

## INCIDENTAL NEST PREDATION IN SONGBIRDS: BEHAVIORAL INDICATORS DETECT ECOLOGICAL SCALES AND PROCESSES

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**Abstract.** Incidental predation occurs when secondary prey items are encountered and subsequently consumed, not through directed search for such prey, but through their consequential encounter by a predator engaged in search for primary prey. We developed a mathematical model that examines the relationships between the abundance of primary prey, patch exploitation (i.e., quitting harvest rates), and the rate of incidental predation on secondary prey items. The model's predictions are dependent upon the spatial scale over which a forager integrates foraging costs and thus determines its quitting harvest rate (QHR). At local (i.e., foraging) spatial scales, we predicted that incidental predation should increase with local food abundance. Also at the foraging scale, local food abundance should not influence QHRs, but local predation risk (from higher trophic levels) should increase QHRs. Therefore, we predicted that incidental predation rates should be negatively correlated with QHRs. Over large (i.e., landscape) spatial scales, greater food abundance and predation risk increase QHRs, and we predicted that predation rates should vary inversely with QHR through two complementary mechanisms: foragers use a greater proportion of space and spend more time foraging as quitting harvest rates decrease.

We experimentally tested the qualitative predictions of the theory in the field using artificial Veery (*Catharus fuscescens*) nests depredated by white-footed mice, *Peromyscus leucopus*, across three spatial scales. We used the technique of giving-up densities to measure QHRs and to determine the scale at which mice integrate different foraging costs. In accord with our predictions, nest predation was positively influenced by the local abundance of food at the foraging scale, and local predation risk to mice and perhaps interference competition from chipmunks resulted in higher giving-up densities and lower nest predation. At the landscape scale, there was an inverse relationship between giving-up densities and nest predation, which was probably the result of large-scale differences in resource abundance between plots. Our study demonstrates how linking theoretical development to the use of empirical behavioral indicators can help determine the relevant ecological scales and processes necessary for understanding predator–prey interactions.

**Key words:** *enemy-free space; foraging ecology; generalist; giving-up densities; incidental predation; nest predation; patch use; quitting harvest rate; Peromyscus leucopus.*

### INTRODUCTION

Some proportion of predation by generalist predators on secondary prey items occurs not through directed search for such prey, but through their incidental encounter by a predator engaged in search for primary prey (Vickery et al. 1992). Alternatively, for food generalists, such as mice of the genus *Peromyscus* (Whitaker 1966, Jones 1970), foraging often may be directed toward patches with the highest cumulative prey availability (see patch use theory; Stephens and Krebs 1986) rather than toward any particular food type. In either example, this type of predation is called incidental predation (Vickery et al. 1992, Schmidt and Whelan 1998).

As we will detail, the magnitude of incidental predation is determined by the predator's behavioral (e.g., functional) response(s) to the abundance and distribution of its primary prey or, alternatively, to the cumulative prey abundance. The predator has no behavioral response to its incidental prey, or at most a weak diffuse response that can be ignored when incidental prey are relatively uncommon. This differs from most predator–prey interactions, which are conceptualized as being driven by the density of predators and their prey (Lotka 1925, Rosenzweig and MacArthur 1963, Taylor 1984). The past decade has seen rising interest in including behavioral responses into models of population dynamics and species interactions (Lomnicki 1988, Fryxell and Lundberg 1997, Peckarsky et al. 1997, Werner 1998, Brown et al. 1999). However, it remains to be seen whether behavioral responses are the driving force of population interactions or whether they are simply “frills” that mildly affect population dynamics or species interactions (Holbrook and Schmitt 1998, Brown et al. 1999).

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Some of the best examples of incidental predation come from detailed studies of nest predation in songbirds (Vickery et al. 1992, Yanes and Suárez 1996). Incidental predation may be common among nesting songbirds because they are characterized by a low encounter rate (daily nest predation rates are generally 2–4% [Martin 1992]) and low prey density ( $\sim 10$  pairs/ha within temperate woodlands; Holmes et al. 1986, Tomiałojć and Wesołowski 1990). Moreover, smaller predators (mice, chipmunks, and shrews) have very restricted home ranges ( $<0.1$ – $1$  ha) that may prevent these predators from having directed responses to songbird nests simply because they are unlikely to encounter more than even a single nest during the summer. For instance, assuming that birds annually produce 30 nests/ha (10 breeding pairs/ha multiplied by 3 nests/pair) and mouse density is 60 individuals/ha, then even if every nest were available and consumed by mice, only half of the mouse population would, on average, consume a single nest.

However, incidental predation should not be confounded with weak predation. On a per capita basis, mice and other small mammals are perhaps inefficient predators of songbird nests. At densities of  $\geq 60$  individuals/ha (Ostfeld et al. 1996, Wolff 1996), they may have strong effects as a population (Ketterson et al. 1996). For example, there are a number of studies in which small mammals were shown to be important predators (Maxson and Oring 1978, Guillory 1987, Reitsma et al. 1990, Hanski et al. 1996, Hannon and Cotterill 1998), despite the fact that studies using quail eggs to measure predation rates may underestimate the importance of small predators (Roper 1992, Haskell 1995a, b).

Here we have built upon predator–prey theory by investigating the relationship between patch-use behavior and incidental predation. We developed a model that examines the relationships between the local abundance of primary prey, patch exploitation, and the rate of incidental predation on secondary prey items. We couched the model's predictions in terms of giving-up densities and local food abundance, and tested the qualitative predictions of the theory in a field experiment using artificial Veery (*Catharus fuscescens*) nests depredated by white-footed mice, *Peromyscus leucopus*.

#### *Incidental predation and enemy-free space*

We considered the model of patch use developed by Schmidt and Brown (1996) to determine the benefit of detecting resource patchiness within a fixed area in which resources are randomly distributed. The further a forager can subdivide the fixed area or patch into smaller “micropatches” and use only those micropatches that are profitable, i.e., those that exceed the forager's quitting harvest rate, the more food is consumed from the entire patch (Schmidt and Brown 1996). This model can also be used to determine the proportion of patch space used by a forager. Those

micropatches that are below a forager's quitting harvest rate are not used; these regions therefore represent enemy-free space (Jeffries and Lawton 1984) from the perspective of the prey.

To illustrate this point, we follow Schmidt and Brown (1996) in envisioning a forager that subdivides a fixed area of space (be it a patch, territory, or home range) into any number,  $n$ , of smaller micropatches whose resources are assessed and harvested independently of each other. For the discussion of scale-specific patterns and processes, we refer to micropatches as the foraging scale (sensu Morgan et al. [1997]; see also Morris [1992]). The intermediate scale refers to an aggregate of micropatches coupled through a forager's daily movements. It is at the intermediate scale, for instance, that foragers assess the average quality of their environment (Brown and Alkon 1990, Morgan et al. 1997). Finally, the intermediate scale is nested within a larger landscape scale. This scale refers to patches that are decoupled or weakly coupled through long-distance dispersal (i.e., that exceed the dispersal range of the forager; Fig. 1).

Assuming that micropatches are equally sized, the mean number of food items per micropatch,  $\lambda$ , is given by the total number of items,  $R$ , divided by the number of micropatches,  $\lambda = R/n$ . Assuming that food is distributed in a Poisson fashion, the probability that  $X$  food items occur in a given micropatch is:

$$\text{pr}(X, \lambda) = e^{-R/n} (R/n)^X / X! \quad (1)$$

We assume that the forager uses a fixed quitting harvest rate (QHR) strategy. That is, the forager exploits only those micropatches that contain a sufficient density of resources ( $>N$ ; where  $N$  is the density of items per patch corresponding to the QHR) such that the forager's instantaneous harvest rate in the micropatch exceeds some threshold. Furthermore, micropatches yield diminishing returns; those micropatches that initially exceed the QHR are exploited until the QHR is reached, after which the forager ceases to use the micropatch. The proportion of micropatches with initial quality that falls below the forager's quitting harvest rate is given by:

$$S_p = \sum_{i=0}^N \text{pr}(X_i, \lambda). \quad (2)$$

The forager's quitting harvest rate may increase for any number of reasons. There may be an increase in the amount of food within the environment, perhaps outside the patch of interest but to which the forager has access, which reduces the overall value of food across an individual's foraging domain (Brown et al. 1992). Alternatively, a reduction in population density may increase access to food through reduced exploitative competition (Bowers et al. 1993, Morris 1997). Finally, there may be increased predation risk from higher trophic levels that increases the QHR. Regardless of the

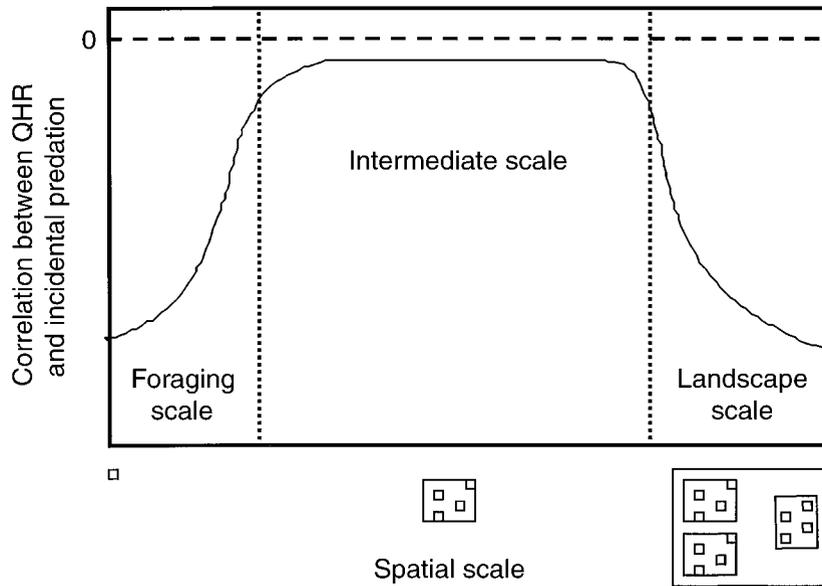


FIG. 1. Hypothesized correlation between quitting harvest rates (QHRs) and rates of incidental predation. At the foraging scale (i.e., micropatch), QHRs are strongly influenced by local predatory risks to the forager and are negatively correlated with incidental predation rates on prey within the micropatch. Food abundance may also be important to incidental predation rates, but is not reflected in QHRs at this scale. Instead, foragers integrate food abundance over intermediate scales (i.e., micropatches coupled through a forager's daily movements) to determine their QHR. However, because incidental predation rates are influenced by local conditions at the foraging scale, there is no correlation between QHR and incidental predation. Intermediate-scale patches are compared at the landscape scale, where, in the absence of strong differences in predatory risks to the forager between intermediate-scale patches, QHRs are primarily responsive to food abundance. QHRs and incidental predation rates are correlated negatively through the mechanisms of enemy-free space (see Fig. 2) and foraging time.

specific mechanism(s), as the forager's QHR increases, it uses a smaller proportion of the total patch area. From the prey's perspective, as a forager's QHR increases, so does the proportion of enemy-free space (i.e., the region of space where the forager is absent). This occurs because fewer micropatches meet the threshold harvest rate at which exploitation is profitable, and the proportion of such unprofitable micropatches increases as the requirement becomes more restrictive (see Fig. 2, which plots  $S_p$  at three different quitting harvest rates and across a range of spatial assessment abilities). There is a positive relationship between the QHR and enemy-free space or, if we equate enemy-free space with an absence of incidental predation in that micropatch, there is an inverse relationship between the QHR and incidental predation across the entire patch.

Our model is somewhat simplistic in that it ignores the possibility that foragers may occur in poor-quality patches as they disperse through landscapes or, alternatively, that poor resource assessment may necessitate a period of sampling each patch before rejecting it and moving on. Although some predation undoubtedly may occur as a forager disperses through the landscape, predation on uncommon, cryptic items, such as songbird nests, is likely to be much lower in this case relative to actively exploiting a patch for food. Likewise, a brief stint of time spent in a patch for sampling purposes may result in incidental nest encounter. However, be-

cause time spent in a patch is proportional to the quality of the patch, these encounters are heavily biased toward the richest patches.

The inverse relationship between incidental predation and the QHR can also occur through a reduction in the total amount of time that the forager spends exploiting resource (micro)patches. For instance, if a micropatch is exploited, the probability that the forager will discover a secondary prey item, should one occur, is a function of its encounter probability with the incidental prey item and the amount of time spent searching for prey in the micropatch. The latter is determined by the resource level of the primary prey:

$$t = (1/a)\log(X/N) \tag{3}$$

where  $t$  is the time within a micropatch spent searching for primary prey,  $a$  is the encounter probability with primary prey, and  $X$  and  $N$  give the initial and final abundance of primary prey within the micropatch. The total time,  $T$ , spent in the entire patch is the sum of time spent within all micropatches:

$$T(n) = (1/a) \sum_{i=1, \dots, n} \log(X_i/N). \tag{4}$$

$T(n)$  likewise decreases as the QHR increases. To illustrate this, we assume that the final abundance of food in a micropatch,  $N$ , is monotonically related to the quitting harvest rate (e.g., Brown 1988, Kotler and Brown

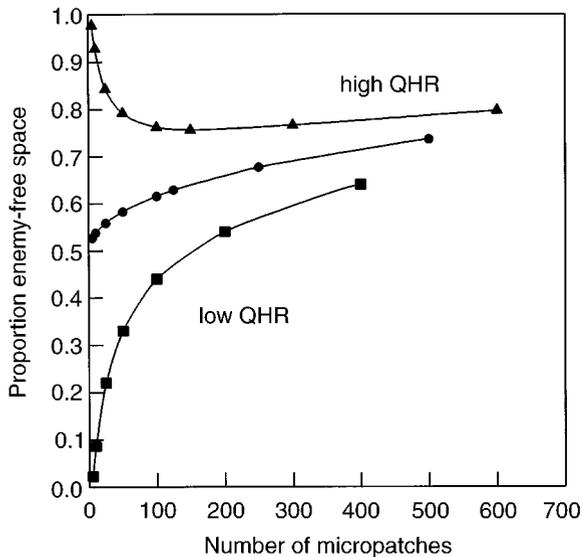


FIG. 2. Proportion of enemy-free space as a function of the scale of patch assessment (number of micropatches) for three magnitudes of quitting harvest rate (QHR). Regardless of patch assessment abilities, the proportion of enemy-free space increases with increasing QHR. These relationships assume 500 randomly distributed food items within a 100-m<sup>2</sup> patch. At high QHRs (>5 items/m<sup>2</sup>), the entire patch represents enemy-free space (i.e., unused space) unless the forager can recognize resource heterogeneity on a scale smaller than the patch. Hence, enemy-free space initially declines with the scale of patch assessment. At lower QHRs, the entire patch is used when resource assessment occurs at the same scale as the patch. As the scale of assessment decreases along the x-axis, the forager more precisely locates resource heterogeneity and uses an overall smaller fraction of the patch.

1990, Morris 1997), and evaluate the sign of the partial derivative:  $\partial T/\partial N = -(1/a)\Sigma(1/N)$ . This relationship is always negative; thus, total foraging time is always a decreasing function of the final abundance of food in a micropatch and therefore the QHR. (Note: Bayesian foraging strategies in combination with clumped resource distributions may yield alternative predictions, e.g., Olsson and Holmgren [1999], and are an avenue for future modeling.)

These two mechanisms, increased enemy-free space and decreased total foraging time, operate at intermediate spatial scales (i.e., the patch) to produce patterns seen at the landscape scale. However, at the foraging scale, incidental predation will be determined by the amount of time spent foraging within a micropatch. This, in turn, is positively influenced by the initial abundance of co-occurring primary prey (all else equal) within a micropatch,  $\partial t/\partial X = (1/aX)$ , which is always positive. However, time spent in a micropatch can also be influenced by additional foraging costs such as predation risk (Brown 1988). Because the QHR is integrated over larger spatial scales (Brown et al. 1992, Morris 1997), there should be no relationship between the abundance of food in a given micropatch,  $X_p$ , and the QHR. Any relationship between QHR and incident

tal predation at the foraging scale, therefore, reflects these additional foraging costs (see Fig. 1).

We undertook studies of predation on artificial songbird nests in 1997 and 1998 to test the following predictions: (1) incidental predation is inversely related to the QHR at the landscape scale; (2) incidental predation is positively related to the abundance of food at the foraging scale; and (3) incidental predation is influenced by additional foraging costs, namely predation risk from a third trophic level, at the foraging scale. To test the latter, we examined the relationship between QHRs and vegetative cover immediately surrounding nests, and related this to levels of incidental predation. We also tested for a relationship between incidental predation rates and QHRs at an intermediate scale. We measured QHRs beyond the immediate influence of local foraging risk surrounding a nest (~5 m away), but at a scale too small for QHRs to integrate food abundance. With these potential influences removed, QHRs should reveal no information on incidental predation rates (Fig. 1).

In 1998, we used giving-up densities (GUD, the remaining density of food within a patch after exploitation by a forager) in experimental food patches as surrogates for quitting harvest rates (Brown 1988), which allowed direct tests of predictions (1) and (3). In 1997, we assessed the density of red maple seeds surrounding nests, which allowed a direct test of prediction (2). Moreover, natural seed density should be strongly and positively correlated with QHRs; thus, we also tested prediction (1) using seed densities in place of GUDs. Concordance of the results from the two analyses should dispel concerns regarding repeatability and should broaden our conclusions across years with different mouse densities.

## METHODS

### Study site

Our field studies were conducted on the property of the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York (41°50' N, 73°45' W), USA. IES property contains ~325 ha of continuous eastern deciduous forest. The forest canopy is dominated by oaks (*Quercus rubra* and *Q. prinus*), with oaks, sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), maple-leaved viburnum (*Viburnum acerifolium*), and witch-hazel (*Hamamelis virginiana*) common in the understory. We used six 2.25-ha forest plots (separated by 0.5–4 km) as sites for both rodent live-trapping and the artificial nest experiment. The plots were arranged as an 11 × 11 array of grid points (one plot used a 12 × 10 array because of topographical constraints), with 15 m between points. We first describe the experimental protocol used in 1998 and, in a separate section, detail how the 1997 protocol differed.

### *Small-mammal trapping*

Two Sherman live traps ( $7.6 \times 8.9 \times 22.9$  cm, H. B. Sherman Traps; Tallahassee, Florida) were permanently placed at each of 121 grid points per plot, for a total of 242 traps per plot. Traps were baited with crimped oats and were covered with a board for protection from the sun and rain. Small mammals were trapped for two consecutive days during monthly trapping session. Traps were set between approximately 1600 and 1800 and were checked between 0730 and 1100 the next morning.

Each small mammal captured (except shrews) was given a numbered metal eartag for individual identification at first capture. At each capture event, we recorded species identification, tag number, gender, age, reproductive condition, body mass, and trap station. Animals were released after processing at the point of capture. Densities of white-footed mice were enumerated as minimum number known alive (MNA) per plot. High capture success of individual mice (>80% per two trap nights) made MNA an accurate method of calculating mouse densities (Hilborn et al. 1975).

These methods were modified on three of the plots designated as chipmunk removal treatments. On these plots, small mammals were trapped for three of every four weeks during June, July, and August, and captured chipmunks were released off site >10 km away. Chipmunks were removed for the purpose of studying Lyme disease dynamics in manipulated host communities in an unrelated study (e.g., Schmidt et al. 1999). Mice appear to have responded behaviorally; but not numerically, to the chipmunk removal (Schmidt et al. 2001). Nonetheless, any responses to the manipulations should in no way alter the model's predictions.

### *Artificial nest experiment*

On 10 June 1998, we placed out 54 artificial stick nests 0–15 cm above ground, mimicking the location of Veery nests. Nine nests were evenly spaced in each of the six plots, with 50-m spacing between the nests. This spacing makes it very likely that no two nests were within the home range of a single mouse. Two days after the nests were distributed within the plots, we baited each nest with one Zebra Finch egg and two blue plasticine eggs measuring  $22 \times 17$  mm, the approximate size of Veery eggs (Harrison 1975). We wore gloves when handling the nests and eggs. We checked nests every two days for the presence and disturbance of eggs, and considered the nest to be depredated if eggs were missing, destroyed, or the plasticine eggs showed tooth or scratch marks. Identifications were made based on imprints on the plasticine eggs. We identified the predators as white-footed mice ( $n = 31$ ), eastern chipmunks (*Tamias striatus*;  $n = 8$ ), raccoon, or opossum (*Procyon lotor* and *Didelphis virginiana*, respectively;  $n = 11$ ), and unidentified ( $n = 4$ ).

For each nest, we scored vegetative cover as 1 (0–

33%), 2 (34–67%), or 3 (>67%) at heights <0.1 m and >0.1–1 m. Cover was estimated in this fashion over a 1 m radius plot centered on each nest and broken into quarter sections, each of which was independently scored. In total, there were eight subscores (four quarters and two heights), and total scores could range from 8 to 24. For the analyses that follow, we collapsed the range of variation such that 1 = scores 8 or 9, 2 = scores 10 or 11, and so on.

### *Giving-up densities*

We used the technique of giving-up densities (GUDs) to assess environmental harvest rates. To collect GUDs, we present a forager with an artificial food patch consisting of, for example, a seed and sand substrate mixture. Given diminishing returns (i.e., the forager's harvest rate declines with time spent exploiting the patch), an optimal forager should exploit a patch until its harvest rate declines to the sum of its foraging costs (including metabolic, predation risk, and missed opportunity costs of not engaging in alternative activities):  $H = C + P + MOC$ . The density at which this relationship is satisfied and the forager ceases exploiting the patch is its giving-up density (Brown 1988, 1992). In the absence of local differences in predation risk and metabolic costs, differences in GUDs will be related to the differences in the mean environmental quality as determined by resource abundance (Charnov 1976). However, when local conditions surrounding artificial patches (e.g., vegetation cover, distance from a refuge) modify predation risks, GUDs will also reflect these additional costs.

After the artificial nest experiment, we deployed artificial food patches (seed trays) composed of a circular plastic tray (30 cm in diameter, 4 cm in height) to which we added 2 L of sifted bank sand and 4 g of unhusked millet seed. We collected GUDs from seven of the nine artificial nest locations per plot, chosen arbitrarily, but also to represent the full range of variation in the number of days that nests had survived. We placed a single seed tray, called the nest tray, at the same location where the artificial nest was placed. We placed two remaining seed trays, referred to as peripheral trays, 5 m away from the nest location in a randomly chosen north–south or east–west orientation. Because mice were responsible for the majority of predation events, we targeted mice for the collection of GUDs. Mice had access to the trays each evening between approximately two hours before sunset (1900) and sunrise (approximately 0500). Trays were sieved between nights to collect the uneaten seeds, which were cleaned of debris and weighed to measure the giving-up density. We collected GUDs on 6 July and for three consecutive days between 9 and 11 July. The first day of data collection was considered a pre-baiting period and was not used in the analyses; nonetheless, on all four days, nearly all trays were found and were heavily exploited by mice. We identified trays that mice had exploited by

footprints and tail drags in the sand and by mouse feces. For the few instances in which we could not identify the animal exploiting a tray, we excluded the data from all analyses.

#### General analyses

Detailed results of the nest predation experiment are the subject of a companion paper (Schmidt et al. 2001); however, we point out that white-footed mice were responsible for 63% (34 of 54) of predation events and, subsequently, were the target of GUD collection. All analyses in this paper are restricted to nest predation events and GUDs ascribed to white-footed mice, unless otherwise noted. For landscape-level analyses, we calculated nest daily mortality rates (DMR) for each plot by dividing the number of nests depredated by mice by the total number of nest exposure days. For the foraging-scale analyses, we used the number of days that a nest survived as our metric of nest survivorship. Giving-up densities were logarithmically transformed to normalize the data and to provide a more linear fit between GUDs and quitting harvest rates (Kotler and Brown 1990).

Based on our model of incidental predation, we predicted an inverse relationship between nest mortality and GUDs at the landscape scale (i.e., between plots). To obtain a better measure of the environmental QHR, we averaged GUDs across each plot (GUD, peripheral trays only) so that local foraging cost associated with any one location simply acts as a random variable. We used linear regression to test the predicted relationship. However, to provide a more linear fit between nest mortality rates and GUDs, we transformed GUDs using the Box-Cox transformation, which employs a maximum likelihood approach to find the best approximation to normality within the family of power transformations (Sokal and Rohlf 1981). We used one-tailed probabilities for these analyses because our model allowed us to predict the direction of putative relationships.

In a second analysis, we tested for a relationship between QHRs and incidental predation at the intermediate scale using linear regression, with each nest and its associated peripheral giving-up densities (mean of the two trays) as an independent data point.

Our third analysis focused on local foraging costs associated with vegetative cover in the immediate vicinity of nest locations, and thus was restricted to GUDs from the nest trays. To test for an effect of cover, we used Spearman's rank correlation for the vegetation score and the variable (GUD – nest GUD). Prior analyses revealed that GUDs influenced nest mortality, consistent with our first prediction. Relative nest GUD, (GUD – nest GUD), eliminates the effect of plot by quantifying the influence of vegetative cover on local GUDs as the magnitude of departure from the plot GUD. Giving-up densities can be used to examine the foraging costs associated with vegetative cover, but

they do not measure other factors associated with vegetation, such as an effect of nest concealment. We discuss these issues below.

#### The 1997 experiment

The previous experiment (initiated on 10 June 1998) was a replication of an earlier experiment (initiated on 25 June 1997), which we now describe. The two experiments differed in several respects. In 1997, (1) nests were constructed of natural materials, such as leaves and grasses; (2) nests were checked every three days for a total of 15 exposure days; (3) smoked aluminum plates surrounding nests further aided the identification of nest predators; and (4) mice, rather than chipmunks, were removed from the three removal plots. These differences may complicate a between-years comparison of nest predation rates, but they do not alter our predictions in any way. Also, in 1997 we did not collect giving-up densities as a surrogate for quitting harvest rates. Instead, following the nest experiment, we assessed the abundance of red maple seeds (the dominant seeds available at the study site during June; C. Canham, unpublished data) in two 1-m<sup>2</sup> sampling plots randomly placed in the vicinity of each nest (~1–2 m). We ranked the abundance of seeds from 1 (seeds rare or absent) to 4 (seeds abundant).

For 1997 analyses, we substituted the mean seed abundance rank in place of GUD for the analyses described earlier, but we did not examine local foraging costs. In the discussion, we justify the similarity of the two measures. In addition, we used linear regression to test the prediction that incidental predation increases with local (i.e., foraging-scale) food abundance. We used the number of days that a nest survived as the dependent variable, and we calculated a relative seed abundance metric as the independent variable. Seed abundance surrounding a nest will, on average, be higher in plots with overall greater seed abundance, and such plots should have lower nest predation rates because greater food abundance at this scale increases QHRs. Therefore, we calculated relative seed abundance as: (mean plot rank – nest rank). This eliminates the landscape effect predicting that predation will decrease with more food through the effects on QHRs, and it more directly tests whether nests surrounded by higher food abundance, relative to a mouse's environment, have higher predation rates.

## RESULTS

### Nest mortality and giving-up densities

We used linear regression to test for a relationship between mouse density and nest daily mortality rate (DMR) per plot. Nest mortality tended to increase with mouse density only in 1997 (for 1997,  $r^2 = 0.62$ ,  $P = 0.064$ ; for 1998,  $r^2 = 0.33$ ,  $P > 0.20$ ). Thus, for 1997 we performed subsequent analyses using the residuals from this regression. In accord with our first prediction,

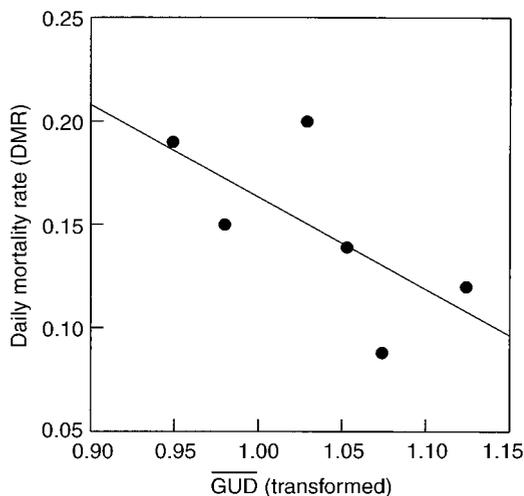


FIG. 3. Nest daily mortality rate (DMR) as a function of the plot giving-up density ( $\overline{GUD}$ , transformed).

DMR decreased (marginally significant) with increasing  $\overline{GUD}$  ( $r^2 = 0.45$ ,  $n = 6$ ,  $P = 0.072$ ; Fig. 3) and residual DMR decreased with increasing mean seed abundance ( $r^2 = 0.59$ ,  $n = 6$ ,  $P = 0.038$ ; Fig. 4). In addition,  $\overline{GUD}$  and mean seed abundance were unrelated to mouse density ( $r^2 < 0.16$ ,  $P > 0.40$  for each). Thus, the negative relationships between nest mortality and  $\overline{GUD}$  or seed abundance were not due to spurious correlations between these variables and mouse density. In accord with our prediction at the intermediate scale, nest mortality was unrelated to giving-up densities ( $r^2 < 0.01$ ,  $n = 31$ ,  $P > 0.90$ ) or to seed abundance (one-way ANOVA:  $F_{3,25} = 0.23$ ,  $P > 0.80$ ).

The enemy-free space mechanism predicts that not only should predation rates decline at higher quitting

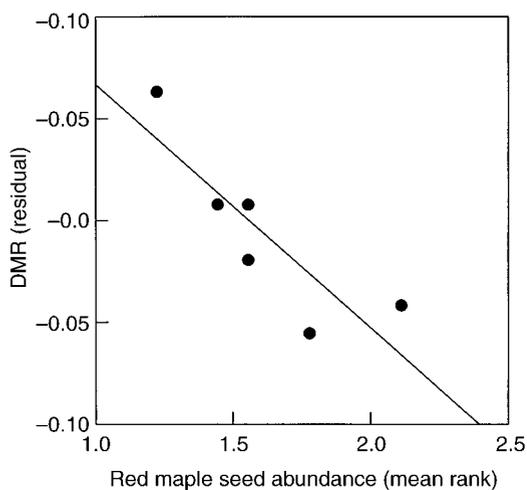


FIG. 4. Residual nest DMR as a function of the mean ranked red maple seed abundance. Residuals result from a prior regression of nest mortality (DMR) against mouse density.

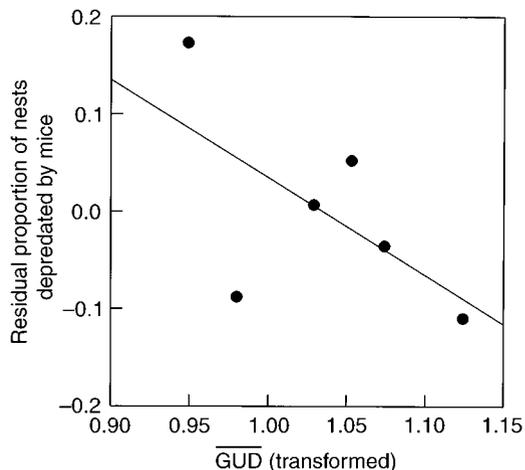


FIG. 5. Proportion of nests depredated by mice (residual) as a function of the plot giving-up density (transformed). Residuals result from a prior regression against mouse density.

harvest rates, but also that fewer nests should be depredated because predators are not in the vicinity of a nest. We tested this prediction by examining the relationship between the proportion of nests depredated by mice (arcsine square-root transformed) and  $\overline{GUD}$ s (1998) or mean seed abundance (1997). As in the earlier analyses, we first regressed the proportion of nests depredated by mice per plot against mouse density. There was a positive relationship in both years (for 1997,  $r^2 = 0.79$ ,  $P < 0.01$ ; for 1998,  $r^2 = 0.73$ ,  $P < 0.02$ ). We next regressed the residuals from these analyses against  $\overline{GUD}$  or mean seed abundance. Residuals were negatively, but only marginally, related to  $\overline{GUD}$  ( $r^2 = 0.41$ ,  $P = 0.087$ ; Fig. 5), and were both negatively and significantly related to mean seed abundance ( $r^2 = 0.60$ ,  $P = 0.036$ ; Fig. 6).

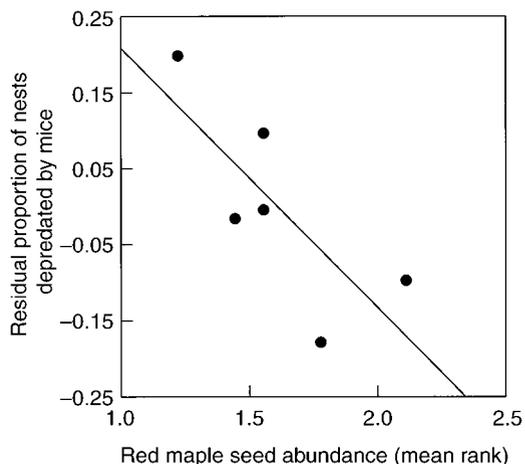


FIG. 6. Proportion of nests depredated by mice (residual) as a function of the mean red maple seed abundance. Residuals result from a prior regression against mouse density.

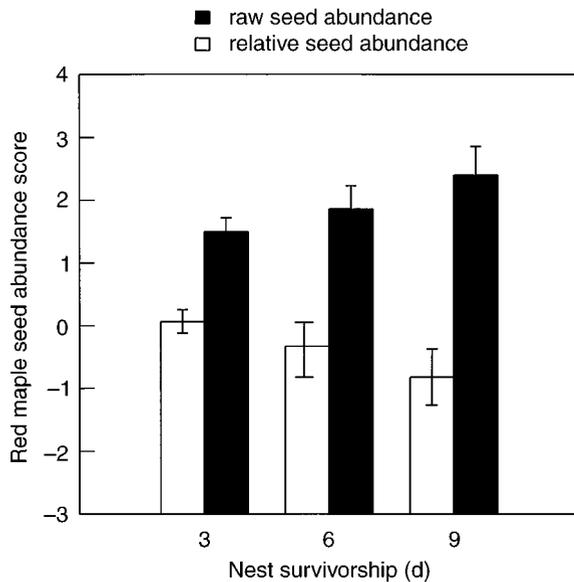


FIG. 7. Mean raw (+ 1 SE; solid bars) and mean relative ( $\pm$  1 SE; open bars) red maple seed abundance scores shown for nests depredated after 3, 6, or 9 days. Means combine nests depredated by either mice or chipmunks.

#### *Nest survivorship and local seed abundance*

In 1997, we regressed nest survivorship against the local abundance of red maple seeds, using both the raw seed abundance ranks and relative seed abundance. We used nests depredated by either mice or chipmunks in this analysis to provide larger sample sizes, and because both species should respond similarly to red maple seed abundance. In accord with our predictions, nest survivorship increased with raw seed abundance ( $r^2 = 0.11$ ,  $P = 0.03$ ,  $n = 34$ ; Fig. 7), but decreased with relative seed abundance, i.e., when abundance was scaled relative to the plot mean ( $r^2 = 0.13$ ,  $P < 0.02$ ,  $n = 34$ ; Fig. 7).

#### *Nest survivorship and local foraging costs*

The influence of vegetative cover on local foraging costs at the nest site differed between control vs. chipmunk removal plots. In control plots, nest GUDs increased relative to the plot GUD as local cover increased. The relationship was weak ( $r_s = 0.34$ ,  $P = 0.09$ ), but two of three plots had much higher correlation coefficients. Small sample sizes precluded any significant results; however, a combined probability test showed a significant effect ( $\chi^2 = 13.0$ ,  $df = 6$ ,  $P < 0.05$ ). Thus, mice were averse to foraging in cover on control plots. In contrast, on the chipmunk removal plots, we found a strong decline in the nest GUDs relative to the plot GUD as local vegetative cover increased ( $r_s = -0.78$ ,  $P < 0.01$ ). Mice were prone to foraging in cover in plots where chipmunks were removed.

Based solely on the relationships between cover and

nest GUDs, we expected to see nest survivorship decline with declining relative nest GUD. However, vegetative cover surrounding a nest may have multiple influences. First, as we have documented, cover is associated with higher or lower foraging costs depending on the presence or absence of chipmunks. Second, cover may conceal a nest from a searching predator, or otherwise increase searching costs (Bowman and Harris 1980). For control plots, these two effects acted in concert: vegetation increased foraging costs and concealed the nest. Indicative of the combined effects, nest survivorship was positively correlated to nest GUDs in the control plots ( $r_s = 0.48$ ,  $P = 0.03$ ). In the removal plots, these two effects acted in opposition. In this case, despite the strong relationship between cover and foraging costs, there was no significant relationship between foraging costs and nest survivorship in the chipmunk removal plots ( $r_s = -0.19$ ,  $P > 0.25$ ).

#### DISCUSSION

Our study of white-footed mouse predation on songbird nests supports the predictions of our model of incidental predation. At the landscape scale, we found a negative relationship between quitting harvest rate (or its correlate, seed abundance) and incidental predation by mice on artificial nests, analyzed using either mortality rates or the proportion of nests depredated. These results were predicted from two separate mechanisms. As quitting harvest rates increase, (1) the amount of space over which a predator forages decreases, and (2) the amount of time spent foraging decreases. The mechanism of enemy-free space differs from the reduced foraging time mechanism in that the former is spatially explicit and may have important consequences for the stability of predator-prey interactions, or may provide mechanisms of coexistence for prey species that share a predator (K. A. Schmidt, *unpublished data*). Both the reduced foraging time hypothesis and the enemy-free space hypothesis predict that nest mortality rates will decline and that, within a specified period of time, fewer nests will be depredated as quitting harvest rates increase. Thus, it may prove difficult to tease apart these two mechanisms without data on predator movement patterns.

Our model also predicts that incidental predation should increase as local food abundance increases. In accordance with this prediction, nests locally surrounded by a higher abundance of red maple seeds had, on average, higher predation rates. These results were particularly informative because predation rates did not simply increase with the raw seed abundance (in fact, they declined), but increased only when seed abundance was scaled relative to the mean. These results reflect our earlier prediction that greater food abundance at a spatial scale on the order of, or greater than, an individual's home range increases quitting harvest rates and thus decreases predation. The effect of local

food abundance only becomes clear once the larger scale influences are removed.

We also predicted that nest predation should be unrelated to quitting harvest rates at intermediate spatial scales. Because our prediction was the same as the null prediction (i.e., no relationship) it perhaps represents weak evidence. Nonetheless, this test serves as a check on our methods in that, at the spatial scale at which we expected no shared influences on QHRs and incidental predation rates, we indeed found no relationship. In fact, our study reveals how giving-up densities themselves can be used to determine at what spatial scale(s) relationships exist between quitting harvest rates and incidental predation (Fig. 1). In this way, GUDs can be used to determine the ecological scales relevant to understanding the subtleties of predator-prey interactions and, aided from theoretical models, the processes occurring at each scale.

Results from 1997 and 1998 were consistent with each another except that statistical trends in the latter were generally marginally significant. This difference may reflect higher mouse densities (1998 densities were roughly double the 1997 densities; Schmidt et al. 2001), which may reduce the amount of enemy-free space (e.g., Gratton and Welter 1999). Although giving-up densities are clearly related to quitting harvest rates (e.g., see Kotler and Brown 1990, Morris 1997, Morris and Davidson 2000), less is known about the relationship between the standing crop of resources in the environment and quitting harvest rates. Numerous studies have shown that quitting harvest rates increase with increasing food in the environment (Brown 1992, Brown et al. 1992, Bowers et al. 1993, Morgan et al. 1997, Olsson and Holmgren 1999), and our results are consistent with this view. Similarly, of the ecological parameters used to characterize the environment and foraging behavior of the Lesser-spotted Woodpecker (*Dendrocopos minor*), differences in average prey abundance across territories explained the greatest variation in giving-up densities (Olsson and Holmgren 1999, Olsson et al. 1999). Thus we feel confident in substituting seed abundance estimates in the place of GUDs. In a cautionary note, conditions greatly removed from equilibrium may obscure the relationship between food abundance and quitting harvest rates, but this should lead to the lack of any relationship between seed density and predation rates, rather than spurious relationships.

#### *Behavioral trophic cascades*

An unexpected result from our study was the differential response of mice to vegetative cover in the presence vs. the absence of chipmunks. In the absence of chipmunks, mice were strongly prone to forage under the protective cover of vegetation. Many studies have shown that increased cover provides foragers with a refuge from predation and reduces foraging costs associated with predation risk (Kotler 1984, Falkenberg

and Clarke 1998). However, interspecific interactions may also mediate the degree to which individuals expose themselves to riskier habitats (Bowers et al. 1987, Kotler and Holt 1989, Ziv et al. 1993, Falkenberg and Clarke 1998). Accordingly, we found that the use of cover by mice appeared to be mediated, in part, by the presence of chipmunks. In the presence of chipmunks, mice were averse to foraging under greater vegetative cover. Moreover, we documented that the foraging costs of cover on mice, as influenced by both predators and chipmunks, had cascading consequences on the next trophic level, songbird nests. Thus, the foraging costs associated with cover in the presence of chipmunks contributed to lower nest predation rates by mice. In the absence of chipmunks, any potential benefit of cover in concealing a nest was apparently nullified by higher foraging activity by mice. These results highlight the importance of using mechanistic approaches to study nest predation. The effects of cover were dual and interactive with other species in the community. Birds may be in a "catch 22:" by attempting to conceal their nests in dense cover, they may consequently expose their nest to higher levels of predator activity in dense cover. Alternatively, some species may avoid dense cover altogether (e.g., Ovenbird, *Seiurus aurocapillus*).

#### *Using artificial nests*

The interpretation of artificial nest experiments has provoked a long and contentious debate in avian ecology (reviewed in Major and Kendal 1996). Although ecologists recognize that predation on artificial nests often does not correspond to predation rates on real nests (Willebrand and Marcström 1988, Yahner et al. 1989, Ortega et al. 1998, Sloan et al. 1998), the underlying patterns are often considered to reflect reality. In this study, we have taken artificial nest studies one step further by investigating the underlying mechanisms that lead to predation on nests. We recommend combining similar mechanistic approaches with artificial nest studies in hope of removing or reducing the stigma of artificial nest studies.

Giving-up densities may be used to collect data on nest predation rates, both as a relative means (e.g., habitat edges vs. interiors) and as an absolute means. We have shown that GUDs are correlated with predation rates, and it should be possible to predict at least qualitatively, if not quantitatively from regression equations, predation rates on songbirds. In addition, GUDs can often be used, as in our study, to target specific predator species.

#### *Giving-up densities as behavioral indicators of ecological processes*

Our results showed that giving-up densities were correlated with nest predation rates, whereas mouse density was either uncorrelated with (1998 experiment), or only marginally related to, nest predation (1997 ex-

periment; perhaps the result of experimental mouse reductions). GUDs, because of their inclusive nature, may be better indicators of nest predation than the population density of predators. GUDs are implicitly sensitive to changes or differences in population density through, for example, the effects of exploitative or interference competition (Bowers et al. 1993, Morris 1997; K. A. Schmidt, *unpublished data*). In addition, GUDs reflect ecological relationships beyond population density, such as the energetic state of the forager and short-term changes in the value of food or predation risk. Finally, GUDs respond quickly to behavioral changes in organisms and thus represent a leading indicator for ecological interactions, whereas population responses involve time lags through dispersal or reproduction. Thus predation rates correlate well with predator population densities over long temporal scales (Ketterson et al. 1996, Jedrzejewska and Jedrzejewski 1998) over which behavioral responses cannot necessarily extend. However, long-term relationships between GUDs, population densities, and nest predation rates are either lacking or extremely uncommon. Validating the usefulness of these alternative approaches over multiple scales would be valuable.

Finally, we hope that this research will shed new light on the ecology of generalist predators. Generalists are often associated with a suite of ecological traits, such as type III functional responses, decoupled predator-prey dynamics, and diffuse interactions. Yet qualitative descriptions of the traits of generalist predators do not begin to describe their complex interactions with their prey. Incidental predation is likely to be an extremely common phenomenon among generalist and, perhaps to a smaller degree, specialist predators. With new importance placed on weak interactions and their potential stabilizing influence on community structure (McCann et al. 1998, Berlow 1999), incidental predation may reveal the importance of generalist predators to community-level phenomena.

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