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# Type 3 functional response of mice to gypsy moth pupae: is it stabilizing?

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We conducted field experiments in 2002 and 2003 to determine whether the functional response of white-footed mice (*Peromyscus leucopus*) to gypsy moth (*Lymantria dispar*) pupae is decelerating (e.g., type 2) or accelerating (e.g., type 3) at low pupal density. In both experiments, live gypsy moth pupae were deployed in June (prior to the appearance of natural pupae) at densities of approximately 1, 8, and 35 pupae per mouse home range in oak-forest grids in upstate New York and monitored over 10 days for signs of predation. Pupae were deployed 1.5-m high on tree boles in 2002, whereas in 2003 the three density treatments were crossed with a height treatment: ground level vs. 1.5-m high. The relationship between daily predation rate (proportion of pupae eaten/day) and pupal density was significantly positive in both years, indicating an accelerating functional response. Daily predation rates on ground-level pupae were substantial in the lowest density treatment, suggesting that dense mouse populations could drive gypsy moths to extinction despite an accelerating functional response. Daily predation rates on elevated pupae increased over several days in the medium and high density treatments, suggesting a lagged shift from ground- to tree-level foraging by mice. Within the high-density treatments, predation rates on pupae showed no apparent relationship with the number of pupae on a tree. Our results disagree qualitatively with simple models of type 3 functional response, in which predation rate of prey approaches zero as prey approach extinction, and support the contention that an accelerating functional response alone may be insufficient to prevent prey extinction.

## Introduction

Through its notoriety as a destructive forest pest, the gypsy moth (*Lymantria dispar*) has become a well-studied model species for testing theories of population regulation, dynamics, and spatial spread, as well as epizootiology and biological control (Elkinton and Liebhold 1990, Berryman 1991, Liebhold et al. 1992, Hajek et al. 1993, Jones et al. 1998, Dwyer et al. 2000, Liebhold et al. 2000). Gypsy moths were introduced to North America from Europe more than 130 years ago (Forbush and Fernald 1896), and since have invaded hardwood forests across much of the eastern USA. Gypsy moth populations achieve intermittent outbreaks that cause extensive forest defoliation and tree mortality (Baker 1941, Kegg 1973), which has stimulated intense field research into factors that might suppress or regulate their populations. A nucleopolyhedrosis virus and various native and introduced parasitoids attack gypsy moths and may have particularly important effects during and immediately after outbreaks, but appear to be much less important during periods of low moth densities (Elkinton and Liebhold 1990, Berryman 1991, Woods et al. 1991, Williams et al. 1992). Therefore, considerable attention has been paid to natural enemies that could potentially suppress or regulate gypsy moth populations at low densities.

In eastern North America, white-footed mice (*Peromyscus leucopus*; hereafter referred to as mice) are major predators of gypsy moth pupae during periods of low moth density. Mice are generalists that feed mainly on seeds, berries, fungi, and arthropods (Wolff et al. 1985). Dense populations of mice can cause severe predation of gypsy moth pupae (Bess et al. 1947, Campbell 1976, Campbell and Sloan 1977, Elkinton et al. 1996). Conversely, pupal predation is greatly reduced when mice are scarce (Elkinton et al. 1989, Elkinton et al. 1996), although invertebrates can partially compensate for low mouse densities in southern forests (Cook et al. 1995, Hastings

et al. 2002). Predation by mice has strong population-level effects at low gypsy moth densities (Elkinton et al. 1996). For example, Jones et al. (1998) experimentally removed mice during the pupation period and observed 10- to 30-fold increases in gypsy moth egg mass density.

Although predation by mice affects gypsy moth populations, the reciprocal effect of gypsy moths on mouse abundance is negligible. Mice lack a numerical (Solomon 1949) or aggregative response to gypsy moth pupae because the pupae are only available for a few weeks in July, when alternative foods are abundant (Wolff 1986, Elkinton and Liebhold 1990), and mouse home ranges are temporally stable (Stickel 1968). Instead, mouse density in summer is strongly linked to abundance of acorns produced the previous autumn (Elkinton et al. 1996, Wolff 1996, McCracken et al. 1999). This numerical dependence on acorns decouples mouse populations from gypsy moth populations, but may release gypsy moth populations from predation during periods of low acorn production (Ostfeld et al. 1996, Liebhold et al. 2000). Predation by mice, in combination with other natural mortality factors, therefore could potentially regulate moths around a low-density equilibrium (Campbell 1975, Berryman 1991). However, in the absence of a numerical or aggregative response, the ability of mice to regulate gypsy moth populations depends on the shape of their functional response (Murdoch and Oaten 1975).

The functional response is a fundamental component of predator-prey interactions (Solomon 1949). Functional responses are typically expressed in terms of the consumption rate of individual predators (# prey eaten $\times$ predator$^{-1}$ $\times$ time$^{-1}$; (Holling 1959b), but effects on the prey population are mediated through the predation rate (# prey killed $\times$ prey$^{-1}$ $\times$ time$^{-1}$). If predator density is independent of prey, regulation of the prey population about a stable equilibrium can only occur if the functional response is accelerating (e.g., type 3), which causes

predation rate to drop as prey become scarce. Regulation is inhibited by a decelerating (e.g., type 2) functional response, which causes predation rate to increase as prey become scarce (Holling 1959b, Murdoch and Oaten 1975). An accelerating functional response can result from predators switching among alternative prey types, selectively foraging in patches of high prey density, or learning through experience (Holling 1959b, Tinbergen 1960, Murdoch 1969, Royama 1970).

Because the white-footed mouse is a generalist with a sophisticated behavioral repertoire, it could exhibit an accelerating functional response to gypsy moth pupae. However, results of previous studies are inconsistent. Campbell and Sloan (1976) reported positive relationships between gypsy moth pupal density and predation rate in observational studies on field populations in New York and Connecticut. Similarly, Smith (1985) found a positive relationship between the density of pupae experimentally deployed in Vermont and predation rate by vertebrates. In contrast, Elkinton et al. (1989) presented observational and experimental evidence that predation rate on pupae is inversely related to pupal density. They found that predation rate and pupal density were negatively correlated over several years on Cape Cod, Massachusetts; however, this correlation was confounded by inverse fluctuations in mouse and gypsy moth densities. Elkinton et al. (1989) also experimentally deployed gypsy moth pupae at varying densities in plots on the forest floor, and found that the proportion eaten generally decreased as pupal density increased across a broad range. However, the experiment was after the period of natural gypsy pupation, so mice may have already had experience with pupae. Also, pupae were only available for a few days, which may not have been sufficient for learning or switching to take place.

Our objective was to experimentally characterize the functional response of white-footed mice to gypsy moth pupae in oak-forest habitats. To do so, we conducted experiments in 2002 and 2003, in which gypsy moth pupae were deployed at varying densities in forest habitats and monitored for predation.

## Methods

Our general approach was to test whether the predation rate (proportion attacked per unit time) on gypsy moth pupae increased or decreased with the abundance of pupae across a range of relatively low pupal densities, indicating (respectively) an accelerating or decelerating functional response (Trexler et al. 1988). In the absence of a numerical response, any change in predation rate with prey density must reflect the functional response of predators. We simultaneously deployed live female gypsy moth pupae at low, medium, and high densities in forest quadrats and monitored them for predation. In both 2002 and 2003, quadrats were arrayed in and around six 2.25-ha grids for live trapping small mammals at the Institute of Ecosystem Studies (IES), Millbrook, New York, USA. These grids acted as blocks in a randomized block design. The grids were arranged in three pairs, with 100-250 m between paired grids and 1-3 km between pairs. All grids were located in mixed-hardwood forest stands dominated by oaks (57-70% oak relative basal area). Each grid was a rectangular array of 11 × 11 ($n$ = 5) or 10 × 12 ($n$ = 1) trap stations, with 15 m between stations and two Sherman live traps placed at each station. Mammal trapping was suspended during periods when experimental pupae were available.

Although the spatial density of pupae can reach values arbitrarily close to zero, the lowest (nonzero) local density a mouse can experience is to have one pupa in its home range. White-footed mice typically forage within relatively stable home ranges of 500 to 1, 000 $m^2$

(Stickel 1968, Wolff 1985), so we used 900 $m^2$ as a conservative estimate of home-range size on which to base density treatments and the size and placement of quadrats. Each quadrat, which comprised one experimental unit, was at least 60 × 60 m in size (approximately four 900-$m^2$ mouse home ranges) and separated from other quadrats by ≥ 30 m (approximately one home range diameter). We made quadrats ≥4-fold larger than a typical mouse home range to reduce the potential aggregation of mice in quadrats with many pupae. Each quadrat was subdivided into 30 × 30-m (900-$m^2$) cells. Thus, we had a hierarchy of spatial scales: each 2.25-ha trapping grid had 3 or 6 quadrats associated with it, and each quadrat contained 4 or 10 cells (Fig. 1).

**Experimental treatments**

Our low, medium, and high pupal density treatments were 1, 8, and 35 pupae per 900-$m^2$ cell (11, 89, and 389 pupae / ha), respectively. These densities are far below densities achieved during gypsy moth outbreaks, when thousands of egg masses may be found per ha (Liebhold et al. 1993, Ostfeld et al. 1996). The medium and high density treatments were applied to 60 × 60 m quadrats, whereas the low density treatment was applied to 60 × 150 m quadrats. Within each grid, experimental quadrats were separated by 30 m, and each grid was randomly assigned one of the eight possible juxtapositions of quadrats (Fig. 1).

Predation risk is consistently greater for gypsy moth pupae at ground level than for pupae above ground on tree boles (Campbell et al. 1975a, Campbell and Sloan 1976, Smith and Lautenschlager 1981, Smith 1985, Cook et al. 1995). In 2002, all pupae were deployed at 1.5 m height above ground and each trapping grid had three quadrats, one for each density treatment (Fig. 1A). In 2003, the three density treatments were crossed with two height treatments (ground level and 1.5 m height) in a factorial design. Therefore, in 2003 each trapping grid had six

quadrats; three quadrats (one for each density treatment) were randomly configured inside the grid, and three others were arrayed ≥ 30 m from the grid boundary. For each density treatment, the height treatments were randomly assigned to the quadrats inside and outside the trapping grid (Fig. 1B).

**Rearing and deployment of pupae**

We established an orthogonal grid of points with 5-m spacing within each quadrat. In each 30 × 30-m cell, we randomly chose (with replacement) the point where each pupa was to be deployed. Thus, in the medium and high density treatments, some points received >1 pupae. In low-density treatments in 2003, a single pupa was placed in the center of each cell. For each chosen point, pupae were deployed on the nearest live tree with dbh > 10 cm. If two candidate trees were approximately equidistant from a point, preference was given to primary gypsy moth host trees (*Quercus* or *Populus* spp.). In several cases, the same tree was the closest tree to >1 point, so the actual spatial distribution of pupae among trees was clumped (range 1 to 10 pupae / tree).

We reared late-instar gypsy moth larvae (USDA APHIS, Otis Plant Protection Laboratory, Otis Air National Guard Base, Massachusetts, USA) to pupation on artificial diet at 25°C. After the onset of pupation, we collected female pupae from the rearing containers every 1-2 days and stored them at 5°C until deployment. Each pupa was affixed with purified beeswax to a small (ca. 5 × 5 cm) burlap square (Smith and Lautenschlager 1981). Latex gloves were worn while handling pupae and burlap squares to minimize contamination with human scent (Duncan et al. 2002). Each burlap square bearing a pupa was stapled to a tree bole under a folded burlap flap (approx. 7 by 15 cm). The burlap flap was meant to mimic a bark flap, a

microsite where gypsy moths often pupate (Campbell et al. 1975a, Campbell and Sloan 1976). Each burlap flap was dipped in molten beeswax and attached to the appropriate tree 5-7 days before pupae were deployed, to allow mice and other predators to become accustomed to the odor and appearance of burlap and beeswax without initially associating them with food.

In each grid, all pupae were deployed on the same day: either June 17 or 18 in 2002 and June 23 or 24 in 2003. Pupae were then checked every 1-2 days for signs of predation until June 28 in 2002 and until July 4 in 2003. Gypsy moth pupation at IES generally begins the first week of July with peak pupation in mid-July (C. G. Jones, unpubl. data), so our experiments took place just before natural pupation each year. After a pupa was depredated, we did not revisit or replace it. We categorized predators as vertebrate or invertebrate on the basis of the pattern of damage and the presence of toothmarks in the beeswax, scat, or holes chewed in the burlap (Smith 1985). This method is not foolproof, in part because invertebrates often feed on pupal remains after a vertebrate attack. Therefore, we consider this to be a minimum estimate of the contribution of vertebrates to pupal predation. Due to the relatively high densities of white-footed mice in this study (see Results) and consistently strong relationship between mouse densities and overall pupal predation (Elkinton et al. 1996, Ostfeld et al. 1996, Jones et al. 1998), we assumed that mice were the primary vertebrate predators.

**Statistical analysis**

Standard survival analyses are based on the assumption that the fates of individuals are independent, but this assumption was almost certainly violated in our experiments. Individual mice are likely to differ in their consumption rates and their foraging activities will be spatially clumped, causing predation risk to be spatially autocorrelated (Koenig 1999, Manson 2000).

Therefore, we conducted our primary analyses using the quadrat as the experimental unit in a randomized block design with trapping grids as blocks.

Our response variable was the transformed daily vertebrate predation rate in a quadrat, defined as $\hat{p}_{ij} = \arcsin\sqrt{1-\left(1-V_{i+\delta,j}/N_{ij}\right)^{1/\delta}}$ where $N_{ij}$ is the number of unattacked pupae on day $i$ in quadrat $j$, $V_{i+\delta,j}$ is the number of pupae found attacked by vertebrates on day $i+\delta$, and $\delta$ is the monitoring interval (days). In 2003, 52 pupae were found to be dead and decomposing at the end of the study with no signs of attack by predators. These pupae might have been dead (and therefore unattractive to mice) when deployed or might have died after deployment. Therefore, we analyzed the 2003 data separately with and without the dead pupae, to determine whether excluding them would affect results. Predations rates varied substantially among days (see Results), so we analyzed the data from each year using weighted repeated measures analysis of variance (RMANOVA; PROC GLM in SAS) with treatment (pupal density only for 2002; pupal density, height, and density × height for 2003) and grid as independent variables. Transformed predation rates were weighted by the initial number of pupae per quadrat. In 2002 all pupae in the high-density quadrats in two of the six grids were consumed by day 7, so RMANOVA was conducted using all grids for days 1-7 post-deployment. In 2003, ground-level pupae were completely gone from 3 quadrats (2 medium-density and 1 low-density) by day 4 and tree-level pupae were gone from one medium-density quadrat by day 6. Therefore, 2003 data were analyzed in RMANOVA using data for days 2-6.

After RMANOVA indicated day × treatment effects (see Results), we performed a separate ANOVA for each day separately with treatment and grid as independent variables and transformed daily predation rate as the dependent variable. In daily ANOVAs, each predation rate was weighted by the reciprocal of its sampling variance: $N_{ij}/(p_{ij}'(1-p_{ij}'))$, where $p_{ij}'$ =

minimum[$p_{ij}$, 0.95] or maximum[$p_{ij}$, 0.05] as appropriate. Hypothesis tests for treatment effects were based on type III sums of squares. When daily ANOVAs indicated significant treatment effects, we applied Tukey Studentized range tests with $\alpha = 0.05$ to make pairwise comparisons of predation rates among treatment levels.

A mouse that finds a pupa might conduct an area-restricted search (Kareiva and Odell 1987) or keep returning to the same tree, causing clumped pupae to experience greater predation risk than lone pupae. Therefore, treatment differences in predation rates could arise due to the presence of clumps of pupae in the high and medium density treatments but not the low density treatment. To address this possibility, we used Cox proportional hazard analysis (PROC PHREG in SAS, SAS Institute, Cary, North Carolina) to test whether pupal survival rates in high-density quadrats differed depending on the number of pupae on the tree bole. This test for a spatial response was stratified by grid to account for differences in baseline predation rates, and was conducted using data from the high-density treatment only.

**Mammal trapping & population estimation**

Population densities of mice vary among grids within a year, which may account for differences in baseline predation rates among grids. Therefore, we used capture-recapture methods to estimate white-footed mouse population size. In each grid, two Sherman live traps were placed at each grid point ($n = 242$ per grid). Live-trapping was conducted for 2 consecutive nights every 3-5 weeks, from May to October 2002 and from May to November 2003. Traps were baited with oats, set in the evening, and checked and closed in the morning. Each mouse captured in a trap was identified by a uniquely numbered ear tag. We used the Jolly-Seber open population model (Jolly 1965, Seber 1965) with heterogeneous survival rates in the program

POPAN-5 (Arnason and Schwartz 1999) to estimate mouse population size during each trapping period. Mouse abundance early in the period when pupae were deployed (June 21, 2002; June 27, 2003) was estimated by linear interpolation between abundance estimates for trapping periods immediately before and after. Mammal trapping and handling were conducted in accordance with an institutional animal care protocol and American Society of Mammalogists guidelines.

## Results

Estimated abundance of white-footed mice on the 6 trapping grids during the 2002 experiment ranged from 64 to 214 mice per 2.25-ha grid, with an average ($\pm$ SD) of 110 $\pm$ 53 mice per grid. Estimated mouse abundance during the 2003 experiment ranged from 39 to 78 mice per 2.25-ha grid (mean $\pm$ SD = 54 $\pm$ 14). Patterns of damage reflected this difference in mouse abundance, indicating that vertebrates (presumably mice) were responsible for at least 861 of 947 (91%) total attacks in 2002 and 1,452 of 1,878 (77%) attacks in 2003.

### 2002 experiment

Daily predation rates were low for all treatments during the first days of the experiment but rose substantially in the medium- and high-density treatments (Fig. 2A), resulting in much higher cumulative predation rates than in the low-density treatment (Fig. 3A). RMANOVA indicated significant day × treatment effects ($F_{10, 50} = 5.4$, $P < 0.0001$ after Huynh-Feldt $\varepsilon$ correction), and univariate ANOVAs detected significant ($F_{2, 10} \geq 4.4$, $P \leq 0.043$) treatment differences on days 3, 4, 5.5, and 7. Post hoc comparison of daily predation rates among treatments indicated a greater predation rate in the high- than low-density treatment on days 4,

5.5, and 7, and greater predation in the high- than medium-density treatment on day 5.5. Predation rates in the high- and medium-density treatments increased while pupal densities were still much higher than the low-density treatment, so this increase was not simply due to reduced satiation as prey density declined. By day 7, all pupae had been eaten in the high-density treatment in 2 grids and $\leq 2$ pupae remained in the medium-density treatment in 3 grids. Because quadrats with high predation rates were no longer represented, overall predation rates appeared to decrease in the medium- and high-density treatments after day 7 (Fig. 2A). Elevated predation rates in the medium- and high-density treatments did not appear to be simply due to spatial responses to trees with >1 pupae. In the high-density treatment, predation risk for individual pupae was not significantly linked to the number of pupae on the same tree (Wald $\chi^2 = 0.09$, $df = 1$, $P = 0.76$; Fig. 4). Grid effects on predation rates (based on least-squares means from univariate ANOVAs) were not significantly correlated with grid-specific mouse density estimates ($r = -0.12$).

**2003 experiment**.

Results of statistical analysis for the 2003 experiment were qualitatively similar whether or not dead pupae were excluded, so we report results excluding dead pupae. Unlike in 2002, predation rates were initially high for all treatments in 2003 (Fig. 2). Throughout the 2003 experiment, predation rates on pupae were substantially higher at ground level (Fig. 2C) than on tree boles (Fig. 2B). Predation rates declined after day 2 for the low-density treatment but either remained level or increased for the medium- and high-density treatments (Fig. 2B,C). In RMANOVA, the main effect of grid was significant, as were the day × density and day × grid interactions (Table 1). There was no evidence of day × height, height × density, or day × height

× density interactions, and the main effect of height was marginally nonsignificant (Table 1). Separate ANOVAs for each day's data detected a significant effect of pupal density on day 6 only ($F_{2,22} = 6.4$, $P = 0.0066$). For day 6, post hoc comparisons indicated that predation rates were higher in the high-density than in the low-density treatment. As with the 2002 experiment, mean predation rates tended to decline toward the end of the experiment (Fig. 2) after pupae were eliminated from quadrats with high predation rates. Cumulative predation rates after 10 days increased with increasing pupal density at both heights (Fig. 3 B,C). Predation rate in the high-density treatment was unrelated to the number of pupae on a tree at both ground (Wald $\chi^2 = 0.003$, $df = 1$, $P = 0.96$) and 1.5-m (Wald $\chi^2 = 1.2$, $df = 1$, $P = 0.28$) heights (Fig. 4). Grid effects on predation rates (based on least-squares means from ANOVAs) showed a nonsignificant positive correlation with grid-specific mouse density ($r = 0.34$)

## Discussion

A positive relationship between prey density and predation rate is often assumed to imply that predation is stabilizing. Accelerating functional responses, which are more typical of generalist than specialist predators, can result in density-dependent predation (Murdoch and Oaten 1975). However, as Murdoch and Bence (1987) and Sinclair et al. (1998) argued, generalist predators are more likely than specialists to cause prey extinction because they may remain abundant despite scarcity of a particular prey species. We found that predation rates on gypsy moth pupae in forest habitats decreased with decreasing pupal density, but predation rates at ground level remained substantial at the lowest relevant pupal density (one pupa per mouse home range), so chronically dense populations of mice may be able to drive gypsy moths to local extinction despite the accelerating functional response. In 2002, predation on elevated pupae

increased over time in the medium- and high-density treatments, suggesting a lagged behavioral response. This lagged response was less evident in the results from 2003, but it appeared to temporarily offset a general decline in predation rates over time. Predation rates were uncorrelated with the number of pupae deployed on a tree, so elevated predation rates at higher pupal densities could not be explained by area-restricted searching for clumped pupae.

Our results provide evidence of an accelerating (e.g., type 3) functional response to gypsy moth pupae. However, our findings also support the assertion by Elkinton et al. (1989) that mice are unlikely to regulate gypsy moth populations in most cases. Regulation of a prey population by predators implies both prevention of high prey densities and relaxation of predation pressure as prey approach extinction (Sinclair and Pech 1996). Fluctuations in mouse abundance owing to factors independent of gypsy moth abundance would indeed be expected to disrupt regulation at the upper end. Still, fluctuations in mouse abundance would not prevent relaxation of predation pressure as gypsy moths became scarce if the per-mouse predation rate approached zero. We found that per-mouse predation rate decreased somewhat but remained substantial at one pupa per mouse home range, especially for pupae at ground level. Elkinton et al. (1989) also observed high predation rates on pupae deployed singly at ground level. Substantial ground-level predation risk at low pupal density could be especially detrimental to gypsy moth persistence because gypsy moths are more likely to pupate close to ground level when their population density is low. Gypsy moths typically pupate in or near larval resting sites (Campbell et al. 1975b) and late-instar gypsy moth larvae rest near ground level during daylight in low-density populations but remain in the canopy when population density is high (Lance et al. 1987). Therefore, predation rates may chronically exceed recruitment in areas with moderate to high mouse density, resulting in local extinction or a source-sink relationship with nearby

populations. Long-term monitoring at IES has documented frequent extinction of gypsy moths at small spatial scales (<1 ha) but continual persistence at larger scales (C. G. Jones, unpubl. data).

To assess whether observed predation rates on ground-level gypsy moth pupae are high enough to exceed gypsy moth recruitment, we can compare them with estimates of fecundity, hatch and larval survival. The empirical model of Williams et al. (1990) indicates mean fecundity of gypsy moths is approximately 705 eggs per egg mass at low density (0.1 egg masses / ha). Data from Campbell (1976) and Moore and Jones (1992) suggest that hatch rate may reach 70%. Finally, survivorship curves published by Gould et al. (1990) indicate ca. 30% survival of gypsy moth larvae to pupation in low-density populations. Using these values, and assuming a 1:1 sex ratio and 100% mating success of adult females, we estimate that each adult female moth produces 74 female offspring that survive to pupation. Multiplying this value by the proportion of pupae that survive to eclosion thus yields an estimate of the annual finite rate of increase ($\lambda = N_{t+1}/N_t$). In our low- and high-density ground treatments in 2003, survival of pupae to day 10 was 13% and 1.2%, respectively. Extrapolating out to a pupation period of 13 days yields estimated $\lambda$ values of 5.2 and 0.24, respectively. These back-of-the-envelope calculations suggest that the level of predation we observed in 2003 (when mouse densities were similar to the long term average at IES) would not drive gypsy moths to extinction but could prevent gypsy moths from reaching high densities. In areas where mean densities were higher, however, mouse predation could conceivably drive pupal survival below the replacement point even at very low pupal density. For example, Hastings et al. (2002) observed 3-day predation rates of 92-99% for pupae deployed singly at several heights in Virginia sites and years with high mouse densities, whereas we observed 80% cumulative predation by day 4 in our low-density ground treatment.

The behavioral mechanism underlying the accelerating functional response of mice to gypsy moth pupae is unknown. In our 2002 experiment, when all pupae were deployed at 1.5 m height, predation rates started low in all treatments but increased over time in the medium- and high-density treatments. As noted previously, this increase in predation rate did not appear to be the result of area-restricted searching for pupae clumped on tree trunks. White-footed mice are semiarboreal, but forage most intensely at ground level (Graves et al. 1988, McMillan and Kaufman 1995) so predation on gypsy moth pupae consistently decreases with increasing height aboveground (Campbell et al. 1975a, Campbell and Sloan 1976, Cook et al. 1995, Grushecky et al. 1998, Liebhold et al. 1998, Hastings et al. 2002), as we found in 2003 (Fig. 3). Gschwantner et al. (2002) found that predation (primarily by small mammals) in Austria on elevated gypsy moth pupae increased over a period of days after initial deployment, becoming more similar to ground-level predation rates. We hypothesize that mice may perceive the forest floor and arboreal microsites as distinct habitat patches, so that a mouse that finds abundant food on one tree trunk may increase the amount of time it spends foraging on tree trunks in general. White-footed mice have been found to increase arboreal activity after encountering attractive bait (peanut butter) on tree trunks (Manville et al. 1992), so they may have a similar response to pupae. This pattern was subtly repeated in 2003: predation rates in 2003 were initially high for pupae at both ground level and 1.5 m height; thereafter predation decreased in the low-density treatment, stayed level for higher densities on the ground, and appeared to increase for higher densities on tree trunks (Fig. 2). Because predation rates increased with pupal density at both ground and tree levels, switching between ground and arboreal microhabitats cannot entirely explain our results. Perhaps mice developed a search image for pupae, or began foraging around the bases of trees more often after several encounters with pupae.

The lagged behavioral response we observed suggests that functional response may take >1 value at a given pupal density, depending on whether that pupal density is the initial value or the result of depletion from higher densities. If the pupal population is sparse at the beginning of the pupation period, then mice may not become "induced" to high predation rates. However, if the pupal density is moderately high at the beginning of the pupation, then mice may continue exerting high predation rates even after driving pupal density to low levels. In other words, dense populations of mice may deplete gypsy moth pupae so rapidly that a delay in responding behaviorally could result in overcompensatory predation. This runs counter to the general assumption that the functional response is very rapid in relation to the time scale of population dynamics.

The apparent lagged response by mice to gypsy moth pupae is relevant to the design of field studies of pupal predation. A 3-day exposure period is often used in field studies on gypsy moth predation (Elkinton et al. 1989, Cook et al. 1995, Grushecky et al. 1998, Liebhold et al. 1998, Hastings et al. 2002), yet in our 2002 experiment daily predation rates approximately doubled between days 1-3 and days 4-7 for the medium- and high-density treatments (Fig. 2). Schauber (2000) analyzed predation rates on freeze-dried gypsy moth pupae deployed in the same six IES grids at 1.5 m height on tree boles during the period of gypsy moth pupation from 1993 to 1998, and found that when mouse density was high, daily predation rates tended to increase as days passed since deployment. This increase in predation rate as prey were depleted was interpreted as evidence for a type 2 functional response (Schauber 2000), but it could also have resulted from lagged behavioral shift by mice in response to the appearance of pupae. Gschwantner et al. (2002) found that predation rates (primarily by small mammals) on deployed gypsy moth pupae in Austria increased dramatically over time within a month. These lines of

evidence suggest that extrapolating from predation rates measured over 3 days to predict overall pupal mortality may be inaccurate.

We found no evidence that mice exhibited a small-scale spatial response to groups of pupae. The lack of a spatial response was unexpected, because foragers exploiting patchy prey can maximize gain by using area-restricted search (Tinbergen et al. 1967, Kareiva and Odell 1987) or other mechanisms of concentrating effort in patches of high prey abundance (MacArthur and Pianka 1966, Charnov 1976). However, the distribution of foraging effort is also constrained by intraspecific interactions such as territoriality (Lewis and Murray 1993), distribution of alternative foods (Schmidt et al. 2001), risk from higher trophic levels (Jefferies and Lawton 1984), locations of nests or other home sites (Orians and Pearson 1979), and habitual travel routes. Perhaps mice only respond spatially to pupae in groups large enough to satiate them, which would slow but not reverse the decline in predation rate as pupal density increased.

On the basis of our results, we recommend the use of more general and mechanistic models of type 3 functional responses. In typical models of type 3 functional response, the per-predator predation rate approaches zero at very low prey densities (Real 1977, Hassell 1978, Turchin and Hanski 1997) so the predator cannot deterministically drive its prey to extinction. A positive minimum predation rate can easily be incorporated into the type 3 functional response by making attack rate a saturating function of prey density with a positive intercept:

$$N_e/N = a[N]/(1+a[N]T_hN) \qquad \text{Equation 1A}$$

$$a[N] = a_{\min} + (a_{\max} - a_{\min})N/(C+N) \qquad \text{Equation 1B}$$

where $N$ is the prey density, $N_e$ is the number of prey eaten per unit of area and time, $a[N]$ is predator attack rate as a function of $N$, and $T_h$ is Holling's (1959a) handling time. This

formulation is mathematically equivalent to that of Juliano (1993). Eq. 1B indicates that $a[N]$ is a saturating function of $N$, with a minimum value $a_{min}$, a half-saturation constant $C$, and a maximum value of $a_{max}$ (Fig. 5A). The type 3 model of Hassell et al. (1977) corresponds to the special case of $a_{min} = 0$. However, there is no *a priori* reason to presume that $a_{min} = 0$. Presuming so would imply that predators completely ignore very rare prey upon encounter, completely avoid patches where rare prey are found, or are completely incompetent at finding or catching novel prey. All of these conditions are unlikely to hold for real generalists, which generally exhibit partial preferences for prey types and patches (Gray 1987, Berec and Krivan 2000). If $a_{min} > 0$, then there exists some predator density that will cause total predation rate to exceed per capita prey recruitment at low prey density and potentially drive prey toward extinction (Fig. 5B), unlike the case of $a_{min} = 0$ (Fig. 5C).

The pattern of $0 < a_{min} < a_{max}$ is probably common for generalist predators attacking preferred prey, according to the model of Joly and Patterson (2003). Their model is based on the assumption that the selectivity of predators with access to two prey types increases in a logit-linear fashion with prey abundance. This model is flexibly capable of producing a type 2 or type 3 functional response, depending on the strength of selectivity. They found that as preferred prey become scarce, per-predator predation rate on preferred prey converges to positive value (analogous to $a_{min}$ in Eq. 1B). When predators are abundant, the model predicts that overall predation rate could exceed population growth of a rare but preferred prey, resulting in its local extinction.

The risk of local prey extinction depends strongly on whether $a_{min}$ varies with predator density. As predators become more abundant, their per-capita impact on prey may decline due to actual or pseudo-interference (Abrams and Ginzburg 2000). However, high mouse density

would likely reduce the abundance of preferred prey other than gypsy moth pupae, which would tend to increase $a_{min}$ according to the Joly and Patterson (2003) model. Thus, the net impact of variations in mouse density on $a_{min}$ is uncertain.

Abundant empirical and theoretical research (Huffaker 1958, Hilborn 1975, Amezcua and Holyoak 2000) indicates that a locally unstable predator-prey system may persist at large spatial scales due to spatial subdivision, structure, and heterogeneity. Large-scale persistence of gypsy moths is particularly likely if the abundance and attack rate of mice vary substantially in space and time, so that areas of low predation risk can serve as sources of emigrants to areas of higher risk. Therefore, mice should not be expected to eradicate gypsy moths at scales relevant to forest management, despite their potential for causing local extinctions. Based on the weak correlations between grid effects and local mouse density that we found, spatial variations in risk may stem from factors affecting attack rate (e.g., abundance of alternative foods or presence of predators that attack mice) as well as variations in mouse abundance.

Our study provides empirical support for the theoretical assertion that an accelerating functional response alone may not be sufficient to prevent predators from driving a strongly preferred prey type to local extinction (Murdoch and Bence 1987, van Baalen et al. 2001, Joly and Patterson 2003). However, we found that predation rates at moderate mouse densities appeared to allow low-density gypsy moths to increase while suppressing population increase at moderate moth densities. Due to spatial variations in long-term average abundance of mice and alternative foods, the effect of predation by mice on gypsy moth populations could range from little effect, regulation at low densities, or even driving moths to local extinction.

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Table 1. Repeated-measures analysis of variance results for 2003 pupal predation experiment, excluding dead but unattacked pupae. Probability (*P*) values for within-subject tests for within-subject effects are adjusted by Huynh-Feldt ε.

| Type of Test | Variable | df | *F* | *P* |
|---|---|---|---|---|
| Between-Subject | Grid | 5 | 4.09 | 0.0089 |
| | Height | 1 | 3.62 | 0.070 |
| | Pupal Density | 2 | 2.24 | 0.13 |
| | Height × Density | 2 | 0.64 | 0.54 |
| | Error | 22 | | |
| Within-Subject | Day | 2 | 0.76 | 0.47 |
| | Day × Grid | 10 | 4.48 | 0.0002 |
| | Day × Height | 2 | 1.15 | 0.33 |
| | Day × Density | 4 | 2.99 | 0.029 |
| | Day × Height × Density | 4 | 0.77 | 0.55 |
| | Error | 44 | | |

Figure Legends

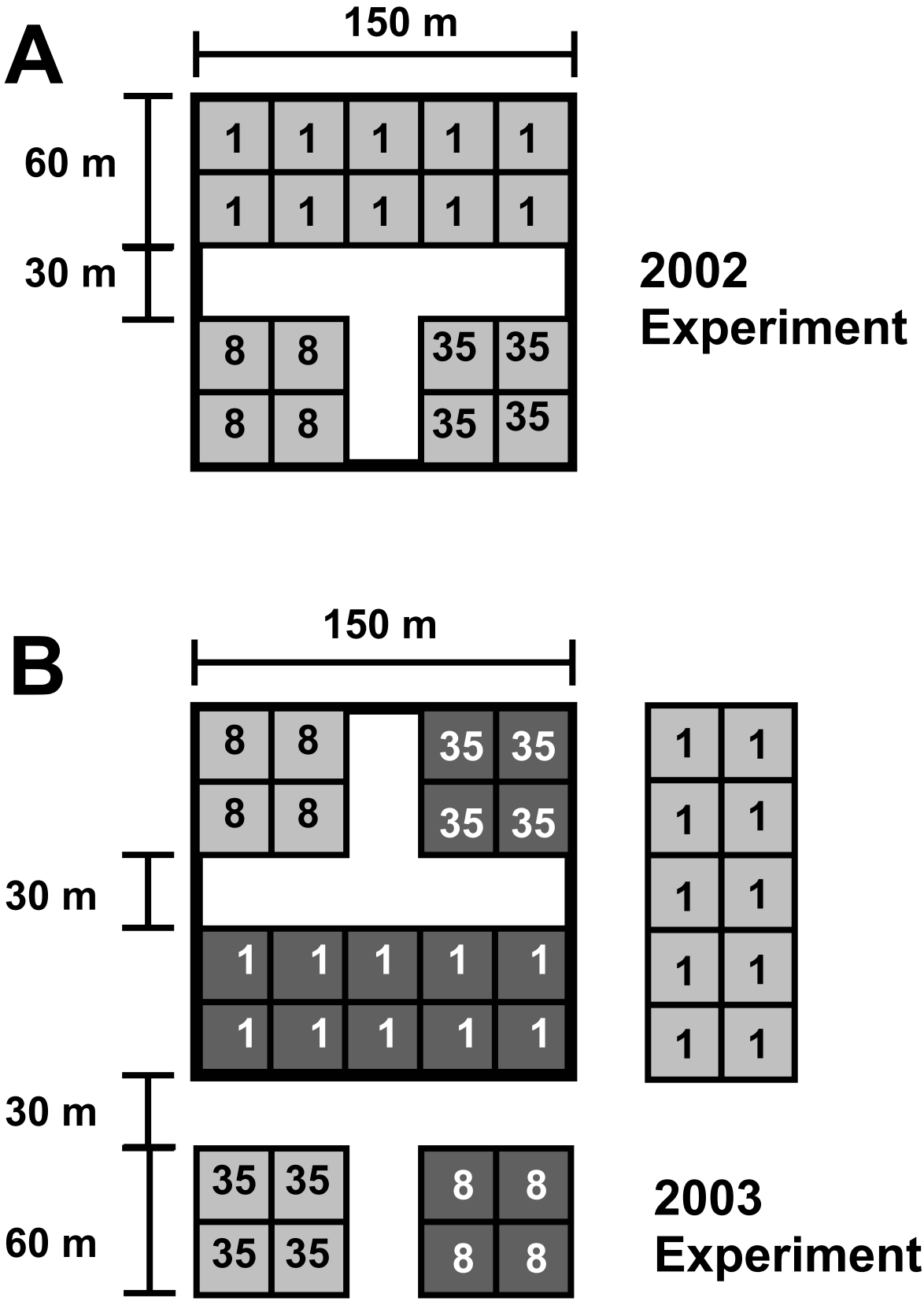
Figure 1. Layout of quadrats for functional response experiments conducted at the Institute of Ecosystem Studies, Millbrook, New York, in 2002 (A) and 2003 (B). Large square with thick black outline indicates a 2.25-ha (150 × 150 m) trapping grid. Quadrats for pupal deployment are depicted with gray fill, with thin black lines designating 30 × 30-m cells within each quadrat. Each cell was approximately the size of a mouse home range. Deployment height is indicated by light gray (1.5 m high) or dark gray fill (ground level). Numbers indicate the number of pupae deployed within each cell.

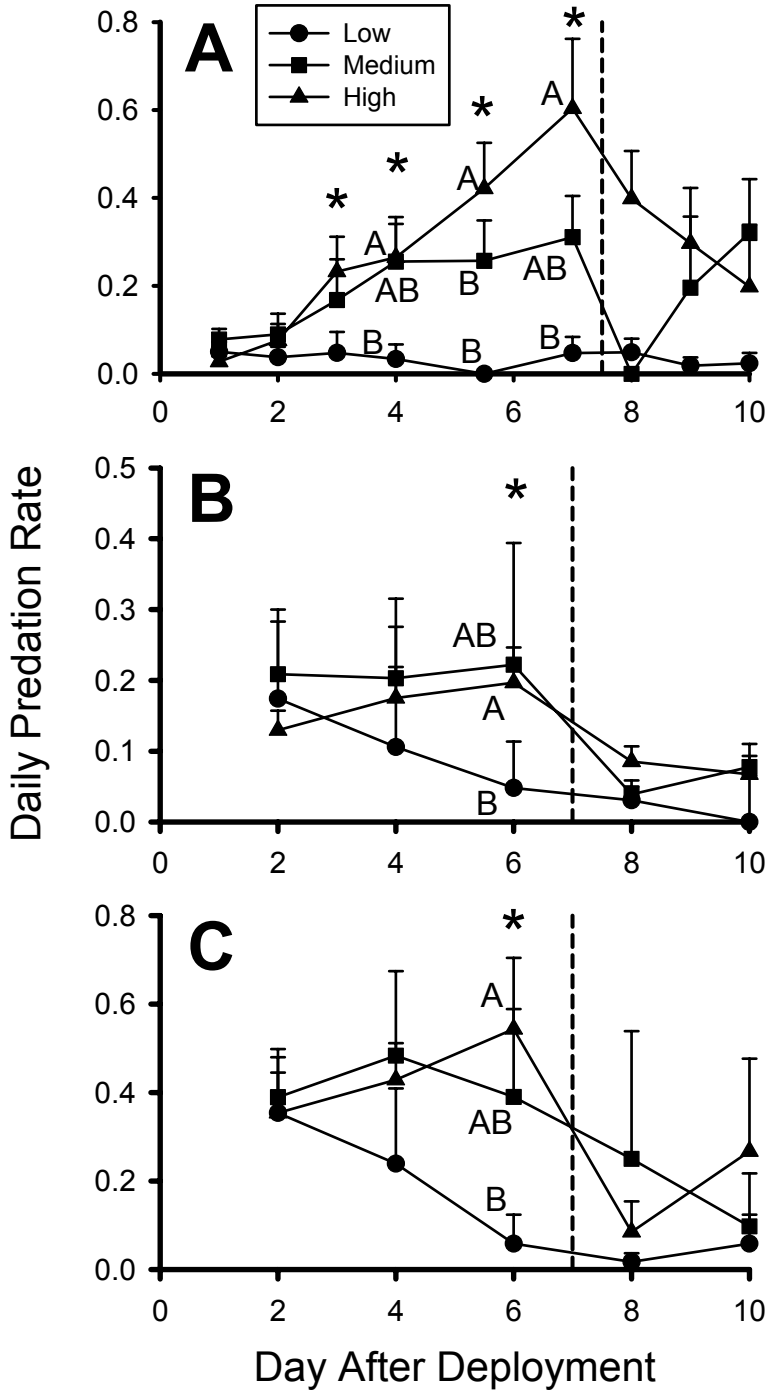
Figure 2. Average (+ 1 SE) daily vertebrate predation rates on live gypsy moth pupae deployed at low, medium, and high densities (1, 8, and 35 pupae per 900 $m^2$, respectively) in 6 forested trapping grids at the Institute of Ecosystem Studies, New York. Results are from (A) 2002 with all pupae deployed 1.5 m high on tree boles, (B) 2003 pupae deployed 1.5 m high and (C) 2003 pupae deployed at ground level. Asterisks indicate significant treatment differences detected by ANOVA. Treatments sharing a letter were not significantly different ($P \geq 0.05$) in post hoc comparisons. After day 7 in 2002 and day 6 in 2003 (indicated by vertical dashed lines), no pupae remained in some treatments and grids.

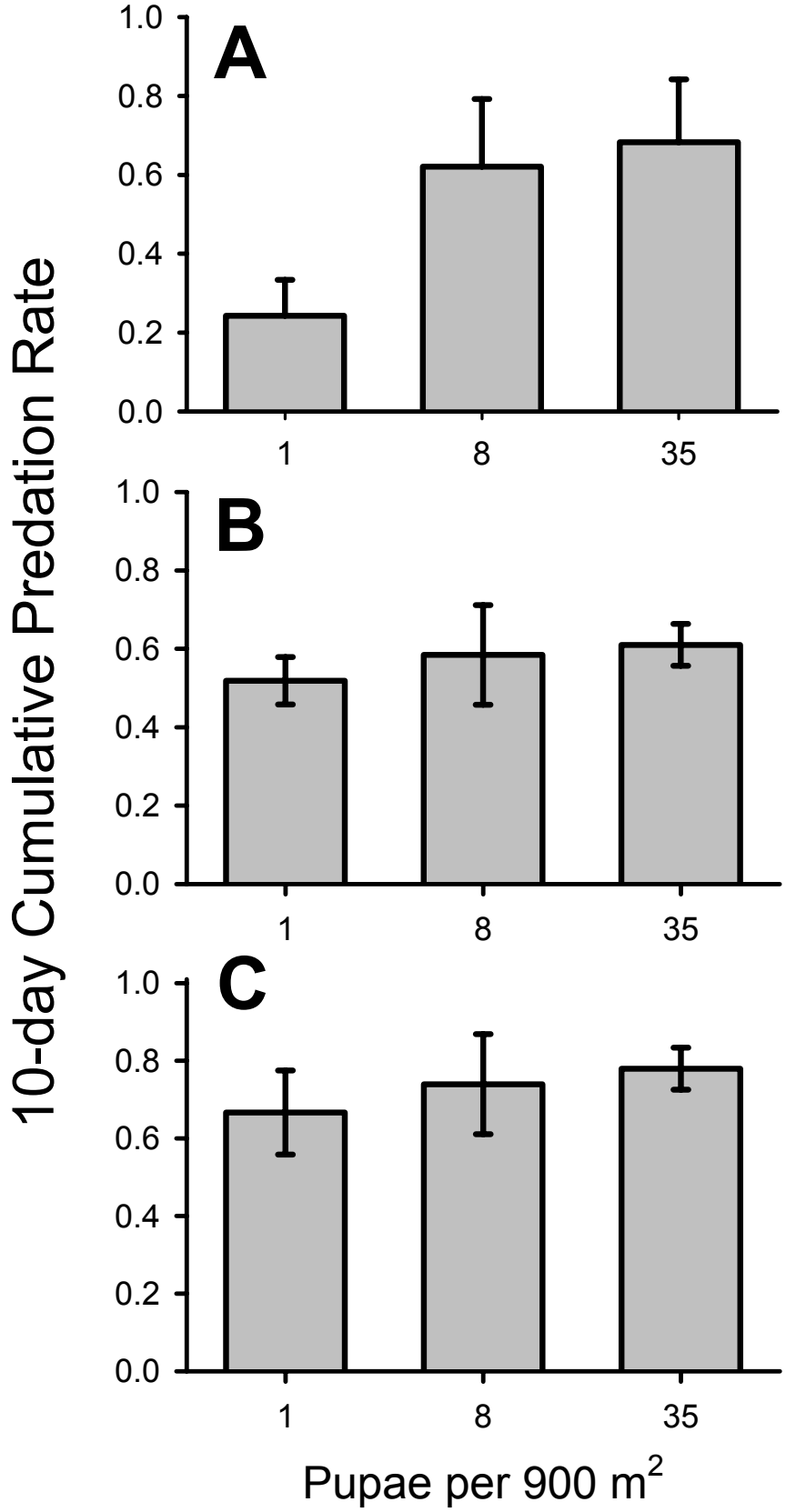
Figure 3. Cumulative vertebrate predation rates on live gypsy moth pupae over 10 days, by density treatment for (A) 2002 pupae deployed 1.5-m high on trees, (B) 2003 pupae deployed 1.5-m high on trees, and (C) 2003 pupae deployed at ground level.

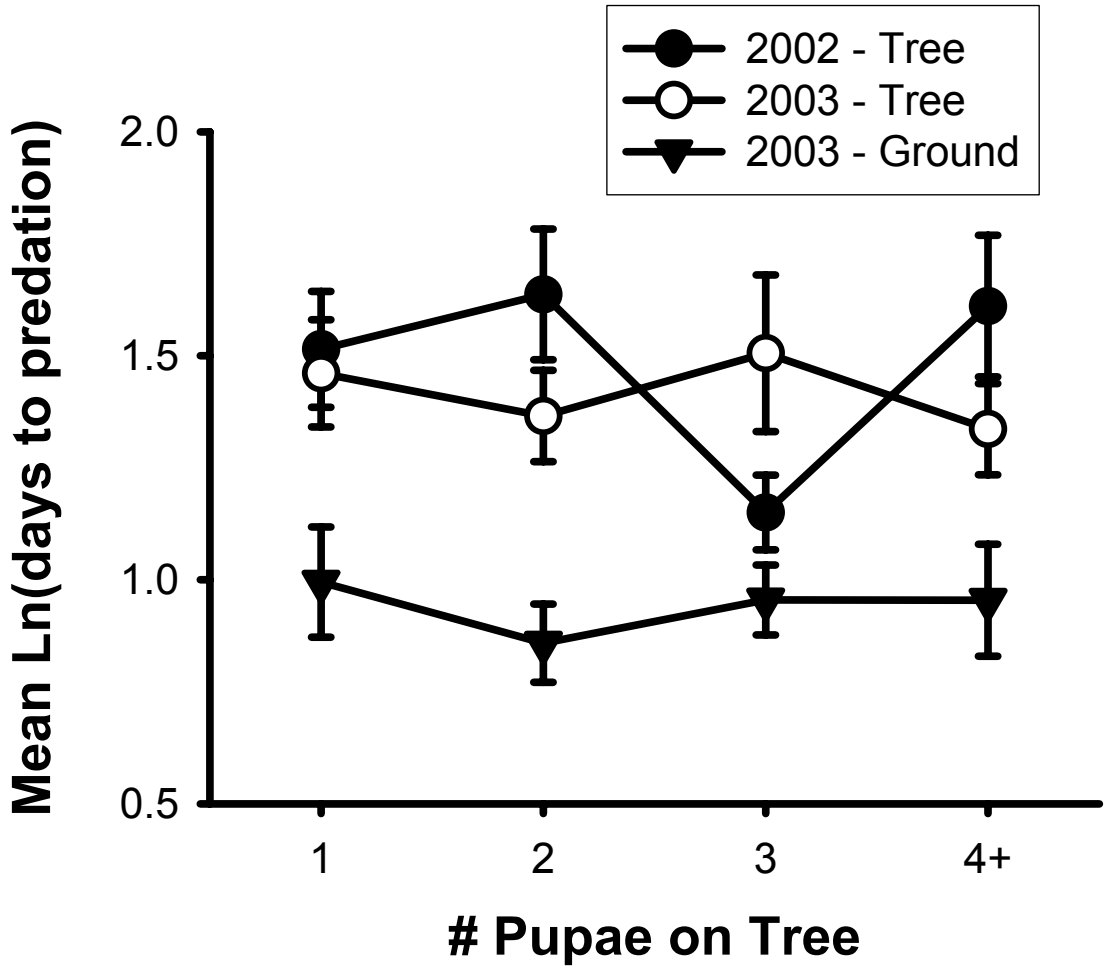
Figure 4. Mean (± 1 SE) time to predation for live gypsy moth pupae in high-density treatments, as a function of the number of pupae deployed on the same tree.

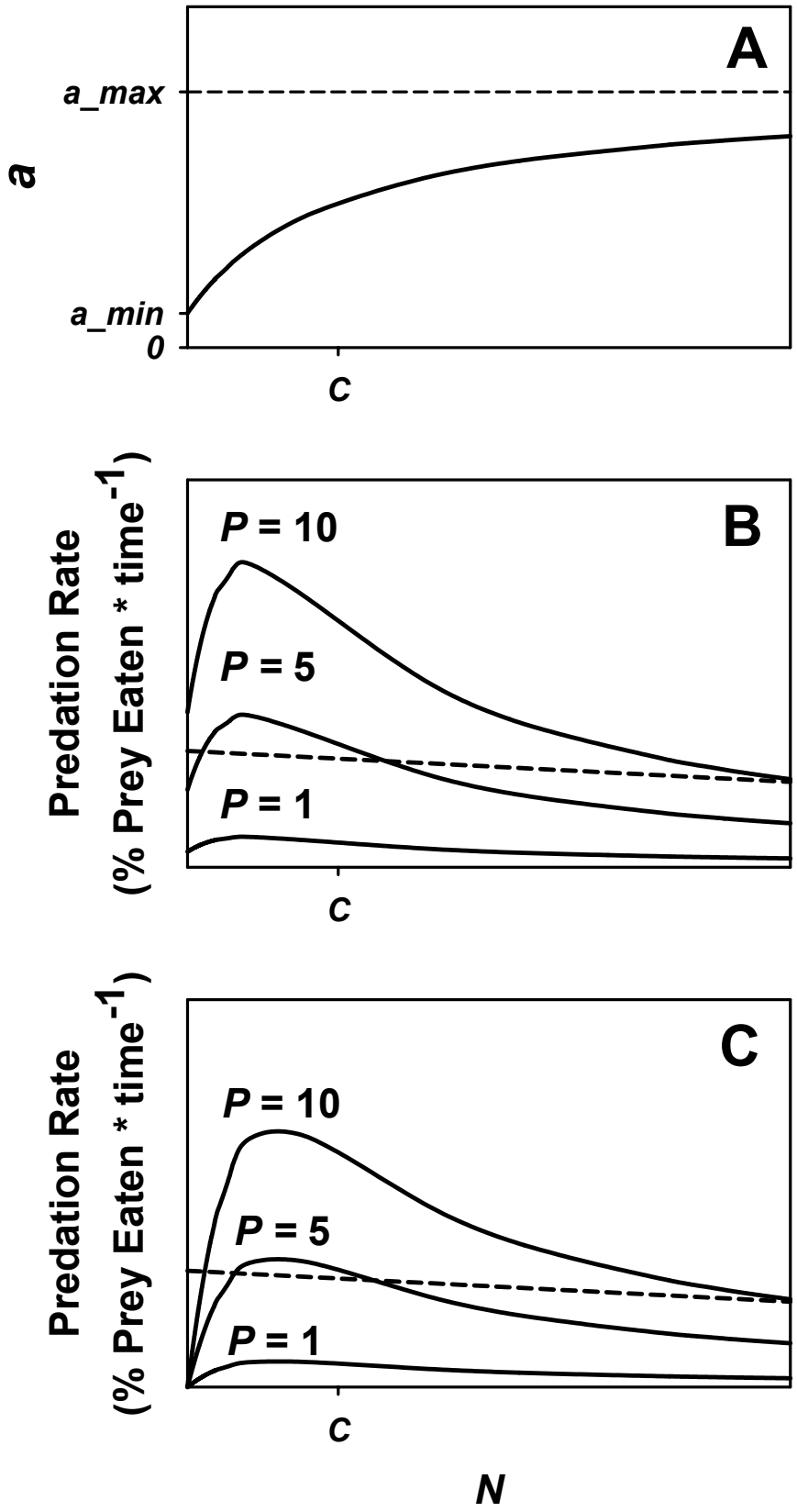
Figure 5. Graphical representation of a type 3 functional response in which predator attack rate approaches a minimum value ($a_{min}$) as prey density approaches zero. (A) Predator attack rate ($a$) as a function of prey density ($N$). (B) Predation rate (solid lines) as a function of predator density ($P$, in arbitrary units), in relation to per capita prey recruitment in the absence of predation (dashed line). Of these 3 predator density scenarios, only $P = 5$ can result in regulation of the prey by the predator. (C) As for (B), except that $a_{min}$ is set to zero, as in standard type 3 models. In this case, any sufficiently dense predator population can regulate the prey at low density.


A
150 m
60 m
30 m
1 1 1 1 1
1 1 1 1 1
8 8
8 8
35 35
35 35
2002
Experiment
B
150 m
8 8
8 8
35 35
35 35
30 m
1 1 1 1 1
1 1 1 1 1
30 m
1 1
1 1
1 1
1 1
1 1
35 35
35 35
60 m
8 8
8 8
2003
Experiment


A
Low
Medium
High
B
C
Daily Predation Rate
Day After Deployment
0.0
0.2
0.4
0.6
0.8
0.1
0.3
0.5
0
2
4
6
8
10
*
A
AB
B


A
B
C
1.0
0.8
0.6
0.4
0.2
0.0
1
8
35
10-day Cumulative Predation Rate
Pupae per 900 m2


2002 - Tree
2003 - Tree
2003 - Ground
Mean Ln(days to predation)
2.0
1.5
1.0
0.5
1
2
3
4+
# Pupae on Tree


A
a_max
a
a_min
0
C
B
Predation Rate
(% Prey Eaten * time-1)
P = 10
P = 5
P = 1
C
C
Predation Rate
(% Prey Eaten * time-1)
P = 10
P = 5
P = 1
C
N