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Quantifying and manipulating spatiotemporal trends in rodent space use and consumption rates on incidentally encountered prey

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QUANTIFYING AND MANIPULATING SPATIOTEMPORAL TRENDS IN RODENT SPACE USE AND CONSUMPTION RATES ON INCIDENTALLY ENCOUNTERED PREY

by

Tyler E. Schartel

B.S., Ursinus College, 2007

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
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in the Graduate School
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THESIS APPROVAL

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Approved by:

Dr. Eric M. Schauber, Chair

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AN ABSTRACT OF THE THESIS OF

TYLER E. SCHARTEL, for the Masters of Science degree in ZOOLOGY, presented on December 17, 2010, at Southern Illinois University Carbondale.

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MAJOR PROFESSOR: Dr. Eric M. Schauber

Spatiotemporal heterogeneity in predator activity can generate and influence the availability of refugia to prey. In eastern forests, white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) are abundant generalist rodents, and large-scale removal experiments have confirmed they are important predators of gypsy moth (*Lymantria dispar*) pupae and songbird nests and eggs. Models predict the extinction of gypsy moth populations when confronted with abundant mouse populations, but small-scale (10s of m) heterogeneity in rodent activity may allow for the persistence of moth populations. I quantified the magnitude, variability, temporal persistence, and spatial structure of white-footed mouse and eastern chipmunk activity, and evaluated the effects of small-scale (30 x 30 m "spots") rodent removal, on 3 pairs of oak-dominated plots for 3, 2-week periods in summers 2008 and 2009 at the Cary Institute of Ecosystem Studies, Millbrook, NY, USA. Small-mammal track activity (1/check) was best fit by a beta-binomial distribution, and the mean and CV ranges of mouse and chipmunk track activity were similar between years. Disattenuated correlations of mouse and chipmunk activity were similar between sampling periods, as well as between years. I found little evidence of spatial structure in rodent activity at the scales sampled (15-250 m). Mean local track activity counterintuitively increased in removal spots compared to control spots for mice in 2008 and chipmunks in 2009. Local, between-year track activity was more strongly correlated and of greater magnitude in persistent removal spots than in non-persistent removal spots for both mice and chipmunks

Environmental factors like abundant alternative food sources can influence predator foraging behavior by concentrating predator space use and altering predation rates on incidental prey items. However, the spatial scale of this aggregative effect, and impact on consumption rates on incidental prey items, are not well understood. In spring 2010, I conducted live-trapping, measured local rodent track activity, and quantified consumption rates on two incidental prey items (almonds [*Prunus dulcis*] and maple [*Acer saccharum*] seeds) on 6 plots provided with 3 supplemental food treatments (control, corn, and sunflower seeds) at Touch of Nature Environmental Center, Carbondale, IL, USA. A half-normal, cosine detectability function best fit our live-trapping data in both pre- and post-experiment trapping sessions, but considerable support remained for other models. Overall mean track activity was greater in control treatments than in sunflower and corn treatments. I found a significant interaction effect of treatment and distance, and significantly increased activity in control treatments at distances of 0, 10, and 40 m. Overall mean almond and maple seed consumption was greater in control treatments than in sunflower and corn treatments, but was greater in corn than sunflower treatments and increased from period 1 to period 3 at all distances. Mean almond consumption by mouse only and mouse + unknown predator groups was greater in control treatments than in sunflower and corn treatments. Mean maple seed consumption by mouse only and mouse + unknown predator groups was greater in control treatments than in sunflower and corn treatments.

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INTRODUCTION

Spatial and temporal heterogeneity are important factors in predator-prey dynamics (Reddingius and den Boer 1970, Roff 1974, Hassell et al. 1991) that can enable competitive coexistence (Cantrell and Cosner 1998, Bonsall 2003). By itself, temporal heterogeneity can promote coexistence for populations of long-lived organisms, but is generally less efficient at promoting coexistence in short-lived organisms (Chesson 1985).Spatial heterogeneity can modify predator-prey and community interactions by generating areas of decreased risk, or refugia, that can allow organisms to escape predators and competitors (Skilleter 1994, Durant 1998). When acting in concert, spatial and temporal heterogeneity can influence refugia availability, as well as species ability to enter and exploit refugia. Prey exploitative ability depends on the temporal consistency of these refugia; prey may exhibit active (habitat selection) and passive (limited dispersal) behavioral responses (Goodwin et al. 2005) as well as win-stay, lose-switch strategies (Fontaine and Martin 2006) to aggregate and increase local abundances within refugia.

Prey able to exploit spatiotemporal heterogeneity may increase in local density within refugia and become biased towards these areas of decreased risk, suggesting a potential mechanism by which persistence probability can be increased for a variety of prey, including rare or endangered, game, and invasive or pest species. The introduction of invasive species into naïve ecosystems can deplete genetic diversity in native species (Mooney and Cleland 2001, Gasc et al. 2010), threaten biodiversity (Mack et al. 2000), and induce behavioral and morphological changes in native predators, consequently disrupting community and ecosystem structure, services, and functions (Flecker and Townsend 1994, Lees and Bell 2008, Greenlees et al. 2010, Nelson et al. 2010).

Empirical evidence suggests generalist native predators may be able to limit the ecological impact of invasive species through opportunistic predation on these prey items (Schoener and Spiller 1995, Gruner 2005). However, few investigations have focused on the role of spatiotemporal heterogeneity in predator activity as a mechanism for promoting the persistence of both native and invasive prey species in complex ecosystem webs. One such web is the interaction of acorn mast production, white-footed mouse (*Peromyscus leucopus*) and eastern chipmunk (*Tamias striatus*) abundance and activity, and population dynamics of the invasive gypsy moth (*Lymantria dispar*) and native ground- and shrub-nesting songbirds.

In eastern forests, the inter-annual population dynamics of the white-footed mouse and eastern chipmunk are driven by acorn production in oaks (*Quercus* spp.), with acorn mast events increasing rodent densities in the following year by up to two orders of magnitude (Ostfeld et al. 1996). As generalists, both rodents are important predators of insects (Marcello et al. 2008), fruits, fungi, and seeds (Linzey and Linzey 1973, Lackey et al. 1985, Schnurr et al. 2004), but they are in turn prey for a suite of predators (Metzgar 1967, Savage 1967, Schmidt and Ostfeld 2003, Randa et al. 2009). White-footed mice are considered primary predators of gypsy moth pupae and larvae (Campbell and Sloan 1977, Jones et al. 1998), and both rodents will depredate songbird eggs and nests (Leimgruber et al. 1994, Schmidt and Ostfeld 2003, 2008). Rodent predation on gypsy moth larvae and pupae can be extensive, occasionally removing nearly all available pupae (Gschwanter et al. 2002, Schauber et al. 2004), and songbird nest mortality rates increase with rodent density (Schmidt and Ostfeld 2003, 2008).

Despite extensive predation, some gypsy moth pupae and songbird eggs and nests survive, implying that spatiotemporal heterogeneity in the activity and foraging patterns of both rodent predators is necessary for the persistence of these prey populations. Therefore, mechanisms that influence the heterogeneous nature of rodent activity patterns and foraging behavior may impact the survival of gypsy moth pupae and songbird nests. In particular, the presence of alternative food can influence rodent space use and predation risk to prey items that are incidentally encountered and consumed opportunistically (Courtney and Fenton 1976, Elkinton et al. 2004). Generalists, like our focal predators, appear capable of selectively choosing prey on the basis of energetic profitability (Stephens and Krebs 1986), so the most profitable prey should be the most preferred and consumed whenever encountered. Therefore, the distribution and profitability of these prey items will determine where predators forage, as well as what prey items are consumed. As a result, areas of abundant and profitable food sources may concentrate predator foraging efforts, and the impact of predation on incidental prey may depend on their profitability in relation to the supplemented food source.

The importance of refugia to the persistence of gypsy moth and songbird populations warrants further research focused on quantifying the spatiotemporal characteristics (magnitude, variability, and temporal persistence) of small-mammal activity, evaluating how manipulation of predator activity through predator removal can generate heterogeneity and increase the likelihood of prey persistence, and clarifying how abundant alternative food sources may influence the spatial scale of predator activity and predation rates on incidental prey items. In Chapter 1, I present the results of a study that used track plates to quantify spatiotemporal trends in small-mammal activity and evaluated the effect of predator removal on these characteristics. I then interpreted these characteristics in terms of heterogeneity, amenability to generating refugia, and persistence of predation risk to both gypsy moths and songbirds. In Chapter 2, I investigated how abundant alternative food sources influenced rodent space use and predation rates on incidentally encountered prey items. I report the spatial scale at which both highly and less-preferred food sources concentrated rodent space use, as well as how predator preference for each supplemental food source influenced consumption rates on two incidental prey items of differing profitability.

CHAPTER 1

QUANTIFYING AND MANIPULATING SPATIOTEMPORAL VARIATION IN RISK TO PREY OF SMALL MAMMALS

INTRODUCTION

Spatial and temporal heterogeneity in predator activity may generate areas of low predation risk, or refugia, which can promote prey persistence (Hilborn 1975, Hastings 1977, Holt 1984, Sih 1987, Cantrell and Cosner 1998, Amarasekare and Nisbet 2001, Schauber et al. 2009). Much attention has focused on the importance of spatial heterogeneity in specialist predator-prey systems (Turchin and Kareiva 1989, Lewis and Eby 2002, Sergio et al. 2003), host-parasitoid interactions (Morrison and Barbosa 1987, Reeve 1988), and shared-enemy assemblages (Walls 1995, Bonsall 2003, Oliver et al. 2009), but the importance of refugia to the prey of generalist predators is less understood. Generalist predators may choose from multiple prey sources, implying that population abundance is not dependent on one particular food source and that sparse or rare prey items may be at increased risk of localized extinction (Sinclair et al. 1998**)**. Predators may avoid areas of high risk to themselves (Taylor 1988, Abramsky et al. 2002), sparse food, and intra- or interspecific antagonistic interactions (Myton 1974, Christopher and Barrett 2006), generating refugia where low-density prey may aggregate and persist (Berryman and Hawkins 2006)**.**

Prey ability to remain within and exploit areas of decreased predation risk depends on the spatial scale and temporal persistence of these refugia. The spatial scale and structure of heterogeneity in predator activity relative to the movement distances of their prey can influence prey ability to find and enter refugia, as well as safely disperse from a refuge or escape predators by relocating to more suitable sites. Predator activity structured at spatial scales exploitable by prey can ameliorate the impact of excessive predation by allowing for localized increases in prey density that can also increase the persistence of prey populations (Goodwin et al. 2005). Previous theoretical work has considered predation risk to be either redistributed frequently (no refugia persistence; Pacala et al. 1990) or permanently fixed in space and time (Snyder and Chesson 2003), but realistic spatial distributions of predation risk, and therefore refugia, likely exhibit a range of persistence levels. The temporal stability of refugia, as well as prey ability to assess and respond to changes in predation risk, influences the potential for prey to exploit these areas. Prey that are able to actively assess predation risk can respond behaviorally (e.g., win-stay, lose-switch strategies; Greenwood and Harvey 1982) to exploit persistent refugia and inform future decisions regarding site selection. Alternatively, prey incapable of site assessment and behavioral responses (e.g., sessile) may remain within persistent refugia (Snyder and Chesson 2003), promoting prey aggregations within these sites. Ultimately, prey exploitation of and bias towards refugia increase if refugia last longer, however, it is not understood exactly how persistent heterogeneity in predation risk must be to alter ecological interactions.

Investigating mechanisms of prey persistence is facilitated by simple predator-prey systems. Two ideal predators are the white-footed mouse (*Peromyscus leucopus*) and eastern chipmunk (*Tamias striatus*), both abundant rodents found throughout much of the eastern United States. The abundance of both species is directly linked to the availability of tree seeds (especially acorns), and may increase by several orders of magnitude in the year following an acorn masting event (McCracken et al. 1996, Ostfeld et al. 1996, Jones et al. 1998, Elias et al. 2004). In the northeastern United States, white-footed mice eat multiple prey items including gypsy moth (*Lymantria dispar*) pupae (Bess et al. 1947, Campbell and Sloan 1977), and both rodents also depredate eggs and nestlings of ground- and shrub-nesting songbirds (Leimgruber et al. 1994, Schmidt and Ostfeld 2003, 2008). Chronically elevated mouse densities may result in localized extinctions of low-density moth populations (Schauber et al. 2004) and increased predation rates on Dark-eyed Juncos (*Junco hyemalis*), Veery (*Catharus fuscenscens*) and Wood Thrush (*Hylocichla mustelina*) nests (Schmidt and Ostfeld 2003, 2008).

The availability of refugia to gypsy moths and songbirds, and the ability of these prey to exploit refugia, are influenced by spatiotemporal heterogeneity in rodent activity. Simulation models indicate that persistent small-scale (10s of m) variability in rodent activity may be important to prey persistence, particularly if the prey species exhibits limited dispersal (Goodwin et al. 2005). Gypsy moth larvae usually disperse ≤ 100m (Frost 1959, Weseloh 1985, 1997), and female gypsy moths are flightless (Montgomery and Wallner 1988) and oviposit at pupation sites (Elkinton and Leibhold 1990). This limited movement prevents gypsy moths from effectively responding to predation risk by relocating to safer sites, bur larvae may instead become passively biased towards these sites by “inheriting” refugia where their mothers survived (Schauber et al. 2007). Like gypsy moth survival, songbird nest success is greater in areas of low rodent activity

(Schmidt et al. 2006). However, unlike gypsy moths, some bird species appear to actively select nest sites based on perceived risk of nest predation (Martin 1988, Martin and Roper 1988, Fontaine and Martin 2006).

Microhabitat features can influence small-mammal habitat use, preference, and activity patterns (Myton 1974, Van Dusen and Kaufman 1977, Lackey 1978, Barry and Francq 1980), so these features also may influence the distribution of predation risk to prey. However, few investigations have quantified the spatial and temporal characteristics of small-mammal activity and evaluated them in terms of amenability to generating refugia for prey (but see Connors et al. 2005 and Schauber et al. 2009). Manipulations of predator activity through small-scale removal are also rare. Although large-scale removal is an effective method of manipulating predator activity, it can generate population-level effects that obfuscate mechanisms of population regulation and persistence that operate at small spatial scales. Thus, predator removal conducted at spatial scales consistent with individual predator home ranges may elucidate how small-scale refugia are generated. In addition, altering the persistence of predator removal may demonstrate the importance of temporally consistent site suitability to prey population dynamics. My objectives were to quantify the spatiotemporal characteristics of heterogeneity in small-mammal activity within an oak-forest ecosystem where rodents are typically abundant, and evaluate their amenability for generating exploitable refugia. In addition, I evaluated the effect of persistent and non-persistent rodent removal on the spatiotemporal characteristics of rodent activity.

MATERIALS AND METHODS

This field study was conducted in summers of 2008 and 2009 on 3 pairs (Green, Henry, Tea) of oak-dominated plots at the Cary Institute of Ecosystem Studies (IES; Millbrook, New York, USA). In addition to oak (*Quercus* spp.), plot overstories were characterized by beech (*Fagus grandifolia*), black birch (*Betula lenta*), eastern white pine (*Pinus strobus*), pignut hickory (*Carya glabra*), shagbark hickory (*C. ovata*), red maple (*Acer rubrum*), and sugar maple (*A. saccharum*). Plot understories were dominated by oak and maple saplings, as well as blueberry (*Vaccinium* spp.), common spicebush (*Lindera benzoin*), and maple-leaved viburnum (*Viburnum acerifolium*). Each pair of plots consisted of an experimental and control plot, and each plots wasoverlaid with an 11 x 11 or 10 x 12 live-trapping grid with 15 m between trapping stations. Each plot contained 12 (Henry and Green Control [HC and GC]) or 16 (all other plots) 30 x 30-m sub-plots ("spots") organized into 4 transects, with 30-m spacing between spots (Fig. 1.1). Four sampling points in a 15 x 15-m square were centered within each spot, and sampling points outside of spots were arranged at 15-m intervals along spot and trapping transects (Fig. 1.1). Since 1995, all plots have been annually live-trapped during May-November to estimate rodent abundances. White-footed mice are the most frequently trapped small mammals, but eastern chipmunks, shrews (*Blarina brevicauda* and *Sorex* spp.), squirrels (*Sciurus* spp.), and southern flying squirrels (*Glaucomys volans*) have also been captured (R. S. Ostfeld, unpublished data).

The 16 spots in each of the 3 experimental plots (Green [GE], Henry [HE], Tea [TE]) were evenly divided between persistent or non-persistent treatments. Four of the 8 persistent treatment spots were unmanipulated both summers whereas the remaining 4 were subjected to removal trapping in both summers. Rodents in spots receiving non-persistent treatments were trapped or left undisturbed in alternate years, with an equal number (4) of these spots being manipulated in each summer. Treatments were assigned to spots systematically with a random start. From May until August, removal trapping was conducted on each experimental plot for 2 consecutive nights in the week immediately prior to track-plate sampling. All captured mice and chipmunks were weighed, inspected for gender and reproductive condition, and animals that were not lactating were transported > 5km away and released. All animal handling procedures were approved by SIUC and Cary Institute Animal Care and Use Committees (SIUC Protocol #07-053, Cary Institute Protocol 06-01).

I quantified local small-mammal activity using track plates, which do not appear to attract or repel small-mammal predators and provide estimates of mouse activity that are strongly correlated with predation risk to gypsy moth pupae (Connors et al. 2005). Track plates were constructed by coating 14 x 22 cm acetate sheets with a graphite-powder suspension (approx. 75% anhydrous ethanol, 20% powdered graphite, and 5% mineral oil). Plot pairs were sampled on a rotating basis for 2-week periods, every 6 weeks, in both years (Table 1.1). At each sampling point, 3 track plates were paper-clipped to aluminum flashing to provide rigid backing and were monitored every 2-3 days (6 checks total) for each 2-week sampling period. At each check, track plates were closely inspected for the presence of tracks (present or absent) and tracks were identified to species. I did not count tracks on each plate, but plates with > 25% of surface tracked were replaced. If tracks covered < 25% of the plate, the tracks were marked to avoid double counting and the plate was reused. Plates that were severely washed out, flipped over, or otherwise unreadable were recorded as such and excluded from all analyses. All track plates were handled while wearing latex gloves throughout the duration of their preparation and use.

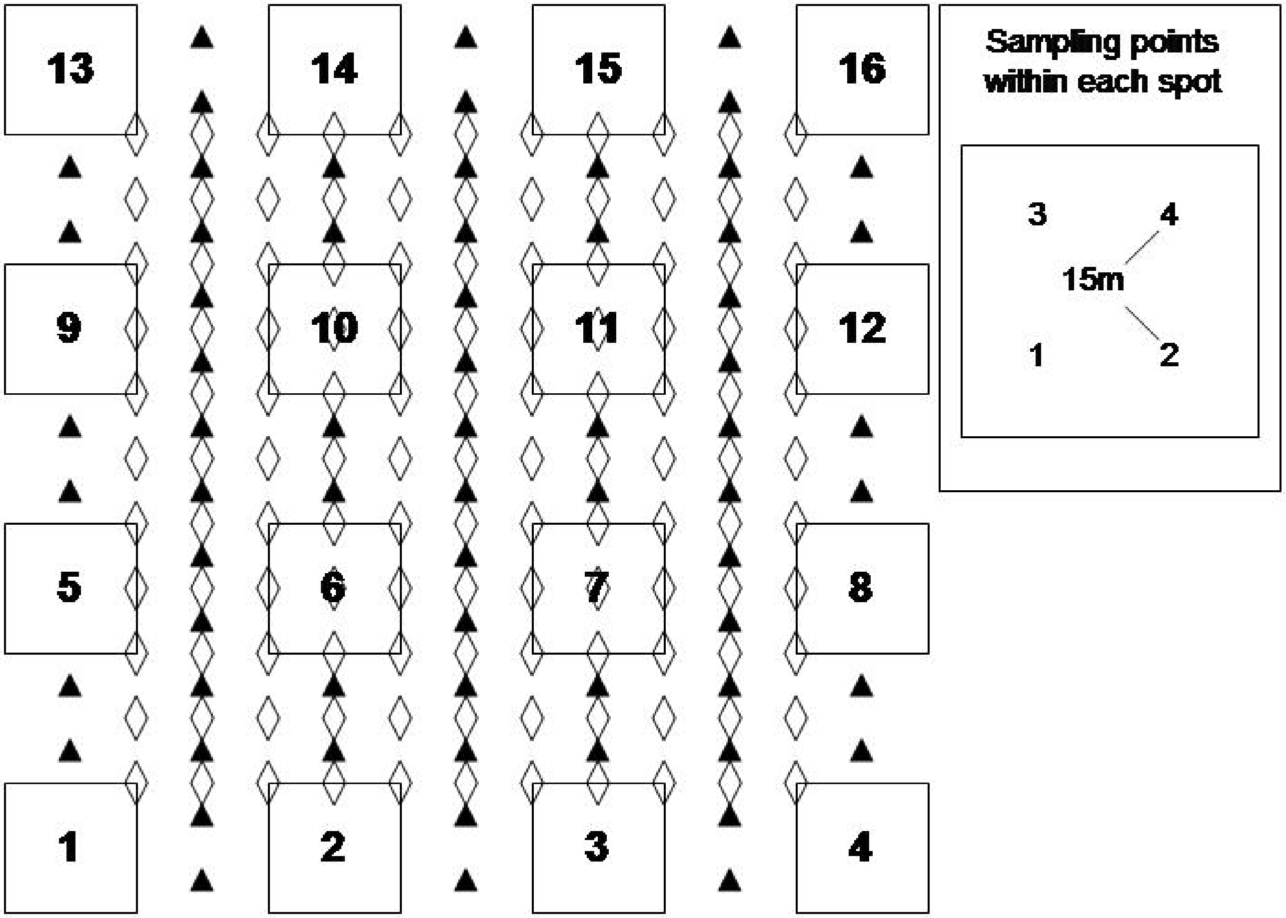

Figure 1.1. Diagram of a study plot showing arrangement of 30 x 30 m spots into four transects, distribution of sampling points (▲) spaced at 15 m intervals within spot transects, and location of trapping stations (◊) and transects containing sampling points spaced at 15 m intervals in 30 m distance between spot transects. The enlargement illustrates the arrangement of 4 sampling points in a 15 x 15 m square centered within each spot.

Table 1.1. Dates of track-plate sampling periods on 3 pairs of oak-forest plots in the summers of 2008 and 2009 at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

		Sampling period		
Year	Plot pair	1	2	3
2008	Green	18 - 30 June	6 - 18 Aug.	17 - 29 Sept.
	Henry	4 - 16 June	16 - 28 July	3 - 15 Sept.
	Tea	21 May - 2 June	2 - 14 July	20 Aug. - 1 Sept.
2009	Green	17 - 29 May	1 - 13 July	12 - 24 Aug.
	Henry	3 - 15 June	15 - 27 July	26 Aug. - 4 Sept.
	Tea	17 - 29 June	29 July - 10 Aug.	7 - 21 Sept.

DATA ANALYSES

I defined small-mammal activity for a given point and sampling period as the frequency at which readable track plates recorded mouse or chipmunk tracks (i.e., tracked plates per readable plate check). Track activity was analyzed separately for each species, plot, and sampling period to quantify the mean, spatial variability, spatial scale, and temporal persistence of small-mammal activity.

I quantified the mean and spatial variability of mouse and chipmunk activity by fitting the beta-binomial distribution to the observed track activity data in each plot and sampling period using maximum likelihood fitting. The beta-binomial distribution disentangles sampling variance from underlying differences among spatial points in the probability of small-mammal visitation (i.e., true track activity) based on the assumptions that true track activity varies among points according to a beta distribution, and that the observed track activity at each sampling point is a binomial random variable conditioned on the true track activity at that sampling point. The 2 parameters of this distribution determine the mean and coefficient of variation (CV) of true track activity among points. I then used likelihood ratio tests to compare the fit of the beta-binomial distribution to that of global binomial and point-specific binomial models. The global binomial represents the null hypothesis that true track activity is equal for all points in a sampling period and plot, so comparing it to the beta-binomial tests whether track activity is spatially heterogeneous. The point-specific binomial estimates a separate track activity for each point in a given sampling period, and so represents a saturated model for goodness-of-fit testing. I used the PopTools utility in Microsoft Excel® for maximum likelihood fitting.

I applied geostatistical analysis to quantify the spatial structure of rodent activity on control plots. I constructed variograms, which depict how variability in measurements between sampling points is related to the distance separating them (i.e., lag distance), using PROC VARIOGRAM in SAS (SAS Institute, Cary, North Carolina, USA). Spatial structure is indicated by lower semivariance of measurements between nearby than between distant sampling points. Measurement errors or very fine-grained spatial variation may result in positive semivariance values (the “nugget”) at zero lag distance, whereas semivariances can approach an asymptote known as the “sill” at large lag distances. The strength of spatial structure is evaluated by the amount by which the sill exceeds the nugget; a variogram with strong spatial autocorrelation will demonstrate a positive slope as it approaches the sill whereas a flat or constant variogram indicates little spatial structure across the spatial scales sampled (Rossi et al. 1992). Because I manipulated small-mammal activity on experimental plots through rodent removal, I restricted variogram analysis of the spatial structure of small-mammal activity to control plots (GC, HC, and TC). For each control plot, I used a high-resolution global positioning system receiver (GeoExplorer 2005 with TerraSync software, Trimble Navigation Limited, Sunnyvale, California, USA) to determine the coordinates of each track-plate sampling point, limiting data to points with horizontal dilution of precision under 3.5. My preferred precision level was 3.0, and I re-collected problem points up to 3 times to improve precision. I set lag-distance intervals at 15 m for variogram analysis of rodent activity as this was the smallest nominal distance between any two sampling points. To account for possible outlying values, I fit a robust variogram (Genton 1998) to the observed rodent track activity within each sampling period.

I calculated Pearson product-moment correlation between sampling periods (June, July, or August) for the observed track activity of each species and plot to evaluate the temporal persistence of spots of high (“hot”) and low (“cold”) mouse and chipmunk activity. Long-term persistence of rodent activity was evaluated by averaging track activity for each species across sampling periods in each year, and then calculating Pearson product-moment correlation between years. Sampling variability reduces Pearson correlation values, therefore I report disattenuated correlation values (Muchinsky 1996, Hancock 1997) that incorporate the reliability of my track activity data to account for this sampling error. For each sampling period (x), I calculated reliability (r_{xx}) by treating the observed track activity at each sampling point as the true probability of recording a track, generating two binomial random variables based on this true probability and the number of readable plates checked per 2-week period at that point, then calculating the average correlation between these simulated data over all sampling points in a plot for 1,000 simulations. I then calculated the disattenuated correlation value (R_{xy}) by $R_{xy} = r_{xy}/\sqrt{r_{xx} r_{yy}}$ where r_{xy} is the correlation of our observed track activity between sampling periods x and y, and r_{xx} and r_{yy} represent reliability for observed track activity in the two sampling periods.

To evaluate the effect of removal trapping on small-mammal activity on each experimental plot, I used the observed point-activity data to generate averaged point-level estimates of track activity in each sampling period. Point-level track activity estimates were then averaged over sampling periods to produce a species-specific, yearly mean estimate of track activity at each point. Yearly mean estimates of rodent activity were averaged in removal and non-removal spots in each plot, and compared using a paired t-test to test if rodent removal influenced track activity. Pearson product-moment correlation values were calculated to quantify the consistency of the spatial pattern of small-mammal activity between years for each treatment combination, and correlation values were compared between persistent and non-persistent treatments using a paired t-test to test whether the persistence of removal treatments influenced the consistency of rodent activity.

RESULTS

Small-mammal track activity data in each plot, sampling period, and year were better fit by a beta-binomial distribution than a global binomial model (all $\chi^2_1 > 22.6$, $P < 0.001$). Both mean and CV ranges of track activity were similar between years for mice (Table 1.2) and chipmunks (Table 1.3). I found little evidence of spatial structure in rodent activity at the scales sampled (15-250 m) as few variograms exhibited declining semivariance at small lag distances (Figures 1.2 and 1.3).

Disattenuated correlation values of white-footed mouse activity between sampling periods ranged from $-0.01 \leq R \leq 0.50$ in 2008 and $-0.12 \leq R \leq 0.34$ in 2009 (Table 1.4) whereas disattenuated correlations of chipmunk activity ranged from $-0.25 \leq R \leq 0.52$ in 2008 and $-0.17 \leq R \leq 0.42$ in 2009 (Table 1.4). The ranges of between-year disattenuated correlations were similar for mice and chipmunks and were generally stronger than correlations between periods (Table 1.4; Mice: $0.20 \leq R \leq 0.66$, Chipmunks: $0.07 \leq R \leq 0.42$). Small-mammal removal counterintuitively increased mean local track activity in removal spots relative to control spots for mice in 2008 (Figure 1.4; 2008: $t = 2.74$, df = 2, $P = 0.051$, 2009: $t = 2.17$, df = 2, $P = 0.081$) and chipmunks in 2009 (Figure 1.5; 2008:

t = 1.74, df = 2, P = 0.11, 2009: *t* = 3.28, df = 2, P = 0.041). Track activity was more strongly correlated between years and was higher in persistent than non-persistent treatment spots for both mice and chipmunks (Table 1.5; Mice: *t* = 4.53, df = 2, P = 0.022, Chipmunks: *t* = 5.17, df = 2, P = 0.018).

Table 1.2. Estimated means and coefficients of variation (CV) of white-footed mouse track activity (tracked plates per plate-check) on 6 oak-forest plots sampled in the summers of 2008 and 2009 at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

			Mean			Variability (CV)	
Year	Plot	June	July	August	June	July	August
2008	Green Control	0.16	0.25	0.15	0.47	0.58	0.72
	Green Experimental	0.10	0.15	0.14	0.65	0.69	1.08
	Henry Control	0.06	0.14	0.27	0.59	0.57	0.54
	Henry Experimental	0.06	0.16	0.26	0.95	0.69	0.52
	Tea Control	0.03	0.07	0.16	1.09	0.83	0.78
	Tea Experimental	0.03	0.10	0.11	0.97	0.66	0.60
2009	Green Control	0.18	0.20	0.21	0.69	0.34	0.26
	Green Experimental	0.19	0.23	0.18	0.55	0.36	0.56
	Henry Control	0.16	0.21	0.24	0.54	0.50	0.46
	Henry Experimental	0.13	0.17	0.19	0.56	0.49	0.52
	Tea Control	0.16	0.20	0.32	0.55	0.47	0.42
	Tea Experimental	0.21	0.22	0.30	0.57	0.46	0.38

Table 1.3. Estimated means and coefficients of variation (CV) of eastern chipmunk track activity (tracked plates per plate-check) on 6 oak-forest plots sampled in the summers of 2008 and 2009 at the Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

		Mean			Variability (CV)		
Year	Plot	June	July	August	June	July	August
2008	Green Control	0.23	0.08	0.05	0.28	0.20	0.79
	Green Experimental	0.16	0.05	0.05	0.51	0.50	1.46
	Henry Control	0.10	0.09	0.08	0.46	0.40	0.57
	Henry Experimental	0.09	0.14	0.12	0.50	0.35	0.62
	Tea Control	0.08	0.10	0.07	0.66	0.58	0.78
	Tea Experimental	0.09	0.13	0.05	0.79	0.48	1.09
2009	Green Control	0.09	0.10	0.08	1.07	0.68	0.51
	Green Experimental	0.06	0.06	0.07	0.93	0.64	0.61
	Henry Control	0.08	0.09	0.04	0.64	1.04	0.94
	Henry Experimental	0.11	0.07	0.04	0.82	0.85	1.34
	Tea Control	0.12	0.08	0.12	0.73	0.69	0.76
	Tea Experimental	0.15	0.08	0.15	0.49	0.70	0.70

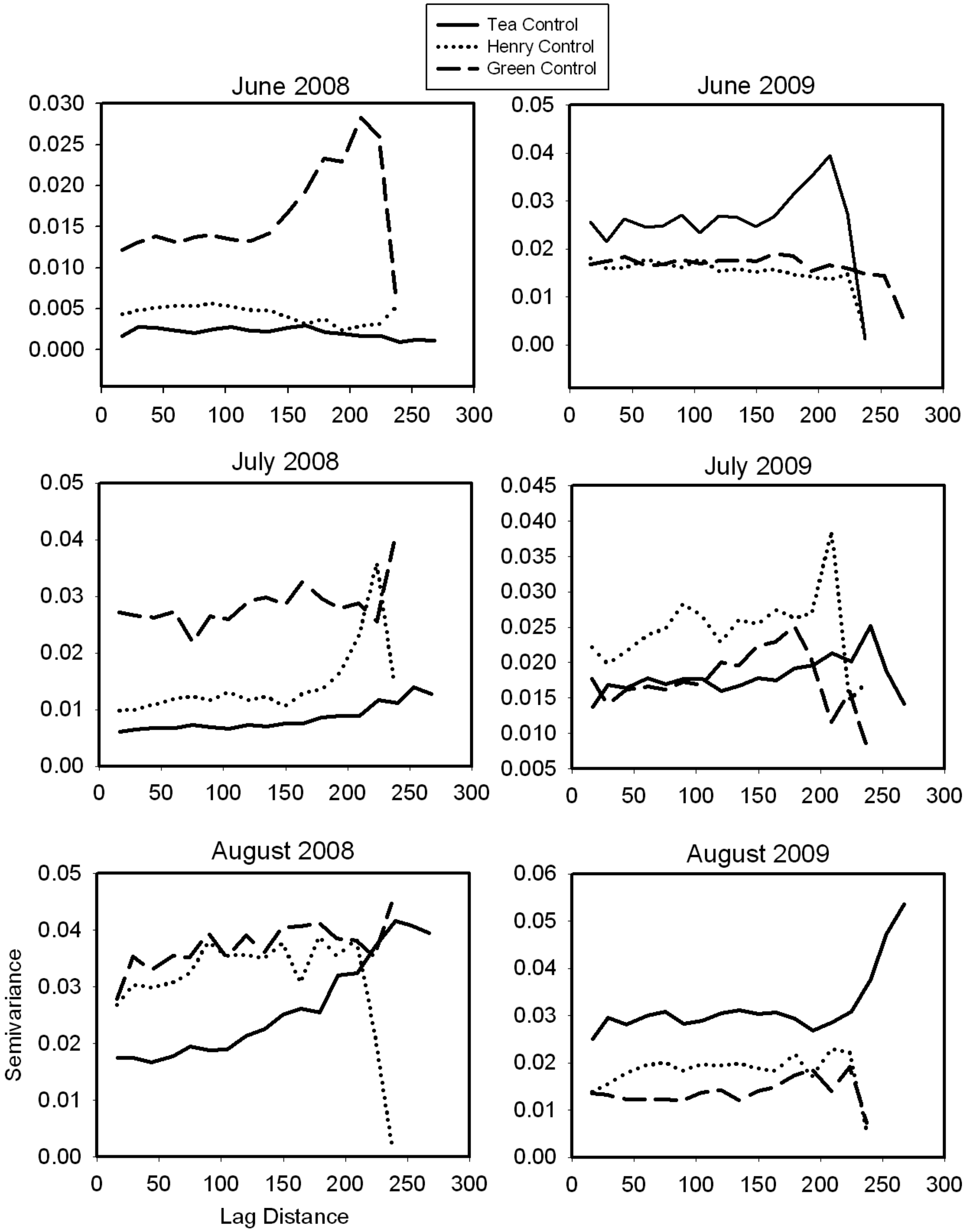

Figure 1.2. Variograms of white-footed mouse activity for 3 sampling periods in 2008 and 2009 on 3 control plots at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

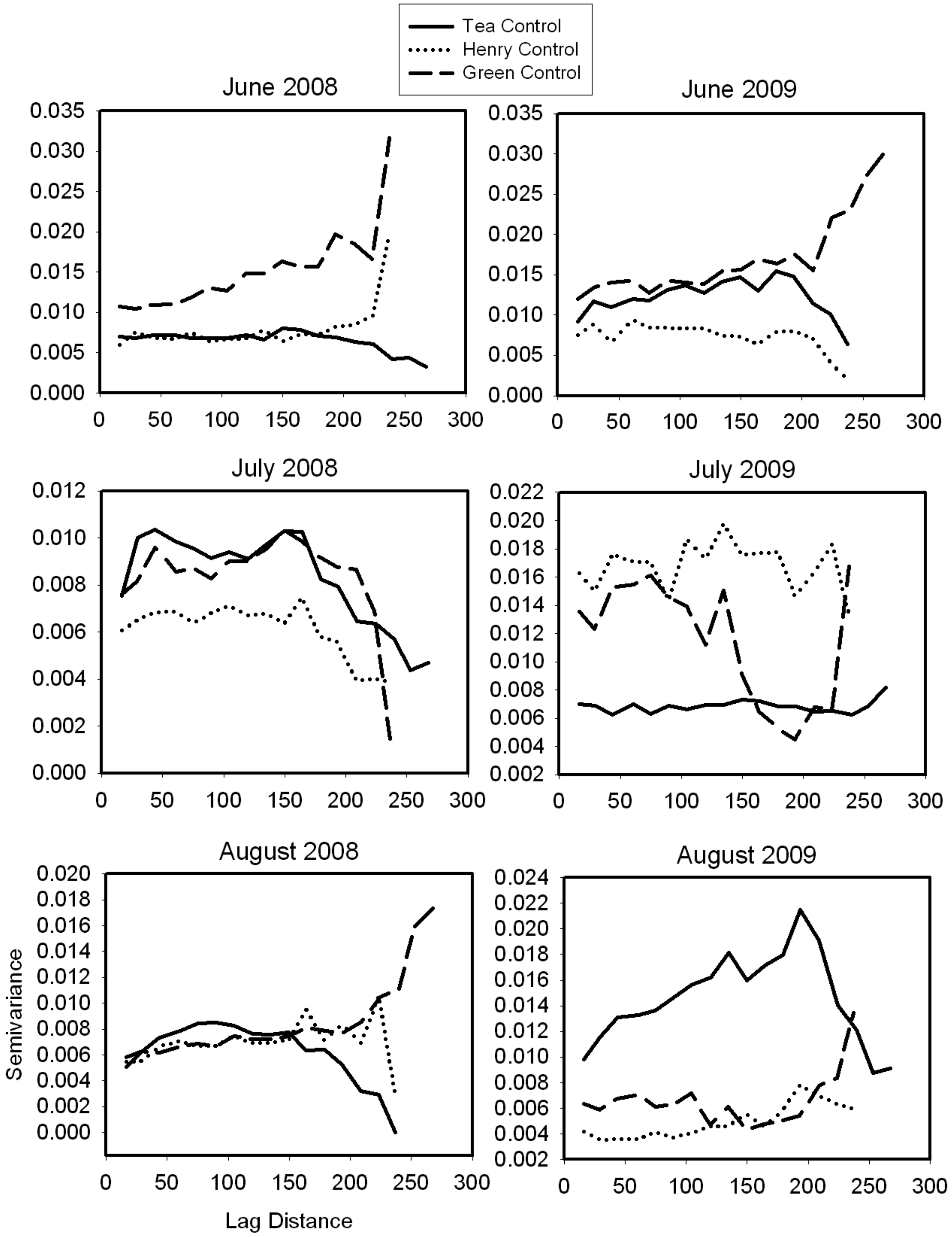

Figure 1.3. Variograms of eastern chipmunk activity for 3 sampling periods in 2008 and 2009 on 3 control plots at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

Table 1.4. Disattenuated correlations evaluating the temporal consistency of rodent activity among sampling periods within a year and between years (2008 and 2009) on 6 oak-forest plots at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

Species	Year	Plot	June vs. July	June vs. August	July vs. August	Between summers
P. leucopus	2008	Green Control	0.27	0.04	0.38	0.62
		Green Experimental	0.18	0.11	0.34	0.45
		Henry Control	0.31	-0.01	0.07	0.66
		Henry Experimental	0.5	0.28	0.12	0.47
		Tea Control	0.02	0.03	0.26	0.2
		Tea Experimental	0.34	0.19	0.15	0.46
	2009	Green Control	0.21	0.19	-0.01	
		Green Experimental	0.33	0.02	0.27	
		Henry Control	0.27	0.08	-0.12	
		Henry Experimental	0.18	0.16	0.3	
		Tea Control	0.1	0.12	0.2	
		Tea Experimental	0.27	0.34	0.25	
T. striatus	2008	Green Control	0.36	0.21	0.52	0.42
		Green Experimental	0.02	-0.21	0.01	0.19
		Henry Control	-0.25	0.38	-0.18	0.15
		Henry Experimental	0.25	-0.1	0.2	0.13
		Tea Control	0.05	0.08	-0.01	0.31
		Tea Experimental	0.29	0.19	0.12	0.07
	2009	Green Control	0.42	0.36	0.25	
		Green Experimental	0.04	0.28	0.33	
		Henry Control	0.34	0.2	-0.17	
		Henry Experimental	0.26	0.2	0.29	
		Tea Control	0.34	0.09	0.28	
		Tea Experimental	0.27	-0.01	0.35	

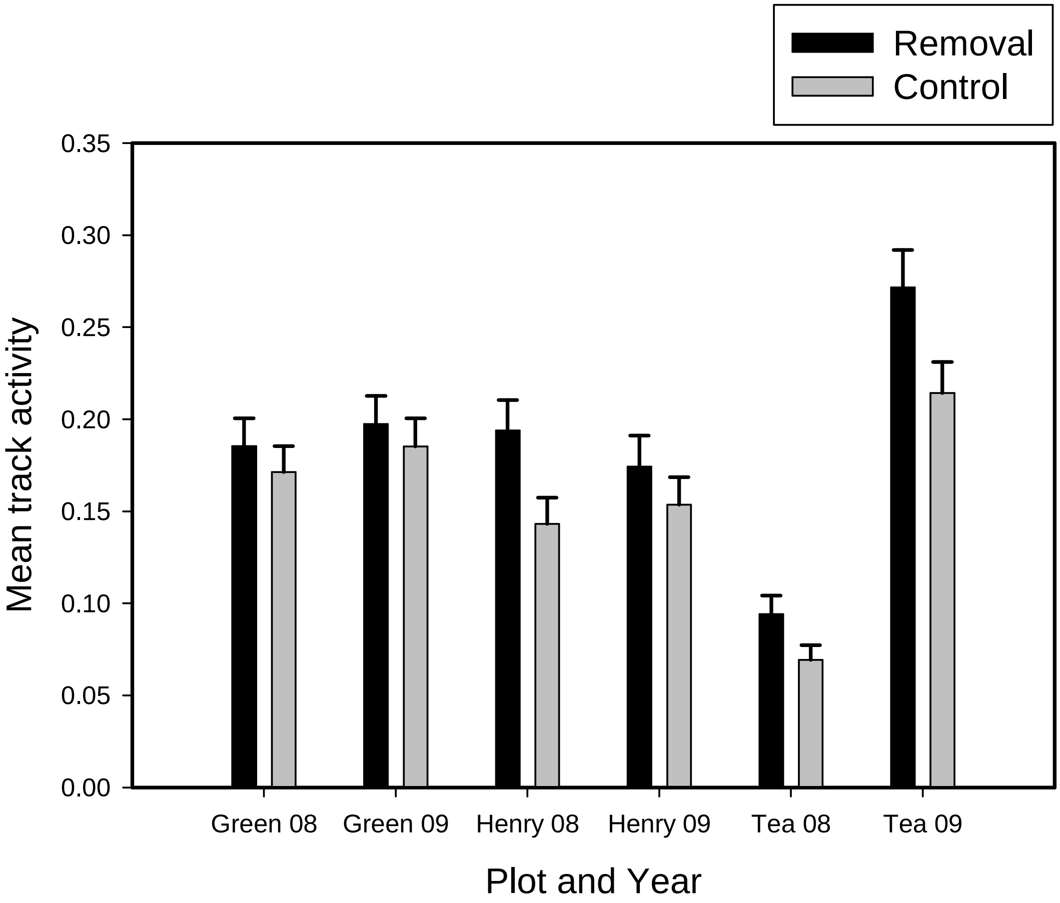

Figure 1.4. Average white-footed mouse track activity (tracked plates/plate-check) + SE in mammal-removal and control spots on 3 experimental plots in the summers of 2008 and 2009 at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

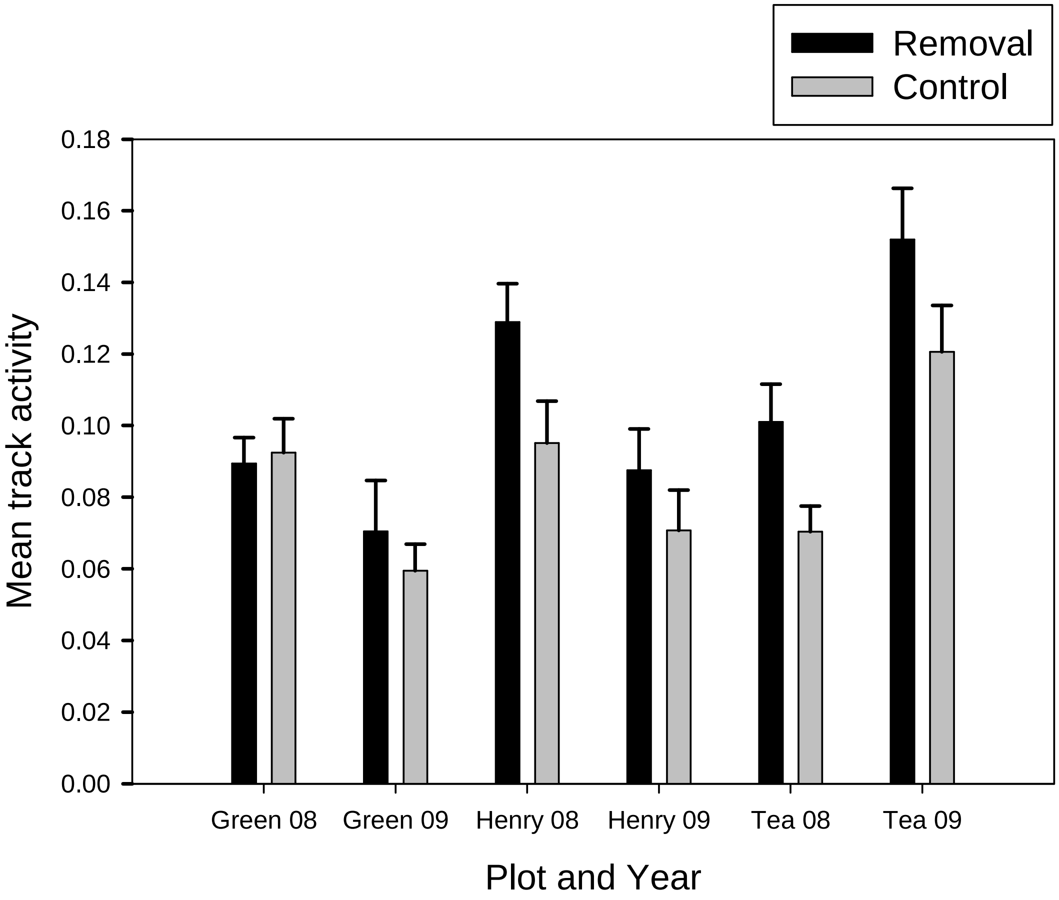

Figure 1.5. Average eastern chipmunk track activity (tracked plate/plate-check) + SE in mammal-removal and control spots on 3 experimental plots in the summers of 2008 and 2009 at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

Table 1.5. Temporal autocorrelations between years (2008 and 2009) of white-footed mouse and eastern chipmunk track activity in persistent (removal or unmanipulated both years) and non-persistent (removal in alternate years) treatment spots on 3 experimental oak-forest plots at Cary Institute of Ecosystem Studies, Millbrook, NY, USA.

	White-footed mice		Eastern chipmunk	
Plot	Persistent	Non-persistent	Persistent	Non-persistent
Green Experimental	0.19	-0.04	0.39	-0.082
Henry Experimental	0.49	0.21	0.40	-0.17
Tea Experimental	0.52	0.054	0.12	-0.16

DISCUSSION

Predator impact on prey can be affected by the strength of refugia, their spatial scale, and their persistence over time. I found considerable heterogeneity in mouse and chipmunk activity in both years, but variogram analysis of small-mammal activity indicated little spatial structure in their activity at the scales sampled (15-250 m). Spatial variations in activity persisted between sampling periods and years for both rodent species. Small-mammal removal counterintuitively increased local track activity of both rodent species, and the temporal persistence of predator activity was greater in persistent than non-persistent treatment spots.

The emergent spatiotemporal characteristics (magnitude of spatial heterogeneity, spatial scale, and temporal persistence) of predator activity in this study system indicate that predation risk varied considerably in space, and this spatial heterogeneity persisted for months to years. Both characteristics are amendable to the generation of refugia exploitable by both gypsy moths and songbirds. My estimates of mean mouse track activity and the CV among sampling points were similar to estimates found by Connors (2005) and Schauber et al. (2009) in years of low mouse abundance. I also found that the temporal persistence of predation risk for both rodents was consistent between sampling periods and years. Between-period persistence of “hot” and “cold” spots of rodent activity may provide information concerning suitable areas for re-nesting attempts for songbirds, as well as temporary refugia where gypsy moths may complete pupation in relative safety. Between-year persistence of “cold spots” in rodent activity can allow gypsy moths to “inherit” refugia (Schauber et al. 2007) and, coupled with limited dispersal and high fecundity (Jones et al. 1990, Weseloh 1997), may result in increased local moth abundances (Goodwin et al. 2005). Songbirds also can benefit from long-term persistence of predation risk as areas of consistent low risk may be manifested in "public information" that can inform decisions regarding future nest site selection (Doligez et al. 2003), particularly for veeries (Schmidt et al. 2006).

The lack of spatial structure in rodent activity makes it difficult to draw substantive conclusions about the size or availability of refugia to gypsy moths and songbirds. Spatial autocorrelation in mouse activity has been found to vary in strength and scale (40 – 155 m) among plots and years, being weakest and least consistent in years of low mouse densities (Connors 2005, Schauber et al. 2009). In addition, rodent predation risk to tree seeds and red maple seedlings has been found to be autocorrelated at even smaller spatial scales (~8m; Manson et al. 2000), so I suggest that my observed rodent activity (and hence, predation risk) was structured at finer spatial scales than I measured. Although gypsy moths typically disperse short distances (≤ 100m), if rodent activity is structured at fine spatial scales (< 15m), dispersing gypsy moths are likely to leave their natal refuge. Furthermore, even if dispersing gypsy moth caterpillars do arrive in refugia, these areas are likely small in size, implying that a limited number of moths are able to aggregate within and exploit these areas. The ability of songbirds to find and exploit refugia is especially important during re-nesting attempts resulting from nest predation. Songbirds with successful nesting attempts may increase future nest success by remaining at the same site, but in instances of initial nest failure, dispersing songbirds tend to have higher nest success than non-dispersers (Powell and Frasch 2000). Nest predation events increase the distance songbirds will move between re-nesting attempts, and the type of predator responsible for the predation event also can influence this distance (Powell and Frasch 2000, Chalfoun and Martin 2010). Both mice and chipmunks have relatively small activity ranges (Mice; ~0.1 ha, Lackey et al. 1985, Chipmunks; 0.03 to 0.40 ha, Snyder 1982), suggesting that forest songbirds may need to disperse short distances to escape areas of high rodent activity. However, as with gypsy moths, dispersing songbirds may encounter difficulties locating and exploiting refugia if rodent activity is structured at fine spatial scales.

Predator distributions, and consequently, enemy-free space, can be manipulated through predator removal. Mouse removal at larger spatial scales (~2.25-ha) has led to increased gypsy moth densities and decreased predation rates on songbird nests (Jones et al. 1998, Schmidt et al. 2001), but the effect of chipmunk removal on songbird nest predation rates was negligible (Schmidt et al. 2001). In contrast, I found that small-scale (30 x 30 m) rodent removal resulted in the counterintuitive effect of increasing local track activity, although spots receiving persistent removal or non-removal treatments had higher correlations in between-year track activity than spots with treatments alternating between years. These findings suggest that persistent small-scale manipulation of rodent activity generated persistent "cold" spots of activity where gypsy moths and songbirds could take refuge, but these refugia were not necessarily the spots where rodents were removed. The counterintuitive increase in observed rodent activity in rodent-removal spots could arise from the release of remaining rodents from conspecific competition (Dooley and Dueser 1996), as well as transient or juvenile individuals moving into newly unoccupied territories and maintaining heightened activity levels during exploratory behaviors (Fairbairn 1978).

This investigation demonstrates that spatiotemporal heterogeneity in predator activity, as well as small-scale predator removal, may be amenable to generating refugia which can promote predator-prey coexistence. Empirically-based models predict the extinction of gypsy moth populations when mouse densities reach ca. 20/ha (Schauber 2000). However, real gypsy moth populations tend to persist even when confronted with high mouse densities (Goodwin et al. 2005), providing a model system for studying how rare or incidental prey can persist when confronted with abundant, generalist predators. These concepts regarding spatiotemporal heterogeneity in predator activity and small-scale predator removal may be applied to other generalist predator/incidental prey systems, including prey species that people actually want to persist. Large-scale removal is an obvious consideration to reduce predation rates on prey of conservation concern. However, interventions (such as small-scale removals) that generate persistent spatial heterogeneity in predator activity, even without changing mean predator densities at larger scales, can generate refugia that are exploitable by prey and promote predator-prey coexistence. I suggest that future research investigate if the counterintuitive increase of rodent track activity in removal spots corresponds with increased predation risk to gypsy moths and songbirds. In addition, refugia size corresponds with the spatial scale and structure of predator activity, but fine-grained predator activity may limit prey ability to access and exploit refugia. As prey differ in their ability to perceive and respond to predation risk, future investigations aimed at quantifying the minimum refuge size necessary for successful prey exploitation may clarify differential use of refugia based on prey response to predation risk and inform future decisions concerning prey species management.

CHAPTER 2:

THE INFLUENCE OF ABUNDANT, ALTERNATIVE FOOD ON SMALL-MAMMAL SPACE USE AND CONSUMPTION OF INCIDENTAL PREY ITEMS

INTRODUCTION

Predator foraging efforts and the resulting distribution of predation risk within a landscape are influenced by what prey are available and where they are located. Optimal foraging theory provides a framework for predicting predator choice of prey on the basis of energetic profitability (Charnov 1976), as well as the spatial distribution of predator foraging efforts in relation to local prey availability (MacArthur and Pianka 1966, Stephens and Krebs 1986). For generalist predators, which are numerically decoupled from the abundance of some prey, increased predator abundance may correspond with increased risk and likelihood of localized extinction for sparse or rare prey items (Sinclair et al. 1998). Prey items that are incidentally encountered and consumed opportunistically during predator foraging for primary prey may be especially vulnerable when generalist foraging behavior is altered (Schmidt et al. 2004). Abundant food sources can supplement predator diets (Griffiths 1975, Vivas and Saether 1987, Speiser and Rowell-Rahier 1991, Musser and Shelton 2003) and influence generalist foraging strategies and space use (Courtney and Fenton 1976, Crabtree and Wolfe 1988), suggesting that the distribution of primary food resources may play a crucial role in determining local risk to incidental prey.

Several mechanisms can influence generalist space use and consumption of primary prey, in turn generating indirect effects on incidental prey. Abundant primary prey sources can act as "buffers" that reduce predation risk for incidental and less-preferred prey items (Ackerman 2002, Sacks and Neale 2002) but, as primary prey abundance decreases, prey switching may be induced and result in increased predation rates on other, less-preferred prey items (Murdoch 1969, Thompson and Colgan 1990, Schmidt and Ostfeld 2003, Sacks and Neale 2007). Alternatively, abundant primary prey can increase predator densities through aggregative and numerical responses (Solomon 1949**,** Schmitt 1987), producing apparent competition that can increase local predation rates on incidental prey that are preferred or highly vulnerable (Holt 1977, Holt and Lawton 1994, Abrams and Matsuda 1996). For example, corn-filled deer feeders concentrate predators such as raccoons (*Procyon lotor*), increasing predation risk for nearby nests of wild turkey (*Meleagris gallopova*) and turtles (Cooper and Ginnett 2000, Hamilton et al. 2002). However, the aggregative effects of abundant supplemental food also can draw predators away from opportunistically consumed prey items like waterfowl nests (Greenwood et al. 1998).

These disparities in predator responses may be explained by the spatial scales at which predators are active, but few investigations have attempted to quantify the spatial scale at which supplemental foods influence predator activity and foraging behavior. In addition, the extent to which predators respond to supplemental food may depend on the preference ranking and abundance of all available prey. Optimal generalist predators should prioritize prey consumption to consume the most profitable prey items available. Therefore, locally abundant and highly profitable (preferred) prey will determine whether less-preferred prey are consumed or disregarded (Elkinton et al. 2004). This reasoning raises a series of questions: (1) at what spatial scale do localized, abundant food sources influence predator space use and foraging behavior, (2) how do abundant food sources influence predator preference for other prey items, and (3) how does the profitability of abundant food influence consumption rates on incidental prey of differing profitability? To answer these questions, I manipulated predator space use and foraging behavior by providing abundant, localized food sources of differing profitability and quantified both predator activity and consumption rates on two incidental prey items of differing nutritional content**.**

The generalist diet and small home range size (~0.1 ha; Lackey et al. 1985, Wolff 1985) of the white-footed mouse make it an ideal predator for this investigation. Distributed widely across North America, the white-footed mouse consumes fruits and fungi (Lackey et al. 1985, Schnurr et al. 2004), but is also an important predator of tree seeds (Ostfeld et al. 1997, Manson et al. 2000), gypsy moth pupae (Bess et al. 1947, Campbell and Sloan 1977, Jones et al. 1998), and songbird eggs and fledglings (Leimgruber et al. 1994, Schmidt et al. 2001, Schmidt and Ostfeld 2003, 2008). Abundant food sources may influence predation risk to gypsy moth pupae, tree seeds, and bird eggs by concentrating rodent space use and altering the relative preference ranking of each prey item. In addition, aggregation of predators around an abundant food source may decrease predation risk and generate refugia for prey items away from this food source. Therefore, this investigation aims to clarify how localized and abundant, highly and less-preferred food resources generate and influence heterogeneity in predation risk, which ultimately impacts the existence of refugia and the ability of prey populations to exploit these areas of decreased risk.

Mouse space use and activity may be concentrated by locally abundant food sources, but highly preferred foods such as sunflower seeds may decrease predation on less-preferred incidental prey items (gypsy moth pupae; Elkinton et al. 2004) while increasing consumption of highly preferred incidental prey. I predicted that white-footed mouse space use and activity would be concentrated around supplemental food sources, especially around highly preferred food sources. I also predicted that the aggregative effect of the feeder and supplemental food would displace mouse activity at intermediate distances (15 and 25 m) and generate an area of decreased activity, but this effect would weaken with distance from the feeder and mouse activity would return to ambient levels at 40 m. Increased mouse activity around the supplemental food sources implies increased mouse encounter rates with incidental prey items close to the feeder. When less-preferred food is provided, I predicted mouse consumption of both highly and less-preferred prey would be high close to the feeder and decrease with distance from the feeder. Alternatively, when highly preferred food is offered, I predicted that consumption of less-preferred prey would be low close to the feeder and increase with distance whereas consumption of highly preferred prey would be high close to the feeder and decrease with distance.

MATERIALS AND METHODS

I conducted this investigation in spring 2010 at Touch of Nature Environmental Center, which is located in the Shawnee National Forest, approximately 13 km south of

Carbondale, IL, USA. Land surveys by Anderson and Anderson (1975) found dominant overstory species included white oak (*Quercus alba*), black oak (*Quercus velutina*), hickory (*Carya* spp.), and northern red oak (*Quercus rubra*). Davis (1987) noted prominent understory species including eastern redbud (*Cercis canadensis*), flowering dogwood (*Cornus florida*), and rusty black-haw (*Viburnum rufidulum*), however non-natives including wild rose (*Rosa multiflora*) and Japanese honeysuckle (*Lonicera japonica*) have invaded the forest interior (Yates et al. 2004).

I established 6 plots, each centered on a feeder in which I deployed food (Figure 2.1). Plots were designed as concentric rings with radii of 0, 5, 10, 15, 25 and 40 m from the feeder. On each plot, I established 8 trapping transects oriented along cardinal (North, South, East, and West) and secondary (NW, NE, SW, SE) directions and flagged the ring distances. All plots were spaced ≥ 100 m apart edge to edge, as well as ≥ 100 m from the forest edge (Figure 2.2).

The feeder on each plot was constructed from a galvanized steel trash can (117 L**)** and lid; 4-cm holes were drilled in the bottom of each can and connected to PVC tubes that allowed rodents to enter and forage, but excluded larger animals. Empty feeders served as control treatments, whereas sunflower seeds and cracked corn were used as supplemental food sources because the energy density and nutritional content of each food item (by weight: dried sunflower seed kernels: 24.4 kJ/g, 1.2 % water, 19.3 % protein, 49.8 % lipids, 24.0 % carbohydrates; cracked yellow corn: 15.3 kJ/g, 10.4 % water, 9.4 % protein, 4.7 % lipids, 74.3 % carbohydrates, USDA 2008) implied that sunflower seeds would be highly preferred food and cracked corn would be less-preferred. Each plot received one, 2-week trial with each of the 3 food treatments (sunflower, corn, or empty) provided *ad libitum* in the periods of 12–23 April, 3–14 May, and 24 May–4 June. Food trial sequence among the 3 periods for each plot was randomly determined (Table 2.1). Food was removed at the end of each trial and the feeder was either refilled with another food treatment or left empty (control) at the start of the following period.

I used trapping webs to estimate mouse densities on each plot. Paired Sherman live-traps (7.6- x 8.9- x 22.9-cm) were placed next to the feeder and along trapping transects at each ring distance (5, 10, 15, 25, and 40 m), giving a total of 82 traps per plot. Each pair of traps was covered with a wood board to provide shelter against environmental conditions. Live-trapping was conducted on all plots during 29 March–9 April and 7–18 June, which bracketed the period when track activity and consumption rates were measured**.** Traps on all plots were baited with oats, provisioned with cotton bedding, and opened Sunday through Thursday at ca. 1600 hr. Traps were checked and closed the following morning at ca. 0800 hr. Each captured animal was marked with a Monel ear tag in each ear, examined to determine sex, reproductive condition, and age, then immediately released.

I quantified small-mammal activity using track plates, which were constructed following methods detailed in Chapter 1. Rings at distances of 0, 5, 10, 15, 25 and 40 m received 4, 4, 8, 12, 20, and 32 pieces of flashing, respectively, for a total of 80 track plates per plot. Track plates were uniformly spaced within rings and monitored at intervals of 1, 2, or 4 days (depending on day of plate deployment and accounting for weekends) for each 2-week trial (same schedule as food treatments). All plates were closely inspected for the presence of tracks and, if present, tracks were identified to species. Tracked plates were marked to prevent double counting and replaced when tracks covered > 25% of the plate.

I used almonds (*Prunus dulcis*) and sugar maple (*Acer saccharum*) seeds as incidental prey items since the energy density and nutritional content of unsalted almonds (by weight; 24.9 kJ/g, 2.6 % water, 22.1 % protein, 52.8 % lipids, 19.3 % carbohydrates, USDA 2008) suggests this prey item should be highly preferred whereas white-footed mice consume sugar maple seeds with intermediate preference (energy density: 20.2 kJ/g; Kendeigh and West 1965, Ostfeld et al. 1997). I investigated the suitability of these prey items by locating a tree-mounted nest box that was inhabited by 5 mice and deploying 4 almonds and 4 sugar maple seeds around the base of the tree. I checked these prey items the following morning; all almonds displayed evidence of mouse depredation whereas 2 maple seeds were depredated. I concluded that both incidental prey items were palatable, but almonds were more readily consumed.

I prepared incidental prey items for deployment by embedding them in unscented beeswax (Strahl and Pitsch Inc., West Babylon, New York, USA) on pieces of burlap (Smith and Lautenschlager 1981). Burlap was cut into 4- x 4-cm squares and then double coated with beeswax. I cut 1.9-cm diameter PVC pipe into 1.3-cm long segments to act as molds and lightly coated their interiors with mineral oil. Each mold was placed on a burlap square, a whole almond was placed inside each mold, and the mold was filled with molten beeswax until most of the almond was encased by wax. The wax was allowed to cool and the PVC mold was removed, leaving the almond affixed to the burlap. Each maple seed was affixed to burlap by spooning molten wax over the seed wing. All prey items were handled with gloves for the entirety of their preparation and deployment.

The schedule for incidental prey deployment was the same as that for food treatments and track plates. Rings at distances of 0, 5, 10, 15, 25, and 40 m received 4, 4, 8, 8, 12, and 12 of each incidental prey item, respectively, for a total of 96 prey items per plot. Incidental prey items were deployed at random compass bearings within each ring and were staked into the ground using a bamboo skewer. Almonds and maple seeds on all plots were monitored every 1, 2, or 4 days (depending on day of prey item deployment and accounting for weekends) for each 2-week food trial. The presence or absence of each prey item was noted and, if depredated, the item was closely inspected to determine predator identity (e.g., mouse, chipmunk, squirrel, raccoon, etc.). The presence of scat was also noted during this inspection. If the item was present and intact, it was left at its current bearing. However, each depredated item was replaced with a new prey item at a new random bearing within the same ring.

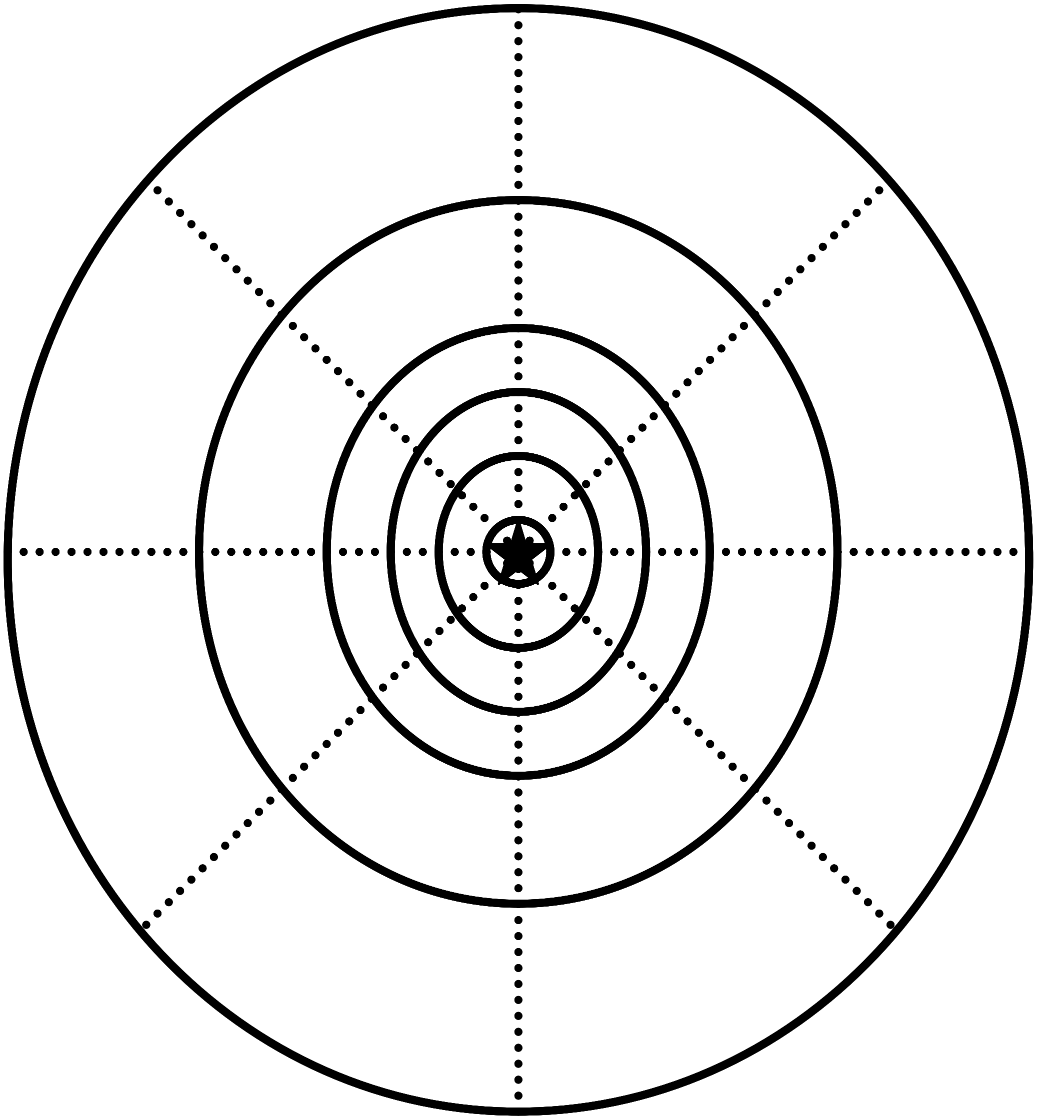

Figure 2.1. Experimental plot design, including central feeder location (star), concentric circles (0, 5, 10, 15, 25, and 40 m), and trapping web (dotted lines). Track plates were uniformly distributed along circle circumferences (4, 4, 8, 12, 20, 32, respectively) whereas incidental prey items were randomly distributed along circle circumferences.

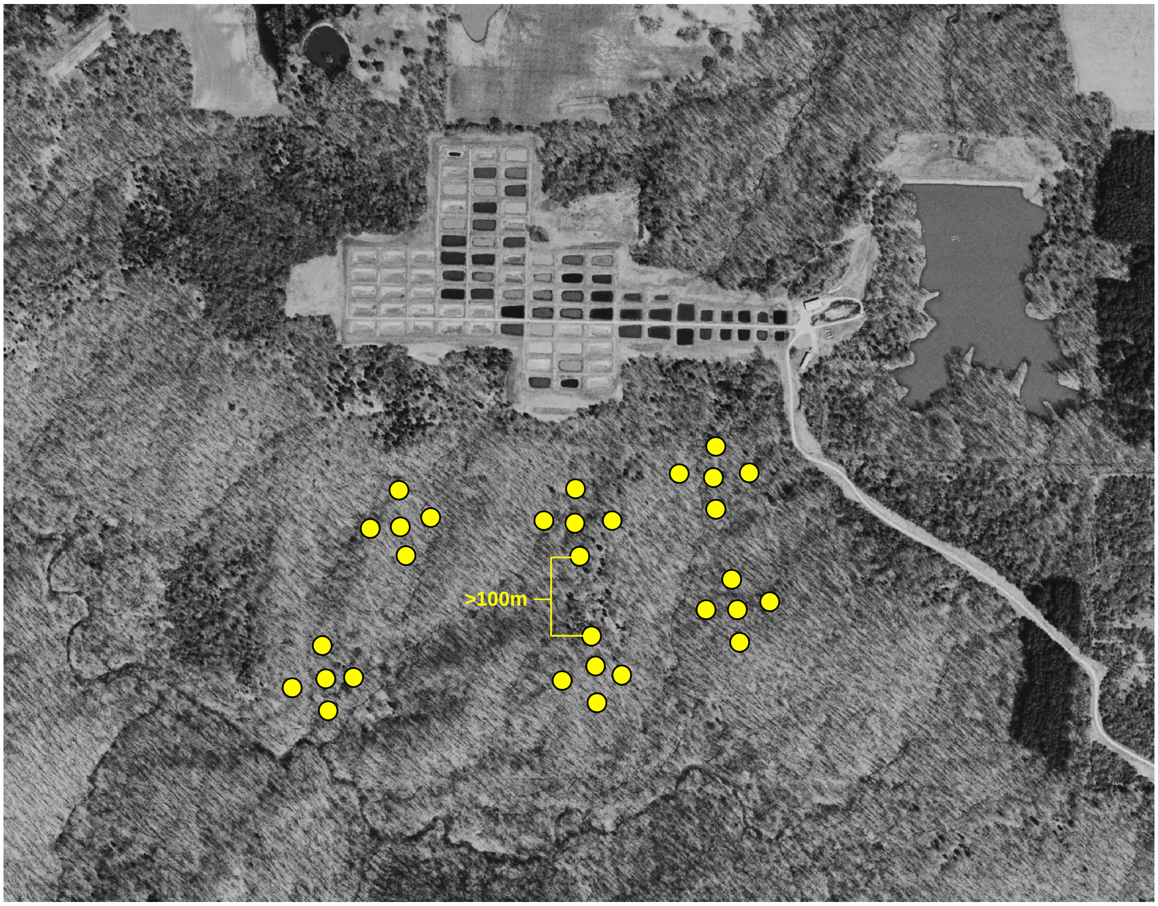

Figure 2.2 Location of 6 plots within the forest interior at Touch of Nature Environmental Center, Carbondale, Illinois, USA.

Table 2.1. Sequence of randomized, 2-week food trials conducted on all Touch of Nature Environmental Center plots, Carbondale, IL, USA, spring 2010.

	Food Treatment Period		
Plot	12 – 23 April	3 – 14 May	24 May – 4 June
1	Corn	Control	Sunflower
2	Sunflower	Control	Corn
3	Corn	Sunflower	Control
4	Control	Corn	Sunflower
5	Sunflower	Corn	Control
6	Control	Sunflower	Corn

DATA ANALYSES

Live-trapping data from each trapping session and plot were analyzed using program DISTANCE to estimate mouse densities (Parmenter et al. 2003) and determine if the presence of abundant food induced a demographic response. I used program DISTANCE to evaluate a variety of detectability functions created using all possible combinations of key functions (half-normal, uniform, and hazard rate) and adjustment factors (cosine, simple polynomial, and hermite polynomial). Akaike's Information Criterion for small samples (AIC_c) was used to select the combination of key function and adjustment term which best balanced bias and variance. All detectability functions were weighted by $w_i = \exp(-\Delta_i/2)/\Sigma\exp(-\Delta_r/2)$, with Δ_i representing the ΔAIC values of model *i* compared to the best fit model and the denominator representing a sum over all models in the model set considered (Burnham and Anderson 2004). Estimated rodent densities were then multiplied by the weight of their respective model, and resulting values were totaled across models to produce model averaged estimates of mouse density for each plot. Model-averaged estimates of pre- and post-experiment mouse densities were then compared using a paired t-test to test whether densities increased during this investigation.

On all plots, I recorded the presence or absence of mouse tracks on each track plate at each check, so track activity was binomially distributed. I conducted repeated-measures logistic regression (PROC GENMOD; SAS Institute, Cary, North Carolina, USA) using general estimating equations (GEE; Liang and Zeber 1986) to test if mouse activity was concentrated by alternative food; plot was the experimental subject, the proportion of track plate-checks that recorded tracks in each ring was analyzed as the response variable, and food treatment, distance from the feeder, interval between track plate checks, sampling period (first, second, or third), and the interaction of distance and food treatment were used as explanatory variables. Score statistics from type 3 GEE analysis were used to determine explanatory variables significantly influencing track activity at $\alpha = 0.05$. A significant interaction of distance and food treatment is implied by my prediction that track activity would be concentrated around the feeder and decrease in magnitude as distance from the feeder increases. When this interaction was indeed significant, I used repeated-measures logistic regression to analyze mouse track activity separately for each distance from the feeder; plot being the experimental subject, the proportion of track plate-checks that recorded tracks at each distance the response variable, and food treatment, interval between track plate checks, and sampling period used as explanatory variables. Once again, type 3 GEE score statistics were used to determine significant explanatory variables at $\alpha = 0.05$. I compared mean track activities at all distances between sampling periods and food treatments (control vs. sunflower, control vs. corn, sunflower vs. corn) using paired t-tests. Together, these analyses would test my predictions that the magnitude and concentration of mouse activity differed between food treatments (i.e., less magnitude and concentrated in less-preferred food treatments) and evaluate if predators exhibited a behavioral response corresponding with the presence of abundant food.

Consumption data on almonds and maple seeds were distributed and analyzed similarly to track plate data. My prediction that mouse consumption rates of both incidental prey items were influenced by the presence of supplemental food and either increased or decreased with distance from the feeder implies a significant interaction of distance from the feeder and food treatment. However, to test my explicit predictions of mouse consumption of each incidental prey item in highly and less-preferred food treatments, consumption rates on both incidental prey items were analyzed by distance from the feeder using repeated-measures logistic regression. Consumption of each incidental prey item was separated into three groups of consumption events: those attributable to mice (mouse-only), those attributable to raccoons, and those with unknown predator. I used the mouse-only predator group and created a mouse + unknown predator group (to account for sampling error in mouse predation events) for this analysis; consumption events attributed to raccoons were not analyzed. Analysis of maple seed consumption by the mouse-only predator group failed to reach convergence, so results are not presented. Repeated-measures logistic regression analysis of mouse-only and mouse + unknown consumption events were conducted for each incidental prey item using the consumption rate as the response variable, and food treatment, distance from the feeder, and sampling period as explanatory variables. Again, score statistics from type 3 GEE analysis were used to determine significant effects at $\alpha = 0.05$. For both incidental prey (almonds and maple seeds) and predator groups (mouse-only and mouse + unknown), mean consumption rates at all distances were then compared between food treatments (control vs. sunflower, control vs. corn, sunflower vs. corn) using a paired t-test.

RESULTS

Comparison of AIC_c values suggested that a half-normal, cosine detectability function best balanced bias and variance in our distance-sampling data for both pre- and post-experiment trapping sessions, but considerable support remained for 2 alternative functions in each period (Table 2.2). A detectability function created using a uniform key function and hermite polynomial adjustment factor failed to reach convergence in the estimation of post-experiment density and was excluded from analyses. Model-averaged estimates of pre-experiment mouse densities ranged from 1.89 to 4.01 mice/ha (mean = 3.05 mice/ha), but increased (t = -3.04, df = 5, *P* = 0.014) to post-experiment estimates of 3.78 to 10.31 mice/ha (mean = 5.65 mice/ha; Table 2.3).

Overall mean track activity was greater in control (empty) treatments than in sunflower (t = 2.60, df = 5, *P* = 0.024) and corn (t = 3.19, df = 5, *P* = 0.012) treatments, but was slightly greater in sunflower than corn treatments (Figure 2.3). This ranking held for all distances from the feeder (Figure 2.3), although I found an interaction effect of treatment and distance (Table 2.4), with higher activity in control treatments than other treatments at distances of 0, 10, and 40 m (Table 2.5). Mean track activities in control treatments were highest in period 2 (Figure 2.4; period 1 vs. period 2; t = -2.91, df = 5, *P* = 0.016, period 2 vs. period 3; t = 4.40, df = 5, *P* = 0.003), but this pattern was not observed in corn and sunflower treatments.

Overall mean consumption rates of both almonds and maple seeds were greatest in control treatments (*t* >2.51, df = 5, *P* < 0.027), but were slightly greater in corn than sunflower treatments (Almonds; *t* = 1.60, df = 5, *P* = 0.085, Maple seeds; *t* = 3.19, df = 5, *P* = 0.012) and increased from period 1 to period 3 at all distances (Tables 2.6 and 2.7,

Figure 2.5). Food treatment affected almond consumption at the feeder (0 m; Table 2.6), but did not influence maple seed consumption at 5 and 15 m from the feeder (Table 2.7). Almond consumption rates by mouse only and maple seed consumption rates by mouse + unknown predators were affected by the interaction of distance and food treatment (Table 2.8), but almond consumption rates by mouse + unknown predators were not apparently influenced by this interaction (Table 2.8). Mean almond consumption rates by mouse only and mouse + unknown predator groups were both greater in control treatments than in sunflower (Mouse only; $t = 2.52$, df = 5, $P = 0.027$, Mouse + unknown; $t = 2.17$, df = 5, $P = 0.041$) and corn (Mouse only; $t = 3.36$, df = 5, $P = 0.01$, Mouse + unknown; $t = 2.33$, df = 5, $P = 0.034$) treatments. Mean maple-seed consumption rates by mouse only and mouse + unknown predator groups were greater in control treatments than in sunflower (Mouse only; $t = 7.10$, df = 5, $P = 0.0004$, Mouse + unknown; $t = 3.89$, df = 5, $P = 0.0057$) and corn (Mouse only; $t = 10.84$, df = 5, $P < 0.0001$, Mouse + unknown predator; $t = 4.44$, df = 5, $P = 0.0034$) treatments (Figure 2.5).

Table 2.2. Detectability functions created using half-normal (HN), uniform (UN), and hazard rate (HR) key functions combined with cosine (COS), simple polynomial (SP), and hermite polynomial (HP) adjustment factors in program DISTANCE to estimate pre- and post-food treatment mouse densities on 6 plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010. AIC_c values are reported due to small sample size.

Period	Name	# params	AICc	ΔAICc
Pre-food	HN+COS	9	311.71	0
	HN+HP	6	313.55	1.84
	HN+SP	6	313.55	1.84
	HR+COS	12	320.37	8.66
	HR+SP	13	320.43	8.72
	HR+HP	13	320.73	9.01
	UN+COS	11	322.81	11.09
	UN+SP	6	327.78	16.07
	UN+HP	11	337.69	25.98
Post-food	HN+COS	12	372.74	0
	HR+COS	12	373.33	0.59
	HR+SP	12	373.33	0.59
	HN+SP	6	379.64	6.9
	HN+HP	6	379.64	6.9
	HR+HP	6	379.64	6.9
	UN+COS	15	387.16	14.42
	UN+SP	6	400.72	27.98

Table 2.3. Mouse density estimates generated from detectability functions in program DISTANCE for pre- and post-food treatment trapping sessions on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA. Model averaged estimates were generated for each plot by totaling initial density estimates weighted by the amount of support ($\Delta \mathrm{AIC}_c$) of their respective model.

			Unweighted density estimates					
Period	Model	w_i	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6
Pre-food	HN+COS	0.54	3.41	5.08	3.31	2.23	1.89	4.31
	HN+HP	0.22	1.7	2.57	3.31	2.23	1.89	2.56
	HN+SP	0.22	1.7	2.57	3.31	2.23	1.89	2.56
	HR+COS	0.01	6.58	6.3	2.34	4.19	1.82	6.32
	HR+SP	0.01	6.58	6.3	45.38	3.82	1.82	6.32
	HR+HP	0.01	6.58	6.3	35.18	3.82	1.82	6.32
	UN+COS	0	1.35	4.49	2.9	1.79	1.46	3.58
	UN+SP	0	1.14	1.7	1.94	1.53	1.27	1.4
	UN+HP	0	0.92	1.94	1.8	1.76	1.43	1.46
Model-averaged estimates			2.73	4.01	3.79	2.26	1.89	3.59
Post-food	HN+COS	0.39	4.85	4.3	2.4	3.57	4	3.98
	HR+COS	0.29	6.82	5.72	16.21	5.21	3.73	4.84
	HR+SP	0.29	6.82	5.72	16.21	5.21	3.73	4.84
	HN+SP	0.01	2.79	2.39	1.24	1.9	2.35	1.86
	HN+HP	0.01	2.79	2.39	1.24	1.9	2.35	1.86
	HR+HP	0.01	2.79	2.39	1.24	1.9	2.35	1.86
	UN+COS	0	4.7	2.53	1.14	3.33	3.42	2.91
	UN+SP	0	1.65	1.57	0.95	1.28	1.33	1.02
Model-averaged estimates			5.91	5.05	10.31	4.46	3.78	4.4

Table 2.4. Results of repeated-measures logistic regression analysis of the frequency of plates tracked vs. study parameters on 6 plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010.

Parameter	df	Wald $\chi 2$	P-value
Treatment*Distance	10	18.46	0.048
Treatment	2	46.99	<0.0001
Distance	5	12.39	0.03
Interval	2	121.02	<0.0001
Period	2	228.36	<0.0001

Table 2.5. Results of repeated-measures logistic regression analysis on the frequency of plates tracked by distance from the feeder (0, 5, 10, 15, 25, and 40 m) on 6 plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010.

		Treatment		Interval		Period	
Distance from feeder	df	Wald χ2	P	Wald χ2	P	Wald χ2	P
0	2	29.57	<0.0001	29.57	0.0009	10.37	0.0025
5	2	3.62	0.081	19.05	<0.0001	27.3	<0.0001
10	2	16.21	0.0004	11.04	0.0041	30.64	<0.0001
15	2	2.11	0.34	23.28	<0.0001	20.26	<0.0001
25	2	2.55	0.48	26.75	<0.0001	59.23	<0.0001
40	2	31.92	<0.0001	49.48	<0.0001	100.59	<0.0001

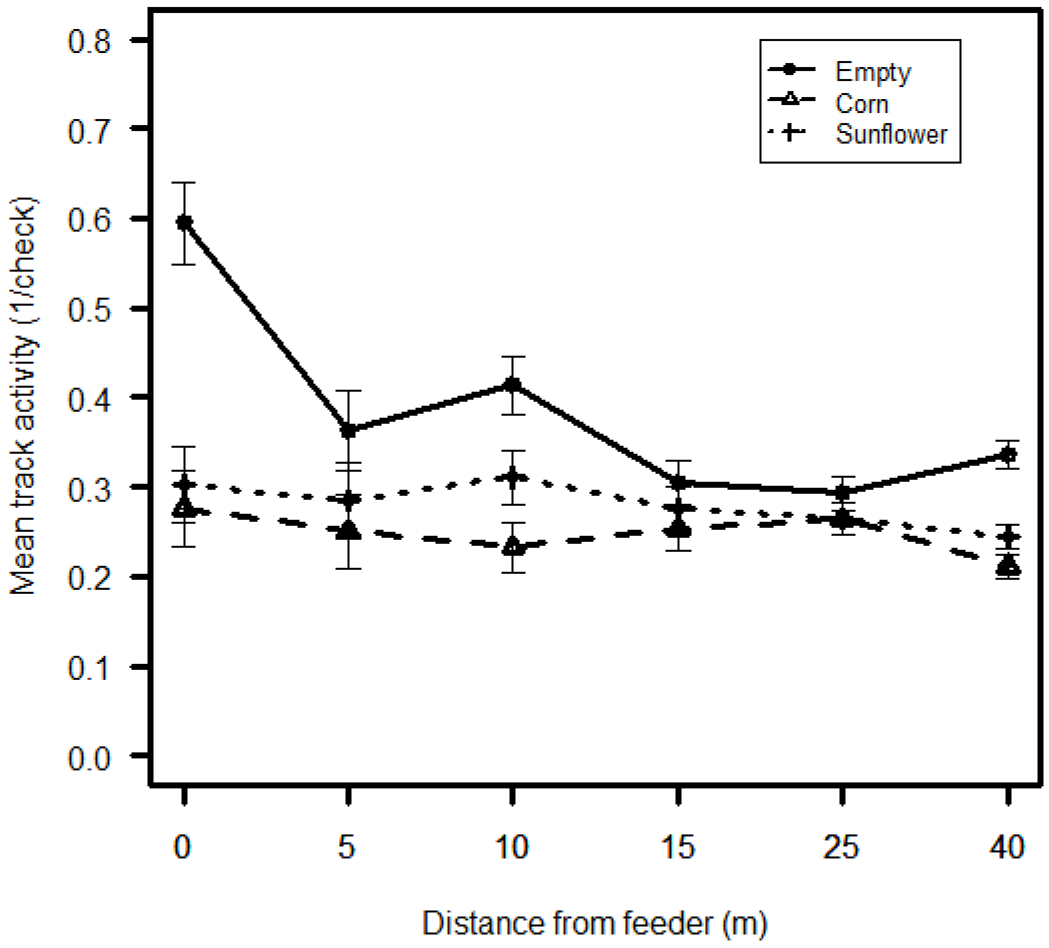

Figure 2.3. Mean mouse track activity (tracked plates per plate-check) by distance from feeder in 3 food treatments (empty, corn, and sunflower) on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010.

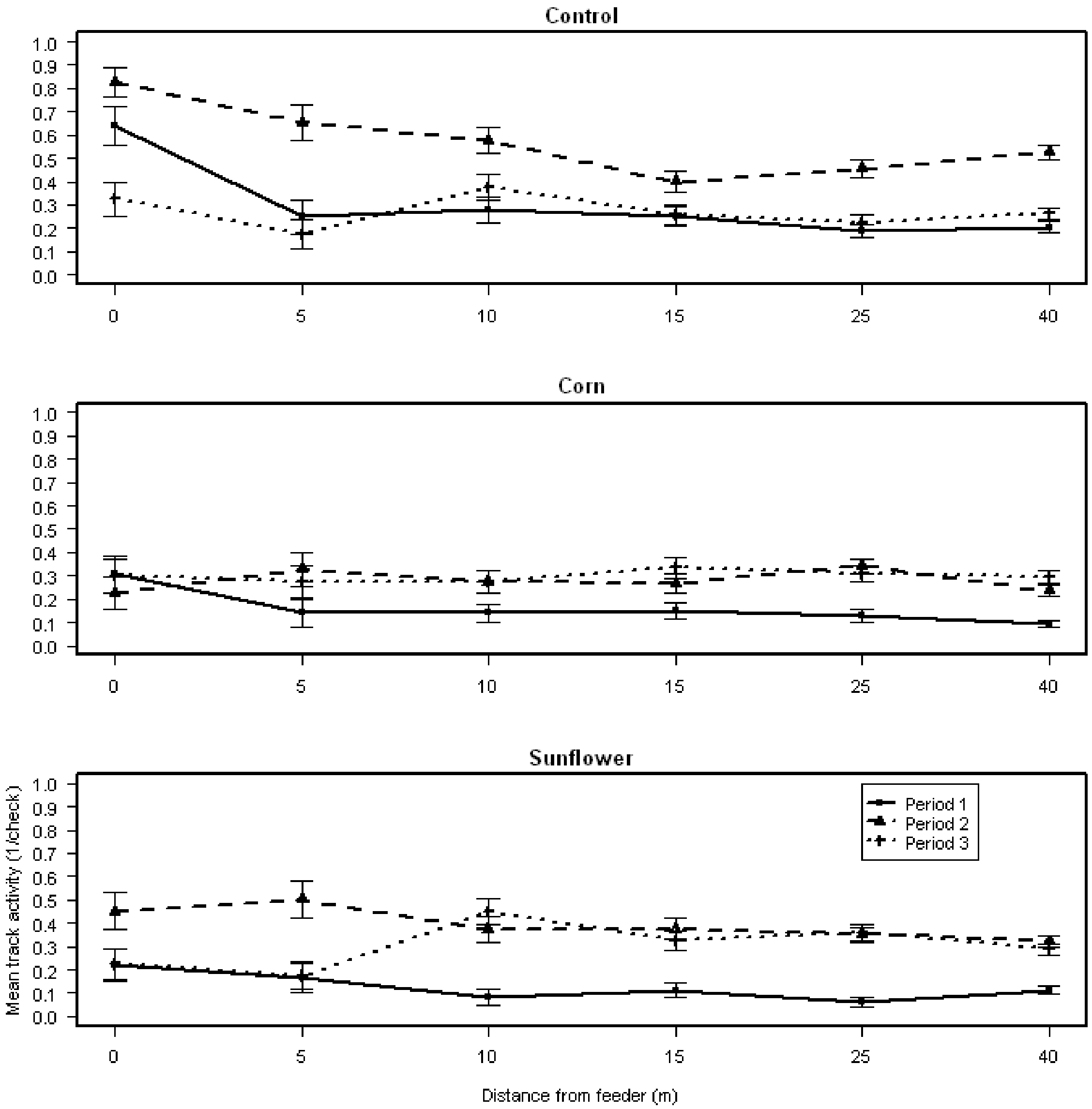

Figure 2.4. Period specific, mean mouse track activity (tracked plates per plate-check) by distance from the feeder in 3 food treatments (control, corn, and sunflower) on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010.

Table 2.6. Results of repeated-measures logistic regression evaluating food treatment effect on consumption of almonds by distance from the feeder on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010.

		Treatment	
Distance from feeder	df	Wald $\chi 2$	P
0	2	10.7	0.0047
5	2	5.54	0.063
10	2	0.91	0.63
15	2	3.05	0.22
25	2	0.04	0.98
40	2	3.58	0.17

Table 2.7. Results of repeated-measures logistic regression evaluating food treatment effect on consumption of maple seeds by distance from the feeder on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010.

		Treatment	
Distance from feeder	df	Wald $\chi2$	P
0	2	55.24	<0.0001
5	2	4.91	0.086
10	2	38.32	<0.0001
15	2	5.58	0.062
25	2	6.97	0.031
40	2	6.53	0.038

Table 2.8. Results of repeated-measures logistic regression on consumption of almonds and maple seeds by predator group (mouse only and mouse + unknown predators) on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010. Results of mouse-only predation on maple seeds are not presented as convergence was not reached during analysis.

Prey item	Predator group	Parameter	df	Wald $\chi 2$	P
Almonds	Mouse only	Distance	5	9.99	0.076
		Treatment	2	28.92	<0.0001
		Distance*Treatment	10	22.74	0.012
		Period	2	210.69	<0.0001
Almonds	Mouse + unknown	Distance	5	13.26	0.021
		Treatment	2	13.28	0.0013
		Distance*Treatment	10	12.94	0.23
		Period	2	309.57	<0.0001
Maple seeds	Mouse + unknown	Distance	5	3.51	0.62
		Treatment	2	55.32	<0.0001
		Distance*Treatment	10	20.37	0.026
		Period	2	304.68	<0.0001

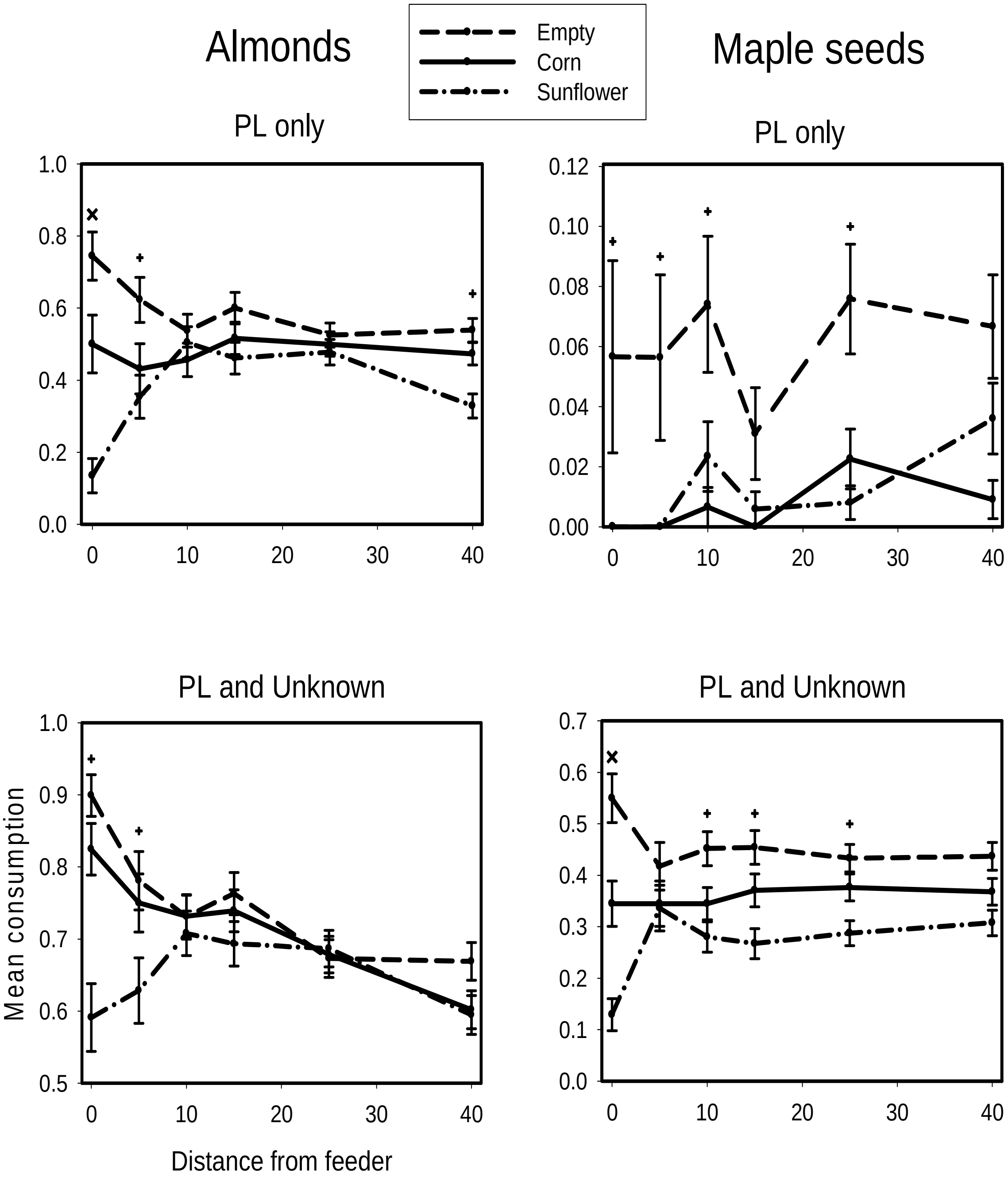

Figure 2.5. Mean consumption (proportion eaten per check (1-4 days)) of almonds and maple seeds by mouse only (PL only) and mouse and unspecified, non-raccoon predator (PL + unknown) groups in 3 food treatment (empty, corn, and sunflower) periods on 6 experimental plots located at Touch of Nature Environmental Center, Carbondale, IL, USA in spring 2010. Distances (m) marked with "+" and "**x**" indicate significant (*P* < 0.05) and highly significant (*P* < 0.0001) food treatment effects, respectively.

DISCUSSION

Environmental factors, like the presence of abundant food sources (Courtney and Felton 1976, Crabtree and Wolfe 1988), can influence predator space use and foraging efforts. Predators can become concentrated by abundant food sources, especially if these sources are highly profitable, resulting in localized foraging efforts that can increase predation on profitable incidental prey items (Martinson and Flaspohler 2003) but decrease search and encounter rates with other, less-preferred prey items (Dixon 1959, Jedrzejewski and Jedrzejewski 1992). I had predicted that both food treatments would concentrate mouse space use (with little effect of control treatments and lesser magnitude of activity around corn-filled feeders); therefore, mouse track activity would be highest near the feeder and decrease with distance. I found that track activity was slightly elevated close to the feeder (< 10 m) in both food treatments, but contrary to my prediction, this effect was most pronounced and significant only in control treatments. This increased, localized activity around empty feeders might have been explained by the initial novelty of the feeder if it only appeared in the first sampling period; however, the increased magnitude of activity observed in the second sampling period suggests a learned behavioral response to the presence of abundant food. When food resources become unavailable, predators may be forced to increase the rate and spatial scale at which they forage for prey (Winkler and Kothbauer-Hellmann 2001, Mols et al. 2004), which may explain why I found mouse activity to increase in control treatments between sampling periods and with distance from the feeder in period 2 and remain at elevated levels in period 3.

Prey profitability influences predator choice of prey, so localized, abundant food sources of differing nutritional qualities may produce discrepancies in consumption rates on incidental prey. For this investigation, I had predicted that abundant food sources would concentrate mouse activity and increase predator encounter rates with almonds and maple seeds near the feeder (0 – 10 m). I also expected that almonds would be more readily consumed due to their nutritional content, and that consumption rates would decrease as distance from the feeder increased. These expectations were generally supported as mouse-only and mouse + unknown predator-consumption rates were greater for almonds than maple seeds and tended to decrease with distance in control and corn treatments. However, almond consumption rates for both predator groups were low near the feeder and increased with distance in sunflower treatments. Low almond consumption rates near the feeder in sunflower treatments suggested greater selectivity in predator diet whereas higher consumption rates far from the feeder imply decreased selectivity in predator diet. These differences in diet selectivity may be explained by the greater handling time associated with almond consumption, as well as the proximity and nutritional quality of the supplemental sunflower seeds, which may have distracted predators from nearby almonds.

My results also supported some, but not all, of my predictions regarding maple seed consumption. I predicted high consumption rates on maple seeds when less-preferred food was provided, but low when highly preferred food was offered. Mouse-only consumption of maple seeds was greatest in control treatments and extremely low around the feeder when supplemental food was provided, suggesting that mouse diet selectivity increased when supplemental food was present. However, I advise that these results be interpreted with caution. It was difficult to ascertain the identity of maple seed predators due to the way maple seeds were prepared for deployment. Mouse predation events may have been recorded as resulting from an unspecified predator, thereby decreasing the sample size of the mouse-only predator group and my ability to accurately interpret my results. So, mouse + unknown predator consumption of maple seeds may better approximate actual mouse consumption rates. Maple seed consumption rates by mouse + unknown predators were highest in control treatments and lowest in sunflower treatments, demonstrating predator diet selectivity decreased when food was absent, and conversely, increased when highly preferred food was provided.

The similar trends in almond and maple seed consumption during control treatments were not in accordance with my predictions. I had predicted little effect of control treatments on predator activity, and consequently, consumption of both incidental prey items. However, consumption rates for both almonds and maple seeds were greatest in control treatments. The lack of food in control treatments suggests these patches were of poor quality, thus forcing predators to consume less-profitable prey items with greater preference (Stephens et al. 1986). Maple seeds are less-profitable than almonds, but I found mouse + unknown predator maple-seed consumption was greater than expected, implying that maple seeds were partially preferred. Partial preferences may be generated by differences in prey size and handling times (Rychlik 1999), so I suggest that maple seeds required less handling time than almonds, which may explain these observed patterns of consumption.

The generalist nature of the white-footed mouse suggests that the findings of this study may be applied to other generalist rodent systems. Abundant food sources can decrease rodent predator activity levels (Pusenius and Schmidt 2002, Sulok et al. 2004), influence site selection (Lacher and Mares 1996, Schmidt 2004) and result in less uniform distributions across small-scale habitats (Schnurr et al. 2004), but the spatial scale of this mechanism is poorly understood. I found that abundant food elevated mouse space use and activity at distances ≤ 10 m, and in turn, predation risk to incidental prey at these distances. However, the concentrative effect of abundant food was less than predicted, suggesting that providing food may not generate refugia for prey by displacing mouse activity and decreasing consumption rates on incidental prey away from the feeder. Rodent diet selection and space use can be influenced by the abundance and profitability of food sources; fox squirrels (*Sciurus niger*) over-utilized poor-quality habitat patches (Morgan et al. 1997) and decreased diet selectivity when the abundance of food sources was increased (Brown and Morgan 1995).

Conversely, removal or depletion of food sources may force predators to increase the rate and spatial scale of their foraging efforts, thereby potentially decreasing encounter and consumption rates on incidental prey. I found evidence that the absence of food resulted in higher mean activity levels, however, predator preference for less-profitable prey, and consumption of incidental prey in general, was greater in the absence of food. Differences in incidental prey consumption between food treatments indicated that the palatability and profitability of an incidental prey item in relation to that of an abundant food source can influence incidental prey consumption. In addition, the distance of the incidental prey item from the food source may contribute to determining whether incidental prey are consumed or disregarded, especially if these prey items are located near the food source.

The results of this investigation may be broadly applied to predator and prey interactions as empirical evidence continues to mount concerning generalist predator deviation from optimal foraging through altered space use and discrepancies in prey consumption. Large predatory mammals, like African lions (*Panthera leo*), deviated from optimal foraging by altering prey choice based on prey group size, prey distance from the hunting group, and prey group composition (Scheel 1993). Avian consumers, when concentrated by bird feeders, exhibited increased preference and localized predation on incidental prey (Martinson and Flaspohler 2003). Differential space use and consumption of prey by predators suggests practical management implications for invasive, endangered, and game species. My data and results suggest that providing abundant food sources near areas of high pest densities may encourage predators to aggregate and increase consumption rates on these incidental prey, provided the pest species is more profitable than the provided food. Alternatively, the placement of abundant food sources away from high densities of desirable species (i.e., game) may distract predators and decrease consumption rates on these prey, so long as the provided food is of high energetic profitability.

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