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Behavioral Indicators of Predator Space Use: Studying Species Interactions Through the Behavior of Predators

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Behavioral indicators of predator space use:

Studying species interactions through the behavior of predators

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ABSTRACT

Predation has major impacts on survival and reproductive success for many species. To quantify these effects, ecologists often choose to intensively study prey populations to measure predation rates and/or estimate predator abundance. But in some cases, predation rates are less strongly related to predator abundance per se than to spatial and temporal patterns of predator space use; thus quantifying the latter may provide meaningful surrogates of predation rates that scale up to larger areas. This is particularly true when safety for prey, especially sessile and vulnerable prey, is strongly linked to predator-free space. Our own research programs have used two general types of behavioral indicators to quantify space use by predators: giving-up densities, as a surrogate for patch quitting harvest rates, and activity density. We discuss two general mechanisms by which predator-free (or predator-poor) space is created and link these mechanisms to behavioral indicators that can be easily collected in the field. We then summarize our past work on predation on passerine nests and moth pupae to demonstrate how using behavioral indicators of space use can reveal much about the impact of a predator on its prey. We demonstrate that behavioral indicators can be used as: (1) leading indicators for predation rates, (2) surrogates for information otherwise difficult to obtain, (3) integrative measures of the strength of species interactions, and may (4) reveal the outcomes of ecological interactions, such as prey persistence.

Keywords: behavioral indicators, foraging theory, GUDs, incidental predation, predator space use

INTRODUCTION

Predation has major impacts on survival and reproductive success for many species. To quantify these effects, ecologists often choose to intensively study predator and prey populations to measure predation rates and/or estimate predator abundance. But in some cases, predation rates are less strongly related to predator abundance per se than to spatial and temporal patterns of predators' space use. The consequence is that predator density can be a lagging or misleading indicator of ecological relationships when the factors that govern predator space use, e.g., the predator's motivational state or patch use decisions based on the local levels of risk and reward, do not scale with or lag behind conspecific population density (Brown et al. 1999, Schmidt et al. 2001a, Pusenius and Schmidt 2002). Under these circumstances, developing informative behavioral metrics (i.e., behavioral indicators) that do scale with predation rates is imperative and of obvious practical value. Two metrics or behavioral indicators of predation rates we consider below are quantifying the amount of space occupied by predators or the intensity at which they exploit space.

Consider nest predation as a specific example of these points. Nest predation is often the leading cause of reproductive failure in birds (Martin 1992) and other nesting organisms (e.g., turtles, Chaloupka and Limpus 1991), and thus is an important determinant of population vital rates. A predator's attack on a songbird nest is the outcome of numerous behavioral decisions made by the predator and prey. Perhaps none are as important as the decisions of where the predator should forage and for how long. To see this, first consider that although parents can actively select nest sites to reduce predation risk, nests themselves cannot move once established and so prey escape tactics are relatively passive. Second, outside colonial species that rely on predator satiation as a means to reduce the magnitude of predation, nests are cryptic as well as ephemeral, dispersed and occurring at low densities, and in some cases outnumbered by their predators. The latter can occur because most nest predators are foraging generalists that rely on a broad prey base and so can out number some classes of prey items. In New York State, for instance, the 2.25-ha trapping grids managed by our colleague, Richard Ostfeld, can hold > 200 individual white-footed mice and eastern chipmunks in some years, whereas breeding bird densities are < 10 pairs/ha and much lower when we consider only ground- or low-shrub nesting species.

Based in part on the ratio of predator/prey abundances, the generalist feeding habitats of most nest predators, and the low intake (nests often comprise $\leq$ 2% of predator diet), that many predation events are incidental in nature (Vickery et al. 1992, Yanes and Saurez 1996); that is, predation occurs as the result of encountering relatively rare and hence “unexpected” prey items while searching for primary prey or simply occupying high quality resource patches. Hence, rates of incidental predation will correlate with patterns of predator space use and exploitation, and developing models or methods to track the latter will benefit from a consideration of the predator’s patch use behavior. We develop these explicit relationships below.

While we have conceptualized our ideas largely based on our empirical studies of breeding songbirds (KAS) and pupae of gypsy moths (EMS), our framework should be amenable to prey that are encountered largely incidentally by generalist predators, including prey organisms that are relatively uncommon or ephemeral, sessile or otherwise are largely inactive during at least one life history stage. For example, this can also include the vulnerable young of cheetahs (Durrant 1998) and deer (Pojar and Bowden 2004). After presenting our conceptual background and supporting empirical studies we expand our framework to consider incidental or non-incidental prey that benefit from alternative mechanisms that ‘anchor’ predators in space in turn creating spatial heterogeneity in predator activity that prey may find refuge in. Through developing a framework and summarizing our past work we argue that behavioral indicators of predator space use can reveal much about the predator’s impact on its prey and hence the habitat quality and reproductive success of the prey. We will demonstrate that behavioral indicators, and the framework from which they emerge, may be particularly valuable as: (1) leading as opposed to lagging indicators of the magnitude of predation, (2) surrogates for information otherwise difficult to obtain, (3) integrative measures of the strength of species interactions, and lastly may (4) reveal novel insights into ecological interactions.

CONCEPTUAL FRAMEWORK

Quitting harvest rates, space use, and incidental predation – The branch of optimal foraging theory known as patch-use theory has developed around the question of how much time to allocate to a resource patch. The answer is generally given in the form of a patch giving-up rule. In the case of prescient foragers with random search the appropriate rule is to forage until the rate of resource harvest (a declining function of time spent foraging in the patch) equals the accrual rate of foraging costs (Charnov 1976, Brown 1988). Brown (1988, 1994) recognized three general foraging costs: predation (P), missed opportunity (MOC; the value of time should it be spent on alternative fitness-enhancing activities) and metabolic (C) costs. This giving-up rule is referred to as a fixed quitting harvest rate (QHR) rule because it results in patches that have equal harvest rates after a forager ceases (i.e., quits) to exploit the patch irrespective of initial patch quality. It can be written as: QHR = P + MOC + C. When the initial harvest rate of a patch is less than P + MOC + C the patch is unprofitable (i.e., the optimal time spent foraging is zero). A forager that can assess and respond to spatial heterogeneity in resource abundance should exploit only those resource patches that it considers profitable (Stephens and Krebs 1986, Schmidt and Brown 1996, Schmidt et al. 2001). Unprofitable and therefore unused space (i.e., predator-free space) can provide refuge that may be especially important for incidental prey; prey too sparse for predators to base patch-use decisions on, yet they are attacked whenever generalist predators encounter them while foraging for more common foods (Vickery et al. 1991).

The giving-up rule also indicates two general routes to patch rejection (see Fig. 1) corresponding to "top-down" and "bottom-up" forces, respectively: predators reject patches associated with a high risk of predation from apex predators (e.g., nest-robbing chipmunks avoid patches associated with greater risk of predation from weasels) and predators reject patches lacking sufficient resources (nest-robbing chipmunks avoid patches with few red maple seeds). These routes are non-mutually exclusive in the sense that patch rejection always occurs because there are insufficient resources to offset the high cost (including the risk of predation; Brown and Kotler 2004) of foraging in the patch. Nonetheless, it is also valuable to separate these two components because the abundance and distribution of resources and apex predators (maple seeds and weasels, respectively, in our chipmunk example) are largely independently determined (but see Sih 1998 for a summary of models that suggest apex predator abundance should match the abundance of resources for its prey).

More formally, Schmidt et al. (2001a) constructed a model explicitly linking generalist predator foraging behavior, space use, and predation rates on incidental prey. In the model, predators assess patch quality and only forage in those resource patches considered profitable (i.e., initial patch harvest rate exceed the predator’s quitting harvest rate, QHR); unprofitable space is unused (Schmidt 2004). By varying the QHR, its relationship to space use and incidental predation rates could be determined (also see Schmidt et al. 2001 for explicit equations). If the QHR is low (i.e., resources are extremely valuable) most patches are profitable and nearly all available space is used. If the QHR is high (i.e., resources are relatively cheap or predation risk is very high) many patches are unprofitable and space use declines. Therefore, changing the QHR drives an inverse but non-linear change in the amount of space predators forage within (Schmidt et al. 2001, Pusenius and Schmidt 2002). In one analysis of the model that included uncommon incidental prey dispersed (independent of primary prey) among the patches, increasing the QHR reduced incidental prey consumption. Overall consumption closely mirrored predator space use when primary prey were distributed in a Poisson fashion (Fig. 3), but this result may not follow for other distributions of prey or if primary and incidental prey are themselves inversely correlated.

Space need not be treated dichotomously as predator-free or predator-occupied and this fact can further strengthen the relationship between the QHR and space use. The QHR is both a qualitative (predator-free/occupied) and quantitative (time spent searching for primary prey) indicator of space use/exploitation. Assuming random search within a patch and holding initial primary prey density fixed, search time (t) is a decreasing function of QHR or the final density of primary prey remaining in a patch (Schmidt and Brown 1996). Predator-free space is equivalent to patches where t=0.

Spatial anchoring and predator space use – Within our framework of incidental predation predator activity is “anchored” to high reward/low risk sites creating predator-free or predator-poor space at other sites. Spatial heterogeneity in predation risk may also arise from alternative mechanisms of spatial anchoring of the predator that may be important for both incidental and non-incidental prey. This includes interactions with conspecifics (e.g., territoriality) and the need to return to a central home location (e.g., nest or den). For example, Sergio et al. (2003) observed that black kite (*Milvus migrans*) territories were aggregated within interstitial areas outside the sphere of influence of its intra-guild predator, the eagle owl (*Bubo bubo*). All black kite nests within 1 km of eagle owl nests were unsuccessful, and kite nests beyond 1 km showed a linear increase in productivity with greater distance from owl nests. Likewise, Mech (1977) noted that wolves form stable territories that are separated by buffer zones up to 2 km wide, into which wolves rarely venture to avoid antagonistic interactions with neighboring packs. Nearly all surviving white-tailed deer in a declining population were within these buffer zones (Taylor and Perkins 1991). In this vein, Schauber (2000) modeled predator-free space as gaps between individual home ranges under different assumptions of territory spacing. Uniform territory spacing creates a linear decrease in predator-free space with increasing predator abundance until all space is occupied, whereas random spacing results in an exponential decrease, as has been observed for white-footed mice (Schmidt et al. 2006). With random territory spacing, some predator-free space persists even at high predator abundance, which was critical for gypsy moth persistence in Schauber's (2000) analysis. Through these mechanisms of territoriality and central place foraging, predator space may not correlate well with predator abundance, leaving the latter a poor indicator of predation risk to prey. Such cases call for measuring space use itself.

We end this section by noting that colleagues have suggested to us that true predator-free space does not exist – eventually predators will move through all available space. This remains to be demonstrated but it does have a ring of truth; predator-free space can best be considered as a transient phenomenon. But despite its transience, predator-free space can be critical when prey vulnerability is short-lived. Examples include gypsy moth pupae (vulnerable for ~ 13 days) and songbird nests (vulnerable for ~ 2-4 weeks) that comprise our own studies, but also includes cheetahs, which are vulnerable to intraguild predation largely as young cubs, and deer, which are vulnerable to predation from coyotes largely as young fawns (Pojar and Bowden 2004, Vreeland et al. 2004). Survival of these prey requires their locations remain predator-free for only days or weeks to have large repercussions. When prey are mobile, as when young cubs or fawns are moved, then even if individual pockets of predator-free space wink on and off, the mean amount of predator-free space is likely to be fairly stable in comparison.

EMPIRICAL STUDIES

Behavioral Indicators: monitoring quitting harvest rates and space use – Quitting harvest rates can be notoriously difficult to monitor in the field. Fortunately, counting the number of resource items remaining within a patch after a foraging bout, known as a giving-up density or GUD, often provides a useful surrogate of quitting harvest rates that is easily measured in the field (Brown 1988). Food patches should yield diminishing returns such that current amount of food in a patch correlates with the instantaneous harvest rate. These conditions are often easily fulfilled through the use of artificial food patches (Brown 1988) created by mixing a small quantity (to prevent satiation) of food (e.g., seeds) within a patch substrate (e.g., sand). Giving-up densities have been widely applied to quantifying individual foraging costs (see recent review by Brown and Kotler (2004), but as discussed above, GUDs collected across larger spatial scales can be used as surrogates for space use (Schmidt et al. 2001).

The technique of giving-up densities is an important tool in the ecologist's toolbox for measuring the landscape of foraging costs perceived by predators and the risk experienced by prey. However, not all prey are distributed within idealized food patches that the GUD technique often requires. Furthermore, the food patches themselves lure animals so that GUDs do not necessarily indicate specific sites predators would not use in the absence of a baited patch.

There are techniques to get around some of these concerns; for example by correlating GUDs to the physical landscape one may learn that a predator around foraging along habitat edges. An alternative to GUDs that we discuss here is directly quantifying predator activity. Predator activity density, i.e., the aggregate use of a site per unit area and time, is a more proximal measure of the landscape of risk experienced by prey. Activity density reflects the total *intensity of use* in a specific area by a number of individuals, rather than quantifying the *number* of individuals. The concept of activity density is similar to the idea of population density, but applies at the spatial scale of individual space use decisions. For instance, one raccoon (*Procyon lotor*) that traverses a given patch of space 6 times in a week should represent greater risk (i.e., higher likelihood of encounter) to prey than 3 raccoons that each traverse the same patch once a week. We have used two different indicators of small mammal activity density, (1) traps with zero captures and (2) track plates.

Case studies – Schmidt and colleagues (2001, Schmidt and Ostfeld 2003) tested the explicit links between QHRs (measured by GUDs), space use (quantified as the proportion single oat grains removed by mice off a lattice grid arrangement) in the white-footed mouse (nest predator), and predation on passerine nests (prey). They used artificial nests to increase sample sizes and have more control of the distribution of nests (Schmidt et al. 2001, Schmidt and Ostfeld 2003). These studies demonstrated the hypothesized relationships between (1) GUDs (collected at random locations within the same 2.25 ha plots where artificial nests were deployed) and space use in mice (Fig 4a) and (2) mouse space use and predation of nests by mice (Fig 4b). In contrast, plot-level mouse density failed to predict space use or predation rates on nests. Noteworthy in this regard, Schmidt and Ostfeld (2003) observed 7-fold variation in the amount of space occupied (based on oat grain removal) among the six study plots that in turn varied less than 2-fold in mouse density. Clearly in this example mouse abundance did not scale with their spatial activity, but it was the latter that determined nest predation. Interestingly, annual variation in mouse abundance does predict annual variation in nest success for the ground-nesting veery (*Catharus fuscescens*) suggesting that intra-annual spatial variability may be greater than inter-annual variability (Schmidt et al. 2006). Unfortunately, we do not have a temporal sequence of spatial activity or GUDs for comparison to mouse density. However, mouse GUDs were by far the highest recorded at the site in 2000 when mouse populations had collapsed and nest predation rates were their lowest.

Spatiotemporal shifts in space use or predation rates – Whereas the above example focused on spatial variability in QHRs and space use, understanding temporal changes is also important and can be addressed using similar techniques. Schmidt and Whelan (1999) documented a reprieve from nest predation for forest songbirds when a mulberry (*Morus spp.*) mast drew raccoons out of the forest within a suburban arboretum. We were first alerted to this through a drop in nest predation and shift from density-dependent to density independent predation mid-way through an artificial nest study. Artificial nests were replenished daily in the experiment, so intact nests remaining after a night of foraging by raccoons represented a giving-up nest density much the same as seeds remaining in a tray of sand after a bout of foraging. We subsequently demonstrated a concomitant drop in nest predation on shrub-nesting birds (American robin, *Turdus migratorius*, and wood thrush, *Hylocichla mustelina*). Importantly, artificial nest GUDs informed us of current temporal changes in predation rates on real nests. Similarly, Schmidt (2006) showed the density of active veery nests drops as much as 20% or more (due to predation) between the full and new lunar phases when white-footed mice demonstrated a 3-fold increase in the amount of space occupied (based again on oat grain removal), typical of nocturnal rodents (Kotler et al. 1991, Mandelik et al. 2003, Abramsky et al. 2004). These observations suggest that GUDs can be used as an indicator of temporal shifts in space use/activity and predation rates as alternative resources rapidly renew (or pulse) in the environment, or through rapid temporal variation in predation risk from apex predators. The two studies described above relied on 'natural' GUDs (or standing crop of nests after a night of foraging by raccoons or mice) instead of using artificial food patches. In these cases the experimenter has little control of resource renewal rates that can cloud interpretation of the data (see Morris and Mukherjeee, this volume). But systems such as these should be amenable to the use of artificial food patches for monitoring and understanding the causes and consequences of temporal shifts in predator behavior and predation rates. Raccoon food patches were developed after Schmidt and Whelan's observations (*Berris, unpublished*). Likewise, Schmidt (2006) did attempt to collect mouse GUDs, but artifacts due to playbacks of owl vocalizations interfered with isolating a moon effect (*KAS, unpublished*).

Variation in the predator community – Coexisting consumer species often differ considerably in their giving-up densities; in fact this observation has become a tool in the search for mechanisms of coexistence between competitors (Brown 1989, Kotler and Brown 1999). However, the relevance of interspecific variation in GUDs for species interactions outside of competition has received far less attention. Our model suggests interspecific variation, through effects on space use and predation, can be far-reaching. For instance, Schmidt (unpublished) collected GUDs from both white-footed mice and eastern chipmunks (*Tamias striatus*) foraging in the same food patches that were replenished between nighttime exploitation by mice and daytime exploitation by chipmunks. Mice (20g) had much lower GUDs than the larger bodied, diurnally-active chipmunk (100g). It is unknown whether body mass, metabolic demands or other life history characteristics might lead to a predictable hierarchy of GUDs among species. Regardless, these species differences, based on our modeling approach, predict that mice should exploit a greater amount of space than chipmunks, all else equal (see Fig. 1). If true, two additional predictions follow: (1) mice should cause higher mortality rates on nests than chipmunks (i.e., mice use more space) and (2) given the greater area of space used, mice will show compensatory predation on nests following chipmunk removal, but not vice versa. Both of these predications have been upheld (see Schmidt et al. 2001b and Fig. 5). Unfortunately, Schmidt and Ostfeld (2003) were unable to quantify space use in chipmunks, so the prediction of interspecific differences in space use commensurate with differences GUDs has not been directly tested.

The assumption of all ‘else equal’ certainly doesn’t hold in this example, and there are numerous alternative explanations for species differences in nest predation rates. For instance, the artificial nests used by Schmidt et al. (2001b) may not have mimicked real nests in important ways, i.e., chipmunks may use begging calls as cues to locate nests (Haskell 1999). Still, the conclusion we hope the reader takes away is that QHRs/GUDs are an empirical tool as well as the center piece of a larger set of conceptual ideas (e.g., mechanisms of coexistence, foraging ecology, incidental predation) that can be applied to individual species as well as communities. As used here, QHR theory and GUD methodology may provide a useful framework toward understanding the distribution of species interaction strengths within communities, or predicting the consequences, such as additive or non-additive predation resulting from the loss or introduction of predator species.

Zero-capture data – Our colleague, Richard Ostfeld, has maintained six 2.25 ha small mammal trapping grids at IES since 1995. We have used small mammal abundance data from these grids to document temporal trends in nest predation rates on ground-nesting birds, such as the veery. In early studies (Schmidt et al. 2001b) we used crude measures of mouse abundance: minimum number known alive (MNA). These studies were later followed by more sophisticated estimates of plot-level abundance through the program MARK (Schmidt and Ostfeld in press). At the same time, we began using a very crude metric of local activity density - simply quantifying the proportion of trap stations where no mice were captured over the course of a capture season. Not only do these metrics vary in their sophistication, but the field and analytical effort needed to produce each estimate varies considerably. In the end, correlating temporal and spatial variability in mouse abundance/activity to nest predation on two thrush species required only the simplest metric, zero-capture trap data (Schmidt et al. 2006).

The proportion of traps with zero mouse captures predicted nest predation in veeries both annually and locally within a 30 × 30m area (nine trap stations centered on each nest; what we called a nest neighborhood; Fig. 6). Zero-capture data also demonstrated an exponential decline in unused space as predicted from the random territory placement model of Schauber (2000) discussed above. However, the decline reached a plateau, not predicted in the model signifying that even at extreme mouse densities a significant proportion (~10%) of space, on average, remained unoccupied (Schmidt et al. 2006). This method of quantifying predator-free space by enumerating information only from trap stations that record no predator activity (i.e., captures) thus provides a useful surrogate for monitoring spatiotemporal heterogeneity in nest predation rates. In some ways, this should not be surprising. If prey are capable of appropriately responding to predation risk then knowledge of where predators are not may be a more meaningful way to track predation rates since the researcher is attempting to assess predation risk in ways that may be similar to what prey use. In our example, this works even though prey (i.e., stationary nests) have to ‘live’ with their choice for 4 weeks. However, if prey were not incidental we suspect predators would quickly respond to the distribution of their prey.

Track plates – When terrestrial predators are identifiable from their tracks, unbaited track plates offer an efficient method to quantify predator activity density at relevant spatial scales without substantially altering predator behavior or their pattern of space use as a result of luring the predator (e.g., traps or cameras baited with food or scent lures; Connors et al. 2005). Connors et al. (2005) designed track plates to use with small mammals by coating acetate transparency sheets with a mixture of graphite powder, mineral oil (for water resistance), and alcohol (carrier). These proved highly effective and convenient for recording tracks and had little evident impact on visitation by white-footed mice (Connors et al. 2005).

We used the activity data obtained from track plates to measure the magnitude, spatial scale, and temporal persistence (over periods of months to years) of hot spots and cold spots in mouse activity density (Connors 2005, Schauber et al. in revision). These characteristics appear to be highly relevant to the persistence of gypsy moths in eastern oak forests, where predatory mice are typically abundant and pupal predation rates are high (Campbell et al. 1975, Elkinton et al. 1996, Jones et al. 1998). The vulnerable pupal stage is sedentary and adult female moths are flightless, so egg masses are most likely to be laid in sites of low predation risk (i.e., spatial selection). We found that track activity at a tree was a strong indicator of predation rate on gypsy moth pupae deployed there (Fig. 7).

If hot and cold spots of predation persist between years and have spatial scales larger than typical dispersal distances of larvae, then larvae can inherit the level of risk their mothers experienced. This combination of spatial selection and inheritance can reduce overall predation on moth populations below the threshold necessary to cause negative population growth (Schauber et al. 2007). However, estimating predation from either naturally occurring or experimentally deployed pupae would likely yield biased results and actually alter the behavior of the foraging mice (Schauber and Jones 2006). Thus, using track plates to measured predator activity density as an indicator of predation risk was the only feasible way to test our hypotheses by quantifying the persistence and scale of relative refugia.

Overall mouse activity decreased greatly between 2004 and 2005, concommittant with a crash in mouse abundance following acorn failure (Connors 2005, Schauber et al. *in revision*). However, only by monitoring the spatial and temporal dynamics of mouse activity were we to fully understand the implications of this crash. Temporal autocorrelation of mouse activity between months was high during years of relatively high mouse density (2003 and 2004), providing stable refugia that prey could exploit, whereas this temporal autocorrelation was considerably lower during the crash year (Connors 2005, Schauber et al. *in revision*). We hypothesize that the increased stability of refugia during periods of high predator density is expected to buffer prey populations from the drastic mast-driven fluctuations that white-footed mouse populations exhibit (Wolff 1996, Ostfeld et al. 1996, McCracken et al. 1999). Such density dependence in space-use stability may arise via greater social stability during periods of high density when summer reproduction is suppressed (Falls et al. 2007), or perhaps just from demographic stochasticity in mouse populations at small spatial scales when overall density is low. These mechanisms are ripe for future empirical investigation, and highlight the insufficiency of predator population density as a sole indicator of risk to prey.

Concluding remarks – Our conceptual approach centers on an animal’s quitting harvest rate for two reasons. First, mechanistically both space use and time devoted to foraging any particular patch are related to the QHR and patterns of adaptive foraging as developed above. Second, the QHR (or GUD) is a phenomenological outcome of a predator’s assessment of its foraging costs and benefits (Brown 1988, Brown and Kotler 2004). The QHR thus presents a window into the world of a predator by reflecting its ecological relationships with its environment, such as its energetic state (influenced by its density and the availability of primary prey), the instantaneous risk of predation from apex predators, and current valuation of food and safety. QHRs/GUDs thereby incorporate the influence of multiple trophic levels (Fig. 1) and may provide a more informative and causal link to space use and rates of predation (i.e., strength of species interactions) than predator density would by itself. GUDs can also reveal the operation of density dependence (see Morris and Mukherjee 2007). For instance, changes in population density of the predator may manifest as a foraging cost (mainly the marginal value of energy increases with density, as resources are depleted; Schmidt et al. 2004) that can be observed through changes in QHRs and GUDs (Bowers et al. 1993, Davidson and Morris 2001, Morris and Mukherjee 2007). As with any ecological model, the set of linkages depicted in Fig. 3 represent a subset of those that actually exist, and some classes of predators may not reasonably fit within the current conceptualization. Nonetheless, we believe the model generalizes a broad and important group of interactions characterizing predator-prey interactions that fall within the purview of incidental predation. It also provides a cornerstone to conceptualizing behavioral mechanisms that anchor predators in space, such as territoriality and central place foraging, that are likely to generalize to both incidental and non-incidental prey (e.g., wolf-deer interactions; Mech 1977).

Although monitoring GUDs reveals insights into the costs and benefits of foraging, the use of artificial food patches to collect GUDs may not reveal predation risk for prey at any specific point, whereas quantifying activity density may. For instance, collecting GUDs in a forested landscape to monitor nest predation levels might tell us that predator space use and predation risk (on nests) in the environment is low but GUDs alone cannot reveal which individual songbird nests (or other prey) are most at risk because overall levels of predation risk and missed opportunity both manifest at large spatial scales. For example, abundant food elsewhere in an animal's territory will influence GUDs collected at a point source (Brown and Alkon 1990, Schmidt et al. 2001a). Likewise, GUDs collected at a relatively risk-free (from the predator's perspective) point in space but in an otherwise high risk environment would fail to accurately reveal the mean likelihood incidental predation outside local site where GUDs were collected. Alternatively, demographic inertia could cause the spatial and temporal distributions of activity of predators to imperfectly reflect the distribution of habitat quality (Schauber et al in revision). Quantifying activity density concomitantly with GUDs can enable researchers to disentangle and compare the landscape of risk experienced by prey (determined by activity density of predators) with the landscape of forging costs experienced by the predator.

It was our goal to promote the use of behavioral indicators as an effective tool to increase our understanding of predator-prey interactions, not as a substitute for measuring abundances and other population-level characteristics. A detailed field study of breeding birds will accurately measure nest predation rates, take video images of nest predators, and collect data on avian demography and possible information on site and individual variation in quality to monitor processes such as density-dependence in reproductive success. Yet many studies or basic monitoring schemes have more modest goals. Even if money is no objective, detailed field studies of breeding populations cannot estimate nest predation in advance of the breeding season - within season estimates will be too late to implement management programs intent on boosting reproductive productivity. In contrast, GUDs and activity density can be collected prior to the breeding season to monitor predator behavior or as surrogates for nest predation rates. Lastly, GUDs and activity density can greatly increase the cost-effectiveness of conservation efforts, particularly in poor nations that cannot mount an effective field effort to monitor avian reproductive ecology and nest predator behavior. Outside of monitoring actual predation events (artificial nests or video images from real nests) the predator has largely been absent from nest predation studies, although some excellent examples exist (e.g., Vigallon and Marzluff 2005). GUDs and activity density are complementary and cost-effective indicators of the "worlds" that predators and their prey inhabit.

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FIGURE LEGENDS

Figure 1. A simplified framework for viewing the operation of patch-use based interactions on prey mortality through the predator. Predator-free or predator-poor space arises through bottom-up and top-down factors that influence the predator's QHR. The QHR is an integrative measure that is influence by, among other factors not shown, the predator's density, and the abundances of primary food and predation risk from apex predators. When possible, we indicate the likely relationship(s) (0, +, -) between two factors when the first is increased, e.g., increasing the QHR creates more behavioral refugia and reduces foraging time.

Figure 2. Creation of nest predator-free space and consequences for incidental prey, i.e., passerine nests. There are two ways to interpret the figure (i) bottom-up and (ii) top-down creation. In (i) local primary prey density decreases from blue to red contour lines, whereas risk of attack from apex predators is homogeneous throughout the environment. The predator has a fixed quitting harvest rate (QHR) that increases from panel (a) → (c). Predator-free space is shown by removing contour lines in panels (b) and (c); i.e., predator-free space occurs where local resource abundance < QHR. A higher QHR creates more predator-free space and fewer nests are vulnerable to predation.

Alternatively, in (ii) contour lines indicate increasing (blue to red) QHR due to local risk from apex predators, whereas the abundance of primary prey is homogeneous throughout the environment. Primary prey abundance

In either case, In nature both scenarios are likely to apply simultaneously; the difference is whether one conceives of spatial heterogeneity created primarily through the distribution or reward (i) or risk (ii). In all cases, predator-free space occurs where local primary prey densities falls below the predator's local QHR. Increasing the QHR changes the distribution and decreases the abundance of predator-free space, which is especially important for incidental prey such as songbird nests (represented by the clutch of eggs). Maybe we should just stick to illustrating bottom-up creation since I am finding it hard to illustrate both in simple terms that will avoid confusion. Ignore the highlighted section if that the case.

Figure 3. (A) Proportion of space used and (B) prey consumption as a function of a predator's giving-up density (GUD) in a simulated landscape produced in MATLAB. Primary (n=1000) and incidental (n=50) prey were randomly and independently assigned to one of 100 patches (this produces a Poisson distribution of prey). Only patches with initial primary prey quality > GUD were foraged, and of these final prey density = GUD. Random search time for a given foraged patch (i) was calculated as: $t_i = (1/a_p) \log (N_i/GUD)$, where a_p is the encounter rate on primary prey and N_i and GUD are, respectively, the initial and final number of primary prey in patch (i). The probability, I_p, an individual incidental prey item was consumed from a foraged patch was calculated as: $I_p = [1-e^{(-aiti)}]$. Actual incidental prey consumption was determined by comparing I_p to a random number (uniform distribution). Figure shows the mean results from 1000 simulations at each specified GUD. $a_p = 0.6$, $a_i = 0.6$.

Figure 4. Relationships between (A) space use (quantified as the proportion oat grains removed by mice off a lattice grid arrangement) and mouse giving-up density (log-transformed) and (B)

the percentage of nests depredated by mice and space use. Each data point represents one of six 2.25 ha plots from which the data were collected. See Schmidt and Ostfeld (2003) for more details of the experimental methods. Figures reprinted with permission from Schmidt and Ostfeld (2003).

Figure 5. Artificial nest daily mortality rates (DMRs = number of nest depredated/nest exposure days; after Mayfield 1975) as a function of rodent abundance. (A) Per capita nest DMR (log-transformed) specific to mice (solid circles) or chipmunks (open circles) as determined by incisor marks on clay eggs. Each data point represents one of six 2.25 ha plots from which the data were collected (3 plots omitted for mice due to an experimental mouse removal). (B) Overall (all predators included) nest DMRs (± SE) on control (n=3) or removal (n=3) plots; mice were removed in 1997, chipmunks in 1998). See Schmidt et al. (2001a) for more details of the experimental methods. Figures reprinted with permission from Schmidt et al. (2001a).

Figure 6. Veery nest success (proportion of nests fledged) as a function of zero-capture data: proportion of the 9 traps stations comprising a trap neighborhood that recording zero mouse captures during spring-summer trapping sessions; see Schmidt et al. 2006 for more details).

Figure 7. Mean (+ SE) daily predation of gypsy moth pupae deployed on (1.5 m height) or at the base of (ground) trees, as a function of the percentage of track plates recording mouse tracks at those trees over a 10-12 day period at the Institute of Ecosystem Studies, Millbrook, New York, 2002-2005.

FIG. 1

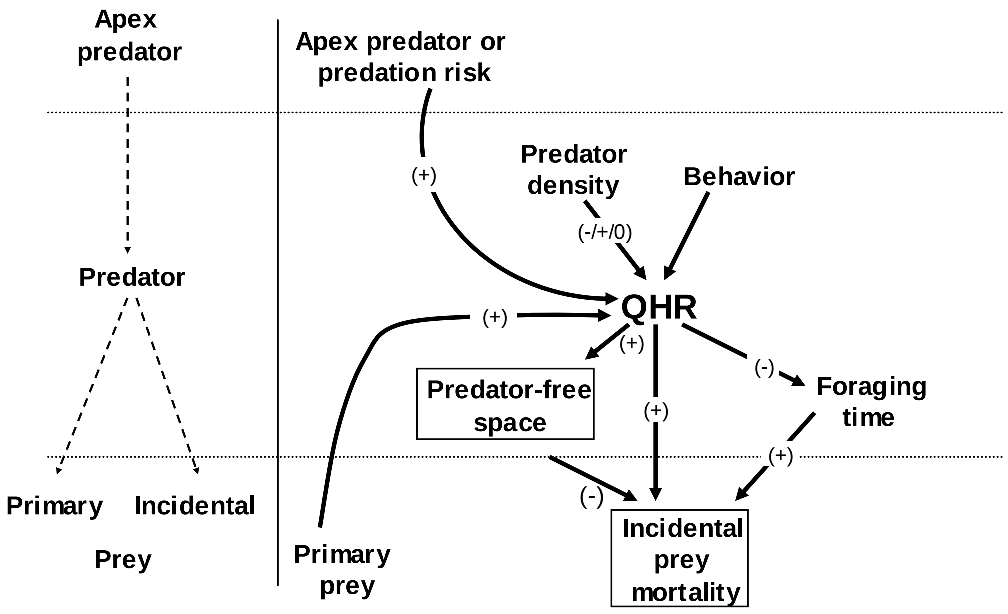
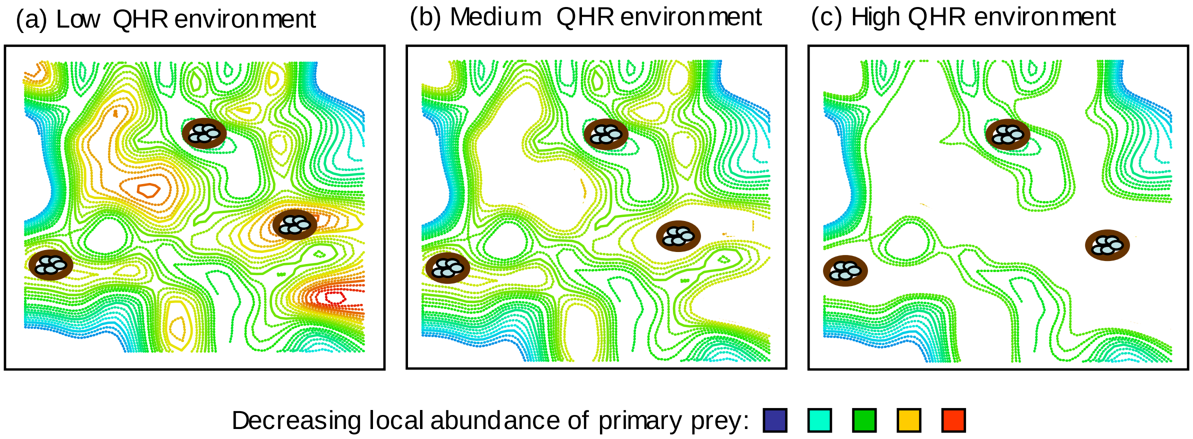

Apex predator
Predator
Primary
Incidental
Prey
Apex predator or predation risk
(+)
Predator density
Behavior
(-/+/0)
QHR
(+)
(+)
Predator-free space
(+)
(-)
Foraging time
(+)
(-)
Incidental prey mortality
Primary prey

FIG. 2

NO REFERENCE TO FIG 2 IN TEXT



(a) Low QHR environment

(b) Medium QHR environment

(c) High QHR environment

FIG. 3

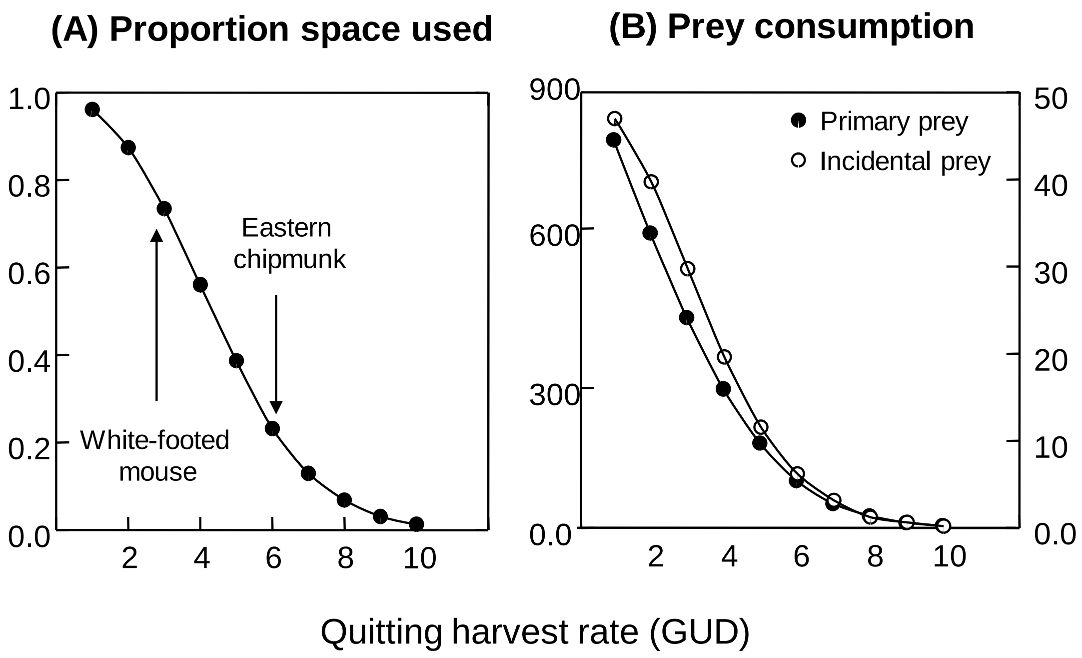

(A) Proportion space used
(B) Prey consumption
1.0
0.8
0.6
0.4
0.2
0.0
Eastern chipmunk
White-footed mouse
2
4
6
8
10
900
600
300
0.0
50
40
30
20
10
0.0
● Primary prey
○ Incidental prey
Quitting harvest rate (GUD)

FIG. 4

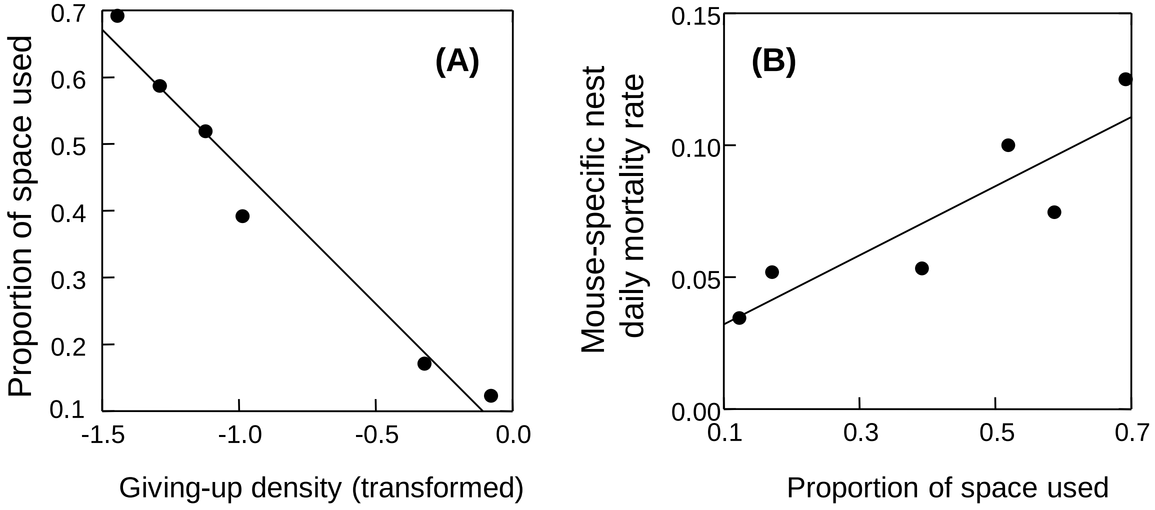

(A)
Proportion of space used
0.7
0.6
0.5
0.4
0.3
0.2
0.1
-1.5
-1.0
-0.5
0.0
Giving-up density (transformed)
(B)
Mouse-specific nest
daily mortality rate
0.15
0.10
0.05
0.00
0.1
0.3
0.5
0.7
Proportion of space used

FIG. 5

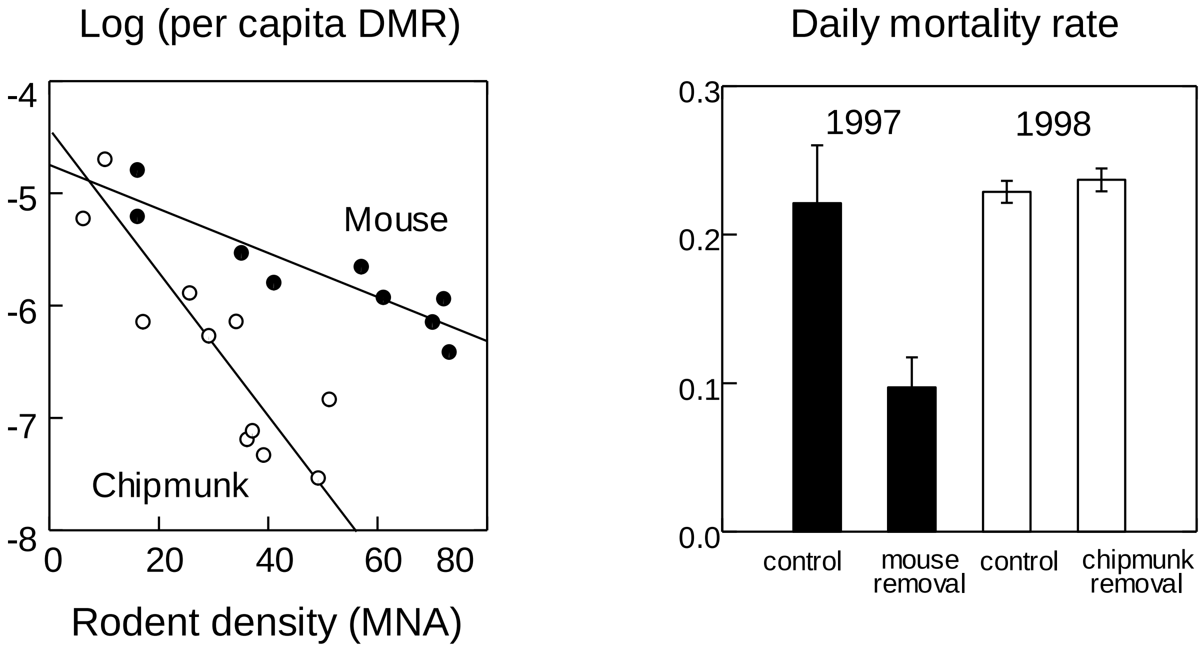

Log (per capita DMR)
-4
-5
-6
-7
-8
0
20
40
60
80
Mouse
Chipmunk
Rodent density (MNA)
Daily mortality rate
0.3
0.2
0.1
0.0
1997
1998
control
mouse removal
control
chipmunk removal

FIG. 6

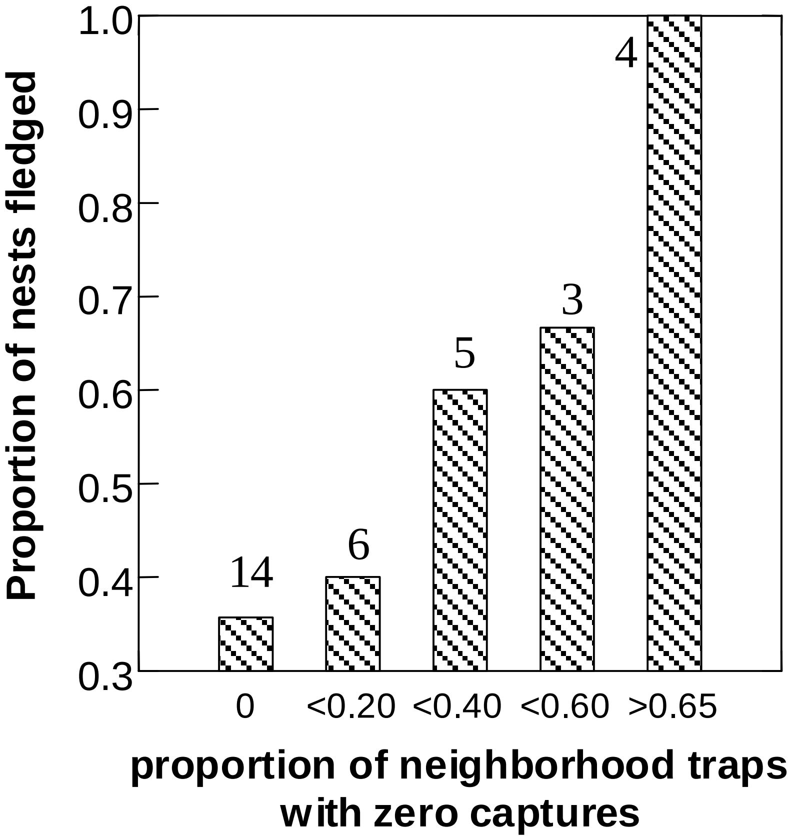
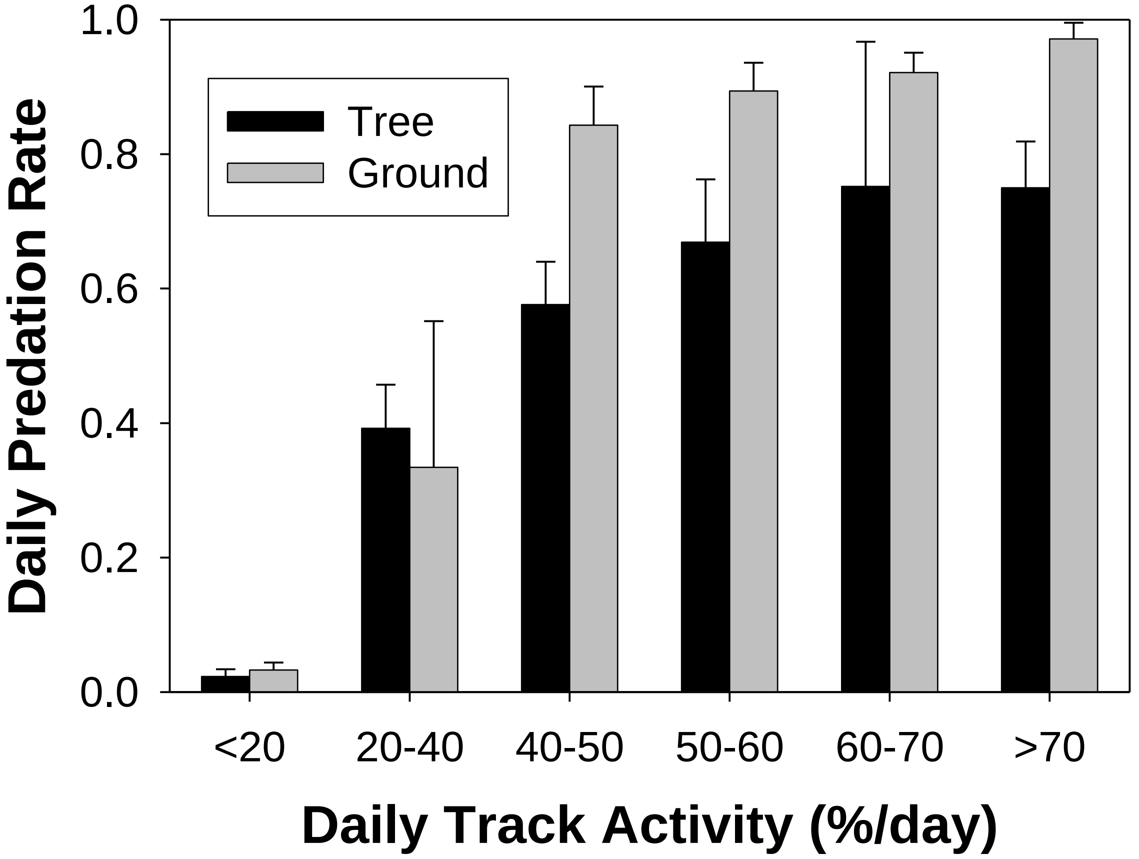

Proportion of nests fledged
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
14
6
5
3
4
0
<0.20
<0.40
<0.60
>0.65
proportion of neighborhood traps with zero captures

Fig. 7



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