

## MICE IN SPACE: SPACE USE PREDICTS THE INTERACTION BETWEEN MICE AND SONGBIRDS

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**Abstract.** The density-dependence inherent in population interactions can be undermined when the behavior or distribution of predators is not predictable from their population density. For instance, unequal use of space by consumers can lead to improper characterizations of their interaction with prey if based solely on population density. Instead, quitting harvest rates (QHRs) from resource patches might provide a useful alternative index of predator impacts. We tested whether space use would predict predation rates of white-footed mice (*Peromyscus leucopus*) on experimental songbird nests and whether QHRs or mouse density would best predict the proportion of space used. Our results indicated that space use was an accurate predictor of nest predation rates. Moreover, space use was significantly related to QHRs, but not to mouse density. In our study, space use is the outcome of behavioral mechanisms that do not appear to scale with or lag behind consumer density. In such cases, we may expect a disjuncture between population density and species interactions.

**Key words:** behavioral indicators; giving-up density (GUD); interaction strength; nest predation rates; *Peromyscus leucopus*; quitting harvest rates (QHR); space use; white-footed mouse.

### INTRODUCTION

All else equal, the rate of predation on a prey species is often assumed to be a function of the predator's population density. The relationship may not be simple or linear due to interference among predators (Beddington 1975, Skalski and Gilliam 2001), complex functional responses (Morgan et al. 1997, Vucetich et al. 2002), behavioral responses of the prey (Abrams 1993, Brown et al. 1999), or interactions with other community members, including higher-order interactions (e.g., Huang and Sih 1991, Werner 1992, Abrams 1993) and short-term apparent competition (e.g., Holt and Kotler 1987, Schmidt and Whelan 1998). Still, one assumes, or hopes, that predator density will be informative for determining a predator's overall impact on a prey population.

However, such density dependence can be undermined when the behavior or distribution of predators is not predictable from their population density. For instance, density can be a lagging or misleading indicator of ecological relationships when behaviors that are essential to the interaction with their prey, such as the motivational state of an individual predator, do not scale with or lag behind conspecific population density (Brown et al. 1999, Schmidt et al. 2001a, Pusenius and Schmidt 2002). The result may be a complicated non-linear relationship between density and interaction strength or no relationship at all. Currently, we do not

know to what extent or under what conditions population density rather than the collective behavior of individuals is more informative.

Spatially explicit models suggest that the amount of space occupied (Schauber 2000, Schmidt et al. 2001a), movement through space (Cuddington and Yodzis 2000), and species' spatial distributions relative to one another (Shigesada et al. 1979, Lewis and Murray 1993, Mitchell and Lima 2002) may be extremely important for species interactions. The unequal use of space by a population of predators can lead to improper characterizations of interactions based solely on their density. For instance, the assumption that prey experience a homogeneous risk of predation may be inappropriate if portions of the environment remain periodically unoccupied by predators. Rather, some knowledge of space use (i.e., proportion of space occupied by predators) and the factors governing it are necessary to properly characterize the interaction.

Incidental predation refers to predation events that are the result of encountering "unexpected" prey items through undirected search (Vickery et al. 1992, Yanes and Saurez 1996). As formulated by Schmidt et al. (2001a), there are explicit links between predator foraging behavior, space use, and predation rates on incidental prey (although the model likely extends beyond incidental encounters; e.g., Pusenius and Schmidt 2002). Predators assess patch quality and exploit only those resource patches considered profitable (i.e., whose current resource density exceeds the forager's quitting harvest rate, QHR). Unprofitable, and therefore unused space, represents a behavioral refuge that may be extremely important for the prey's persistence

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(Schmidt 2003). The amount of space used is itself determined in part by the forager's QHR: Set a very low QHR (i.e., resources are extremely valuable) and nearly all available space becomes profitable, set a very high QHR (i.e., resources are relatively cheap) and very little space meets the demands of the forager. The QHR, therefore, is predicted to be inversely related to the amount of space predators forage within (Schmidt et al. 2001a, Pusenius and Schmidt 2002).

The QHR is, in turn, the phenomenological outcome of a consumer's assessment of its foraging costs and benefits. Exploitative competition (intra- or interspecific) is manifest as a foraging cost thus linking QHRs to changes or differences in population density (Bowers et al. 1993, Davidson and Morris 2001). QHRs reflect additional ecological relationships, such as the energetic state of the forager, the instantaneous risk of predation, and current valuation of food and safety. QHRs thereby incorporate the influence of multiple trophic levels and may provide a more informative and causal link to space use and the strength of species interactions than consumer density would by itself.

Predictions based upon the model of incidental predation relating QHRs to the magnitude of predation rates have been upheld in two unique systems (Schmidt et al. 2001a, Pusenius and Schmidt 2002). Schmidt et al. (2001a) correlated QHRs and predation rates on artificial songbird nests attacked by white-footed mice (*Peromyscus leucopus*). However, the link between QHRs and space use was not explicitly tested experimentally. We returned to the system investigated by Schmidt et al. (2001a) to examine the link between the foraging behavior of the white-footed mouse, its patterns of space use, and predation by mice on songbird nests. We tested whether predation rates on experimental nests are a function of the amount of space over which mice forage and whether mouse behavior (assessed through giving-up densities) or mouse density better predicts space use.

#### METHODS

We conducted our field studies on the property of the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York, USA (41°50' N, 73°45' W). Our experiment utilized six permanent small-mammal trapping grids measuring 2.25 ha and consisting of an 11 × 11 array of trap stations with 15-m spacing between stations and two traps per station (see Jones et al. 1998). We used these grids as sites for: (1) small-mammal trapping and density enumeration, (2) an artificial-nest experiment, (3) collection of giving-up densities, and (4) assessment of space use through the removal of seeds from a lattice grid.

We trapped and ear-tagged small mammals (white-footed mice [*P. leucopus*] and eastern chipmunks [*Tamias striatus*]) for two days at least once per month between early May and mid-November. Traps were opened from ~2 h prior to sunset until 2 h after sunrise.

Trapping rotated among three pairs of grids, with each grid trapped for two days in its respective week and every fourth week designated as a non-trapping week. We enumerated densities of mice as the minimum number known alive (MNA). Our high capture success of individual mice (>80% per 2 trap nights; R. S. Ostfeld, unpublished data) made MNA an accurate method of calculating mouse densities (Hilborn et al. 1975; see Jones et al. [1998] for further description and justification of our procedures). Density estimates for statistical procedures in the artificial-nest/space use experiment were calculated for the approximate date of 12 June. Because individual grids were trapped 1–2 weeks apart and not necessarily during the target date, we took a weighted average of MNA estimates bracketed around 12 June when necessary.

#### Artificial-nest experiment

We distributed 59 nests among the six grids between 15 June and 3 July such that there were never more than seven active nests per grid at any one time. We replaced nests that were depredated at a different location in the same grid, usually >50 m away. Because predation rates differed per grid, relocation schedules differed slightly, and by the end of the experiment each grid received between 9 and 11 total nests. We baited each nest with one blue clay egg measuring the approximate size of Veery (*Catharus fuscens*) eggs, a common ground-nesting thrush at the site. Previous experiments (Schmidt et al. 2001b) indicated that predation rates on nests were similar regardless of the presence of an additional real egg (e.g., Zebra Finch eggs) as bait; therefore we did not use one. We wore gloves when handling the nests and eggs. We checked nests every three days for the presence of eggs and considered a nest depredated if eggs were missing, destroyed, or the clay egg showed tooth or scratch marks. Identification of predators was based on tooth impressions on the clay eggs. Nests that were not depredated after 15 days of exposure were considered successful, and the nest was picked up. For calculation of predation rates, we assumed predation occurred during the midpoint of the rechecking interval. We converted predation rates into mouse-specific daily mortality rates (MDMR) by dividing the number of nests depredated by mice (as identified from marks on the clay eggs) by the number of nest exposure days (Mayfield 1975, Schmidt et al. 2001a, b). The MDMR measures the rate of predation, but greater unused space by mice should lead to overall fewer nests consumed by mice. To tests this, we also compared the percentage of nests depredated by mice (Percent Mice) between plots.

#### Giving-up densities

We collected giving-up densities (GUDs; the amount of food remaining within a patch after a forager has quit harvesting food) from artificial food patches to measure mouse quitting harvest rates. Food patches

were a mixture of seed and sand substrate. As mice forage within the patches, they deplete the seed and their instantaneous harvest rate concomitantly declines. Mice eventually quit foraging and vacate the trays once they have reached their quitting harvest rate. Provided that harvest rates are proportional to the amount of food within a patch (e.g., Brown 1988, Davidson and Morris 2001), GUDs provide a surrogate for the quitting harvest rate.

After the artificial-nest experiment, we deployed 12 artificial food patches per plot. We arbitrarily chose 12 trap stations that provided relatively even coverage of each plot. Starting at the station, we walked off a previously determined number of meters (randomly chosen between 1 and 10) in one of eight directions (randomly chosen from possibilities at 45° intervals) and placed the tray directly on the ground. Each patch was composed of a circular plastic tray (30 cm diameter, 4 cm height) to which we added ~1.5 L of sifted bank sand and 5 g of unhusked millet seed. Because mice were responsible for the majority of predation events, we targeted mice for the collection of GUDs. Mice had access to the trays each evening between ~2 h before sunset (1800 hours) and 1 h after sunrise (~0600 hours). We sieved the trays between nights to collect the uneaten seeds that were then cleaned of debris and weighed to measure the giving-up density. We collected GUDs on 12, 13, 14, and 19 July. Each night nearly all trays were found and heavily exploited by mice; nonetheless, we considered the first night as a pre-baiting period and excluded the data from the analyses. We identified trays that mice had exploited by their footprints and tail drags in the sand and by mouse feces. Any GUDs we could not associate with mice we excluded from the analyses. We logarithmically transformed GUDs to normalize the data and to provide a more linear fit between GUDs and quitting harvest rates (Kotler and Brown 1990). We then averaged GUDs from each plot over time (3 d of collection) and space (12 stations/plot) to arrive at the average plot-specific GUD to use in the analyses. Averaging GUDs over space is necessary to prevent local predation risk, which is proportional to the amount of surrounding vegetation (within ~3 m; Schmidt et al. 2001a), from exerting the dominant influence on GUDs. Average GUDs instead reflect overall risk or, more likely, missed opportunity costs as influenced by the background level of food and the number of competitors within the plot. Missed opportunity costs are not influenced by local differences in, e.g., food availability (e.g., Brown and Alkon 1990, Brown et al. 1992). Therefore, averaging GUDs reduces the noise related to local differences in predation risk (also see Schmidt et al. [2001a] for full discussion of GUDs and the spatial scaling of foraging costs).

#### *Space use: seed grid experiment*

We used the proportion of seeds removed from an experimental grid (Thompson et al. 1991, Pusenius and

Schmidt 2002) to quantify space use in each plot. Between 21 and 22 June 2001, we established 40 transects measuring 65 m in length in each plot. We placed a single oat grain on the ground at 2.5-m intervals. To prevent the grains from being carried away by unwanted predators (e.g., invertebrates and birds), each oat grain was partially embedded in a drop of unscented beeswax (Strahl and Pitch, Incorporated, West Babylon, New York, USA) affixed to a small strip of burlap. We used 30-cm wooden cooking skewers to impale the burlap to the forest floor. Because foraging mammals often left tooth impressions on the wax when removing the seed, this technique facilitated their identification. Transects were spaced 5 m from each other and from trapping transects on either side. We alternated the starting position of transects from opposite sides of the experimental plots. Because transects were only 65 m, whereas the plots were 150 m in length, seeds were not laid out on a perfect lattice grid. This method reduced the time necessary for setup and seed checks while providing relatively even coverage of each plot. On two of the plots, topographical constraints prevented us from fully using this design, and several neighboring transects were started at the same end of the plot.

We surveyed the transects 3, 6, and 9 d after placing out the seeds (beginning on 24 June). During each census, we noted the presence or absence of each seed, examined the wax for tooth impressions, and noted any other signs indicating the presence of animals. We often observed mouse feces on the burlap strips, and recorded these as depredated by mice whether or not tooth impressions were present. This is justified since we were ultimately interested in whether mice had visited particular points (and the proportion of all points visited) rather than predation on seeds per se. Chipmunks, slugs, and unidentified predators took the remainder of eaten seeds. This combination of predators removed nearly all seeds after six days on several plots, and thus we did not consider space use after this period. We transformed the proportion of seeds consumed by mice after three days ( $M_{space3}$ ) or six days ( $M_{space6}$ ) using the arcsine square-root method. We used these variables as our measure of the percentage of space used (i.e., space use) by mice in the analyses. Seed predation by mice after three and six days was highly correlated ( $r > 0.99$ ), as were both variables to total seed predation after their respective time period ( $r > 0.91$ ).

#### *Small-scale activity levels*

We used two methods to quantify mouse activity levels at small spatial scales with nests rather than trapping grids as the sampling unit. First, we quantified mouse activity by determining both the number of individual mice and the total number of captures (i.e., includes recaptured individuals) at each of the 121 trap stations within each grid throughout the trapping period between May and July 2001 (because the trapping

schedule rotated among three pairs of plots, the exact dates differ by  $\pm 1$  wk). From this data set, we determined activity at both the single nearest trap station and nine nearest trap stations centered on each artificial nest. If nests were placed at the edge of the trapping grid, we only examined the nearest trap data. At either scale, the number of individuals and total captures were highly correlated (nearest trap  $r = 0.887$ ,  $n = 59$ ,  $P < 0.001$ ; nine nearest traps  $r = 0.945$ ,  $n = 49$ ,  $P < 0.001$ ). Therefore, we used the individual data for subsequent analyses regressing activity vs. nest survivorship. We used both logistic (successful = 0, depredated = 1) and linear regression methods. For the latter, we used the number of days a nest survived as the dependent variable, scoring successful nests as surviving 15 days.

In addition to using raw count data, we expressed mouse activity per station (or nine stations) as units of standard deviation above or below the mean station activity per grid. This was calculated as:  $(I_T - p_i)/(SD_T)$ , where  $I_T$  and  $SD_T$  are the mean and standard deviation of the number of individuals per trap (averaged over each grid), and  $p_i$  is the number of individuals per the  $i$ th ( $i = 0, 1, \dots, 121$ ) trap station. This metric is useful since previous analyses suggested that there are both large-scale (i.e., plot) and small-scale (i.e., within plot) effects, with the latter obscured unless the plot effect is first factored out (Schmidt et al. 2001a). Using standard deviation units provides a means of estimating local hot or cold areas of mouse activity that can be standardized across plots.

A second measure of small-scale activity was provided by an experiment conducted in 2002 to examine the probability of nest predation as a function of a predator's minimum detectable distance from a nest. We randomly placed artificial nests across  $\sim 50$  ha of our study site and baited each with one clay egg as described in *Methods; Artificial-nest experiment*. At the same time, we placed four spokes of oat baits emanating from each nest in the four cardinal directions. We placed a single oat grain at 0.2-, 0.5-, 1.0-, 2.0-, and 3.0-m distances from the nest along each spoke for a total of 20 oats per nest. We examined the grains and nest daily for predation and terminated the trial after the nest was depredated or disturbed. We used 31 nests in total initiated over four days between 18 and 24 June. We placed all but seven nests directly on the ground, with the remainder placed in low bushes never exceeding 30 cm above ground. Furthermore, 14 of the 31 nests were old Veery nests remaining in their original location that had either previously fledged young or were depredated at least one week prior. All experimental nests were depredated within 10 days; thus, it is possible that disturbance to the area while placing out the oat seeds may have attracted predators and inflated predation rates. Therefore, we terminated the experiment after only 31 trials (i.e., nests) and pursued other techniques to address our original question.

Although predation rates may be artificially high, there appears no reason why predator activity and distance should not be related to nest predation rates in this experiment. We tested whether small-scale activity determined through oat consumption predicted nest predation rates. With individual nests as the sample, nests that survive longer may have more seeds consumed simply because they were observed for a longer period of time. Therefore, we focused on the rate of seed consumption as the appropriate variable to measure the level of predator activity. We calculated the seed consumption rate by multiplying each seed by the number of days it was exposed until consumed. Uneaten seeds were assigned the number of days the experiment lasted (i.e., until the nest was depredated). We divided the number of seeds consumed by the sum of seed exposure days to arrive at a daily seed consumption rate. We regressed this metric against nest survivorship (in days) as the dependent variable.

Second, we hypothesized that if proximity to the nest is a good measure of the risk of predation, then seeds consumed closest to the nest should more closely approximate the date of predation of the nest than seeds consumed farther from the nest. Therefore, we calculated the mean (per distance) number of days that seeds were lost to predators before the nest was depredated. For instance, if a seed was consumed on the same day as the nest it was scored a zero; if consumed three days before the nest was depredated it was scored as a 3. Uneaten seeds were not scored to prevent differences in the percentage of consumed seeds across distance categories from biasing the data. Using nests as the sampling unit, we compared mean seed consumption scores across the five distance categories using ANOVA with nest placement (ground vs. raised  $\sim 30$  cm) and nest type (artificial vs. Veery nest) as additional independent variables.

Statistical significance was based on  $\alpha < 0.05$ , and all  $P$  values are based on two-tailed analyses.

## RESULTS

### *Relationships with mouse density*

Mouse density varied little among the six plots (range = 31–49 mice). We used linear regression to examine the relationships between mouse density and the variables: MDMR, Percent Mice, Mspace3, Mspace6, and GUD. None of the relationships were significant (Table 1).

### *Space use*

In contrast to mouse densities, we observed considerable variation in the percentage of oat grains removed by mice. After three days, mice removed between 4.8% and 63.5% of seeds from the individual plots, and between 12.3% and 69.2% after six days. Space use at either three or six days was significantly related to GUDs (3 days,  $r^2 = 0.977$ ,  $P < 0.001$ ; 6 days,  $r^2 = 0.980$ ,  $P < 0.001$ ; Fig. 1).

TABLE 1. Statistical results of linear regression analyses between mouse density and the ecological measures used in this study.

Factor	$r^2$	$P$
MDMR	0.010	0.85
Percent Mice	0.017	0.81
Mspace3	0.208	0.36
Mspace6	0.224	0.22
GUD	0.327	0.23

Note: Abbreviations are: MDMR, mouse-specific daily mortality rates; Percent Mice, percentage of nests depredated by mice; Mspace3, proportion of seeds consumed by mice after 3 d; Mspace6, proportion of seeds consumed by mice after 6 d; and GUD, giving-up density.

#### Nest predation rates

Forty-six of 59 nests were depredated after 15 days of exposure. Mice were responsible for 32 predation events (raccoons and chipmunks taking the remainder), and mouse-specific daily mortality rate (MDMR) varied from 3.5% to 12.5% per day (mean = 6.8%) among plots. MDMR was significantly related to space use measured after six days (Fig. 2;  $r^2 = 0.772$ ,  $P < 0.01$ ). The percentage of nests depredated by mice (Percent Mice) varied from 36.4% to 72.7% among plots and was significantly related to space use measured after six days (Fig. 3;  $r^2 = 0.858$ ,  $P = 0.008$ ).

#### Small-scale activity

The number of days a nest survived was not significantly related to the number of individuals captured in the single nearest (range = 0–6 mice) or nine nearest (range = 5–24 mice) trap stations whether analyzed as a logistic regression (depredated vs. successful) or as a linear regression using the number of days surviving as the dependent variable. In contrast, at the smallest scale (nearest station) there was a significantly negative

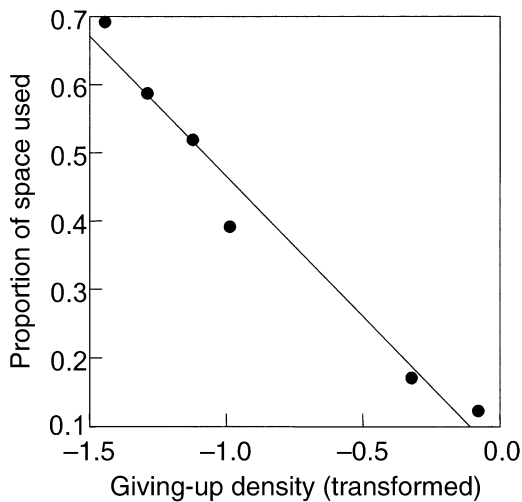


FIG. 1. Relationship between the proportion (untransformed) of seeds removed by mice after six days (Mspace6) and giving-up densities.

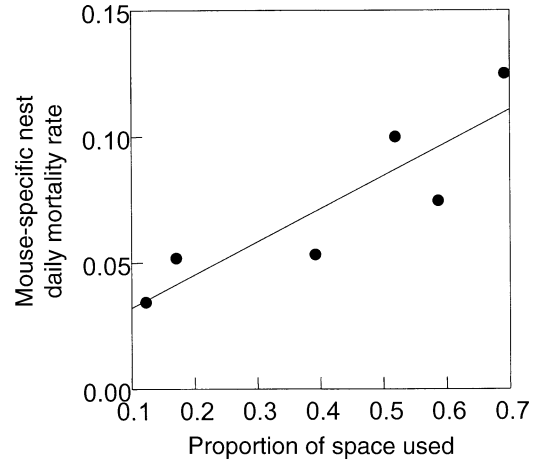


FIG. 2. Relationship between the mouse-specific nest daily mortality rate (MDMR) and the proportion (untransformed) of seeds removed by mice after six days (Mspace6).

but weak ( $r^2 = 0.11$ ,  $P = 0.01$ ,  $n = 59$ ) relationship between mouse activity, based on units of standard deviation, and the number of days a nest survived. This relationship disappeared at the larger (nine stations) scale of analysis ( $r^2 = 0.03$ ,  $P > 0.25$ ,  $n = 49$ ).

There was a significantly negative relationship between nest survivorship and seed consumption rate (Fig. 4;  $F_{1,27} = 11.21$ ,  $r^2 = 0.315$ ,  $P = 0.002$ ), whereas nest type and placement were not significant ( $F_{1,27} = 0.61$ ,  $P > 0.40$  and  $F_{1,27} = 0.06$ ,  $P > 0.80$ , respectively). We found no spatial relationship between nest predation and seed consumption, i.e., there was no significant difference in the mean date of seed consumption, relative to nest predation, as a function of the distance of seeds to the nest (Fig. 5;  $F_{1,265} = 0.23$ ,  $r^2 = 0.001$ ,  $P > 0.60$ ).

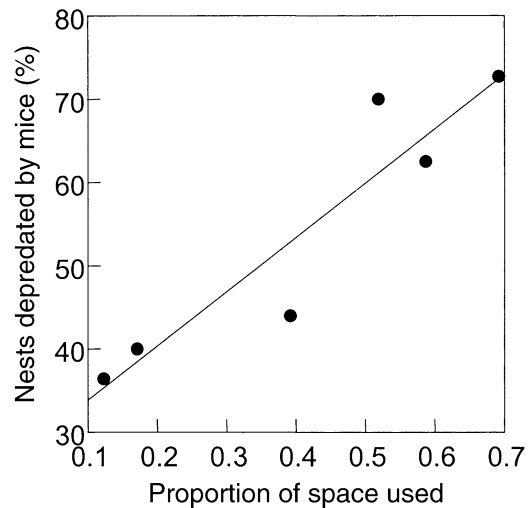


FIG. 3. Relationship between the percentage of nests depredated by mice and the proportion (untransformed) of seeds removed by mice after six days (Mspace6).

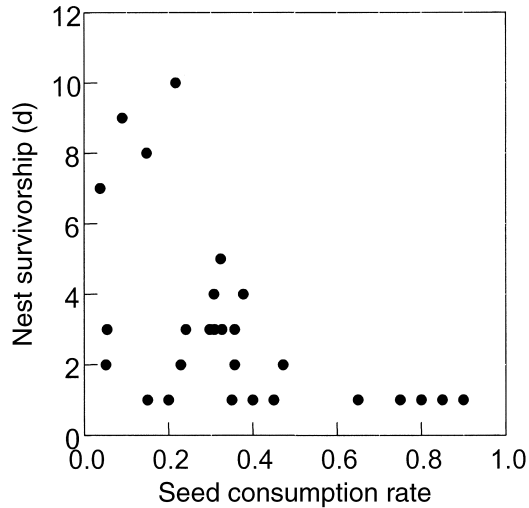


FIG. 4. Relationship between nest survivorship and seed consumption rate from the small-scale experiment in 2002.

#### DISCUSSION

An important implication of this work is the disjuncture between species interactions (specifically, predation rates on nests) and the density of consumers (i.e., mice). Instead, predation was significantly related to the percentage of space over which mice foraged. Moreover, space use was not related to mouse density, but rather to a behavioral index: the quitting harvest rate (i.e., GUDs; also see Pusenius and Schmidt 2002). While low inter-grid variability in mouse density may have reduced the power to detect a density effect, the priority of GUDs over densities has been consistently replicated in our system. Including the results of Schmidt et al. (2001a), we have now shown for three different years a correlation between quitting harvest rates and nest predation rates. Mouse density was either uncorrelated (1998 and 2001) or only marginally related to nest predation (1997). In the latter instance, we conducted a concurrent experimental mouse removal from half the plots. Only in these extreme (many vs. very few mice) and manipulated conditions did mouse density have a marginal effect on nest predation rates. In contrast to the rather low variability in mouse population size, the amount of space used by mice varied substantially among grids. For space use to vary considerably (from 10% to 70% between plots; Fig. 2) in the presence of weak variability in mouse densities suggests that space use is perhaps more strongly determined by alternative factors summarized by quitting harvest rates.

An alternative explanation for our large-scale results is that our packaged oat seeds do not actually measure space use, but rather selectivity on the part of mice in their willingness to consume seeds. This is nothing more than a scaling issue with regard to our original hypothesis that states as their quitting harvest rates increase mice become more selective on resource

patches (i.e., space) rather than diet. Changes in diet selectivity do not rule out concurrent changes in space use, although the relationship between seed consumption and space use may not be linear in such cases. Nonetheless, given the high consumption rate of oat seeds across all grids, partial selectivity by mice does not seem likely, nor is this explanation consistent with results of the small-scale analyses.

At the smaller scale of analyses, mouse abundance based on trapping data was again relatively uninformative, although considering the spatial and temporal scales over which these data were collected, we view this more appropriately as a measure of mouse activity rather than abundance per se. For only a single analysis, based on the departure from the mean activity per plot, did we find a significant effect of activity on nest predation, and it explained a meager 11% of the variation. Quantifying activity based on seed consumption rate was more successful at predicting nest predation rates; predation rates increased with the rate of local seed consumption. Interestingly, there was no spatial relationship within 3 m of a nest. Seeds consumed 20 cm away from a nest were no more likely to signify an imminent nest predation event than seeds consumed 3 m away. We interpret these results as consistent with incidental predation: Greater mouse activity (i.e., higher seed consumption rate) near a nest is more likely to result in a predation event, but the encounter itself at a small scale is a random event (i.e., there is no detectable spatial element in the data).

Our results suggest that both empirical and theoretical approaches to studying species interactions may need to incorporate more spatially explicit behavioral mechanisms in order to correctly assess (1) the nature and strength of species interactions (Fryxell and Lund-

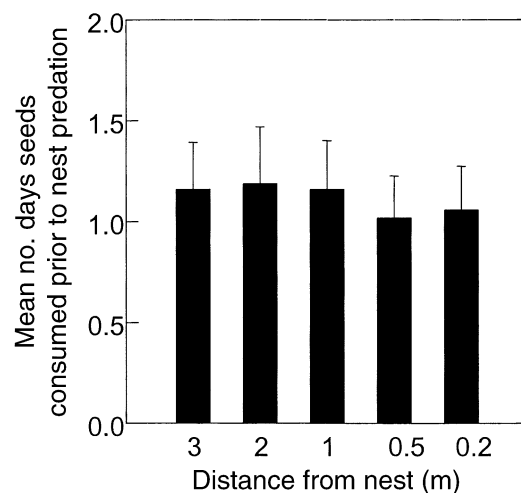


FIG. 5. Mean (+1 SE) relative date of seed consumption (i.e., the value indicates the mean number of days prior to nest predation when seeds were consumed) as a function of distance from the nest. Data are from the small-scale experiment in 2002.

berg 1997, Schmidt 2003), (2) population stability (Brown et al. 1999), and (3) mechanisms of species coexistence (Vincent et al. 1996, Richards et al. 2000, Schmidt 2003). Brown et al. (1999) said it best in their succinct summary, "Ignore behavior at your peril." Quitting harvest rates are associated with the assessments of foraging costs and benefits, including, but not limited to, the value of time, energy, and predation risk. The relative importance of these underlying influences on QHRs remains unexplored, yet the causes and consequences of variability in these underlying factors relative to space use is significant.

For instance, the magnitude of space use varied considerably among our experimental plots in relation to differences in quitting harvest rates (i.e., GUDs). We suggest the differences observed in GUDs reflect differences in foraging opportunities for mice. The density of mast-producing trees (oak and hickory) and red maples (whose seeds are an important spring resource for mice) differ substantially between plots. Furthermore, there is a correlation between mouse density peaks during population booms and density troughs during population crashes (R. S. Ostfeld, *unpublished data*). Differences in food availability and population lags may create heterogeneity in foraging opportunities throughout the forest. If so, mice do not appear to quickly equalize these differences through dispersal, perhaps because they occur at a spatial scale much greater than the dispersal range of an individual mouse. Alternatively, plots that contain greater numbers of recent immigrant mice may show less effective use of space (Pusenius and Schmidt 2002).

Despite the clarity of our results at the scale of our experiments, species interactions may be a function of population density at larger spatial and temporal scales (Schmidt et al. 2001b). For instance, mortality rates on Veery nests at our site (>200 ha) are strongly and significantly related to rodent densities over a 5-yr period (Schmidt and Ostfeld 2003). We have not made behavioral measurements across this scale for comparison, but they would unlikely alter this conclusion. Given the extreme interannual variability observed in mouse densities (Ostfeld et al. 2001), much unused space may exist as "vacant" territories during population crashes. A large proportion of these vacancies become filled during population booms, thus explaining the proportion of unused space by the number of territory holders (i.e., mouse density). Thus, discontinuities in the explanatory variables used to characterize species interaction across spatial and temporal dimensions may indicate the presence of new mechanisms (Schmidt et al. 2001a).

Quitting harvest rates have been successful at predicting space use, which in turn predicts predation rates, in systems where prey are immobile: rodents attacking songbird nests and voles consuming tree seedlings (Pusenius and Schmidt 2002). Mobile predators must approach a potential prey item within a threshold

detection distance in order to attack. The general assumption that encounter rates scale with the population density of consumers was not supported in our study, although such density-dependent relationships do occur at much larger temporal and spatial scales. Instead, the proportion of space used by the predator was the best predictor of encounter/attack rates, and this appears to scale nonlinearly with density. In contrast, QHRs do scale linearly with space use and suggest that food availability and predation risk underlying variability in QHRs are important determinants of species interactions. Whether these results will hold up to a predator-prey system where both species are mobile awaits experimental tests.

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