

Voles competing with mice: differentiating exploitative, interference and apparent competition using patch use theory

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ABSTRACT

We derived unique sets of predictions from patch use theory to differentiate apparent, exploitative and interference competition. Armed with these predictions, we used field enclosures to determine whether white-footed mice (*Peromyscus leucopus*) perceived meadow voles (*Microtus pennsylvanicus*) as apparent competitors. The enclosures were sited at forest-field ecotones. Within them, we manipulated vole density, food patch microhabitat (i.e. predation risk) and distance from the forest edge. We studied the effect of these variables on giving-up densities of white-footed mice. Giving-up densities increased in response to higher vole activity. Under higher vole activity, mice increased foraging costs associated with risky, open microhabitats. These results were consistent only with apparent competition. Thus shared predators may be contributing to the pattern of habitat selection between mice and voles along forest-field ecotones.

Keywords: apparent competition, competition, ecotone, giving-up density, habitat selection, interference, *Microtus*, patch use theory, *Peromyscus*.

INTRODUCTION

Individuals of two or more species may experience reduced interspecific competitive interactions through mechanisms, such as habitat selection, that result in their separation in time or space and ultimately permit their stable co-existence (MacArthur, 1972; Rosenzweig, 1981; Kotler and Brown, 1999; Morris *et al.*, 2000; Martin and Martin, 2001). Rarely is separation so complete that individuals of the two species never interact. For example, species' boundaries along ecotones are seldom so abrupt that two species, each of which specializes on a different habitat, never come into contact. Ecotones therefore provide an opportunity to examine the

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ecological interactions between species that seldom overlap in space and infer what type of interactions are currently maintaining their separation or habitat choices.

This includes three unique forms of competitive interactions: exploitative competition (i.e. through the consumption of shared resources), interference competition (i.e. aggressive interactions over access to potentially shared resources) and apparent competition (i.e. enhanced predation risk in the presence of a competitor mediated through the response of a shared predator) (Holt, 1977; Holt and Kotler, 1987). Each form has been implicated to contribute to patterns of habitat selection in small mammals (Brown, 1992; Kotler *et al.*, 1993; Morris, 1999). However, the role of apparent competition in determining habitat choice, largely ignored in earlier studies, has received increased interest in recent years through recognition of its ubiquitous nature (Menge, 1995; Chaneton and Bonsall, 2000). For instance, recent studies using unmanipulated populations of mice (*Peromyscus*) and voles (*Clethrionomys*) suggest that these two rodents may be apparent competitors rather than interference or exploitative competitors (Morris, 1999). Morris further suggested that habitat switching by generalist predators may mediate the co-existence of mice and voles, an example of the Ghost of Predation Past (Morris, 1999; Morris *et al.*, 2000).

Similarly, white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*) are common inhabitants of forest-field ecotones throughout the eastern United States, and their relatives compete in similar habitats throughout temperate ecosystems in the northern hemisphere. Across the eastern United States, white-footed mice are among the most abundant vertebrates in many forest ecosystems (e.g. Whitaker and Hamilton, 1998), whereas meadow voles are similarly the most abundant small mammal within adjacent herbaceous habitats. Voles apparently inhibit the presence of mice in open habitats (Grant, 1972; M'Closkey and Fieldwick, 1975; Ostfeld *et al.*, 1997), and this has generally been thought to reflect aggressive interference by the larger voles (~40 g versus ~20 g). However, as voles and mice appear to share few dietary or habitat resources along these ecotones (Batzli, 1985), the benefit of energetically expensive aggression on the part of voles, if it occurs, is a mystery. Alternatively, voles can reach incredible densities (~1000 individuals per hectare in some years; Pusenius and Schmidt, 2002) that are likely to result in a numerical response of their predators (Craighead and Craighead, 1956; Pearson, 1985). Thus, mice may avoid areas where voles are abundant because their risk of predation is enhanced by the presence of voles (i.e. apparent competition). Here, we combined the methodology of giving-up densities and predictions derived from patch use theory to test whether white-footed mice inhabiting forest-field ecotones avoid voles largely due to exploitive, interference or apparent competition.

PATCH USE THEORY AND COMPETITIVE EFFECTS

We developed a method of differentiating exploitative, interference and apparent competition based on differences in relative patch use between safe and risky habitats under different intensities of competition. We followed Brown's (1988, 1992) procedure for determining the optimal time allocation among depletable resource patches given a forager that experiences predation risk while foraging. Brown's (1992) result is depicted as a patch-quitting rule; an optimally foraging animal should quit harvesting a resource patch when:

$$f = \mu(F + 1)/(\partial F/\partial e) + \phi_1/p(\partial F/\partial e) + C \quad (1)$$

where f = the benefit of further resource harvest (i.e. quitting harvest rate), μ is the instantaneous mortality rate, p is the probability of surviving to the point at which fitness benefits

$(F + 1)$ accrue, ϕ_t is the marginal value of time, $\partial F/\partial e$ is the marginal value of energy, and C is the rate of metabolic expenditure. The three terms on the right-hand side of equation (1) represent the foraging costs of predation, missed opportunities and metabolic expenditure, respectively.

Brown (1992) further considered two patches that are identical in all respects save predation risk, μ . Subtracting the quitting harvest rate expression (i.e. equation 1) of a safe (subscript S) resource patch from the quitting harvest rate of a risky (subscript R) resource patch yields an equation representing the difference in quitting harvest rate between the two patches:

$$f_R - f_S = [(\mu_R - \mu_S)(F + 1)]/(\partial F/\partial e) \tag{2}$$

As the relative difference in predation risk increases ($\mu_R - \mu_S$), or as the value of energy decreases ($\partial F/\partial e$), the difference in quitting harvest rates between the two patches grows larger. These results have been confirmed in many empirical studies that selectively manipulated predation risk by placing artificial food patches close to and far from protective cover (e.g. Brown *et al.*, 1992; Kotler, 1997; Thorson *et al.*, 1998; Olsson *et al.*, 2002). For the remainder of this section, we consider this two-patch system where patches differ in predation risk by their location in different, but nearby, habitats. We ask how individuals of a focal species vary their relative use of the two habitats given the existence of exploitative, interference or apparent competition in the presence of a second species.

Consider first what happens in the presence of exploitative competition. Exploitative competitors depress the mean resource abundance of the environment and thus increase the value of the remaining food – that is, increase $\partial F/\partial e$. This has two consequences for the focal species. First, overall quitting harvest rates decrease irrespective of habitat type (risky or safe patch) because predation and missed opportunity costs are lowered ($\partial F/\partial e$ is in the denominator of equation 1). Second, because the cost of predation is an increasing function of the value of energy, the differences in predation costs and hence the difference in quitting harvest rate between the safe and risky patches similarly declines ($\partial F/\partial e$ is in the denominator of equation 2; Table 1).

For interference competition, we modified equation (1) by adding an additional cost term, I , to reflect the additional energy expenditure due to interference. With the incorporation of interference costs, equation (2) now becomes:

$$f_R - f_S = [(\mu_R - \mu_S)(F + 1)]/(\partial F/\partial e) + (I_R - I_S) \tag{3}$$

Consider again two patches that differ in terms of predation risk. Interference competition will be greater in the safer of the two habitats ($I_S > I_R$) as more competitive dominants will

Table 1. Predicted directional changes in overall giving-up densities (GUDs) and GUDs in risky (i.e. open) patches relative to a fixed GUD in the safe (i.e. shrub) patch as vole activity or density is increased

	Overall GUDs	Ratio of risky to safe GUDs
Exploitative	↓	↓
Interference	↑	↓
Apparent	↑	= or ↑

be present and/or active in the safer habitat (e.g. Abramsky *et al.*, 2000; Pusenius and Schmidt, 2002). Thus, there is a trade-off between a low cost of interference but a high cost of predation in the risky habitat and vice versa in the safe habitat. Because the interference cost is biased towards and increases disproportionately in the safer habitat, the difference in quitting harvest rates between safe and risky habitats decreases. This is the same prediction for exploitative competition; however, unlike exploitative competition, interference competition raises overall foraging costs and thus overall quitting harvest rates increase (Table 1).

Apparent competitors increase predation costs by increasing the likelihood of predation, thus overall quitting harvest rates will increase. But how is the increased predation risk experienced between relatively safe and risky patches? There are two likely scenarios. First, if safe and risky habitats are distributed in a fine-scale mosaic (e.g. shrub versus open habitat), then the presence of a putative competitor may increase predation risk through apparent competition simultaneously in both safe and risky microhabitats by a constant amount, k_S and k_R respectively (and where $k_R = k_S$). The numerator of (2) becomes $[(\mu_R + k_R) - (\mu_S + k_S)](F + 1) = [(\mu_R - \mu_S)](F + 1)$. Under this scenario, foragers do not change their relative use of safe versus risky patches. However, it is more likely that the presence of a predator, attracted to high densities of the apparent competitor, will cause a relatively greater increase in predation risk within the already riskier habitat – that is, $k_R > k_S$. In this case, apparent competition increases the difference in foraging costs between safe and risky habitats, and patch use is even more biased towards safer patches. Regardless of which of the two scenarios apply, apparent competition never decreases the difference in quitting harvest rates between a safe and risky patch as predicted by the two alternative forms of competition. (*Note:* A third scenario may occur if the predator biases its activity towards higher prey densities in the safe habitat. This is more likely to occur under coarse-grain habitat diversity whereby time allocated by the predator to one habitat is mutually exclusive to others. However, this is unlikely in the fine-scale mosaic that we consider above and in the empirical study that follows.)

In summary, we have three unique sets of predictions with which to distinguish among the three forms of competition (Table 1). We tested these predictions by comparing overall quitting harvest rates (using giving-up densities from experimental food patches as a surrogate for quitting harvest rates; Brown, 1988; Schmidt *et al.*, 1998) in mice in response to experimentally manipulated vole density.

METHODS

Study site and vole enclosure plots

Our field studies were conducted on or near the property of the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York (41°50'N, 73°45'W). We used three previously constructed sets of vole enclosure plots (see Manson *et al.*, 1999, 2001) for the present study. Each replicate consisted of two adjacent 40 × 40 m vole enclosure plots located along forest-field edges. Three sides of the enclosures were made of 0.9-m high 1.2-cm mesh galvanized hardware cloth buried to a depth of ~0.4 m and covered with ~20 cm of aluminium flashing. The forest edge functioned as the fourth side of each enclosure due to strong forest and forest edge avoidance by voles (Tamarin *et al.*, 1984). Similarly, a 0.5-m strip on either side of the fence was mowed every 2 weeks to further enhance the

effectiveness of the enclosure of voles, which avoid open areas. In contrast, white-footed mice were free to move between the adjacent enclosure, forest or oldfield habitat. Herbaceous cover in oldfields included a mixture of grasses (*Schizachyrium scoparium*, *Bromus inermis* and *Phleum pratense*), forbs (*Solidago juncea*, *S. rugosa*, *Galium tinctorum* and *Centuria maculosa*) and two species of sedges (*Carex* spp.). Dominant shrub species at the site included multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera morrowii*) and grey dogwood (*Cornus racemosa*). A previous study (Manson *et al.*, 1999) showed no significant changes in vegetation cover with distance from the forest edge. We refer the reader to Manson *et al.* (1999, 2001) for a detailed description of our trapping protocol. In brief, a randomly chosen enclosure of each pair was assigned as a high vole density treatment, and density differences were maintained between paired enclosures from 1994 to 1998 by translocating most juvenile and sub-adult voles from the low- to high-density enclosure at another site. Vole activity (number of captures) was doubled, on average, in the high vole density treatment (Manson *et al.*, 2001). Also relevant for this study, vole activity increased threefold from 5 to 15 m from the forest edge (Manson *et al.*, 2001).

Giving-up densities

We measured the foraging activity of white-footed mice by collecting giving-up densities (the amount of food remaining in a patch after a forager quits its foraging activity) from artificial food patches (seed trays). Food patches were composed of a circular plastic tray (30 cm diameter, 4 cm height) to which we added 2 litres of sifted bank sand and 4 g of unhusked millet seed thoroughly mixed into the sand. An optimal forager experiencing diminishing returns (i.e. the forager's harvest rate declines with time spent exploiting the patch) should exploit a patch until its harvest rate declines to the sum of its foraging costs (including metabolic, predation risk and missed opportunity costs of not engaging in alternative activities: $H = C + P + MOC$). The remaining density of food at which this relationship is satisfied and the forager ceases exploiting the patch is its giving-up density (Brown, 1988, 1992).

We established replicate sets of seed trays at three study sites where the vole density manipulation experiments were being conducted (see above). Within each vole density plot (high versus low), we laid out three pairs of trays (stations) at two distances (0–5 m and 15–20 m) from the forest edge. Each pair of trays consisted of one tray placed under a shrub to represent a relatively safe microhabitat and the second tray placed ~1 m away in more open herbaceous cover to represent a relatively risky microhabitat. The total number of trays at a site was 24 (3 stations \times 2 distances \times 2 microhabitats \times 2 vole density plots), and three replicate sites resulted in a total of 72 trays. However, as foraging activity was extremely low at one of the three sites, data from this site were subsequently eliminated from the analyses.

Mice had access to the trays each evening between approximately 2 h before sunset (19.00 h) until sunrise (approximately 05.00 h) to minimize visits from diurnal seed consumers such as chipmunks, which were present but rare at the study sites (Manson *et al.*, 1999). Trays were sieved between nights to collect the uneaten seeds that were cleaned of debris and weighed to measure the giving-up density. We collected giving-up densities over three nightly sessions, each consisting of three consecutive evenings: 4–6 August, 20–22 August and 11–13 September 1998. The first and last session corresponded with the full moon, whereas the middle session corresponded with the new moon. We identified trays that mice

had exploited by their footprints and tail drags in the sand and by mouse faeces. For the few instances in which we could not identify the animal exploiting a tray, we excluded the data from all analyses. We saw no signs that voles were utilizing the trays, and their preference for herbaceous matter (Batzli, 1985) likely precludes them from utilizing the trays.

To test the prediction regarding the direction of changes in overall giving-up densities, we used an analysis of variance (ANOVA) with giving-up density (logarithmically transformed to provide a more linear fit to quitting harvest rates; Kotler and Brown, 1990) as our dependent variable. Giving-up densities were averaged over the three nights of data collection within each foraging session to prevent problems with repeated measures of the same individuals. In a hierarchical ANOVA (with day nested within session), day was not significant ($F_{2,6} < 0.50$, $P > 0.50$), thus dispelling statistical concerns about pooling among days. The independent variables included moon (full versus new), vole density (low versus high), distance (~5 m and ~15 m), risk (shrub versus open) and station ($n = 3$), as well as the two interactions: vole \times moon and vole \times risk.

We ran a similar ANOVA using the number of patches foraged by mice as the dependent variable; moon, vole, distance, risk and station as the main effects; and the two interactions, vole \times moon and vole \times risk. Patch use data were collected over six nights (two 3-day sessions) under a full moon versus three nights under the new moon. Therefore, before running the analysis we divided the number of patches visited under the full moon in half to adjust for the number of exposure nights.

We tested the predictions regarding the relative use of risky (i.e. open) versus safe (i.e. shrub) patches using analysis of covariance (ANCOVA). The ANCOVA compares the value of a risky patch under the two vole densities while statistically controlling for the value of the safe patch. If interference competition is present and overwhelms other potential competitive effects, greater abundance of voles under shrub cover should decrease the relative cost of open patches, since these patches provide a refuge from interference (i.e. fewer voles; Korpimäki *et al.*, 1996). If apparent competition is present and overwhelms other competitive effects, greater abundance of voles should increase (or at least should not decrease) the relative cost of open patches, since predation risk is enhanced at high vole density/activity (Table 1). We used giving-up density in the open tray as our dependent variable, giving-up density in the shrub tray as the covariate, and station, vole density, moonlight and distance as group variables, plus the interaction terms between the main effects (except station) and the covariate. For this analysis, giving-up densities were used only if both the shrub and open trays at a station were foraged on the same night. When we tested for homogeneity of slopes, we found a positive interaction term between vole density and the covariate ($F_{1,79} = 9.50$, $P = 0.003$), which may complicate the interpretation of ANCOVA results if the regression lines cross (Sokal and Rohlf, 1981). By plotting the data in graphic form, we saw that this interaction was the result of a vole density \times moonlight interaction; mice foraged little in open trays at high vole density under a full moon, but foraged more heavily at low vole density under a new moon. Therefore, we re-ran the ANCOVA using a composite of these two treatments: we compared low vole density under a full moon versus high vole density under a new moon, dropping the main effects of vole density and moonlight, which no longer had any variation. This comparison seems reasonable in light of: (1) the full moon will cause voles to reduce their nightly activity (Doucet and Bider, 1969; Halle, 1995), thus pairing the full moon with low vole density seems reasonable; and (2) both mouse giving-up densities and mouse activity (number of trays foraged) showed similar responses to both full moon and high vole density (see Results section), and thus these two variables act in complementary fashion.

RESULTS

Giving-up densities

Mice had significantly lower giving-up densities when foraging under shrubs ($F_{1,83} = 9.22$, $P = 0.003$; Fig. 1), at low vole densities ($F_{1,83} = 4.30$, $P = 0.041$; Fig. 1) and under a full moon ($F_{1,83} = 26.41$, $P < 0.001$; Fig. 1). The increase in giving-up densities at higher vole densities is consistent with either interference or apparent competition, but not exploitative competition. Station and distance from the forest edge did not significantly influence giving-up density ($F_{2,83} = 2.03$, $P > 0.10$ and $F_{1,83} = 0.02$, $P > 0.80$, respectively; Fig. 1), and neither of the two interaction terms was significant (vole \times risk: $F_{1,83} = 1.65$, $P > 0.20$; vole \times moon: $F_{1,83} = 3.11$, $P > 0.08$).

Number of patches foraged

Mice foraged in fewer patches in the open ($F_{1,83} = 16.47$, $P < 0.001$; Fig. 2) and at higher vole densities; however, the latter effect was not statistically significant ($F_{1,83} = 1.28$, $P > 0.20$; Fig. 2). These results are consistent with higher foraging costs (i.e. giving-up densities) associated with the treatments. In contrast to the results from the giving-up density analyses, mice visited fewer patches under a full moon ($F_{1,83} = 24.29$, $P < 0.001$; Fig. 2) and

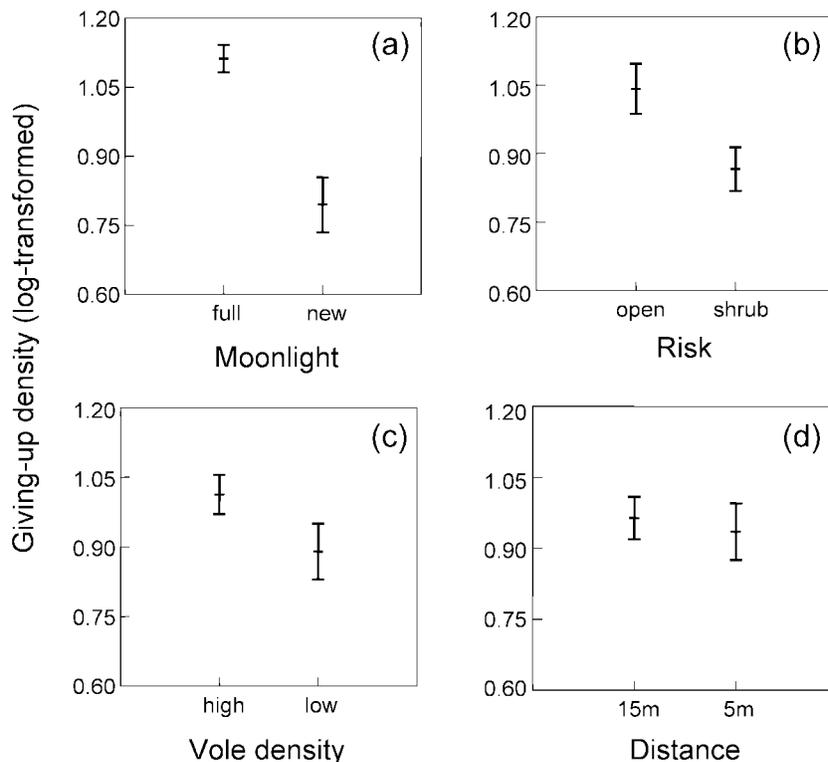


Fig. 1. Mean giving-up densities (log-transformed) as a function of (a) moon phase, (b) risk, (c) vole density and (d) distance. Error bars denote ± 1 standard error.

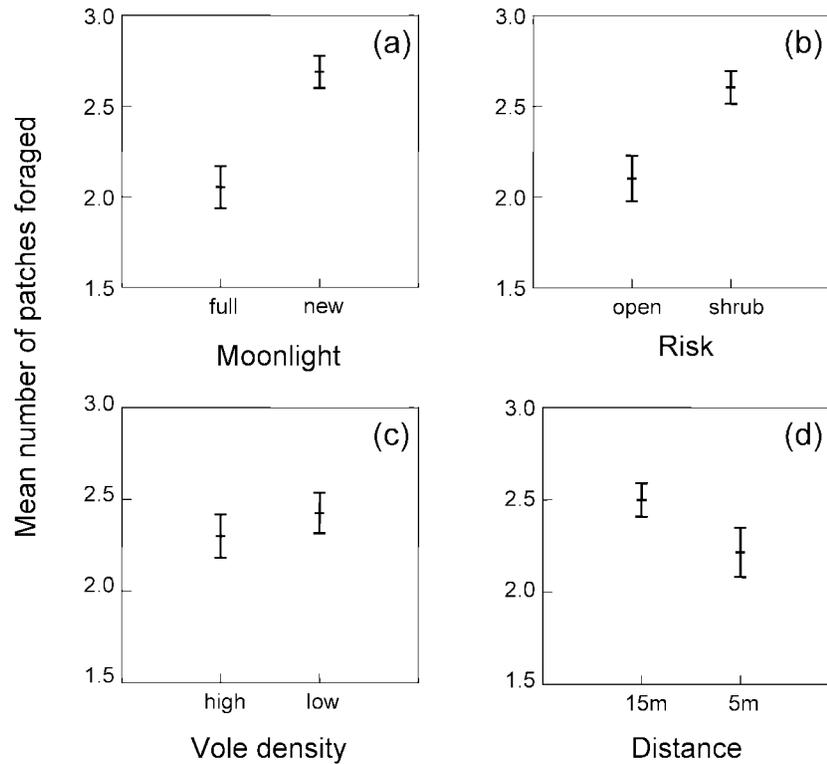


Fig. 2. Mean number of food patches foraged in over a 3-day period as a function of (a) moonlight, (b) risk, (c) vole density and (4) distance. Error bars denote ± 1 standard error.

visited fewer patches at the 5-m distance than at the 15-m distance ($F_{1,83} = 5.84$, $P = 0.018$; Fig. 2). There were also significant differences between stations ($F_{2,83} = 7.91$, $P = 0.001$), but no significant interaction effects (vole \times risk: $F_{1,83} = 1.28$, $P > 0.20$; vole \times moon: $F_{1,83} < 0.10$, $P > 0.50$).

Relative use of safe versus risky patches

The composite variable of vole density and moonlight significantly influenced value of risky open patches relative to a fixed giving-up density in safer shrub patches (Table 2, Fig. 3). Open patches were relatively more risky at high vole density under a new moon than at low vole density under a full moon (Fig. 3), which is only consistent with voles as apparent competitors of mice. Interestingly, when distance was examined in the data set using only stations in which both shrub and open trays were utilized, there was a significant risk \times distance interaction (two-way ANOVA: $F_{1,170} = 5.97$, $P = 0.016$; Fig. 4).

DISCUSSION

Our results suggest that meadow voles and white-footed mice are apparent competitors where they overlap at forest-field ecotones. Within experimental plots with enhanced vole

Table 2. Results of ANCOVA examining the effects of station, distance and vole activity (composite variable of density and moonlight) on the relative risk of open to shrub (covariate) giving-up densities

Source	d.f.	MS	F-ratio	P
Station	2	0.663	1.87	0.167
Distance	1	1.577	4.45	0.041
Vole/moonlight	1	0.663	7.22	0.010
GUDshrub (covariate)	1	4.761	13.44	0.001
Error	41	0.354		

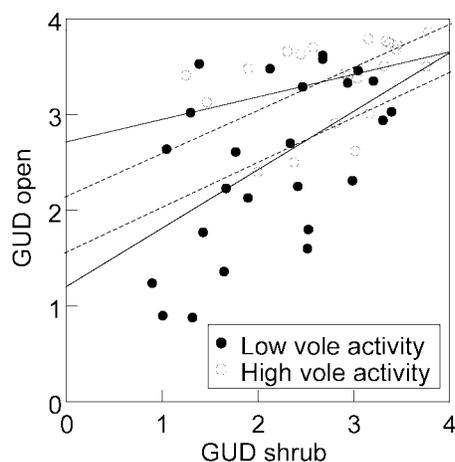


Fig. 3. Relationship between giving-up density in the open tray relative to giving-up density (GUD) in the shrub tray as influenced by vole activity (i.e. high vole density and new moon versus low vole density and full moon). Solid lines denote least-square regressions; dashed lines denote adjusted least-square relationships. The higher open GUD at a fixed shrub GUD indicates open trays are relatively riskier microhabitats under higher vole activity.

density, mice had higher giving-up densities and were less likely to forage within our resource patches compared with low vole density plots. These results were also observed in time. Mice had higher giving-up densities during the new moon when vole activity should be at its highest due to reduced predation risk on voles (see Doucet and Bider, 1969; Halle, 1995). These results rule out exploitative competition, which predicted decreased giving-up densities under higher vole densities. The lack of support for exploitation competition is not surprising given the lack of dietary overlap: meadow voles consume approximately 60–80% herbaceous material (see studies summarized in Batzli, 1985), whereas white-footed mice consume considerable quantities of seeds in oldfields (Ostfeld *et al.*, 1997; Manson *et al.*, 1998). Alternatively, exploitative competition might be most evident during winter food shortages, whereas our study was conducted during the summer months. However, it should be borne in mind that our methods can only measure a cumulative competitive effect and do not rule out alternative forms of competition. Rather, they suggest that exploitative competition (or interference competition considered below), if present, must be relatively weak.

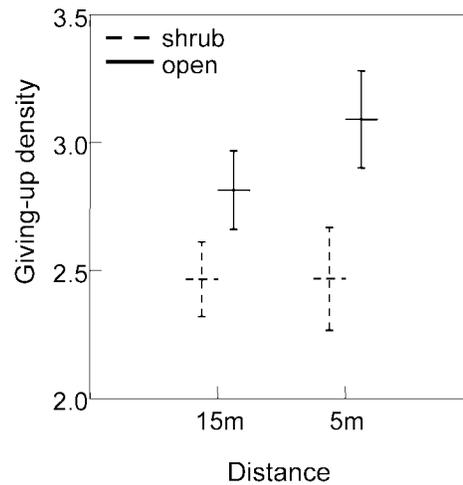


Fig. 4. Giving-up densities (± 1 standard error) as a function of risk (open versus shrub trays) and distance from the forest edge. Data are for all day and station combinations in which both the open and shrub tray were foraged.

For our result to distinguish between interference and apparent competition, we must look at the relationship between the foraging costs of risky open patches (at a fixed value of a safe shrub patch) as vole density/activity increases. Results showed that spatial and temporal increases in vole density/activity led to a relative increase in foraging costs in risky open habitats that is consistent only with apparent competition. Below we consider these effects in greater detail.

Vole density

Higher densities of voles reduced overall giving-up densities and resulted (when combined with moonlight effects) in relatively riskier open patches for mice in comparison to the low vole treatment (Table 2, Fig. 3). These effects are consistent with the view of voles as apparent competitors. The number of patches visited declined, but not significantly so, under the high vole density treatment (Fig. 2). This may reflect somewhat lower mouse densities in these plots (Manson *et al.*, 2001) or, consistent with apparent competitive effects, reduced travel under higher predation risks (Mandelik *et al.*, 2003).

Moonlight

Mice had lower giving-up densities in response to greater moonlight and riskier foraging (Fig. 1). This latter effect is atypical of rodent foraging responses in relation to moonlight (Kotler, 1984; Falkenberg and Clarke, 1998). We suggest that during the full moon voles have decreased nocturnal activity (Doucet and Bider, 1969; Halle, 1995), thereby reducing the cost of predation risk for mice to a greater extent than increased moonlight enhanced predation risk. At first, this may seem an unlikely proposition; however, closer inspection suggests a plausible mechanism. The number of patches visited by mice decreased under the full moon (Fig. 2), suggesting that mice may be more inclined to reduce their activity travelling to and from

food patches as a response to increased predation risk (Mandelik *et al.*, 2003). In turn, this suggests that predation risk on mice is greatest while travelling rather than foraging, as has been noted in other nocturnal rodents (e.g. Mandelik *et al.*, 2003). Lastly, combining the effect of moonlight (i.e. higher vole activity under a new moon) with the vole density treatment led to a relative increase in foraging costs in the risky open patches at higher vole density and activity (Table 2, Fig. 3). This effect is consistent with voles as apparent competitors of mice.

Distance

Voles tend to be more abundant away from the forest edge (Ostfeld *et al.*, 1997; Manson *et al.*, 1999, 2001). For instance, Manson *et al.* (1999) reported an approximately 50% increase in vole trapping capture probability over a distance of 5 to 15 m from the forest edge, which suggests that moving 10 m further away from the forest edge may lead to significantly more frequent encounters between mice and voles. If distance can be used as a surrogate for vole activity in space, such as moonlight was used for vole activity in time, we would expect giving-up densities to be higher at patches 15 m from the edge than 5 m from the edge. However, predation risk may decrease with distance from the forest edge if edges are used as perching sites for avian predators. Voles attract primarily avian predators, such as owls (weasels are rare at our study site; J. Pusenius, personal communication), and avian predators elicit a stronger fear response in voles than do weasels (Korpimäki *et al.*, 1996). Because changes to these potential inputs to the cost of predation act in opposite directions with respect to distance from the forest edge, the effect of distance on giving-up densities is not intuitive. The analysis of giving-up densities using stations where both open and safe trays were utilized the same day demonstrated a significant distance \times risk interaction. This was caused by an increase in giving-up densities in the risky patches (open) near the edge (Fig. 4) and, with reduced activity of mice (fewer trays foraged) near the forest edge (Fig. 2), is consistent with the view that edges are a riskier microhabitat than even 10 m further out.

Voles and mice as apparent competitors

The perception that mice are predator-avoidance specialists, whereas voles fall easy victim to predators, abounds in the literature (e.g. Pearson, 1985; Halle, 1988, and references therein). Clearly, if this is the case, mice run additional risks within areas of high vole abundance and/or activity since these sites should similarly attract larger numbers of predators (e.g. Craighead and Craighead, 1956; Pearson, 1985; Salamolard *et al.*, 2000). Therefore, it is necessary for mice to respond to the presence of an apparent competitor by reducing their activity during times and in places when and where vole density or activity is high.

It is important to point out that our techniques allow us to measure only the increase in perceived predation risk mediated through voles (i.e. apparent competition), rather than an actual demonstration that greater vole density leads to increased predation on mice. Nonetheless, regardless of whether actual apparent competition occurs, the subsequent behavioural changes made by foragers in response to perceived risk are often ecologically relevant and at times may be far more significant than changes in density through actual mortality (Huang and Sih, 1991; Lima and Dill, 1990; Lima, 1998; Werner and Peacor, 2003). In light of our results, we suspect that previously inferred mechanisms of habitat selection or other forms of ecological separation between species may be explained solely by the action of apparent

competition or apparent competition in addition to one or more alternative forms of competition. While apparent competition may not have been the initial mechanism driving the habitat selection of white-footed mice and meadow voles (this would be extremely difficult to prove), it may be sustaining, wholly or in part, their current habitat preferences. Our study is the second to suggest that the limited habitat overlap of voles and mice (at least at forest-field ecotones) may be caused by apparent competition, rather than or in addition to interference competition (Morris, 1999). By establishing a protocol that can be used to differentiate the various forms of competition, we hope that previously inferred interactions between putative competitors will be re-evaluated in the future.

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