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Running head: Spatial Heterogeneity in Predation

QUANTIFYING A DYNAMIC RISK LANDSCAPE: HETEROGENEOUS PREDATOR ACTIVITY AND IMPLICATIONS FOR PREY PERSISTENCE

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Abstract: Spatial heterogeneity in predation risk can ameliorate impacts on prey populations, particularly for prey of generalists. Spatially heterogeneous risk implies the existence of refugia, and the spatial scale of those refugia and their persistence over time affect whether prey can avoid predation by aggregating therein. Our objective was to quantify the magnitude, spatial scale, and temporal persistence of heterogeneity in risk of predation by white-footed mice (*Peromyscus leucopus*), an abundant generalist predator of gypsy moths (*Lymantria dispar*) and songbirds. We used track plates to measure white-footed mouse activity at >170 trees in each of 3 forest plots in upstate New York during summers of 2003-2005. We quantified the mean and coefficient of variation of track activity among trees by fitting the beta-binomial distribution to data from each plot and study period. We measured temporal persistence by disattenuated autocorrelation, and spatial scale by fitting exponential variograms. Mice were much less abundant in 2005 than the other 2 years, leading to lower overall track activity but higher coefficient of variation among trees. Mouse track activity at individual trees was positively autocorrelated between monthly study periods in 2003 and 2004, and even between the two years, whereas temporal autocorrelation in 2005 was much weaker. Track activity showed positive spatial autocorrelation over lag distances from ca. 30 to >1000 m. These findings indicate that mouse activity, and hence risk to their prey, varies substantially in space at spatial and temporal scales that appear responsive to mouse population dynamics. The spatial scale and temporal persistence of that variation imply that prey may benefit from returning to, or failing to disperse from, refugia.

Key words: activity, autocorrelation, *Peromyscus leucopus*, persistence, predation, refugia, spatial heterogeneity, spatial scale, track plates, white-footed mouse

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INTRODUCTION

Spatial heterogeneity in predation risk and the resulting refugia are important to predator-prey dynamics (Gause 1934, Huffaker 1958, Murdoch and Oaten 1975, Hilborn 1975). Specialist predator-prey systems have received the most attention by researchers in this regard (Luckinbill 1974, Turchin and Kareiva 1989), but spatial heterogeneity in risk may be especially important to incidental prey of generalist predators (Schmidt 2004a). Because generalists switch to more abundant prey types when a focal prey type becomes scarce, abundance of generalist predators is affected modestly, if at all, by rarity of the focal prey (Holt 1977, Murdoch and Bence 1987, Sinclair et al. 1998). This numerical decoupling means that rarity is not a refuge for prey of generalists. However, the numerical decoupling of generalists predators can benefit prey when spatial refugia persist over time, because prey can become aggregated in refugia without strongly increasing local predator abundance. Specialist predators would be expected to show an aggregative or numerical response to such heterogeneity in prey abundance, but these responses are likely to be weak or absent for generalists. Aggregation of prey in refugia generates negative spatial covariance between predator and prey abundances, and may further reduce predator impact through local satiation of predators (Goodwin et al. 2005).

The white-footed mouse (*Peromyscus leucopus*) is a generalist forager that consumes many prey types and shows only weak food limitation during the growing season (Wolff et al. 1985, Wolff 1986), but its abundance in many areas is strongly linked to availability of tree seeds (especially acorns) during winter (Elkinton et al. 1996, Wolff 1996, Jones et al. 1998, McCracken et al. 1999). Dense mouse populations following bumper crops of acorns are associated with intense predation on various prey, including gypsy moth (*Lymantria dispar*) pupae (Bess et al. 1947, Campbell and Sloan 1977, Smith and Lautenschlager 1981) and the eggs and nestlings of certain songbirds (Schmidt et al. 2001, Schmidt and Ostfeld 2003, Clotfelter et al. 2007). In low- to moderate-density populations of gypsy moths, both pupal survival and population growth rates are negatively related to mouse densities (Elkinton et al. 1996, Ostfeld et al. 1996) and removal of mice can cause >10-fold increases in gypsy moth abundance (Jones et al. 1998). Similarly, nest predation of veeries (*Catharus fuscescens*) and dark-eyed juncos (*Junco hyemalis*) is strongly correlated with fluctuations in white-footed mouse abundance (Schmidt et al. 2001, Schmidt 2003), yet songbird eggs and nestlings represent an incidental food source to the mice (Schmidt et al. 2001).

For both gypsy moths and nesting songbirds, the existence and persistence of refugia are important in avoiding local predator-driven extinction. Because mice are generalists yet readily attack gypsy moth pupae even at low pupal densities, chronically dense mouse populations could potentially drive gypsy moths locally extinct (Schauber et al. 2004). However, simulations and analytical models indicate that persistent spatial heterogeneity in predation risk coupled with limited gypsy moth dispersal can enable gypsy moth populations to withstand high densities of white-footed mice (Goodwin et al. 2005, Schauber et al. 2007). Gypsy moth larvae typically disperse short distances (tens of m; Mason and McManus 1981, Weseloh 1997, Erelli and Elkinton 2000) and adult female gypsy moths are flightless (Montgomery and Wallner 1988). Therefore, gypsy moth population growth is enhanced because larvae "inherit" refugia where their mothers survived to lay eggs (Goodwin et al. 2005, Schauber et al. 2007). Similarly, veery nest success is higher in locations with relatively low use by mice, and nesting songbirds may be able to assess and actively select such refugia (Schmidt et al. 2006, Fontaine and Martin 2006). Even if birds are unable to assess risk before committing to a nest site, they can benefit from using a win-stay/lose-switch strategy if "hot" and "cold" spots of risk persist over time (Greenwood and Harvey 1982, Schmidt 2001, Hoover 2003, Schmidt 2004b).

Many studies (reviewed by Jorgensen 2004) have examined the small-scale activity patterns of white-footed mice and similar small mammals. However, such studies have typically focused on identifying the microhabitat features to which small mammals respond (i.e., causes), rather than the emergent spatiotemporal characteristics (magnitude, scale, and persistence) of spatial heterogeneity in activity that affect the consequences for prey. Our objective was to quantify these spatiotemporal characteristics of white-footed mouse activity in an oak-forest ecosystem where mice are typically abundant, to assess whether movement strategies of focal prey species could enable them to exploit refugia of low mouse activity. Throughout, we use the term "activity" to indicate a quantity that is analogous to "abundance" or "population density" yet applies at scales smaller than an individual home range: i.e., how much time mice (in aggregate) spend in particular locations. To meet this objective, we used track plates to measure mouse activity around individual trees, and from these data estimated the variation and autocorrelation of activity in time and space.

MATERIALS AND METHODS

Study area and mouse abundance

All field studies were conducted on three, ca. 2-ha oak-dominated forest plots (Green, Henry, and Tea plots) at the Cary Institute of Ecosystem Studies, Millbrook, New York, USA. Live-trapping for small mammals on these plots has continued from 1995 until the present. Each trapping grid consisted of an 11×11 or 12×10 array of trap stations with 15 m between stations and two Sherman live-traps at each station. During 2003-2005, 2-day trapping sessions were conducted on each plot at 3-week intervals from late May until late October or early November each year. Traps were baited with oats, and cotton batting was provided as insulation during cool weather. Traps were set in the late afternoon and checked and closed the following morning. Each captured mouse or chipmunk was marked with a uniquely numbered ear tag and released at the site of capture. Because each trap session was too short for closed-population estimators, we estimated white-footed mouse abundance (mice per plot) during individual trap sessions in 2003-2005 using the Jolly-Seber open population model with heterogeneous mortality rates, implemented in program POPAN5 (Arnason and Schwartz 1999). We report abundance estimates interpolated to the 15th day of each month. White-footed mice were by far the most frequently trapped small mammals on these plots, although shrews (*Blarina brevicauda* and *Sorex cinereus*.), eastern chipmunks (*Tamias striatus*), and southern flying squirrels (*Glaucomys volans*) were also captured frequently.

Measuring activity

Predation risk can be measured by observing predation on naturally occurring prey, but stationary prey that survive long enough to be found by researchers under-represent sites of especially high risk, introducing bias (Zens and Peart 2003, Schauber and Jones 2006). Prey could also be deployed, but deploying enough prey in a small area to precisely estimate the local predation rate could alter the foraging behavior of mice (Schauber et al. 2004). Instead, we measured local activity of white-footed mice, based on the assumption that risk of being attacked by mice is determined by the local activity of mice. High activity at a location could result from intense use by a single mouse or moderate use by several mice, with similar implications for sparse prey because individual predators are unlikely to become satiated. Space use of small mammals has been measured by the frequency of capture at live-trap stations (e.g., Mengak and

Guynn 2003, Schmidt et al. 2006) but mice often respond behaviorally to the presence of traps and trapped animals cannot move, which can bias observed space use (Douglass 1989).

We measured white-footed mouse activity by the frequency at which mice left tracks ("track activity") on plates placed around individual trees during the summers of 2003-2005. Track plates were constructed of 14×22-cm acetate sheets coated with graphite powder suspended in an ethanol/mineral oil mixture (Connors et al. 2005). To provide rigid backing, track plates were clipped to pieces of aluminum flashing, which had been deployed in the field at least 1 week before to allow mice to become accustomed to them. Mouse track activity is a strong predictor of predation on gypsy moth pupae at the scale of individual trees, and the plates do not appear to attract or repel mice (Connors et al. 2005). Tracks of white-footed mice are readily distinguished from those of chipmunks, shrews, or flying squirrels. Southern red-backed voles (*Clethrionomys gapperi*) and meadow voles (*Microtus pennsylvanicus*), whose tracks could be mistaken for mouse tracks, have been captured very rarely on the plots.

Each plot comprised 100 15×15-m cells. In 10 randomly selected cells per plot, we placed plates around all trees > 7 cm diameter at breast height (dbh). In each of the remaining cells, we randomly selected one of four candidate sample points 7.5 m apart and placed three track plates around the nearest tree > 7 cm dbh. Universal Transverse Mercator coordinates of each sample tree were measured with a global positioning system unit (Garmin GPS 12; Garmin International, Inc., Olathe, Kansas, USA). Track plates were placed around 183, 187, and 171 sample trees on Green, Henry, and Tea plots, respectively, and the same trees were used in all years except for 1 tree on Henry plot that fell after the 2003 field season.

Track plates were monitored every 2 days during ca. 2-week study periods in June, July, and August each year. A tracked plate was replaced when available untracked area reached <50

% of the total graphite-coated area of the plate. We marked tracks on plates left in the field to prevent double counting. Track plates with unknown or unidentifiable tracks were replaced and removed from the field for later examination. Due to inclement weather and time constraints, data-collection days per study period varied from 5-8 among plots and study periods in 2003 and 2004 (always 7 data-collection days in 2005). In each plot and study period, the sample size (in "plate-checks") at a tree was the number of data-collection days multiplied by 3 plates. In 2003, plates were monitored 19 June – 3 July, 14 – 28 July, and 6 – 19 August. In 2004 plates were monitored 14 – 30 June, 14 – 28 July, and 14 – 27 August. In 2005 plates were monitored 8 – 21 June, 7 – 20 July, and 3 – 16 August.

Analyzing activity data

We measured mouse track activity at a tree by the proportion of plate-checks that recorded mouse tracks. We analyzed track activity separately for each study period, plot, and year to quantify the magnitude, spatial scale, and temporal persistence of heterogeneity in mouse activity among trees. All our analyses addressed the problem of disentangling spatial and temporal variation in the true activity of mice (i.e., the probability of recording mouse tracks on a given plate-check) from the sampling variation inherent to proportional data.

Magnitude of Spatial Heterogeneity. – To quantify variation in true track activity among trees, we fitted the beta-binomial distribution (Kendall 1998) to observed track activity data from each plot and study period. The beta-binomial distribution is often applied to model how the probability of an event varies among subjects, such as detectability of individual animals (McClintock et al. 2006) or disease incidence at individual sites (Gent et al. 2006). In our case, this procedure is based on two assumptions: (1) true track activity varies among trees according to a beta distribution and (2) observed track activity (plates tracked per check) at a tree is a binomial random variable conditioned on the true track activity at that tree. We obtained maximum likelihood estimates for the mean and coefficient of variation (CV) of the underlying beta distribution (Evans et al. 2000) for each plot and study period using the PopTools add-in in Microsoft Excel®, employing a wide array of initial parameter values to ensure convergence to a global maximum. We used profile likelihood to place 95% confidence intervals on the mean and CV of track activity for each study period and plot. To test the null hypothesis that track activity was equal among trees, we used a likelihood-ratio test to compare the fit of the beta-binomial distribution to that of a binomial distribution in each plot and study period. Finally, we performed a Chi-square goodness-of-fit test to test for lack of fit by the beta-binomial model, which would indicate deviations from the assumptions that true mouse activity follows a beta distribution and that observed track activity is a binomial random variable.

Spatial Scale. –We applied geostatistics to quantify the spatial structure of mouse activity. This approach describes how the dissimilarity of measurements taken at different points in space depends on the distance between those points (lag distance), in the form of a variogram (Fig. 1). In geostatistics, this dissimilarity is typically expressed by the semivariance, which is calculated like the variance except using only measurements below the overall mean (Cressie 1993). If the quantity being measured is spatially autocorrelated then nearby measurements are expected to be more similar, resulting in a lower semivariance among measurements at small than at large lag distances. If measurements were perfectly repeatable then semivariance would equal zero at lag distance zero, but measurement errors or fine-grained spatial structure can produce a positive semivariance value (known as the nugget) at lag distance zero. In many cases, semivariance can be expected to level off at a maximum value (called the sill) at large lag distances. If the measured quantity shows strong spatial autocorrelation (also described as strong spatial structure), then nearby measurements will be much more similar than distant ones, so the relative amount by which the sill exceeds the nugget (i.e., relative structural variability) is often used to indicate the strength of spatial autocorrelation (Isaaks and Srivastava 1989). The absence of spatial autocorrelation is indicated by a flat variogram. The spatial scale of autocorrelation is typically measured by the lag distance at which semivariance approaches sill; this distance is called the effective range. If data are collected at a small scale relative to the scale of autocorrelation (i.e., maximum observed lag distance < effective range), then estimating effective range and the sill requires extrapolation beyond the range of the data and consequently is imprecise. The spatial pattern of the quantity being measured is described as isotropic if the variogram is unaffected by the direction in which lag distance is measured (e.g., east-west or north-south; Cressie 1993).

We used PROC VARIOGRAM in SAS (SAS Institute, Carey, North Carolina) to produce an empirical variogram from mouse track activity data in each plot and study period. To more concisely characterize spatial structure and scale, we use PROC NLIN to fit an isotropic, exponential variogram model to data from each plot and period. The model is: $\gamma(h) = C_0 + C_1(1 - \exp(-\alpha h))$, where $\gamma(h)$ is the predicted semivariance at lag distance h, C_0 is the nugget variance, and $C_0 + C_1$ gives the sill (Cressie 1993). We defined effective range (A) as the lag distance at which the variogram curve was 95% converged to the sill ($A = 3/\alpha$). Each model was fitted by weighted least squares, weighting data in the bin centered on distance i by $n(i)/\gamma(i)^2$, where $n(i)$ is the number of observations in the bin (Cressie 1993). Initially, we analyzed data from each plot separately, binned in 5-m distance intervals up to a maximum of 155 m (i.e., the plot extent). However, estimates of A were often greater than the plot extent, producing highly imprecise estimates of the effective range and sill. Therefore, we also fitted exponential variogram models to data pooled from all three plots in each period, binned in 20-m distance intervals up to a maximum of 5000 m. Relative structural variability (RSV; Isaaks and Srivastava 1989) is defined as RSV = 1 - $C_0/(C_0+C_1)$. Because of imprecise estimates of the sill, we calculated a within-plot RSV for each variogram model, replacing the sill (denominator) with $\gamma(155)$. For variograms fitted to data pooled from all plots, we calculated RSV with $\gamma(5000)$ in the denominator. With the fitted variogram model, we used point kriging (PROC KRIGE2D in SAS) to interpolate track activity within each plot and study period.

Temporal Persistence. – We calculated between-period (June, July, or August) correlations (Pearson product-moment correlation, r) in track activity around sample trees in each plot and year. To measure the persistence of mouse activity between years, we averaged track activity around each sample tree over the 3 study periods in each year, and calculated the pairwise correlations in average track activity among the 3 years. We determined statistical significance of raw correlations using SAS but report disattenuated correlations (Muchinsky 1996) to adjust for the reduction in correlation coefficient magnitude due to sampling variability. Each observed correlation between vectors x and y (r_{xy}) was disattenuated by $R_{xy} = r_{xy} / \sqrt{r_{xx} r_{yy}}$, where r_{xx} is the reliability of the data in vector x (i.e., data from a given plot and study period). We used a parametric bootstrap to estimate reliability for each plot and study period. To do so, we treated the observed track activity at each tree as the true probability of recording a track, generated two binomial random variables (using PopTools add-in in Microsoft Excel®) based on that true probability and the number of plate-checks, calculated the observed correlation between the two random variables over all trees, and took the average correlation over 1,000 simulations.

RESULTS

Mouse abundance, mean activity, and magnitude of spatial heterogeneity

Track activity was measured with >62,400 plate-checks per year. Activity data were significantly better fit by a beta-binomial distribution than a binomial distribution, indicating that true track activity varied among trees, for all plots and study periods (all $\chi^2 > 7.7$, d.f. = 1, $P < 0.006$) except Henry plot in June 2005 and Tea plot in July 2005 ($\chi^2 < 0.32$, d.f. = 1, $P \geq 0.57$). Although statistically significant lack of fit generally remained after beta-binomial fitting (all $\chi^2 > 219$, d.f. ≥ 169, $P < 0.04$; except Tea plot in July 2005 -- $\chi^2 = 156.2$, d.f. = 169, $P = 0.75$), observed track frequencies closely followed model predictions (**Appendix A**). Over all grids and study periods, estimated mean and CV of track activity were similar (ca. 0.3-0.35) in 2003 and 2004 (Fig. 2), when mouse abundances were generally >60 mice/plot. However, acorn failure in fall of 2004 precipitated a crash in mouse abundance in 2005 to $\leq$6 mice/plot; consequently, track activity in 2005 averaged only 0.06 but exhibited high spatial heterogeneity, with estimated CV averaging 0.58 (Fig. 2).

Spatial scale

The strength and scale of spatial structure scale varied among plots and years (Appendix B). Variograms for 2003 from the Henry plot tended to peak at 40-80 m whereas those from the Green plot increased approximately linearly out to 155 m, indicating spatial autocorrelation out to and perhaps beyond the plot scale (Fig. 3). In 2004 and 2005, most variograms had shallower initial slopes than in 2003, suggesting weaker spatial autocorrelation, and most 2005 curves leveled off at $\leq$ 80 m (Fig. 3). These patterns are reflected in the estimates of A and RSV from the fitted variogram models (Table 1). Green plot variograms in 2003 had $A > 1000$ m, whereas those from Henry plot in 2003 had $33 \leq A \leq 70$ m. RSV in 2003 varied from 0.46 to 0.72 with a median of 0.61, consistently greater than 2004 or 2005. Variogram data from 2005 exhibited the lowest RSV and inconsistent *A*. Variograms based on data pooled from all plots indicated little spatial structure at scales larger than the extent of our plots (150-200 m), except for August 2005 (Fig. 4).

Temporal persistence

Within each year, track activity was significantly autocorrelated among study periods on Henry and Tea plots in 2003 and 2004 and on Green in 2003, but not on Green in 2004, with disattenuated correlations between periods ranging from 0.16 to 0.55 in these 2 years (Fig. 5A, Table 1). Between-period correlations were weaker in 2005 ($-0.18 \leq R \leq 0.36$) and all were nonsignificant, except June vs. July for Green plot. Track activity averaged over study periods in a year also was autocorrelated between 2003 and 2004 for all plots, with $R \approx 0.5$; observed correlations between 2004 and 2005 were also positive but lower ($R \leq 0.21$), and were not statistically significant (Fig. 5B, Table 1). Disattenuated correlations between 2003 and 2005 were near 0.21 for all grids but were marginally nonsignificant for Tea plot (Table 1).

DISCUSSION

We found that the spatiotemporal characteristics of mouse activity, as measured by track plates, were amenable to exploitation by prey. In 2003 and 2004, when mice were abundant, mouse activity varied substantially among trees with spatial structure over tens to hundreds of m and temporal autocorrelation over months to years. In 2005, when the mouse population was lowest, the CV of activity among trees was higher than in other years, but spatial structure and temporal autocorrelations were weak. These characteristics indicate that limited dispersal by gypsy moth larvae could enable them to "inherit" low-risk sites where their mothers survived as pupae (Schauber et al. 2007), and that songbirds could benefit from electing to re-use successful nest sites (Schmidt 2004b). The spatial scale and temporal persistence of relatively low-activity sites, and hence their contribution to prey population growth, appear to be greatest when mice are most abundant and therefore most important as predators.

The spatial scale of predator activity relative to prey movement distances is integral to the ability of prey to exploit cold spots and escape hot spots of risk. On our plots, the effective range of mouse activity was often similar to or larger than the typical dispersal distances of moths (< 100 m; Weseloh 1997, Erelli and Elkinton 2000), indicating that many dispersing larvae may remain within their birth refuge. This correspondence of scales can ameliorate predation impact on moth populations by allowing local build-up of moth densities in temporally stable refugia (Goodwin et al. 2005). The spatial scale of predation risk can also determine the optimal distance for birds to move when re-nesting after nest predation (Powell and Frasch 2000). The effective ranges of mouse activity we observed were often similar to or greater than territory size in veeries (Martin 1960), suggesting that territory abandonment may be necessary for breeding dispersal to be an effective response to predation by white-footed mice.

Temporal persistence of hot and cold spots of risk also affects the impact of predation. After accounting for sampling variability, mouse activity showed substantial temporal autocorrelation between months and, when averaged over months, between years. Within-season persistence is needed for nest predation events to provide information about the likely success of re-nesting attempts in the same area. Between-year consistency is necessary for nest success to provide information relevant to nest-site philopatry decisions. Between-year consistency is also necessary for limited dispersal to enable gypsy moths to inherit refugia where their mothers survived. In our mouse-moth system, if a refuge persists for > 1 year, the high fecundity (Moore and Jones 1987, Jones et al. 1990) and limited dispersal of gypsy moths can cause a substantial increase in local moth populations with a concomitant expansion of the area with moth densities high enough to satiate mice and hence an expansion of the refuge. Both within- and between-year persistence of mouse activity were greatest in years when mouse abundance was relatively high, suggesting that the spatiotemporal characteristics of predation risk in this system act to ameliorate intense predation risk associated with high mouse densities.

We found that most of the spatial structure in mouse activity was at scales below ca. 50 m, similar to the typical home range radius for white-footed mice (ca 0.1 ha; Wolff 1985). This scale is considerably greater than the scale (ca. 8 m) of spatial autocorrelation in seed and seed predation by small mammals documented by Manson (2000). We also found some instances of spatial structure at scales equal to or larger than the scale of our plots (150 m). Such larger-scale pattern could arise from behavioral responses to larger scale spatial variations in the determinants of habitat suitability for mice, or from the build-up of local matrilineal clusters due to female philopatry (Wolff and Lundy 1985). At smaller scales, local activity of *Peromyscus* is often associated with microhabitat features such as understory cover (McCracken et al. 1999) and coarse woody debris (Greenberg 2002, Mengak and Guynn 2003) and, although few studies have linked such small scale features to individual fitness, Manning and Edge (2004) found that *P. maniculatus* with sufficient woody debris within their home ranges had higher survival. Other microhabitat features selected by mice may be more ephemeral. For example, Schmidt et al. (2001) found that local abundance of red maple seeds was associated with increased predation by small mammals on songbird nests, suggesting that rapid predator responses to resource pulses could weaken the persistence of hot/cold spots. However, Connors (2005) did not find that mouse track activity on our plots was related to volume of coarse woody debris, tree size, or tree species. Mouse track activity did appear to be related to local tree seed production, but that relationship was inconsistent among plots (Connors 2005).

Demographic inertia could also generate or exacerbate spatial heterogeneity in mouse activity. At the scale of our plots, mouse abundance in summer is tightly linked to acorn production the previous autumn (Jones et al. 1998, Ostfeld et al. 2006), so current density can be a carryover from high habitat quality in the past. Given that female white-footed mice are often philopatric (Wolff and Lundy 1985), differential reproductive success among females at one point in time could similarly lead to spatial variation in mouse activity later. Such inter-female differences in reproductive success can stem from differences in female quality, local habitat quality, or simply demographic stochasticity. Thus, demographic inertia could cause the spatial and temporal distribution of activity for mice (or other species with female philopatry) to imperfectly reflect the distribution of features related to habitat quality.

The magnitude of spatial heterogeneity in risk (and other determinants of population growth) necessary for a prey population to persist can depend on the spatial scale and temporal persistence of that heterogeneity relative to exploitive strategies employed by the prey. In other words, only a small degree of heterogeneity may be necessary if that heterogeneity is persistent and at a spatial scale that prey can efficiently find and exploit. Therefore, the significance of our findings about heterogeneous predation risk is tied to prey behavior. Schmidt et al. (2006) found that ca. 75% of veery nests were found near (<8 m) trap stations where fewer than average mice were captured, suggesting that veeries may effectively recognize and select refugia for nesting. In contrast, gypsy moth larvae prefer to feed on oak trees, which elevate local mouse abundance via acorn production. In fact, gypsy moths often pupate (with predictable results) inside mouse-inhabited nest boxes on our plots. Therefore, gypsy moths do not appear capable of selecting low-risk sites for pupation. Instead, the offspring of mothers that happen to pupate in persistent refugia may exploit those refugia through limited dispersal, thereby "inheriting" the relatively low risk that favored their mothers.

Elevated spatial heterogeneity of mouse activity (as measured by CV) in the year of low mouse density could have resulted from habitat selection or social regulation. Under an Ideal Free Distribution (Fretwell and Lucas 1970), animals in a low-density population should only occupy the sites of highest quality, moving into lower-quality sites as only density increases. At coarse examination, our finding that the degree of spatial heterogeneity in local activity was be greatest at low regional abundance broadly agrees with the Ideal Free Distribution. For example, at small scales, *Peromyscus* select sites based on habitat features related to cover and food, and ultimately fitness (Morris 1991, Morris and Davidson 2000, Manning and Edge 2004). Also, Schnurr et al. (2004) found that *Peromyscus* were more uniformly distributed among small-scale habitat types at high density than in a year of low density. However, we found that temporal persistence of mouse activity was lower in the low-density year (2005), suggesting that sites of high local activity might not necessarily reflect highly preferred patches. Alternatively, high spatial heterogeneity with low temporal persistence in low-density years could occur if aggressive social interactions arise when local density exceeds a threshold (Wolff 1985). Widespread aggression in years of high overall density would tend to spatially homogenize local activity levels by driving animals away from areas of high local activity, whereas activity can vary in time and space with less constraint when population density is low. Several studies support a role for aggression in population regulation of white-footed mice (Sadleir 1965, Healey 1967, Dooley and Dueser 1996) but its impact on the spatial scale and magnitude of heterogeneity in mouse activity is unclear.

To our knowledge, this is the most comprehensive analysis of the spatiotemporal characteristics of the predation-risk landscape experienced by prey. We consider our system of mice attacking gypsy moths and songbird nests as a model for circumstances in which rare, incidental prey are confronted with predation from abundant generalist predators. The spatial and temporal distribution of risk are critical considerations in endangered species management, reintroduction programs, and other instances where the conservation of rare prey is desired (Sinclair et al. 1998). Increasing the spatial heterogeneity and temporal consistency of predation risk could be useful for protecting desirable or native species from predation. Conversely, homogenizing the distribution of risk in space or time by altering predator activity may be effective for managing undesirable and introduced species, such as the gypsy moth. Confirming these possibilities will require experimentally manipulating not only the spatial differences of risk, but the persistence of those differences over time, and monitoring the performance of prey populations.

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Table 1. Effective range (*A*, in m) and relative structural variability (RSV) calculated from exponential variogram models fitted to mouse track activity data from oak-forest plots in Millbrook, New York. Variograms were fitted either to data from each plot individually or from all plots pooled.

		2003		2004		2005	
Plot	Period	*A*	RSV	*A*	RSV	*A*	RSV
Green	June	>1,000	0.58	>1,000	0.38	214	0.37
	July	415	0.55	>1,000	0.36	50	0.39
	Aug	>1,000	0.36	>1,000	0.09	48	0.36
Henry	June	67	0.51	44	0.44	106	0.11
	July	34	0.65	>1,000	0.26	18	0.43
	Aug	39	0.55	18	0.43	>1,000	0.36
Tea	June	107	0.55	210	0.60	44	0.54
	July	>1,000	0.44	250	0.45	>1,000	0.29
	Aug	20	0.51	100	0.41	----[a]	0
All	June	78	0.52	166	0.47	90	0.26
	July	131	0.48	259	0.41	>10,000	0.16
	Aug	46	0.49	745	0.29	>10.000	0.61

[a] Flat variogram.

Table 2. Disattenuated temporal autocorrelations of mouse track activity on 3 oak-forest plots in Millbrook, New York, 2003-2005. Values in bold indicate $P < 0.05$.

	Plot		
Period	Green	Henry	Tea
June-July 03	**0.55**	**0.30**	**0.49**
June-Aug 03	**0.35**	**0.36**	**0.37**
July-Aug 03	**0.53**	**0.45**	**0.34**
June-July 04	0.18	**0.43**	**0.54**
June-Aug 04	0.20	**0.30**	**0.56**
July-Aug 04	0.16	**0.33**	**0.55**
June-July 05	**0.36**	-0.01	-0.01
June-Aug 05	-0.18	0.17	-0.09
July-Aug 05	0.01	0.23	0.001
2003-2004	**0.55**	**0.43**	**0.54**
2004-2005	0.18	0.14	0.21
2003-2005	**0.21**	**0.23**	0.21

Figure 1. A hypothetical variogram indicating the nugget, sill, and effective range of the relationship between true semivariance and lag distance (solid line), as well as semivariance estimates calculated from observed data (symbols). Note that effective range would be much more difficult to estimate precisely from data collected only at smaller lag distances (triangles) than from data collected over a wide range of lag distance (circles).

Figure 2. Monthly abundance and track activity of white-footed mice in 3 2.25-ha oak-dominated forest plots (symbol shapes) at the Cary Institute of Ecosystem Studies, Millbrook, New York, 2003-2005. (A) Mean track activity (open symbols) estimated by maximum likelihood fitting of the beta-binomial distribution and mouse abundance (filled symbols) estimated by Jolly-Seber model and interpolated to 15th day of each month. (B) Coefficient of variation of mouse track activity among trees estimated by maximum likelihood fitting of the beta-binomial distribution. In both panels, error bars indicate profile 95% confidence intervals.

Figure 3. Standardized variograms of white-footed mouse track activity measured on each of 3 oak-forest plots at the Cary Institute of Ecosystem Studies, Millbrook, New York, 2003-2005, during 3 monthly periods (line types) per year. Data for each plot and period are standardized relative to modeled semivariance at 155 m.

Figure 4. Standardized variograms of white-footed mouse track activity measured on 3 oak-forest plots at the Cary Institute of Ecosystem Studies, Millbrook, New York, 2003-2005, during 3 monthly periods per year (symbol shapes). Solid lines indicate fitted exponential variogram

models for the 3 periods. Data for each period are standardized relative to modeled semivariance at 5000 m.

Figure 5. Maps of observed and interpolated (based on point kriging) spatial variations in white-footed mouse track activity among trees on one oak-forest plot ("Tea") at the Cary Institute of Ecosystem Studies, Millbrook, New York. Triangles indicate the locations of trees where track activity was monitored. Warmer colors indicate higher mouse activity. (A) Monthly mean activity from 3 monthly periods during 2004, showing strong persistence of "hot spots" and "cold spots" within that year. (B) Yearly mean track activity data for 2003-2005, showing between-year persistence of spatial variations, especially 2003-2004. Note that the scale of activity data for 2003-2004 is 10-fold higher than for 2005.

FIGURE 1

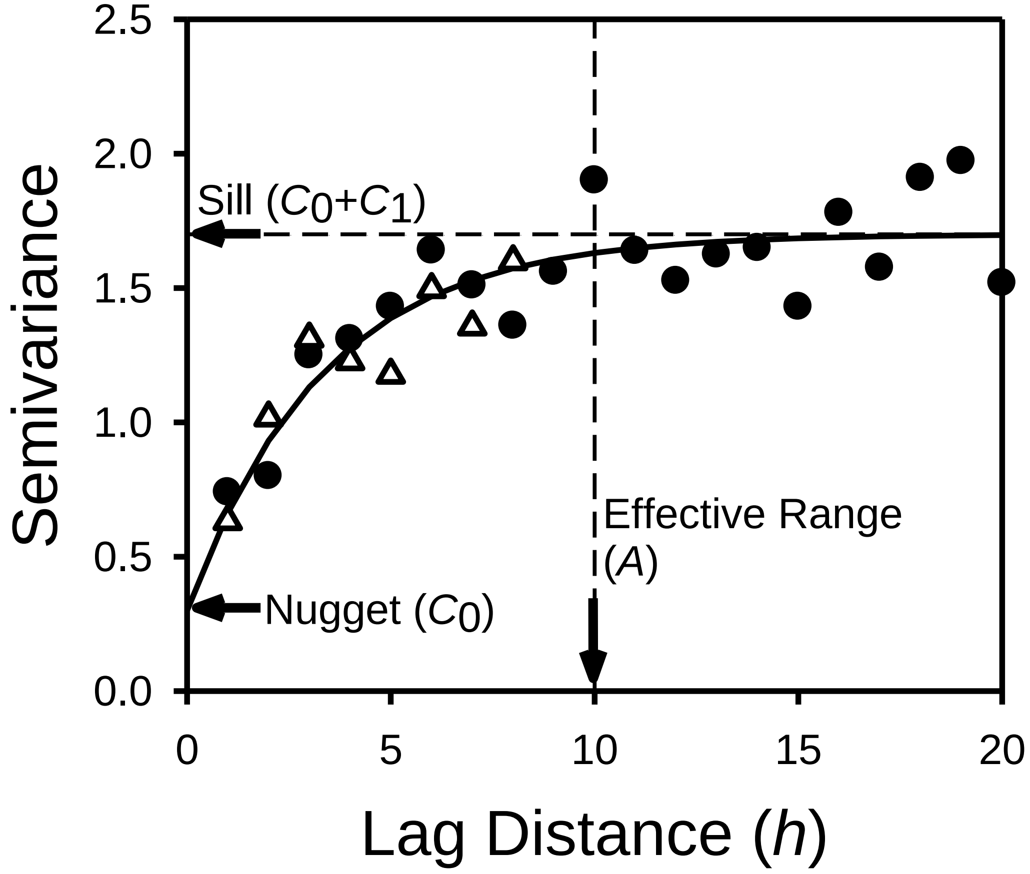

Semivariance
Lag Distance (h)
Sill (C0+C1)
Nugget (C0)
Effective Range (A)
0.0
0.5
1.0
1.5
2.0
2.5
0
5
10
15
20

FIGURE 2

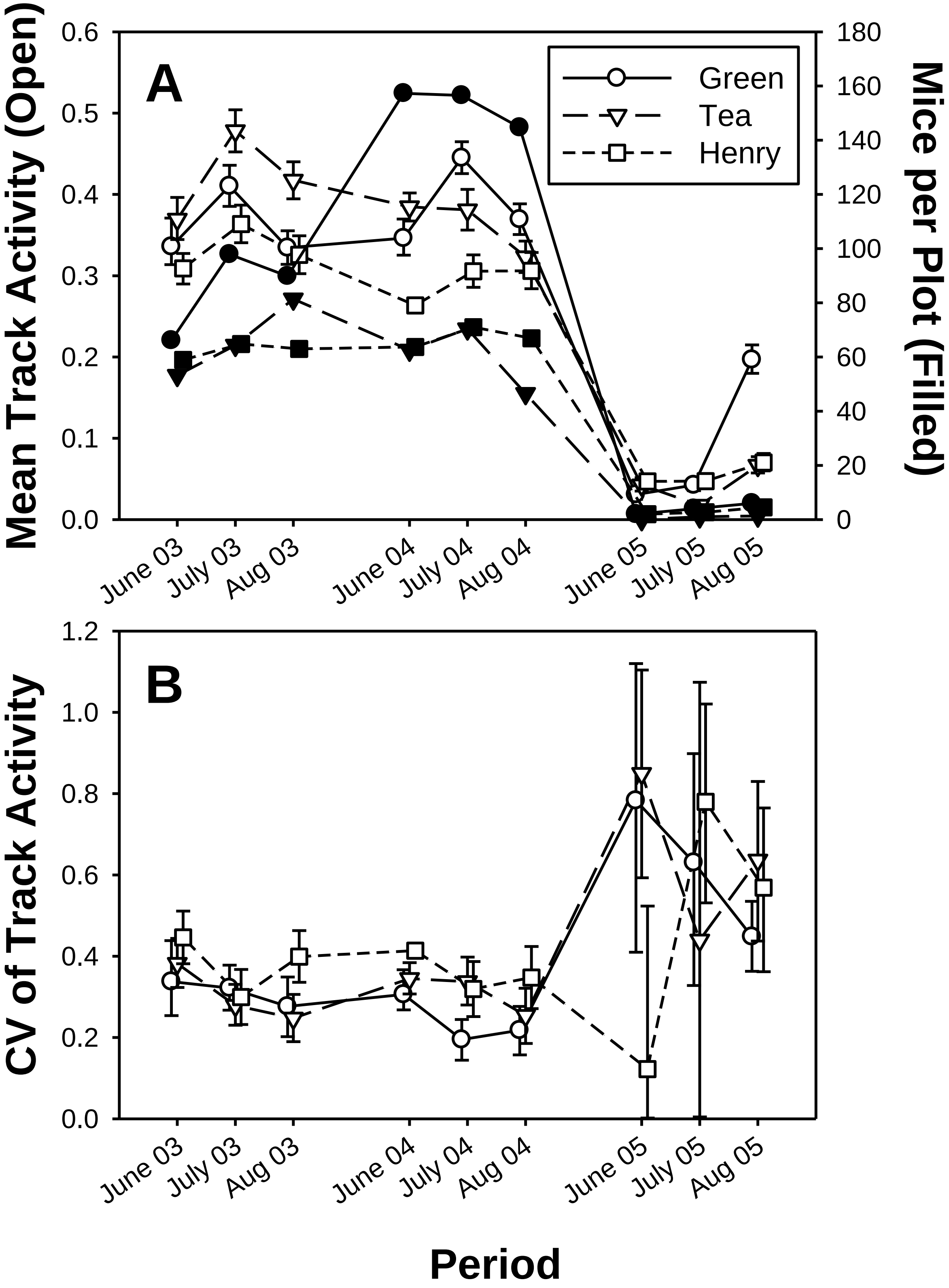
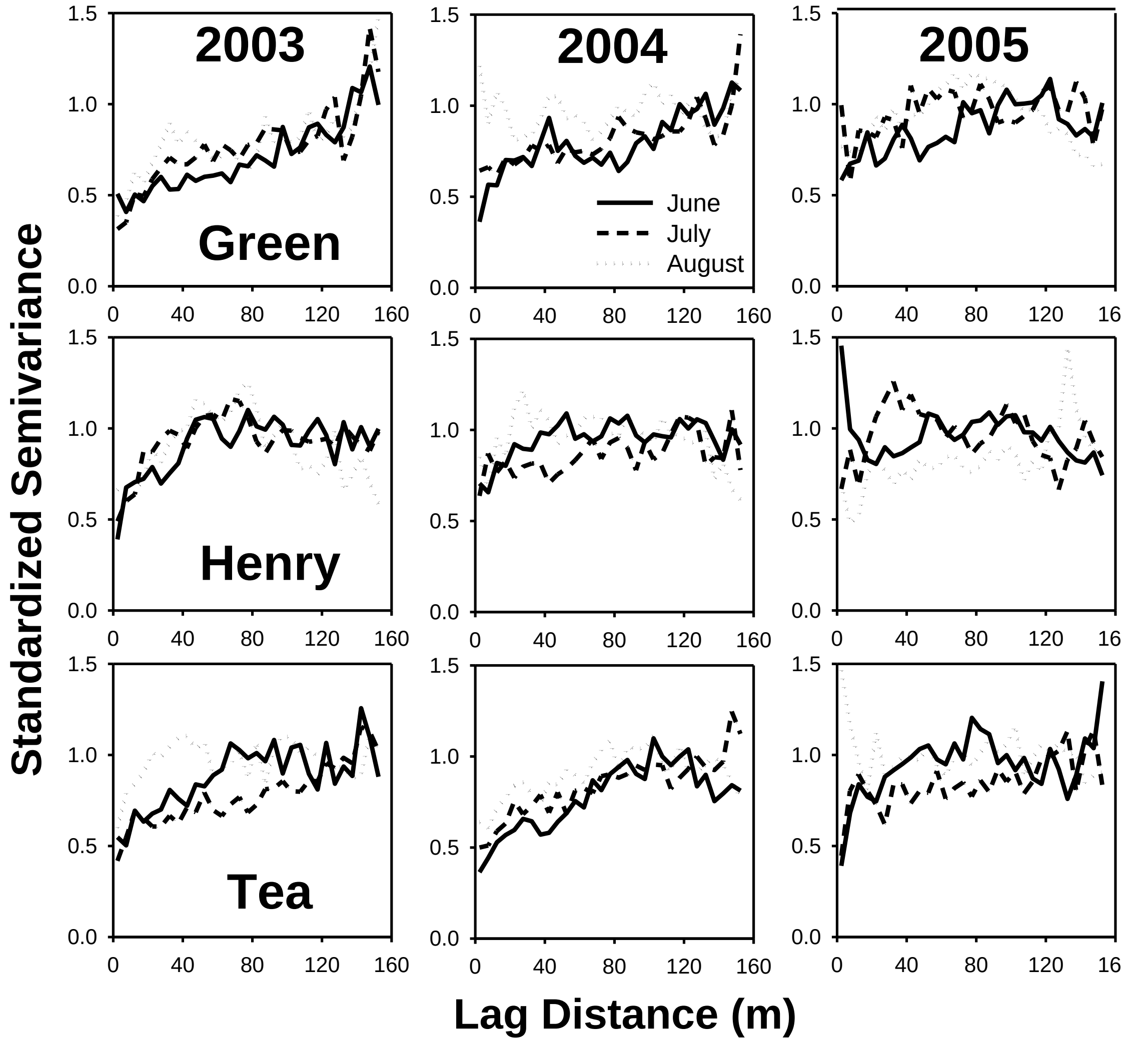
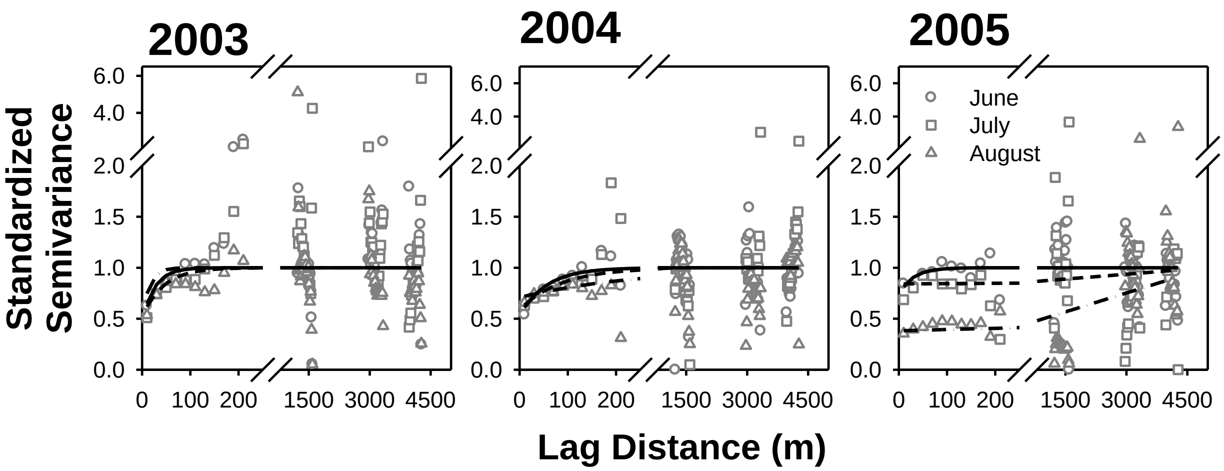

A
B
Mean Track Activity (Open)
Mice per Plot (Filled)
CV of Track Activity
Period
Green
Tea
Henry
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
20
40
60
80
100
120
140
160
180
0.0
0.2
0.4
0.6
0.8
1.0
1.2
June 03
July 03
Aug 03
June 04
July 04
Aug 04
June 05
July 05
Aug 05

FIGURE 3


2003
2004
2005
Green
Henry
Tea
June
July
August
Standardized Semivariance
Lag Distance (m)
0.0
0.5
1.0
1.5
0
40
80
120
160

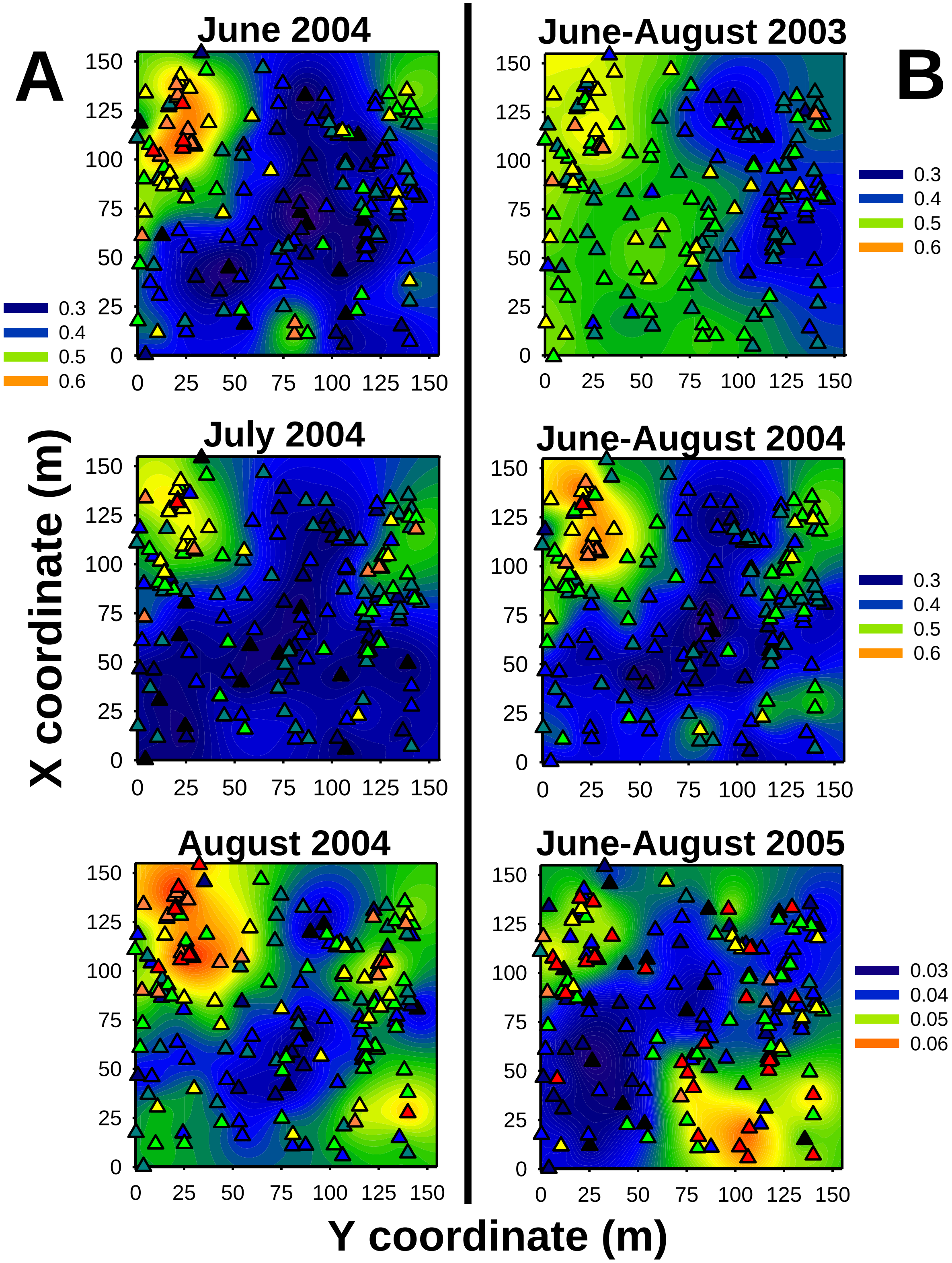
629 FIGURE 4



630

631

FIGURE 5


A
B
June 2004
July 2004
August 2004
June-August 2003
June-August 2004
June-August 2005
0.3
0.4
0.5
0.6
0.03
0.04
0.05
0.06
0
25
50
75
100
125
150
X coordinate (m)
Y coordinate (m)