energy decreases the difference in GUDs between covered and open patches, here it actually increases the difference.

The response of *Myodes* to variation in the local abundance of *Microtus* also suggests an unappreciated effect of scale. If patch use by *Myodes* depended on total density of *Microtus*, then patch use should have been constant through time. The significant effect of local abundance of *Microtus* suggests a sophisticated small-scale assessment of risk by *Myodes* that varied with use by *Microtus* of different foraging stations during the experiment. Increased marginal value of energy associated with both scramble competition and interference with *Microtus* likely caused *Myodes* to forage to a lower GUD in covered patches. Note that *Microtus* actually foraged to the lowest GUD in the patches with the most competition (demonstrated in the analysis of GUD by the final forager in a patch), but even so, *Myodes* still increased its PRT when *Microtus* depressed GUDs to these low values.

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 1 red-backed vole was eaten by an ermine), but *Myodes*, when competing with few *Microtus*, expressed no preference 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, 2007b; Andruskiw et al. 2008; Lemaitre et al. 2010). We suspect that these apparently divergent results might reflect unknown cues of predation risk in addition to those associated with covered and open patches. The 2 types of foraging patches may, for example, be incapable of reducing predation risk from ermine that enter the 25 × 25-m quadrants of the enclosure where escape is through the single exit hole to the next quadrant (indeed, the ermine feces with our unfortunate vole's radiofrequency identification tag was found adjacent to one of the exits).

Our experiment was confined to a single enclosure with 4 different pairs of sample sites for which we measured GUDs and PRTs 8 times over 10 days. Although we controlled for site differences with repeated measures, we did not replicate the entire experiment (we remind readers that pseudoreplication [Hurlbert 1984], at some scale, is inherent in all experiments). Regardless, it is possible that other individual *Myodes* (or those that disappeared during the experiment) may not react to *Microtus* the same way as in our experiment. They might even

exhibit different innate patch preferences. Although our application of strong inference (Platt 1964) unambiguously documents indirect interference additive to predation risk, we encourage further testing of apparent predation risk (and its mechanisms) in this and other systems.

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 our experiments, and those by Morris (2009), suggest that competition and predation risk may act synergistically to influence patch use. With these complexities in mind, astute ecologists would do well to control for competition in experiments focused on predation risk, control for predation risk in experiments focused on competition, and examine both processes simultaneously when attempting to infer factors structuring ecological communities.

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APPENDIX I

Model selection for analyses of aggression scores, patch-residence times of *Myodes*, and giving-up densities from experiments with 2 species of voles in northern Ontario, Canada. For competing models ($\Delta AIC_c < 2$), the model with the least number of parameters, “most parsimonious,” was selected (boldface type; see Tables 2–5).

TABLE 2.—Selection of models describing how species and competition affect aggression score using bias-corrected Akaike’s information criterion (AIC_c). All models included order of trial nested within individuals as a random effect. Boldface type indicates the selected model. K = number of parameters.

Model	K	AIC_c	ΔAIC_c
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 3.—Model selection for the “best” model (boldface type) of mean patch-residence time (PRT) of *Myodes* using the bias-corrected Akaike’s information criterion (AIC_c). Binary logistic regression with patch type, number of *Microtus*, and total PRT of *Microtus* as independent binary variables. An asterisk (*) represents a competing but less-parsimonious model. K = number of parameters.

Model	K	AIC_c	ΔAIC_c
<i>Myodes</i> mean PRT = number of <i>Microtus</i>	4	90.73	0
<i>Myodes</i> mean PRT = number of <i>Microtus</i> + patch type	5	91.62	0.89*
<i>Myodes</i> mean PRT = number of <i>Microtus</i> + patch type + number of <i>Microtus</i> × patch type	6	93.61	2.88
<i>Myodes</i> mean PRT = <i>Microtus</i> total PRT + patch type + <i>Microtus</i> total PRT × patch type	6	95.67	5.94
<i>Myodes</i> mean PRT = <i>Microtus</i> total PRT + number of <i>Microtus</i> + patch type + <i>Microtus</i> total PRT × patch type + number of <i>Microtus</i> × patch type + <i>Microtus</i> total PRT × number of <i>Microtus</i> × patch type	10	98.91	8.18

TABLE 4.—Model selection for the “best” model (boldface type) of giving-up density (GUD) using Akaike’s bias-corrected information criterion (AIC_c). Binary logistic regression with patch type and 2 metrics of patch use of *Myodes* and *Microtus* as fixed effects. An asterisk (*) represents a competing but less-parsimonious model (fewer parameters [K]). PRT = patch-residence time.

Model	K	AIC_c	ΔAIC_c
GUD = patch type + number of <i>Microtus</i> + number of <i>Myodes</i> + patch type × number of <i>Microtus</i>	7	79.64	0
GUD = patch type + number of <i>Microtus</i> + number of <i>Myodes</i> + patch type × number of <i>Microtus</i> + patch type × number of <i>Myodes</i>	8	81.62	1.98*
GUD = patch type + number of <i>Microtus</i> + patch type × number of <i>Microtus</i>	6	83.40	2.76
GUD = patch type + <i>Microtus</i> total PRT + <i>Myodes</i> total PRT + patch type × <i>Microtus</i> total PRT + patch type × <i>Myodes</i> total PRT	8	88.63	8.99

TABLE 5.—Selection of models describing how mean patch-residence time (PRT) of *Microtus* was affected by patch type and the number of *Microtus* based on bias-corrected Akaike’s information criteria (AIC_c). Binary logistic regression with station nested within day as a random effect. An asterisk (*) represents a competing but less-parsimonious model (fewer parameters [K]).

Model	K	AIC_c	ΔAIC_c
<i>Microtus</i> mean PRT = patch type	4	71.21	0
<i>Microtus</i> mean PRT = patch type + number of <i>Microtus</i>	5	71.70	0.49*
<i>Microtus</i> mean PRT = patch type + number of <i>Microtus</i> + patch type × number of <i>Microtus</i>	6	69.77	2.56

APPENDIX II

The distribution of voles in each quadrant through time in an experiment with *Microtus pennsylvanicus* and *Myodes gapperi* at the Lakehead University Habitron in northern Ontario, Canada (See Fig. 6).

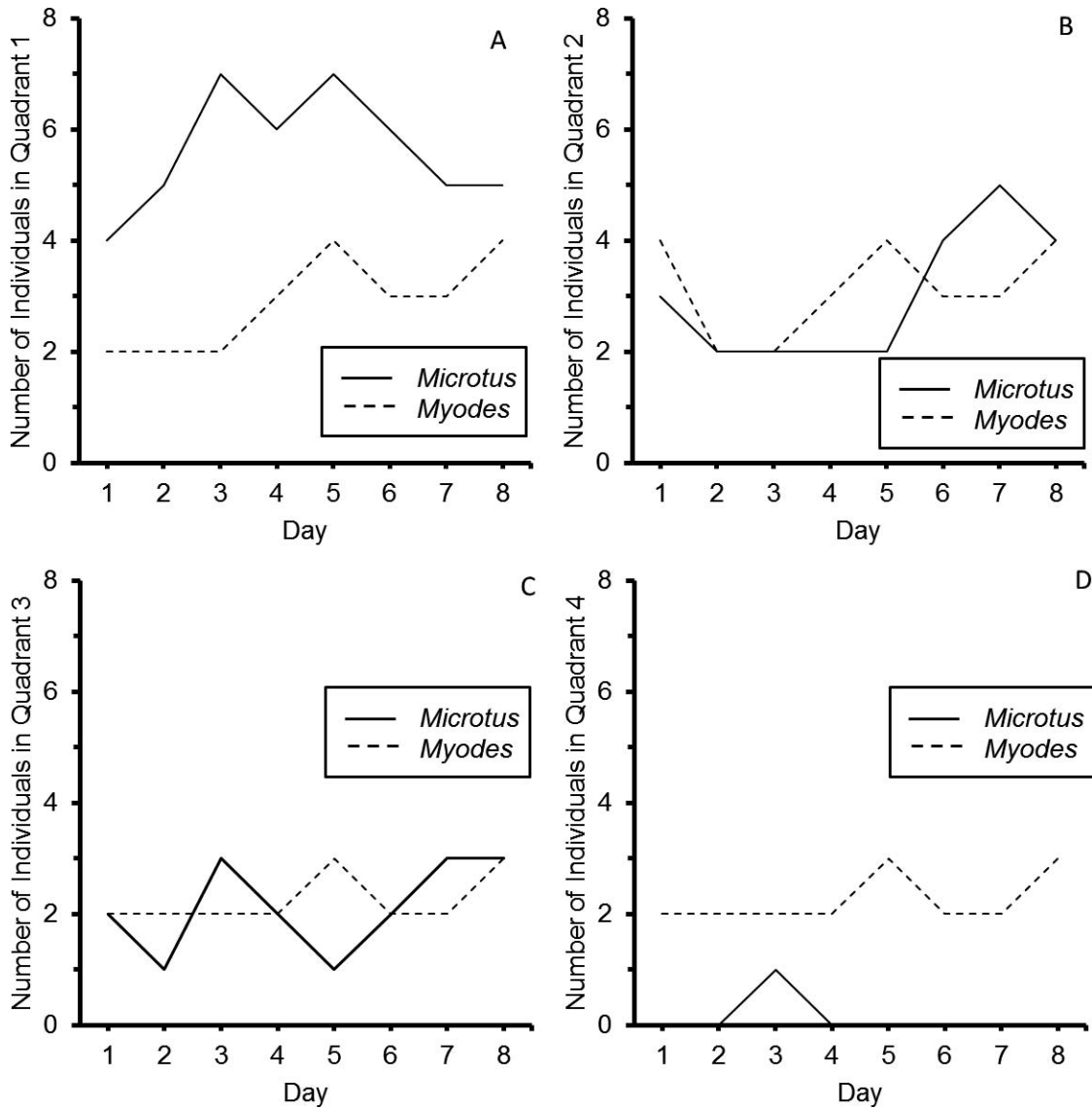


FIG. 6.—Trends in the number of individuals of 2 vole species in each of the 4 quadrants (panels A–D) used in an experiment with *Microtus pennsylvanicus* and *Myodes gapperi* at the Lakehead University Habitron in northern Ontario, Canada. Includes only the number of voles that used foraging trays during each day (21.5-h foraging period).

APPENDIX III

Scatter plots illustrating that giving-up density (GUD) declined more or less linearly with patch-residence time (PRT) in experiments evaluating competition between *Myodes gapperi* and *Microtus pennsylvanicus* (See Fig. 7).

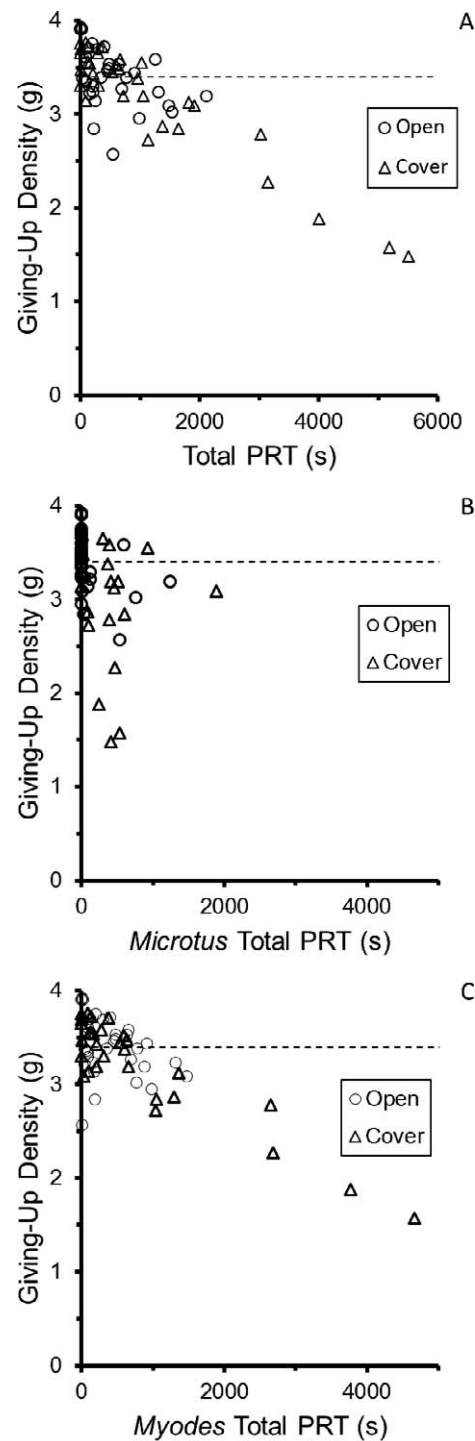


FIG. 7.—Giving-up density (GUD) decreases as the total patch-residence time (PRT) of both *Microtus* and *Myodes* increases in both patches. A) The pattern between GUD and the additive effect of total PRT of both *Microtus* and *Myodes*. B) The pattern between GUD and total PRT of *Microtus*. C) The pattern between GUD and total PRT of *Myodes*. GUD is typically lower in covered than in open patches. The dashed line represents the median GUD used in binary logistic regressions.