

EXPERIMENTAL REMOVAL OF STRONG AND WEAK PREDATORS: MICE AND CHIPMUNKS PREYING ON SONGBIRD NESTS

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Abstract. We examined the effects of separate removal experiments of two generalist consumers, the white-footed mouse (*Peromyscus leucopus*) and the eastern chipmunk (*Tamias striatus*), on nest predation rates of forest songbirds. Mice are numerically dominant at our study sites and were shown to be strong predators in other predator–prey interactions, such as those involving gypsy moths. Therefore, we hypothesized that removal of mice would result in decreased levels of nest predation relative to control treatments with a complete predator assemblage, but that the removal of chipmunks would not result in decreased nest predation. Both hypotheses were supported. Mice depredated >60% of artificial nests in control plots (mouse populations intact), whereas chipmunks depredated ~20%. Daily nest mortality rates in mouse removal treatments were less than half the rates in controls but were virtually identical between chipmunk removal and control treatments. Nonetheless, when we examined predation rates across plots in which the density of mice varied naturally, total daily mortality rates declined as the density of mice increased. This pattern occurred because mortality from non-mouse predators decreased as the density of mice increased and overwhelmed increasing mortality from mice to drive the overall dynamics of the system. Analysis of the relationships between the density of mice and predation rates by mice as a function of the abundance of natural food in their environment revealed probable reasons for these conflicting results. We suggest that high local densities of mice deplete resources for larger, non-mouse predators, which preferentially occupy areas of few mice and high local food abundance. In these areas, songbirds may be faced with higher overall nest predation dominated by non-mouse predators. Mice thus influence nest predation rates through both direct and indirect pathways.

Key words: *indirect interactions; nest predation; Peromyscus; predator compensation; songbirds; strong interactions; Tamias; white-footed mouse.*

INTRODUCTION

Not all predators have equivalent impact on their prey populations. Variability in interaction strength among species (to generalize beyond predators) has important consequences within the realm of theoretical ecology (Lawton and Brown 1994, Kokkoris et al. 1999) and conservation biology (Mills et al. 1993). Identifying strong interactors simplifies what are otherwise complex ecological systems into subsets of interactions (i.e., interaction webs, sensu Menge et al. 1994; also see Wootton 1997) that encapsulate those interactions that drive population dynamics (Navarrete and Menge 1996) and, in the case of keystone predation, may determine community composition (Paine 1966, Power et al. 1996). This approach may work well provided that interaction strength is primarily dependent on the identity of the interacting species, with little

or no role of the surrounding community. The alternative is that the strength of species interactions may vary depending on the specifics of the community in which the interactions are embedded (Navarrete and Menge 1996, Kokkoris et al. 1999).

We characterize for our present purpose strong predators as those predators that are responsible for the majority of predation events on a particular focal prey species and whose dynamics drive the interaction between predator and prey. By this latter point, we mean that the magnitude of total predation experienced by a prey population depends upon the population density of strong, but not weak, predators. This implies that reduction in the numbers of strong predators cannot be completely compensated by the remaining guild or assemblage of predators. In contrast, strong predators can completely compensate for the reduction in the density of weak predators (Navarrete and Menge 1996). This definition makes no reference to whether effects of a predator on its prey are direct, indirect, or both, and corresponds with Navarrete and Menge's (1996) definition of community importance.

Songbird communities in the deciduous forests of southeastern New York have a large and diverse assemblage of potential nest predators including corvids (e.g., Blue Jay, Common Crow), rodents (e.g., mice,

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chipmunks, squirrels), insectivores (e.g., *Blarina* shrews), and medium-sized mammals (e.g., opossums, raccoons, foxes, skunks, weasels). It is likely, however, that many of these predators have weak predation rates and thus negligible impacts on songbirds. We postulated that white-footed mice, *Peromyscus leucopus*, are strong predators, based on the fact that mice are the numerically dominant rodent at our sites (Ostfeld et al. 1996) and mice predominantly influence other predator-prey interactions at our sites, such as those involving gypsy moth pupae (Jones et al. 1998). In contrast, eastern chipmunks (*Tamias striatus*) are less abundant and play a minor role in at least some predator-prey interactions at our sites.

Mice have been identified in many studies as potential nest predators (Maxson and Oring 1978, Guillory 1987, Reitsma et al. 1990, Beletsky and Orions 1991, Bayne et al. 1997, Darveau et al. 1997, Hannon and Cotterill 1998). However, often these studies have used artificial nests, and whether mice are effective predators on real nests that possess a guarding parent remains an open question. In a nine-year study in Virginia Ketterson et al. (1996) demonstrated that the failure of Dark-eyed Juncos (*Junco hyemalis*) was positively correlated to the density of mice. Long-term studies in Białowieża Forest by Jędrzejewska and Jędrzewjeski (1998) provide a wealth of similar correlative evidence that nesting success of ground-dwelling birds declines as the density of small rodents increases. Finally, ongoing studies on breeding success of songbirds at our study site, the subject of a forthcoming paper, document precipitous declines in nest predation in Veeries and Red-eyed Vireos concurrent with a crash in mouse populations (K. A. Schmidt, *unpublished manuscript*). Interpretation of these results is complicated by a positive correlation between densities of mice and chipmunks. Thus, an experimental manipulation of rodent densities is paramount in demonstrating the relative effects of each predator. However, the difficulty of removing rodents on a spatial scale sufficient to find a large sample of nests, necessitates the use of artificial nests.

We removed white-footed mice and eastern chipmunks in separate experiments conducted in 1997 and 1998, respectively, and monitored the survivorship of artificial songbird nests on control and predator removal plots. We tested whether the remaining predator assemblage compensated for the removed predators, i.e., whether total predation rates were comparable between treatments. In addition, we examined nest predation rates by predator groups over both years in plots within which the density of mice and chipmunks varied naturally. Finally, we estimated and corrected for potential biases between predation rates on artificial vs. real nests using a natural Veery (*Catharus fuscescens*) population as our model. We used these results to test the hypothesis that interactions between predators and songbird prey were strong for mice and weak for chipmunks.

METHODS

Study site

We conducted our field studies at the Mary Flagler Cary Arboretum at the Institute of Ecosystem Studies in Dutchess County, southeastern New York. The Arboretum's grounds consist of 800 ha, of which ~325 ha is continuous forest with a canopy dominated by oaks (*Quercus rubra* and *Q. prinus*). Oak and sugar maple (*Acer saccharum*) saplings, maple-leaved viburnum (*Viburnum acerifolium*), and witch hazel (*Hamamelis virginiana*) are common in the understory. We conducted our experiments using three pairs of 2.25-ha plots as sites for rodent trapping. Pairs were separated by 0.5–4 km and consisted of one control and one rodent removal plot separated by at least 150 m. Each plot consisted of an 11 × 11 array of grid points with 15 m between points. We placed two Sherman live traps (7.6 × 8.9 × 22.9 cm; H. B. Sherman Traps, Tallahassee, Florida) at each point for a total of 242 traps per plot.

Small mammal trapping

We live-trapped rodents on the plots beginning each year in early to mid-May and ending in early to mid-November. We baited traps with crimped oats, covered them with a board for protection from sun and rain, set traps between ~1600 and 1800, and checked them between 0730 and 1100 the next morning. On control plots, small mammals were trapped for two consecutive days during monthly trapping sessions. On experimental plots, rodents were trapped twice a week during removal periods (see below), before and after which we followed the same protocol as control plots.

Captured white-footed mice and eastern chipmunks were given a numbered metal eartag for individual identification at first capture. At each capture event we recorded species, tag number, gender, age (juvenile, subadult, or adult; mice only), reproductive condition, body mass, and trap station. Animals were released after processing at the point of capture with the exceptions noted for removal periods. In 1997, we removed mice from experimental plots from mid-June through August, and in 1998, we removed chipmunks from early June through August. We adjusted timing of trapping sessions during chipmunk removal to improve trapping success and removal efficiency. In both years, removed animals were released off site ~10 km from the study plots.

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; R. S. Ostfeld, *unpublished data*) made MNA an accurate method of calculating mouse densities (Hilborn et al. 1975). Lower trapping success of chipmunks (~50% per two trap nights), necessitated the use of more sophisticated estimators of population size to avoid unacceptable bias. We used the program CAP-

TURE to enumerate chipmunk densities, which accounts for variation in the capture probabilities among individual animals, over time, and in response to previous capture. More details on estimating densities can be found in Schmidt et al. (1999). Both mice and chipmunk population densities are expressed below as the number of individuals per plot.

Artificial nest experiments

On 25 June 1997 and 10 June 1998, we placed 54 artificial stick nests 0–15 cm above the forest floor in or at the base of shrubs or near fallen logs to simulate nests of the Veery, a common ground-nesting thrush at the site. In 1997, we constructed nests from leaves, grass, rootlets, and bark. In 1998, we used commercially available artificial stick nests. Nine nests were evenly spaced in each of the six plots with 50-m spacing between nests to reduce possible encounters of more than a single rodent predator (Sloan et al. 1998). After 2 d to simulate a period of nest building, we placed a single Zebra Finch egg ($\sim 16 \times 12$ mm) and two blue plasticene clay eggs (20×15 mm, the approximate size of Veery eggs, Harrison 1975) in each artificial nest. To avoid scent contamination, we wore latex gloves when handling nests and eggs. In 1997, we inspected nests every 3 d for a total of 15 d. If eggs were missing or destroyed, or if the plasticene eggs had tooth or scratch marks, we considered the nest depredated. Predation was assumed to occur during the midpoint of the rechecking interval. Predation rates were converted into daily mortality rates (DMR) by dividing the number of nests depredated by the number of nest exposure days (Mayfield 1975). In 1998, we were concerned that higher mouse densities would depredate nests more quickly, and therefore we increased the frequency of nest checking to 2-d intervals for a total of 14 d. In both years, we identified nest predators by imprints left on plasticene eggs, and in 1997, four smoked plates (10×8 cm) placed around each nest recorded predator tracks and further aided the identification of nest predators. All predators were identified in 1997, while four nests in 1998 were attacked by an unknown predator as a result of missing plasticene eggs. For purposes of the analyses, since the eggs were carried off we assumed larger predators (raccoons or opossums) depredated these nests.

Assessing resource abundance

In 1998, we collected giving-up densities (GUDs) from artificial food patches to investigate the behavioral influences of resource abundance on nest predation rates (Schmidt et al. 2001). GUDs provide a surrogate for a forager's quitting harvest rate, and thus the level to which a forager exploits its environment. For example, under lower foraging costs, mice deplete food patches (artificial or real) to lower resource levels (Brown 1988, Brown et al. 1992, Morgan et al. 1997, Olsson and Holmgren 1999, Olsson et al. 1999). Pre-

vious studies (Schmidt et al. 2001) have shown that the level of patch exploitation is related to the rate of incidental nest predation through increased time spent foraging and greater use of space in the environment (K. A. Schmidt and J. Pusenius, *unpublished manuscript*).

To collect GUDs, we used patches consisting of 4-g millet seed thoroughly mixed into 2 L of sifted sand. As the food in the patch is depleted, a forager exploiting the patch experiences a decline in harvest rate. Assuming the forager can reasonably assess resource abundance, it should remain in the patch until its instantaneous harvest rate (the benefit to the forager) declines to the point where the benefit of further harvest is offset by the costs of foraging (predation, energetic and missed opportunity costs). The amount of food remaining in a patch thus abandoned by a forager is its giving-up density and can be measured by sieving the tray and weighing the amount of uneaten food. To collect GUDs, we distributed 14 food patches in each plot shortly after completion of the artificial nest experiment. We opened trays during the night to target mouse foraging activity. We collected GUDs for three consecutive evenings (plus 1 d of prebaiting). For analyses, we used only GUDs attributed to mice (as determined by footprints and spoor). We logarithmically transformed GUDs to provide a more linear fit between GUDs and quitting harvest rates (Kotler and Brown 1990), and averaged GUDs for each plot across all three nights of collection.

Assessing biases of artificial nests

Predation rates on artificial nests may not be directly comparable to natural predation rates if artificial nests attract or repel potential predators. Possible biases include odors associated with distributing nests (Whelan et al. 1994) or with using clay eggs, lack of a parental bird guarding the nest (Schmidt 1999), differences between nest sites selected by the researcher and nest sites selected by birds, and visual cues associated with artificial nests (Martin 1987). To investigate these potential biases, we located and monitored the success of 21 natural Veery nests both on and adjacent to the study plots in 1998. After these nests fledged young or were depredated, we placed either a single blue plasticene clay egg or a single Zebra Finch egg in each nest to monitor their fates. Most nests were used twice, varying the order of placement of the finch or plasticene egg. We let several days elapse between a nest's natural fate and the beginning of the first trial and between trials. We did not disturb nests prior to or during the interval between their natural fate and the experiments, with the exception of two occasions in which a Veery nest was translocated to a site where the original nest had been destroyed. We monitored nests and calculated DMRs in the manner described above.

Because nests and nest sites were used multiple times, there is the potential for memory among pred-

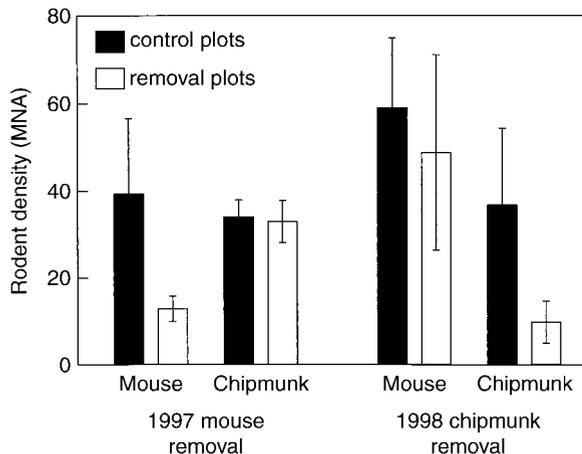


FIG. 1. Density estimates (MNA = minimum number known alive) of mice and chipmunks on control and removal plots during the two experimental removal periods. Error bars denote standard errors.

ators to affect predation rates. We first tested for an effect of predator nest revisitation by comparing DMRs (using the program CONTRAST, Hines and Sauer 1989) of eggs deployed in natural nests that (1) fledged young, and thus were not previously visited by a predator, and (2) were depredated, and found no difference ($\chi^2 < 0.10$, $df = 1$, $P > 0.90$). We also compared DMRs between the first and second trials of the experiment and found no difference ($\chi^2 = 1.34$, $df = 1$, $P = 0.25$). Therefore, we conclude that depredated nests were not likely to be revisited due to predator memory.

General data analysis

Densities of rodents used in the analyses below were determined for the trapping period closest to the artificial nest experiments. For control plots, this was at most one week before or after the experiment. Because rodents were trapped more frequently on experimental plots, we estimated rodent densities from trapping sessions during nest exposure, and in the case of 1997, used the mean density estimate over two trapping sessions.

For each plot in each experiment, we calculated species-specific daily mortality rates (or lumped predator species to calculate non-mouse DMRs) as the number of depredated nests attributed to a species, based on predator identification, divided by the total number of nest exposure days. We calculated standard errors using the method of Johnson (1979), and used the program CONTRAST (Hines and Sauer 1989) to statistically compare total DMRs. We analyzed DMRs rather than the number of nests depredated per treatment because the former is better suited to resolve differences between treatments. This is particularly true since DMRs on our artificial nests were inflated relative to natural nests (see *Results: Patterns of predation*). As such, as the number of days nests are exposed increases, the

proportion of nests depredated will converge to one despite potential differences in predation rates.

We converted mouse-specific DMR and chipmunk-specific DMR into per capita DMRs by dividing each by its respective density in a given plot. The purpose of calculating per capita DMRs was to examine differences between mice and chipmunks and effects of the treatments rather than documenting a decline in per capita predation with density. We examined trends in species-specific or per capita DMRs using linear regression or ANCOVA. More details are given in the *Results*.

RESULTS

Mouse removal

Mouse populations on removal plots were reduced below one-third their densities on control plots (Fig. 1). Moreover, populations on removal plots were likely to be effectively smaller as they consisted largely of immigrant individuals that concentrated around plot edges (R. S. Ostfeld, *unpublished data*). Fewer total nests were depredated (21 vs. 25) and daily mortality rates were much lower on mouse removal plots than on control plots ($\chi^2 = 7.96$, $df = 1$, $P < 0.005$; Fig. 2). Mice depredated the majority of nests in control plots while predation was more evenly distributed among predator species in removal plots (Fig. 3a). Both a decline in mouse density (Fig. 1) and a decline in per capita DMR (removal plots outside 95% confidence interval; Fig. 4a) appear to have contributed to lower mouse DMRs in removal plots (Table 1). Neither chipmunk densities (Fig. 1) nor chipmunk per capita DMRs (Fig. 4b) differed substantially between mouse-removal and control plots. Finally, the DMR of raccoons and

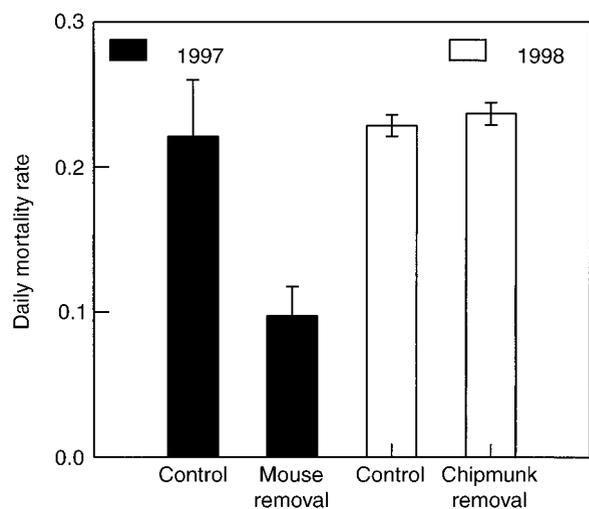


FIG. 2. Daily mortality rates (no. nests depredated/no. nest exposure days) for the experimental treatments in 1997 (mouse removal and its paired control) and in 1998 (chipmunk removal and its paired control). Error bars denote standard errors.

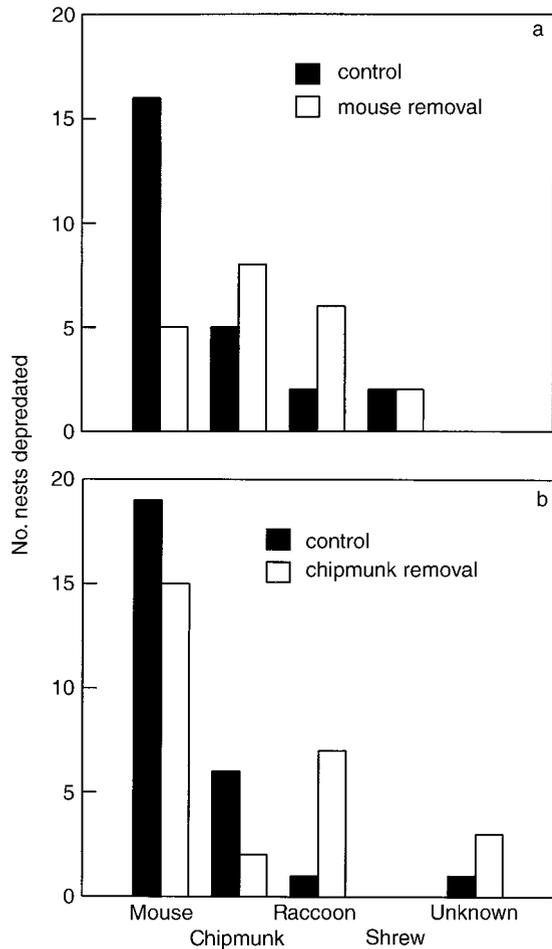


FIG. 3. Number of nests depredated by predator category across the treatments. The raccoon category also includes predation by opossums.

opossums showed a nonsignificant increase ($\chi^2 = 0.37$, $df = 1$, $P > 0.50$; Table 1) in removal plots.

Chipmunk removal

Chipmunk populations on removal plots were reduced to approximately one-third their populations on control plots (Fig. 1), although as with mice, they consisted largely of immigrant individuals concentrated at plot edges. In both control and chipmunk removal plots, all nests were depredated by the end of 14 d of exposure. There were no differences in DMRs between treatments ($\chi^2 = 0.04$, $df = 1$, $P > 0.80$; Fig. 2). Mice depredated the majority of nests in both control and removal plots (Fig. 3b). Chipmunk DMRs declined as a whole (Table 1), but their per capita effects do not fall outside the 95% confidence intervals (Fig. 4b). In contrast to 1997, raccoons and opossums depredated significantly more nests in removal plots (Fig. 3b) with resulting higher DMRs ($\chi^2 = 4.85$, $df = 1$, $P < 0.03$; Table 1).

Combined experiments

Predation on artificial nests on the control plots was very similar between years. Daily mortality rate was 0.221 in 1997 and 0.229 in 1998. Moreover, mice consumed similar numbers of nests (Fig. 3), had similar DMRs (Table 1), and per capita effects in line with their densities (Fig. 4). These similarities also extended for non-mouse predators (Figs. 3 and 4, Table 1). Thus, while experimental protocols differed slightly between 1997 and 1998, results were highly consistent between years.

We used ANCOVA to test for differences in per capita DMRs between chipmunks and mice. Each species' removal treatment was excluded from the anal-

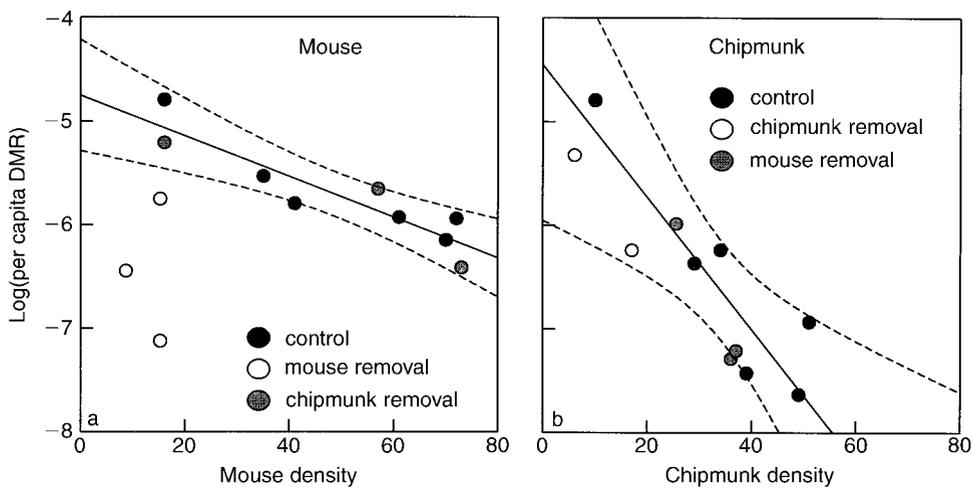


FIG. 4. Log per capita daily mortality rates (DMR, measured as no. nests depredated/no. nest exposure days) decline with conspecific density for both (a) mice and (b) chipmunks. Dashed lines represent 95% confidence intervals and were calculated in the absence of each species' respective removal plots (shown by the open circles). Control plots are denoted by black circles, conspecific removal plots are denoted by open circles, and alternative predator removal plots are denoted by gray circles. Figures were drawn on the same axes to illustrate the faster decline in per capita DMR for chipmunks.

TABLE 1. Predator-specific daily mortality rates.

Treatment	Mouse	Chipmunk	Raccoon	Shrew	Other
Control (1997)	0.1416	0.0442	0.0177	0.0177	0
Mouse removal	0.0231	0.0370	0.0278	0.0093	0
Control (1998)	0.1610	0.0508	0.0085	0	0.0085
Chipmunk removal	0.1316	0.0175	0.0614	0	0.0263

Note: The raccoon category also includes predation by opossums.

ysis. We used density as the covariate and predator type as a group variable. Mice and chipmunks had indistinguishable per capita effects as densities approached zero (nonsignificant intercept term: $F_{1,14} = 0.39$, $P = 0.54$), but differed greatly in the rate at which the per capita DMR declined with increasing density (predator \times density interaction: $F_{1,14} = 13.99$, $P < 0.002$). As densities increased, mice produced higher per capita effects than did chipmunks (Fig. 4).

We regressed DMRs against plot-specific mouse density to determine if nest predation on the artificial nests was driven by the density of mice. We dropped the mouse removal plots in 1997 because lower per capita effects of mice on those plots (Fig. 4a) may be related to their recent immigrant status (see *Discussion*). We used ANCOVA with year as a group variable and mouse density as a covariate. We varied the dependent variable across three analyses we performed: (1) total DMR; (2) mouse DMR; and (3) non-mouse DMR. Year did not influence DMRs in any analysis ($F_{1,6} = 1.21$, $P > 0.30$; $F_{1,6} = 0.059$, $P > 0.80$; $F_{1,6} = 4.98$, $P =$

0.07, for the three analyses, respectively). Total DMRs showed a marginally nonsignificant decline with mouse density ($F_{1,6} = 5.43$, $P = 0.06$; Fig. 5). This was due to strongly declining non-mouse DMRs ($F_{1,6} = 42.42$, $P = 0.001$; Fig. 5), which overpowered a smaller and nonsignificant increase in mouse DMRs with increasing mouse density ($F_{1,6} = 3.00$, $P = 0.134$; Fig. 5). Similar analyses regressing DMRs (total, chipmunk, and non-chipmunk) against chipmunk densities as the covariate (dropping chipmunk removal treatments) resulted in no trends (all $P > 0.25$).

Giving-up densities and nest predation

We analyzed giving-up densities (in 1998) to infer behavioral changes that may account for the contrasting patterns of predation across the natural variation in mouse density. Prior analyses have shown that mouse DMRs declined with GUDs in accordance with a theory of incidental predation (Schmidt et al. 2001). Here we are interested in the relationship between GUDs and DMRs from non-mouse predators. Because GUDs were collected from mice, no relationship between non-mouse DMRs and mouse GUDs was expected in the absence of any behavioral interactions or modifications between mice and other predators. Specifically, we consider the role of exploitative competition between mouse and non-mouse predators (alternative hypotheses are considered in the *Discussion*). Under exploitative competition, we predict GUDs to decrease with increasing mouse density as a consequence of the high valuation of food when mouse densities increase and resources become scarce (Morgan et al. 1997, Morris 1997, Olsson et al. 1999). In this scenario, GUDs are proportional to habitat quality and nest predation from larger predators (raccoons and opossums) should increase with GUDs if they themselves seek high quality patches to forage in.

To test these predictions, we used linear regression to examine GUDs and mouse density. GUDs declined with mouse density ($r^2 = 0.59$, $P < 0.001$), but only in control plots. In chipmunk removal plots, GUDs increased as a whole compared to control plots ($F_{1,29} = 12.58$, $P = 0.001$). This relationship is likewise consistent with chipmunks as exploitative competitors; the removal of a competitor increases the availability of resources for mice and consequently GUDs are predicted to increase. To analyze the relationship between giving-up densities and DMRs, we used ANCOVA with GUD (plot mean) as the covariate and predator type

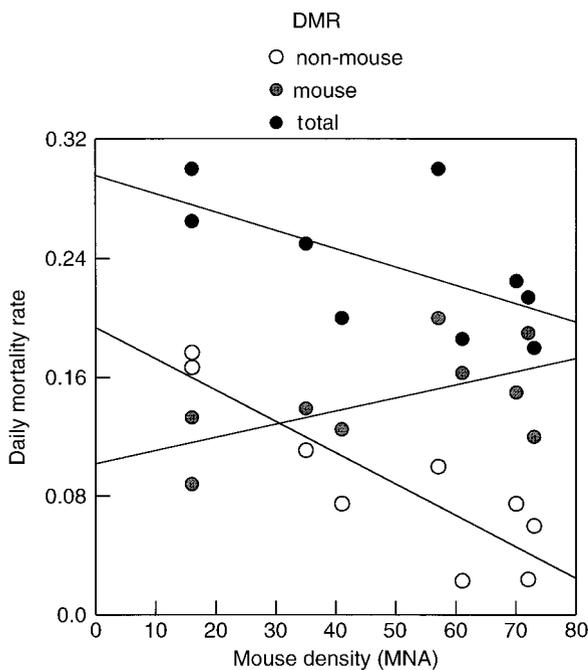


FIG. 5. Daily mortality rates (units as in Fig. 4; total, mouse, and non-mouse) in relation to the abundance of mice. The 1997 mouse removal plots are excluded from the figure. MNA = minimum number alive.

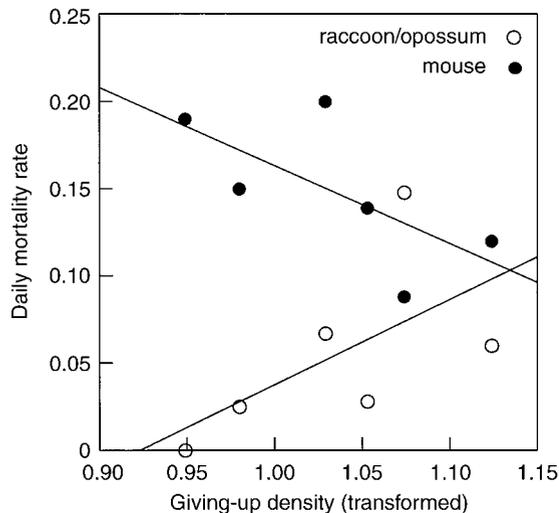


FIG. 6. Daily mortality rates (units as in Fig. 4) as a function of giving-up densities (GUDs). GUDs are used in this case as a surrogate for the availability of alternative food. Mouse DMRs and non-rodent DMRs show opposite patterns in response to increasing GUDs (i.e., increasing food availability see *Results: Giving-up densities*). GUDs were transformed, using the Box-Cox transformation, which uses a maximum-likelihood approach to find the best approximation to normality within the family of power transformations (Sokal and Rohlf 1981).

(mouse vs. raccoon/opossum) as the group variable (we did not include chipmunk predation because of their near absence in the removal plots and dispersal between plots is rare). Overall, nest predation was greater by mice ($F_{1,8} = 6.27$, $P = 0.037$; Fig. 6) and declined with mouse GUDs. In contrast, nest predation by larger predators increased with mouse GUDs showing the opposite pattern as mice (predator \times GUD interaction: $F_{1,8} = 5.23$, $P = 0.051$; Fig. 6).

Patterns of predation on natural nests and biases of artificial nests

We monitored a total of 19 natural Veery nests in 1998 from which we calculated DMR = 0.0613. Veery nests in experimental (chipmunk removal) plots had higher survivorship than those nesting outside the experimental plots (including nests located on control plots). The magnitude of this difference in DMRs (experimental, 0.0339; control, 0.0719) was large, but small sample sizes (experimental, 2 of 4 nests depredated; control, 11 of 15 nests depredated) precluded statistical significance ($\chi^2 = 1.45$, $df = 1$, $P = 0.23$). The absence of visual (birds flying to and from a nest) and auditory (begging chicks) cues at artificial nests may have underestimated the effects of diurnal chipmunks, and the trend toward higher Veery nest success in chipmunk removal plots is supportive of this claim. If chipmunks are more frequent predators on real nests and use these cues to locate nests, we would expect predation rates on natural Veery nests to occur pri-

marily during the nestling phase when both types of cues are at their maximum. However, during a 3-yr study (1998–2000) of Veery nesting success at our site, 20 of 32 depredated Veery nests contained eggs at the time of predation in contrast to 8 of 32 nests containing chicks (and 4 nests at an unknown stage at the time of predation).

Mean DMRs of Zebra Finch eggs and plasticene eggs placed in natural Veery nests did not differ significantly (finch = 0.182, plasticene = 0.171; $\chi^2 = 0.04$ $df = 1$, $P > 0.80$), and thus we concluded that odors from plasticene eggs did not influence predation rates. Likewise, DMRs on plasticene or finch eggs did not differ significantly between natural nests and artificial nests from control plots (0.176 vs. 0.229; $\chi^2 = 1.27$, $df = 1$, $P > 0.25$), and thus we concluded that placement of artificial nests and/or their appearance did not influence predation rates.

Instead, we interpret the difference in predation rates between artificial nests used in our experiments and natural Veery nests as a result of the absence of parental guarding, whether by outright defense or by sheltering the nest. We can calculate the efficacy of nest guarding by determining the reduction in predation rates on artificial nests that must be accounted for to match natural predation rates, 0.0613. Dividing the DMR from natural Veery nests by the DMR from artificial nests provides an estimate of the probability that an encounter between a predator and a real nest results in a successful predation event: artificial nests, $0.0613 / 0.229 = 0.27$; clay/finch eggs in natural Veery nests, $0.0613 / 0.176 = 0.35$. These calculations suggest that only 27–35% of nests encountered by a predator are successfully depredated, whether through parental defense, gape-limited predators that cannot break the larger songbird eggs, or alternative mechanisms. This bias may actually differ among the predator species (see Schmidt 1999); for instance raccoons are unlikely to be deterred by a parental bird. If we subtract the effect of raccoons (0.0085 from 1998 control plots), the rate of successful predation by rodents is further reduced, e.g., $(0.0613 - 0.0085) / 0.229 = 0.23$.

DISCUSSION

The primary goal of our research was to determine if mice and chipmunks are strong and weak predators, respectively, on songbird nests. While chipmunks depredated >20% of nests in plots in which their populations were unmanipulated, chipmunk removal did not result in lower nest daily mortality rates. DMRs (mouse-specific, chipmunk-specific, or total DMR) did not vary with chipmunk density, and chipmunks showed no evidence of compensating for the reduction of mouse populations. Artificial nests lack sounds of begging chicks or activity of parental birds that may attract diurnal predators such as chipmunks (Haskell 1999). The absence of these factors may have underestimated the effects of chipmunks. In particular, pre-

dation on Veery nests was lower in chipmunk removal plots, but low sample sizes preclude any conclusions being drawn.

In contrast, mice at unmanipulated densities depredated >60% of nests, and the removal of mice resulted in a dramatic drop in daily mortality rates (Fig. 2). These results suggest that mice are strong predators whose effects cannot be wholly compensated by other predators, at least on the time scale of our manipulations. However, contrary to our expectation derived from the previous results, total predation by all predators declined with increasing mouse density (Fig. 5). We consider three alternative hypotheses for the different directional trends in mouse vs. non-mouse predator impacts: predator compensation, habitat selection along an environmental gradient, and patch dynamics of non-mouse predators.

If alternative predators compensated for the removal of mice, we would expect the decline in mouse DMR to be, at best, offset by an increase in non-mouse DMR such that total predation remained constant throughout the range of mouse density. A null model of compensation based on attack rates would predict a more modest increase in non-mouse DMR. Regardless, as mouse densities declined, DMRs by non-mouse predators increased over twice as fast as DMRs by mice decreased (Fig. 5). This gross overcompensation suggests that other predators were not simply finding nests that mice did not, but rather that the density and/or behavior of non-mouse predators was influenced by the density of mice. A second alternative is that mice and non-mouse predators have distinct habitat preferences along an environmental gradient that results in a negative correlation between their densities and/or activities without any behavioral interactions between one another. This would account for the pattern in Fig. 5, but distinct habitat preferences seem unlikely given that the predators we have identified are habitat generalists, no obvious environmental gradients occur between plots, and the relationship between non-mouse DMR and mouse GUDs is difficult to explain in the absence of interactions between predators.

Instead, the relationships between DMRs and GUDs (Fig. 6) and the pattern of declining GUDs with increasing mouse density suggest that the level of resources within the local environment is negatively correlated with the density of mice (also see Morris 1997, K. A. Schmidt and J. Pusenius, *unpublished manuscript*). At higher mouse densities and higher levels of resource exploitation, mice are expected to encounter and depredate more nests through what is likely incidental predation (Vickery et al. 1992, Schmidt et al. 2001). However, heavy resource depletion by high densities of mice in localized areas may deter the use of these areas by larger, non-mouse (particularly non-rodent) predators, which frequently consume the same resources. Instead these predators may select foraging sites that contain fewer mice and consequently have

higher resource levels. Therefore, non-mouse predators depredate more nests in areas with fewer mice, above and beyond that expected from compensation alone.

This interpretation requires a rigorous experimental protocol for its validation. The spatial requirements would be considerable, but the alternative, examining the effects of predator removals at spatial scales smaller than the range over which large predators forage, may limit our ability to detect the significance of alternative predators. In addition, the relationships between DMRs and GUDs may have been caused by factors not considered above. For instance, if raccoons/opossums prey on mice, they may have dispersed into sites with higher mouse densities (instead of dispersing from these sites as argued earlier) and more frequently consumed nests encountered incidentally. This alternative, however, predicts that non-mouse DMR should increase with GUDs, the opposite as shown, and thus can be ruled out.

Finally, we point out that Navarrete and Menge (1996) working with an invertebrate predator-prey system in the rocky intertidal noted similar dispersal patterns in response to resource exploitation. Seastars (*Pisaster*) influenced mussel predation by whelks (*Nucella* spp.) at least partially through a negative correlation between predator densities stemming from whelk dispersal in response to food depletion by *Pisaster* (Navarrete and Menge 1996). In both Navarrete and Menge's study and ours the weaker predator dispersed from patches heavily exploited by the stronger predators. That two very different systems can show potentially similar predator-predator interactions suggests these interactions may be common.

Rodent predation on forest songbird nests

Our results suggest that mice can be important nest predators of forest songbirds, but at the same time, suggest artificial nests do in fact overestimate predation rates and this bias appears to be related to the absence of parental guarding. We estimated that ~60–75% nest encounters by rodents may be repelled through either passive or active parental defense of the nest, or perhaps some proportion of rodents are gape-limited and cannot break the shells of larger songbird eggs. Nonetheless, studies using video recordings have shown that mice are capable nest predators (e.g., Pietz and Granfors 2000) that can consume eggs much larger than themselves and that mice may take advantage of opportunities when parental birds are absent from the nest (Blight et al. 1999). Furthermore, gape-limitation does not apply when mice encounter small hatchlings within nests (see Pietz and Granfors 2000). While individual mice are perhaps inefficient predators, the sheer number of mice in some years may dramatically reduce songbird nest success (Guillory 1987, Jędrzejewska and Jędrzejewski 1998). In contrast, predation rates on natural Veery nests are >6 times higher than predation by chipmunks on the same nests that contain clay eggs

(K. A. Schmidt, *unpublished data*). While these nests may lack begging chicks that diurnal predators, such as chipmunks, use to locate nests (Haskell 1999), our studies of Veery nesting success indicate that most nests are depredated during the egg phase when real nests lack these cues as well. Unfortunately, constraints and trade-offs in effort, replication, and the scale of experimental manipulations necessary to obtain sufficient sample sizes of real nests necessitates use of indirect evidence to compare predator impacts. Even so, a mass of evidence is accruing to suggest mice are important nest predators for some species of songbirds.

Reconsidering strong and weak predators

Inferring the strength of species interactions without regard to the community context in which they occur can be problematic. First, species interactions are likely to be context dependent. Heterogeneity in mouse densities, which may be necessary for mediating dispersal of other predators in the system, is likely a by-product of the distribution of oaks and the magnitude of masting events (Jones et al. 1998). Thus, the detection of these interactions may be dependent upon acorn production and/or time since the most recent masting event. The effect of larger predators in the absence of the heterogeneity imposed on the system by mice (or oaks) may be substantially different. Second, interaction strength may be scale dependent, and thus comparisons across species must be made at the appropriate scale(s). In our study we suggest that the interaction strength of larger predators may have been masked by an experimental system that operated on a scale smaller than foraging distances of some nest predators. Third, as indicated by the differential decline in per capita interaction strength between mice and chipmunks (Fig. 4), the strength of species interactions, or even the identity of strong or weak interactors, may vary depending on the absolute and relative abundance of species in a community. These points encapsulate the idea that not only species interactions, but interaction strength as well, are embedded within an ecological community.

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