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Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes

Abstract The ability of prey to find and use predator-free space has far-reaching consequences for their persistence and interactions with their predators. We tested whether nest survivorship of the ground-nesting veery (*Catharus fuscescens*) and shrub-nesting wood thrush (*Hylocichla mustelina*) was related to the local absence of a major nest predator, the white-footed mouse (*Peromyscus leucopus*). Mouse-free space was defined by trap stations that failed to trap a mouse during the avian breeding season (∼May through July). In addition, mouse activity was quantified at individual trap stations based on the number of captures during the same period (six 2.25-ha trapping grids, each containing 121 trap stations trapped repeatedly throughout the summer between 1998 and 2002.) Annual mouse-free space was correlated with other measures of mouse activity based on trapping data. Both mouse-free space and activity metrics were significantly related to annual rates of nest predation (i.e., nest daily mortality rate) in veery but not wood thrush. Likewise, mouse-free space and mouse activity within the nest neighborhood (∼30×30 m² surrounding each nest) was significantly related to nest survivorship in veery but not wood thrush. More trap stations had consistently greater (hotspots) and lesser (coldspots) mouse activity than expected by chance, and veeries were significantly more likely to nest near stations that

had below the grid-average trapping success. Our study thus documented significant spatial variability in predator activity and its relationship to nest predation and nest-site selection in a ground-nesting songbird.

Keywords Nest predation · Predator-free space · Predator–prey interactions · Spatial heterogeneity in predator activity · Veery

Introduction

The ability of prey to find and use predator-free space has far-reaching consequences for their persistence and the ecological and evolutionary relationships with their predators (Durrant 1998; Schmidt and Ostfeld 2003a; Schmidt 2004a). Predator-free space may be most important for prey species that are relatively stationary and whose principal or sole mechanism of escape is to avoid initial detection by their predators (Schmidt et al. 2001a). Bird nests are one such example. Against many predators, parental birds may be relatively helpless in guarding their young and instead have invested in behaviors that prevent predators from foraging in the proximity of their nests. This includes arctic tundra-nesting species (e.g., snow goose, red-breasted goose) that nest in close proximity to nesting raptors (e.g., rough-legged hawk, snowy owl *Nyctea scandiaca*, peregrine falcon), which aggressively defend large areas as much as 0.5-km radii around nests against potential predators, indirectly benefiting the geese (Bety et al. 2002; Quinn and Kokorev 2002; Quinn et al. 2003). Similarly, the dusky warbler (*Phylloscopus fuscatus*) avoids its major nest predator, the Siberian chipmunk (*Tamias sibiricus*) by nesting in isolated shrubs that chipmunks avoid due to their own risk of predation (Forstmeier and Weiss 2004). Female warblers are significantly more likely to mate with males possessing territories with fewer resident chipmunks (Forstmeier and Weiss 2002), demonstrating that warblers are capable of assessing chipmunk abundance (or some

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surrogate). Alternatively, some species capitalize on predator-free space created through alternative mechanisms that "anchor" the predator in space. For instance, black kites (*Milvus migrans*) reduce nest predation by eagle owls (*Bubo bubo*) by living in relatively owl-free zones created through the owls' own central-place behavior—owls are tied down to their own nests (Sergio et al. 2003). A similar example is played out by white-tailed deer (*Odocoileus virginianus*) that occupy gaps that exist between adjacent wolf (*Canis lupus*) packs (Mech 1977; Lewis and Murray 1993).

At smaller spatial scales, predator-free zones may exist within predator territories when heterogeneity in the distribution of resources, either food or safety, necessitates that some areas will not be used for economic reasons. As overall habitat or territory quality increases, fewer low quality (or excessively risky) patches within the territory are worth exploiting and consequently animals use less space and encounters with prey should decline. In accord with this reasoning, Schmidt and Ostfeld (2003a) found a significant negative relationship between the environmental-level of patch exploitation (assessed via giving-up densities; Brown 1988) and space use in the white-footed mouse (*Peromyscus leucopus*). Space use in turn was significantly related to mouse predation on experimental nests while mouse density had no effect either on space use or nest predation rates.

Spatial heterogeneity in predator activity as a research focus is well represented in both the empirical and theoretical literature. Nonetheless, there are three questions that have not been adequately addressed through empirical studies: (1) which metric, predator abundance, predator-free space or some measure of predator activity, best predicts rates of predation; (2) over what range of scales are these metrics informative for predicting predation rates; and (3) does variation in predator abundance or predator-free space over time explain temporal variability in predation rates? Here we address these questions through our on-going research on nest predation on forest songbirds. Our studies focus on the veery (*Catharus fuscescens*), a small (28 g) ground-nesting thrush whose major predators include the ground-foraging white-footed mouse and the eastern chipmunk, *Tamias striatus* (Schmidt and Ostfeld 2003b; Schmidt, in review and this study). We contrast this species with the larger (50 g) wood thrush (*Hylocichla mustelina*), which experiences far less predation by small rodents likely through its habit of building nests in the shrub and sub-canopy layers.

Materials and methods

Studies were conducted in eastern temperate deciduous forest located on the property of the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York. These forests are characterized by oaks (*Quercus rubra* and *Q. prinus*) and sugar maple (*Acer saccharum*) dominant in the canopy, and oaks, maple (*Acer* spp.), maple-leaved viburnum (*Viburnum acerifolium*) and witch-hazel (*Hamamelis virginiana*) common in the understory (Schmidt et al. 2001a).

Trapping protocol and density/activity enumeration

We used 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). Between approximately mid-May and mid-November trapping rotated weekly between three pairs of grids, with each pair of grids trapped for two consecutive days in its respective week and every fourth week designated as a non-trapping week. Traps were opened at approximately 1700 hours (at least 2 h before sunset) and checked between 0800 and 1100 hours the next morning, and all captured white-footed mice and eastern chipmunks given ear tags for individual identification. Mouse density was enumerated as the minimum number known alive (MNA) for each grid for the target date of approximately 12 June in each year (see details in Schmidt and Ostfeld 2003b). To determine annual variation in MNA we averaged MNA across the six trapping grids each year.

For examining rodent activity at smaller spatial scales we quantified trapping success per individual trap each year from 1998 to 2002. We selected trapping dates that closely overlap the breeding season of most Neotropical migrant songbirds (i.e., May through July). For each trap and each rodent species we tallied the number of captures and the minimum number of individuals captured (i.e., individuals recaptured multiple times were only counted once). In total, we had six potential metrics of rodent activity: three categories (mice, chipmunks, or combined) × two measures (total captures or minimum number of individuals). These six metrics were highly correlated to one another (~80% of correlations $r > 0.85$ and more than 50% of correlations $r > 0.90$) with the exception of total rodent versus total chipmunk. We chose to use the total number of mice captured as our single metric of rodent activity with which to compare to avian nest success. We considered the number of mouse captures to more accurately reflect surrounding activity of mice than the number of individuals. For instance, with respect to predation pressure on passerine nests, an individual mouse captured 6 times throughout the year at the same location likely poses greater risk than two individuals each caught only once. Traps remained open primarily throughout the night thereby providing a more accurate measure of mouse activity than chipmunk activity, hence the poorer correlations between total rodents and total chipmunks. Nonetheless, chipmunks have also been observed depredating veery nests (K.A.Schmidt, unpublished data) and, if they have correlated levels of activity, may contribute in part to the results we obtained.

The dates and total number of trapping days varied between grids and years as annual summer trapping began at different dates in each year. In most cases, eight trapping days (four 2-day trapping sessions) were conducted between ~May and July each year. However, on a few occasions total trapping days varied (range 4–10). This was corrected by expressing mouse activity in units of captures per trap night. A second potential bias might be produced along the outermost trap line of grids where fewer trap lines "compete" with neighboring lines for rodents. The outermost trap line (or shell when considering the two-dimensional grid) lacked neighboring traps on one side. Therefore, the outer shell may have higher trapping success than interior shells that are surrounded on all sides by neighboring traps. We tested for this artifact using ANOVA with mean total mouse captures per shell as the dependent variable and plot ($n=6$), year ($n=4$; 2000 was excluded due to very low rodent densities), and shell ($n=4$; a fifth shell is possible, but would consist of only eight traps and so we decided to exclude it) as main effects; all interactions were non-significant and dropped from the analyses. All main effects, but in particular shell ($F_{3,84} = 15.2$, $P < 0.001$), were highly significant. Tukey post-hoc comparison among shells revealed that the outer shell had greater trapping success than all interior shells ($P < 0.001$ in all comparisons), which in turn did not differ significantly from one another ($P \geq 0.25$). The outer trap shell had 1.604 greater number of captures, on average, than the interior shells. Therefore, we adjusted total mouse captures for trap stations in the outer shell by dividing by 1.604.

Nesting data

We searched IES property from May to August 1998 to 2003 for songbird nests and monitored all active nests following standard protocols (Martin and Geupel 1993). We typically monitored nests every 3 days (more often when fledging was imminent) until depredated or until all fledglings had left the nest. Nests were considered successful if they fledged at least one young. Nests with obvious signs of predation or whose chicks disappeared before the earliest possible fledgling date were considered depredated. We quantified nest predation rates in each year as the daily nest mortality rate (DMR) by dividing the number of depredated nests by the sum of nest exposure days (after Mayfield 1975). The DMR quantifies the probability a nest is killed per day of exposure.

Quantifying rodent activity

For each nest, we determined mouse activity at the focal trap nearest the nest (focal mouse activity) and mouse activity of the nest neighborhood (neighborhood mouse activity), defined as the focal trap nearest the nest plus its eight nearest neighboring traps (i.e., the nearest trap at each 45° interval). The neighborhood for nests located at the edges of grids was represented by only six total traps rather than nine given the absence of a trap line in one direction. Nests located at grid corners (very rare) had a neighborhood of only four traps.

An alternative metric for mouse activity considers only trap stations where mice were absent or at least were not caught during the breeding season of both thrushes. We refer to such sites as mouse-free space (MFS). MFS was calculated for each grid in each year as the proportion of traps that failed to catch any mice during the thrush breeding season, and averaged across grids to determine annual variation in MFS. For smaller scale analyses, for each nest located on a grid we quantified mouse-free space as the proportion of the nine trap stations surrounding a nest (i.e., neighborhood scale) that caught zero mice (neighborhood MFS). Note that the standardizations applied to MNA used above are not applicable to MFS because zero rodent activity cannot be adjusted downward (or upward) based on a multiplier correcting for edge effects or fewer trapping days.

To verify that focal traps or neighborhoods constituted independent sampling units, we calculated Moran's I to examine spatial correlation in mouse activity across all 30 grid × year combinations. Moran's I was calculated at 15-m intervals (i.e., the minimum inter-trap distance) and significance tests performed by the program AutocorQ v.2.00 (http://www.ulb.ac.be/sciences/lagev/autocorq.html) using a permutation test with 1,000 permutations to assign variance to I and calculate a P-value (Kaluzny et al. 1998). We used a Bonferroni corrected $\alpha = 0.0017$ for determining statistical significance. Less than 1% of all tests gave significant results, and we concluded that spatial correlation is absent in our trapping data.

Analyses

Nest predation (large-scale temporal trends)

We used linear regression to examine the relationships between the annual nest daily nest mortality and the two metrics of mouse activity: MFS and MNA. We used the log-transformation of nest daily mortality rate (expressed as a ratio of two variables) and the arcsine square root transformation of MFS (expressed as a proportion). We calculated annual nest daily mortality rates using all nests located during the respective year, i.e., nests found on and off trapping grids (sample sizes, 1998–2003, respectively: wood thrush: 43, 27, 15, 46, 40, 36; veery: 21, 19, 12, 23, 31, 36). MFS and MNA were calculated as the mean from the six trapping grids and are assumed to be representative for the site as a whole. We evaluated which metric, predator abundance (MNA) or predator-free space (MFS), was the better predictor of annual variation in the daily rate of nest mortality in veeries (only veeries showed significant patterns, see

Results) by comparing Akaike's Information Criterion corrected for small sample sizes (AIC$_C$, Burnham and Anderson 1998). In general, the best fitting model is the one with the lowest AIC$_C$ score. Models with relative AIC$_C$ scores (ΔAIC$_C$) < 2 show strong support, between 4 and 7 show some support, and scores > 10 are poorly supported (after Burnham and Anderson 1998).

Nest predation (small-scale spatial trends)

A moderate number of birds nested within the six trapping grids between 1998 and 2002 and were amenable to small-scale analyses between nest predation and local rodent activity. For these analyses, we used only nests built in or within ~10 m (15 m is the minimum distance between traps) of the six trapping grids. Sample sizes were considered sufficient for two species: veery (32 nests, 15 of which were depredated) and wood thrush (62 nests, 31 of which were depredated). We used logistic regression to examine the relationship between nest success and: (1) neighborhood MFS, (2) focal mouse activity, and (3) neighborhood mouse activity. Lewis (2004) recommended logistic regression over other approaches when analyzing binary data such as nesting success. Year and plot were also included as independent variables. Lastly, we compared model performance using AIC$_C$ scores using the full models (i.e., including terms for year and plot) for MFS, focal mouse activity and neighborhood activity.

Mouse density, activity, and mouse-free space

We analyzed the relationship between mouse-free space and mouse abundance or activity at three scales: (1) temporal correlation using the entire study site as the spatial unit, (2) across the six trapping grids, and (3) between neighborhood MFS and neighborhood mouse activity. We used Pearson and Spearman's Rank correlation (reporting only the former for lack of qualitative differences) for the temporal and neighborhood analyses. For the neighborhood analysis, there are 81 possible neighborhoods per grid, but at most only 12 non-overlapping neighbors. Therefore, we calculated correlation coefficients for each of 100 random samples of 360 neighborhoods (12 neighborhoods per grid × 6 grids × 5 years = 360) to prevent non-independence from overlapping neighborhoods. Because the significance of all 100 correlation analyses was identical there was no need to further quantify their distribution to assess significance.

For the analyses across trapping grids, we used MFS and MNA separately for each grid × year combination. Schauber (2000) modeled mouse-free space as gaps between predator territories by generating hypothetical mouse home ranges randomly located in space. Under this assumption, the proportion of space outside all predator home ranges is given by the zero-term of a Poisson distribution where a is the area of each home range and P is the density of predators: MFS $= e^{(-aP)}$. Therefore we fit an exponential decay model to our dataset and compared models using AIC$_C$ with and without an asymptotic plateau to MFS using the software GraphPad Prism v.4.00.

Temporal correlation and avian settlement patterns

To examine temporal correlation in mouse activity at individual trap stations for each grid × year combination, we determined each station's departure from its grid-specific mean mouse activity in units of standard deviation (SD). We summed the number of negative departure SD values over the 5 years of data, which could range from zero (hotspots; consistently above average mouse activity) to five (coldspots; consistently below average mouse activity). We compare the distribution of summed negative departures (0–5) against the expected values using Chi-square analysis. Expected values were derived from the binomial distribution in which the probability of a negative SD at any given trap station in any given year was determined from the proportion of negative SD values for the respective grid-year combination.

We then examined whether the two thrush species nested in areas with low (i.e., less than the mean) mouse activity more than be expected by chance by comparing the number of nests placed nearest a trap station with either greater or lesser activity than its grid-specific average for the same year. To determined significance we calculated the cumulative probability that nests would be placed nearest to trap stations with less than average mouse activity the same number of times or greater based on the binomial distribution.

Results

Nest predation (large-scale temporal trends)

For veery, nest daily mortality rate was strongly and negatively correlated with annual mouse-free space (MFS; $r^2 = 0.924$, $P = 0.002$; Fig. 1) and strongly positively correlated with mouse abundance (MNA; $r^2 = 0.840$, $P = 0.01$; Fig. 2). Neither MFS nor MNA were significantly related to the daily mortality rate for wood thrushes after the removal of a significant outlier, year 2000 (Fig. 1; $r^2 < 0.03$, $P > 0.40$ for either analysis). Although not a significant outlier for veeries, removal of the 2000 data point did not qualitatively change the results ($r^2 > 0.70$, $P < 0.04$ for either analysis). While MNA better predicted annual variation in daily mortality rate of veeries (MNA AIC$_C$ = 5.183, MFS AIC$_C$ = 6.033) both models show strong predictive power (ΔAIC$_C$ = 0.850 for the MFS).
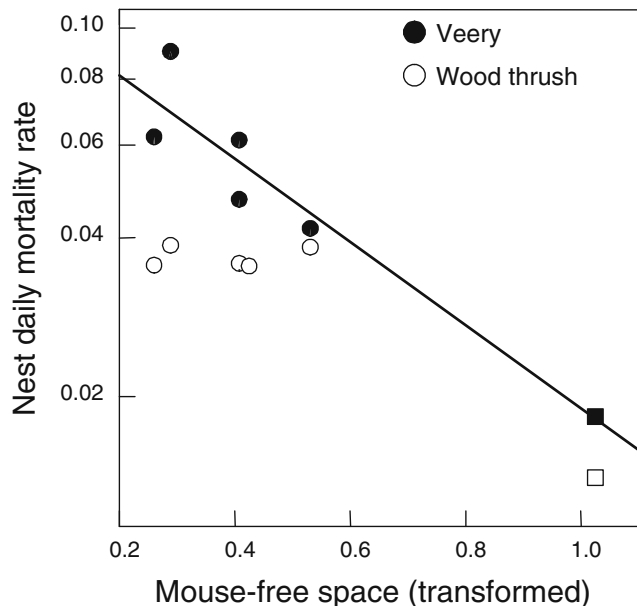
Fig. 1 Relationship between annual nest daily mortality rate (probability per day of exposure) on veeries (*Catharus fuscescens*) (*filled symbols*) and wood thrush (*Hylocichla mustelina*) (*open symbols*) and annual mouse-free space (MFS). Each data point represents 1 year. Least square regression line is shown only for the veery. Annual MFS was calculated as mean proportion of traps without mouse captures across six 2.25-ha trapping grids and is arcsine square-root transformed. Year 2000 is represented by *squares*; all other years are represented by *circles*. Note: the two centermost data points for wood thrush are offset slightly to facilitate viewing

Nest predation (small-scale spatial trends)

None of our measures of mouse-free space or activity (focal or neighborhood scale) were significantly related to nest success in wood thrush (Table 1). In contrast, nest success in veeries significantly increased with greater neighborhood MFS and neighborhood mouse activity, whereas focal mouse activity was not significant (Table 1). Model selection procedures gave a somewhat different interpretation. Neighborhood MFS was the best ranking model (Table 1) followed closely by focal mouse activity ($\Delta AIC_C < 1$), whereas neighborhood mouse activity showed considerably less support ($\Delta AIC_C \sim 4$).

Correlations between mouse activity and mouse-free space

We observed negative correlations between annual MFS and annual MNA at the site level ($r = -0.90$, $n = 6$, $P < 0.01$) and between neighborhood MFS and neighborhood mouse activity (all samples $r < -0.70$, $n = 360$, $P < 0.001$). Across grids, an exponential decay with a plateau gave the best fitting model ($MFS = e^{(-0.071 \times MNA)} + 0.1014$; $r^2 = 0.914$; Fig. 3) compared with either a non-plateau model ($\Delta AIC_C = 11.71$) or linear model ($\Delta AIC_C = 52.31$).
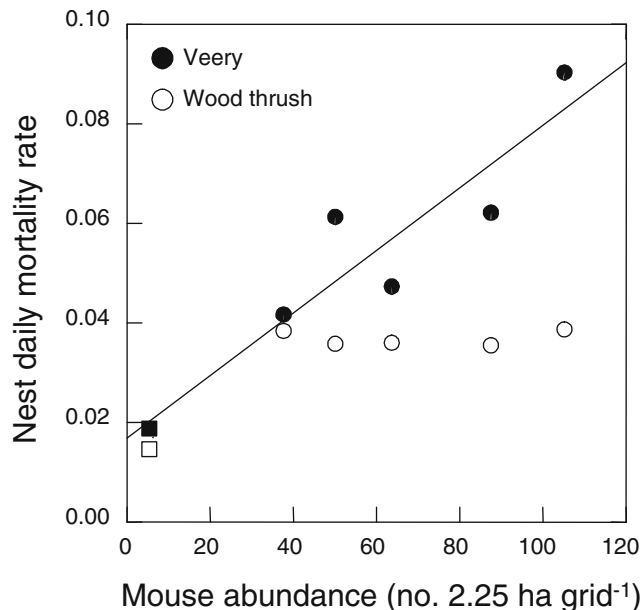

Fig. 2 Relationship between annual nest daily mortality rate (probability per day of exposure) and annual mouse abundance for veeries and wood thrushes. Mouse abundance was estimated as the mean minimum number alive (MNA) on six 2.25-ha trapping grids. Each data point represents 1 year. Least square regression line is shown only for the veery. Wood thrush regression was non-significant after removal of year 2000, whereas results for veery were qualitatively unaffected (year 2000 is represented by *squares*; all other years are represented by *circles*)

Temporal correlation and avian settlement patterns

We found a significantly greater number of hotspots and coldspots of mouse activity than predicted by chance on five of the six grids ($\chi^2_5 > 34.3$, $P < 0.01$) and a similar, although non-significant trend on the last grid ($\chi^2_5 = 10.52$, $P < 0.10$). Cumulatively across the six grids, the expected number of cold- and hotspots was 63 trap stations (8.7%), whereas we observed 152 (21%). Twenty-four of 32 (75%) veery nests were located nearest trap stations with lower than average mouse activity ($P = 0.052$), whereas 34 of 72 (47%, $P > 0.50$) wood thrush nests were located similarly.

Discussion

Variation in mouse activity or mouse-free space in time and space was significantly related to predation rates on veery nests across multiple temporal and spatial scales. In contrast, we observed no significant relationships between mouse activity or mouse-free space and nest predation in wood thrushes, with the possible exception that predation on wood thrush nests declined precipitously during a crash in the mouse population (Fig. 1). The absence of significant relationships with this species is not surprising given the wood thrush's greater body mass and habit of nesting in the shrub layer or higher, which reduces accessibility to the nest by primarily

Table 1 Summary of logistic regression analyses relating metrics of mouse activity and mouse-free space to nest success in veery (15 of 32 nests depredated) and wood thrush (31 of 62 nests depredated)

Model	Coefficient (*t*-ratio)	P	AIC$_C$	ΔAIC$_C$
Veery				
Focal mouse activity: Wald $\chi^2_7 = 10.11$, $P = 0.18$			−60.226	0.779
Year	−0.65	0.52		
Activity	−0.95	0.35		
Neighborhood mouse activity: Wald $\chi^2_7 = 15.75$, $P = 0.027$			−57.033	3.972
Year	−0.68	0.50		
Activity	−2.01	0.045		
Neighborhood MFS: Wald $\chi^2_7 = 18.01$, $P = 0.012$			−61.005	0.000
Year	−0.01	0.99		
MFS	1.99	0.047		
Wood thrush				
Focal mouse activity: Wald $\chi^2_7 = 7.41$, $P = 0.39$				
Year	1.04	0.30		
Activity	0.88	0.38		
Neighborhood mouse activity: Wald $\chi^2_7 = 15.75$, $P = 0.027$				
Year	1.80	0.07		
Activity	−1.42	0.16		
Neighborhood MFS: Wald $\chi^2_7 = 8.64$, $P = 0.28$				
Year	1.96	0.05		
MFS	1.71	0.09		

Full models also included plot effects, but for brevity these are not shown; all plot effects were non-significant ($P > 0.90$). Significance is shown for each full model and individually for year and mouse activity metrics. AIC$_C$ and ΔAIC$_C$ scores are shown for each full model in the case of veeries

ground-foraging rodents. The remainder of our discussion therefore focuses on the veery.

Across our study site, the annual rate of predation on veery nests was strongly and significantly related to annual variation in mouse abundance. Likewise, at the local scale, nest predation was significantly related to mouse activity within the neighborhood of a nest (mouse abundance, such as MNA, would not be meaningful at this scale). All three metrics, neighborhood MFS, focal, and neighborhood mouse activity, were supported by one or more analyses, although neighborhood mouse activity received the least support from information theoretic analyses. Several lines of evidence indicate that mouse attacks on songbird nests are examples of incidental predation (Schmidt et al. 2001a; Schmidt and Ostfeld 2003a), that is, predation resulting not from

Fig. 3 Relationship between grid mouse-free space (MFS, proportion of traps without mouse captures) and grid mouse abundance (MNA). Data points represent grid × year combination (6 grids × 6 years = 36 in total). *Solid line* gives the best fitting ($r^2 = 0.91$) exponential equation: $MFS = e^{(-0.071 \times MNA)} + 0.1014$

directed search for nests, but rather a consequence of encounters between mice and nests while mice are searching for other prey items. Therefore, nests that are attacked are likely detected only at close range leading to the expectation that local heterogeneity in mouse activity will be strongly correlated with the vulnerability of nests.

Our metric of mouse-free space enumerated information only from trap stations that recorded no mouse activity (i.e., captures). It is not a true measure of mouse-free space for the simple reason that MFS was determined based on occasional trapping events throughout the season rather than a continuous record of mouse absence. Nonetheless, MFS proved to be a reliable indicator of nest predation on veeries (Table 1). Nest success increased with the amount of neighborhood mouse-free space measured within a 30×30 m^2 area centered on a nest. Likewise, annual variability in MFS was a highly significant predictor of annual variability in nest daily mortality rate. The predictive power of MFS persisted despite small unequal sampling rates between years and biases in the likelihood of capturing rodents along the outermost trap lines—issues corrected with the mouse activity metrics.

Mouse density, activity, and mouse-free space were all determined from the same set of trapping data, and consequently were strongly correlated with one another. Whether this would be true if we had an independent measure of mouse-free space is uncertain. Previous studies in our system that used independent measures of mouse-free space did demonstrate poor and non-significant relationships between mouse-free space and mouse abundance (MNA) at the scale of 2.25-ha trapping grids (Schmidt et al. 2001a; Schmidt and Ostfeld 2003a). Also in these studies, mouse-free space predicted mouse predation rates on artificial nests whereas in two of three years mouse abundance did not.
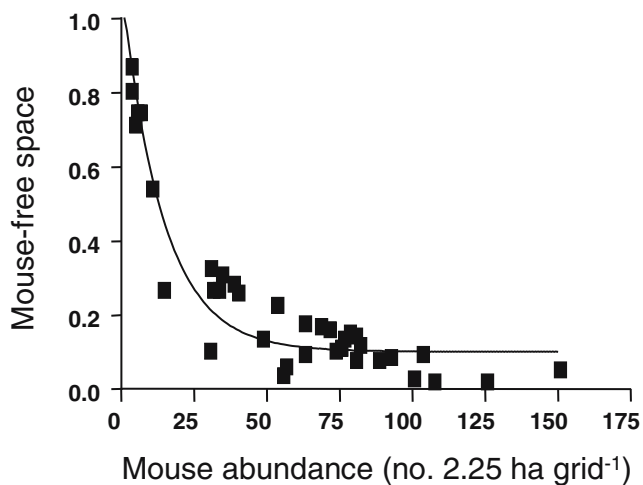
Analyses conducted at the scale of 2.25-ha trapping grids demonstrated an exponential decline in MFS as mouse density (MNA) increased that is consistent with Schauber's (2000) model of random territory placement. However, by itself this observation does not provide sufficient evidence for such a mechanism. We did not measure mouse-free space as gaps in territories as assumed by Schauber, and random placement of territories seems unlikely in light of other studies (e.g., Schnurr et al. 2004). Moreover, MNA was estimated at a point in time (mid-June), whereas MFS was based on cumulative captures over the breeding season. What is most interesting about the relationship between MFS and MNA at this scale is the rapid decline in MFS at low MNA. Fifty percent of space is rapidly occupied (i.e., 50% of trap stations recorded the presence of mice through captures) at low mouse density (∼6 mice/ha). Mouse-free space then reaches a plateau at ∼18 mice/ha. Further increases in mouse density do not appreciably increase MFS beyond ∼10% of available space, on average. Therefore, even during periods of high mouse density mouse-free space will likely be available for prey, such as nesting songbirds, to utilize. Moreover, because the relationship is flat throughout a large range of densities only in years with low mouse densities (the steep decline in MFS in Fig. 3) might we expect a strong relationship between MFS and MNA at this scale.

Are veeries assessing rodent activity?

Several studies suggest that passerines are capable of assessing and avoiding avian predators on nests and adults (Sergio et al. 2003; Roos and Pärt 2004), but there are far fewer demonstrations that passerines assess mammalian nest predator abundance or some corresponding metric such as activity level. Such examples that do exist typically involve rodent predators whose populations vary dramatically among years (summarized in Forstmeier and Weiss 2004) as in our system (Schmidt and Ostfeld 2003b). Examples include the dusky warbler (nest predator is the Siberian chipmunk; Forstmeier and Weiss 2004) and the wood warbler (*Phylloscopus sibilatrix*) (nest predators are *Apodemus* rodents; Jędrzejewska and Jędrzejewski 1998). In extremely variable environments it may be both easier to determine relative predator abundance and more profitable to have such information.

The observation that veeries tend to nest at sites associated with below average mouse activity suggests that veeries may in someway assess nest predator abundance/activity and avoid the riskiest sites. Veeries may directly assess mouse abundance or they may simply be choosing sites with physical features that mice avoid (e.g., sites lacking runways along fallen limbs and trunks, or adequate vegetation cover). Alternatively, veeries and other passerines may be able to assess predation risk based on previous breeding experiences and thereby exhibit fidelity to successful territories or nest sites (Schmidt 2001, 2004b) while dispersing from unsuccessful sites. Such a mechanism requires temporal autocorrelation in risk between years (Schmidt 2001, 2004b; Doligez et al. 2003), which the presence coldspots of mouse activity, i.e., trap locations that repeatedly scored below average mouse activity, confirms.

In conclusion, the relationships between spatial heterogeneity and temporal variability in mouse abundance/activity and nest predation on veeries suggest that inferences regarding the importance of mice as nest predators from artificial nest studies (Schmidt et al. 2001b; Schmidt and Ostfeld 2003b) were warranted. At the same time, the presence of spatial heterogeneity in mouse activity and mouse-free space provides veeries a means to potentially avoid their nest predators. We have not yet examined the mechanisms that create spatial heterogeneity in mouse activity in our system, but those mechanisms apparently create significant temporal autocorrelation in the form of coldspots and hotspots of activity. Veeries appear to utilize coldspots, but whether they assess these locations directly, indirectly, or through other factors correlated with nest-site selection is unknown.

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