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## Effects of alternative prey on predation by small mammals on gypsy moth pupae

Received: 15 August 2003 / Accepted: 6 April 2004 / Published online: 20 May 2004  
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**Abstract** Previous work shows that predation by small mammals is a dominant cause of mortality of low-density gypsy moths in North America and that declines in small mammal density result in increases in gypsy moth density. Here we examined whether predation by small mammals is density dependent by way of a type III functional response, and how predation is influenced by alternative prey. First we showed that the preference of predators for gypsy moth pupae was low compared to other experimental prey items, such as mealworm pupae and sunflower seeds. Predation on gypsy moth pupae was characterized by a type II functional response with percent predation highest at the lowest prey densities, whereas the functional response to sunflower seeds was characterized by a type III functional response in which predation increased with increasing prey density. These results suggest that predation by small mammals is unlikely to stabilize low-density gypsy moth populations.

**Keywords** *Lymantria dispar* · Lepidoptera · Lymantriidae · Small mammals · Functional response · *Peromyscus leucopus*

### Introduction

Most of the literature on the regulation of insect populations has focused on specialist predators and parasites (Hassell 1978). However, there is increasing agreement that generalist predators play an equal or greater role than specialist enemies in the control of many forest insects (Buckner 1969; Murdoch and Marks 1973; Hassell and May 1986; Latto and Hassell 1988; Hanski 1990). Because generalist predators, by definition, have many prey, the numerical response of predators to particular prey populations may be limited or non-existent (Hanski 1990). Therefore, if generalist predators regulate prey populations, this must occur via the functional response to prey density (Holling 1965).

Many herbivorous insects spend time on or near the ground, and this behavior exposes them to predation by ground-dwelling vertebrates and invertebrates. Several studies have reported that small mammals are major predators of insect herbivore populations, especially when they exist at low densities (Bess et al. 1947; Holling 1959a; Buckner 1969). Although there is compelling evidence that predation by small mammals is sometimes intense, the role of predators in regulating herbivore populations has not always been clear. Reproduction by small mammals is typically limited by overwintering food availability and space; for these reasons, small mammals are unlikely to respond numerically to prey population densities in mid-summer.

In contrast, the functional response of small mammal populations to prey density may be quite pronounced. Holling's (1959a) classic work with small mammal predation on forest insects indicated that for some predator-prey systems, the proportion of prey consumed declined with prey density; he referred to this as a type II functional response. In other systems, the proportion of prey consumed increased with host densities up to a maximum level and then declined again at higher densities. This latter response, termed a type III functional response, has been recognized as capable of regulating

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prey populations via negative feedback (Holling 1965; Hassell 1978).

Predation has been identified as the major cause of mortality in low-density populations of gypsy moth, *Lymantria dispar* L (Bess et al. 1947; Campbell 1975). Furthermore, there is good evidence that most of this predation is caused by small mammals (Bess et al. 1947; Campbell et al. 1977; Weseloh 1988, 1990; Smith 1989; Elkinton et al. 1989, 1996; Grushecky et al. 1998; Jones et al. 1998). Despite this knowledge, however, there are differing theories as to how predator populations interact with the dynamics of gypsy moth populations and how they affect the onset of gypsy moth outbreaks. Campbell (1975) argued that predation by small mammals on gypsy moth populations was density dependent and therefore responsible for regulation of low-density populations. Elkinton et al. (1989) and Gould et al. (1990) measured rates of pupal predation in experimental populations that ranged from low to high density. They reported inversely density dependent predation, a finding compatible with Campbell's suggestion that satiation of generalist predators allows gypsy moth populations to escape from low density into outbreak phase in which predators cause negligible mortality. However, Elkinton et al. (1989) argued that even though small mammals cause high levels of mortality in low-density gypsy moth populations, there is no evidence that they cause positive density dependent predation at these low densities. More recently Elkinton et al. (1996) confirmed that variation in rates of predation by small mammals was a major determinant of inter-generational changes in the density of low-density populations. However, they reported that variation in predation rate was not strongly affected by gypsy moth densities, but instead was determined by variation in predator densities, which in turn appeared to be determined by mast abundance.

The apparent lack of positive density dependence in predation on gypsy moth is in stark contrast with several classical studies of the functional response of vertebrate predators to prey densities. Predation by small mammals and other vertebrate predators on various prey species has been often characterized by a type III functional response (Holling 1965; Hassell 1978). However, Holling noted that the functional response of predation to prey density can be modified both by the palatability of the prey item relative to alternative items and the abundance of alternative items.

In this study we examined the relative preference of predators for gypsy moth pupae compared to other prey items. We hypothesized that gypsy moth pupae may be an unpalatable food item compared to other prey items in the forest. Furthermore, pupal palatability may be crucial in determining the functional response of predators to gypsy moth pupal densities. Unfortunately, little information about the palatability of gypsy moth larvae and pupae compared to other prey items is available. Smith and Lautenschlager (1978) gave a brief description of the preference of hairless cankerworm

larvae over gypsy moth larvae in laboratory feeding trials to white-footed mice (*Peromyscus leucopus* L.). In studies presented here, we show how the availability of alternative prey might affect predation on gypsy moth populations. To address this question we experimentally evaluated the effect of the presence of alternative food sources both during the winter, when they affect predator survival and reproduction, and during the spring, when they compete with gypsy moth pupae as prey.

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## Materials and methods

### Measurement of predation

Predation was measured by monitoring the disappearance of food items in the field. Food items were glued individually to 15×15 cm burlap squares using melted beeswax. Burlap squares were placed on the forest floor. Over each of the following 1–3 days, each burlap square was visited and the condition of the prey item was recorded. Condition was recorded as intact, partially eaten, or completely missing. Similar methods have been used in several previous studies to measure predation on gypsy moth pupae (Smith 1985, 1989; Cook et al. 1994; Elkinton et al. 1989, 1996).

### Experiment 1: prey preference

Predation on gypsy moth pupae was compared with predation rates on two other items: mealworm (*Tenebrio molitor*) pupae and sunflower (*Helianthus annuus*) seeds. This study was replicated in spring (early May), summer (early July), and fall (early September) in 1995 and 1996 in a mixed hardwood stand located in the Powdermill Nature Reserve, Westmoreland Co., PA. USA. Gypsy moth egg mass densities were very low in the stand in both years; egg mass counts in twenty 0.01 ha plots indicated that densities were < 5 per ha. Prey items were deployed along eight 300 m transects that were located ca. 20 m apart. Along each transect, the three prey items were glued to burlap squares and placed alternately on the forest floor at 10 m intervals for a total of 80 replicates of each prey item. The proportions of mealworm pupae and sunflower seeds consumed were compared with the proportion gypsy moth pupae eaten using a two-tailed *G*-test with  $\alpha=0.0047$ , adjusted for 11 pairwise comparisons using Šidák's inequality (Sokal and Rohlf 1981).

### Experiment 2: functional response

We next examined the functional response of predators to a full range of experimentally set densities of gypsy moth pupae and sunflower seeds so as to characterize the shape of the functional response curve for both prey items. We conducted this experiment in August 2000 on a 10 km oval transect on the Prescott peninsula in the

Quabbin Reservoir in western Massachusetts. We deployed either laboratory-reared pupae or sunflower seeds in 20 m×20 m plots. Plots were located at intervals of ca. 80 m and alternated between the two food types. This distance was chosen so that mice that encountered one plot would be unlikely to also encounter other plots. Each plot was stocked with 6, 12, 25, 50, 100, 200 or 400 gypsy moth pupae or seeds spread evenly over the plots. For both pupae and sunflower seeds there were eight plots with 6 prey items, four plots with 12, and two plots at each of the higher densities. These levels of replication assured that at least 48 seeds or pupae were deployed at each density. Densities were assigned to plots at random. We also deployed a total of 50 single seeds and 50 single pupae in alternate fashion at the midpoints (ca. 40 m) between the plots and along another nearby transect. We measured predation rates by all predators during a single night. We also recorded the presence of mouse feces on the burlap squares and tooth marks in beeswax holding the pupae and seeds in place. The feces of *P. leucopus* are quite distinct from that of other forest-dwelling small mammals that might feed on pupae or seeds, including the eastern chipmunk (*Tamias striatus*) and the northern short-tailed shrew (*Blarina brevicauda*).

To analyze the functional response data in Experiment 3, we followed the two-step process recommended by Juliano (1993). First, we used logistic regression (PROC LOGISTIC, SAS Institute 1989; Trexler et al. 1988) to determine whether the functional response was type II or type III (Holling 1965). The procedure entailed fitting a polynomial model of seed or pupal density (numbers per plot) to the logit-transformed proportion consumed during the one-day test period. We began with a cubic model and eliminated any non-significant highest-order terms. We then plotted the resulting best-fit model against seed or pupal density and examined it for regions of positive or negative density dependence. Positive density dependence would indicate a type III functional response. Negative density dependence over all prey densities would indicate a type II response.

We then used SAS NLIN (Juliano 1993; Juliano and Williams 1987) to fit our data to the appropriate model. For a type II functional response we fit the Holling (1959b) disk equation:

$$N_e = \frac{aTNP}{1 + aT_h N} \quad (1)$$

where  $N$  is the number of seeds or pupae presented,  $N_e$  is the estimated number of seeds or pupae eaten,  $T$  is the total time available (we assigned  $T=1$  day),  $T_h$  is the handling time per seed or pupa and  $a$  is the instantaneous attack rate.

For a type III functional response we fit the equation suggested by Hassell (1978):

$$N_e = \frac{dNT + bN^2T}{1 + cN + dNT_h + bN^2T_h} \quad (2)$$

Experiment 3: effect of the availability of alternative prey items

In Experiment 3, we tested the effect of the availability of alternative prey items on predation on gypsy moth pupae by distributing large quantities of a more palatable alternative food item (sunflower seeds) and then measuring predation on deployed pupae. At the same time we tested the effect of winter-feeding (with a wheat-based mouse chow) of small mammal populations on predation in the following summer. We hypothesized that winter-feeding of small mammal populations would increase winter survival of small mammal populations and cause their population densities to be elevated in the following summer, which in turn would increase total levels of predation on gypsy moth pupae. In contrast, we hypothesized that increasing the availability of alternate prey items during the summer would greatly decrease predation on pupae because it would satiate predators (Murdoch and Oaten 1975).

These experimental manipulations were conducted in eight 4 ha forest stands located in the Quabbin Reservoir located in western Massachusetts. These forests were oak-dominated and have been described in more detail elsewhere (Gould et al. 1990; Elkinton et al. 1996). In the year that these experiments were conducted (1986) naturally occurring populations of the gypsy moth were extremely low, such that it was virtually impossible to find any life stages. Each stand was divided into four 1 ha plots and one of three treatments was randomly assigned to each of three of the four plots (the remaining plot was unused).

The three treatments consisted of elevation of the availability of alternate food items, winter-feeding, and control (no treatment). Availability of alternate food was elevated by distributing 91 kg of unshelled sunflower seeds onto the forest floor throughout the plot in early July (the approximate time of gypsy moth pupation). Seeds were uniformly distributed by traversing through the plot and using a cyclone broadcast seeder to distribute the seed. We estimate that this resulted in a density of approximately 100 seeds per m<sup>2</sup>.

Winter-feeding was accomplished by stocking nine feeding stations per plot with Purina Mouse Chow (a wheat-based food blended to supply the nutritional needs of mice). Feeding stations consisted of 0.75 m×0.75 m×0.75 m plywood boxes with openings at ground level. Mouse chow was provisioned from above in a steel mesh that allowed mice to feed on the chow but prevented them from removing large pieces that could be cached.

Predation on gypsy moth pupae was measured in July as described above except that 12 pupae were attached to a single burlap strip placed at ground level instead of using single pupae glued to individual strips. Within each plot, 36 strips were placed in a 6×6 grid with 15 m between each strip. The fate of each pupa was monitored

over the next 4 days. If the pupa was dead, the cause of death was classified (vertebrate vs invertebrate) based upon pupal remains (Smith and Lautenschlager 1981). We assumed that small mammals preyed upon pupae that were entirely missing after a single night.

The statistical significance of differences in mean levels of predation by small mammals was compared between each of the two treatments and controls using a Wilcoxon signed-ranks test (Conover 1980) on paired predation rates from the same plots.

## Results

### Experiment 1: prey preference

Rates of predation on items deployed at the Powdermill Nature Reserve are shown in Table 1. Predation on gypsy moth pupae was usually lower than predation on mealworms and sunflower seeds in all three seasons and in both years. There was little difference in predation on mealworms versus sunflower seeds. Thus, mealworm pupae and sunflower seeds both appeared to be more preferred prey items than gypsy moth pupae. Predation on gypsy moth pupae appeared to be slightly lower in the fall than it was in the spring and summer, likely because of a greater availability of more desirable naturally occurring prey items in the fall. For example, the availability of abundant mast in the fall may cause a decrease in predation on gypsy moth pupae (Smith and Lautenschlager 1978). Since gypsy moth pupation occurs in the summer but hard mast is produced in the late summer or early fall in most climates, mast is unlikely to be an alternative prey item in most populations.

### Experiment 2: functional response

In Experiment 2 predation was evaluated across a wide range of prey densities to assess the form of the

**Table 1** Percentage of prey items eaten 3 days after deployment at low densities, Powdermill Reserve, Pa. ( $n=80$ ). Percentages of mealworm pupae and sunflower seeds followed by “\*” are statistically different than percentages for gypsy moth pupae in the same row [two-tailed  $G$ -test,  $\alpha=0.0047$ , corrected for 11 pairwise comparisons using Šidák’s inequality (Sokal and Rohlf 1981)]. *NT* not tested

| Year | Season | Percentage predation |                |                 |
|------|--------|----------------------|----------------|-----------------|
|      |        | Gypsy moth pupae     | Mealworm pupae | Sunflower seeds |
| 1995 | Spring | 56.3                 | 91.6*          | 91.6*           |
| 1995 | Summer | 60.0                 | 96.3*          | 90.0*           |
| 1995 | Fall   | 33.7                 | 92.7*          | 80.5*           |
| 1996 | Spring | 74.3                 | 94.6*          | 87.8            |
| 1996 | Summer | 85.0                 | 100*           | 98.7            |
| 1996 | Fall   | 40.0                 | NT             | 98.8*           |

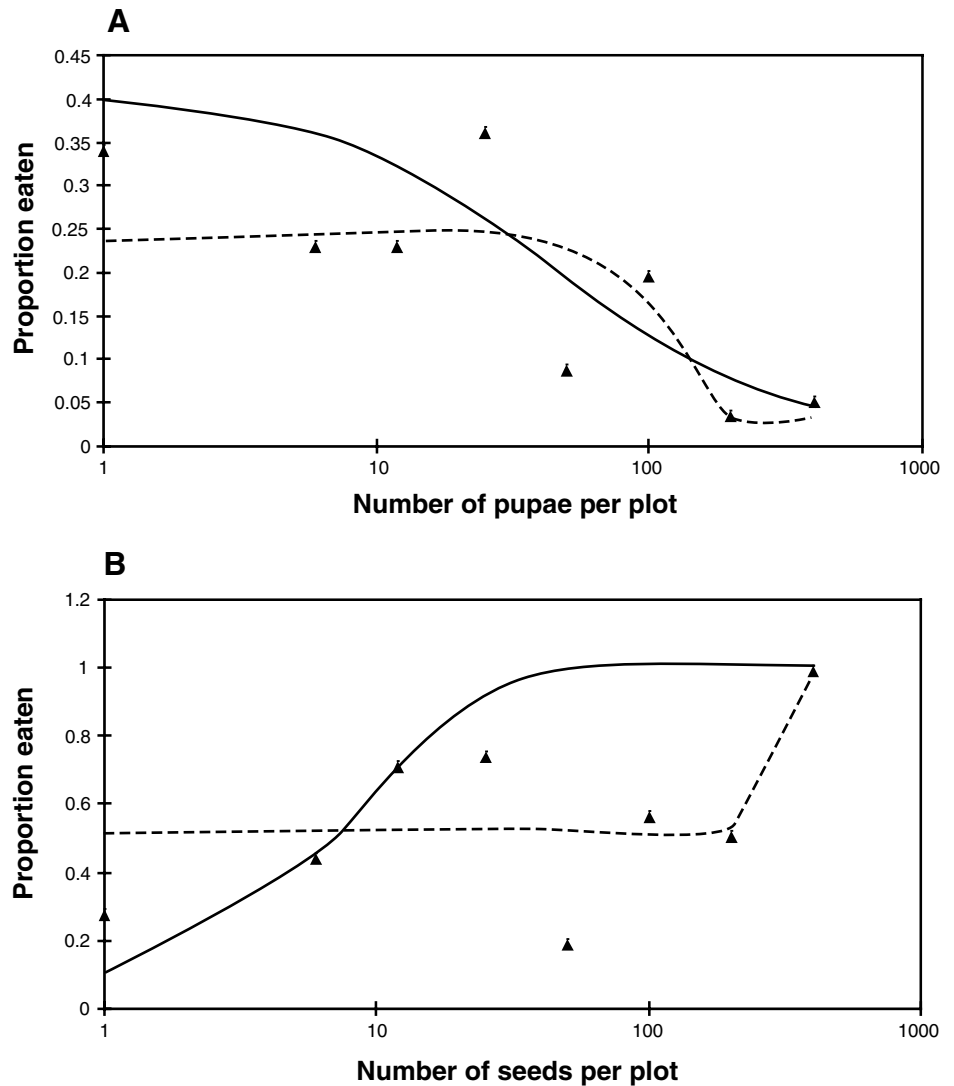
functional response. The proportion of pupae consumed declined from the lowest to highest pupal density, whereas the proportion of sunflower seeds consumed increased (Fig. 1). The parameter values for the cubic term in logistic regression models (Juliano 1993; Trexler et al. 1988) were significant ( $P<0.05$ ), for both pupae and sunflower seeds (Table 2), so we retained that model as our best-fit logistic regression equation. For pupae, the plots of the resulting model had a slope close to zero at the lowest densities (density independent) followed by a steadily decreasing slope at densities above 50 per plot (Fig. 1A), which indicated that the functional response was type II. Accordingly, we fit the Holling disc equation (Fig. 1A). For sunflower seeds, the slope was also close to zero at lowest densities and then steadily increased towards the highest densities. (Fig. 1B). Such a model is compatible only with a type III response, wherein all the densities presented were below the density of maximum consumption rate above which satiation or handling time constraints cause the proportions consumed to decline as prey densities increase. Accordingly, we fit the type III model (2) of Hassell (1978). Estimated parameter values for each of these models are given in Table 2. Our data were inevitably “noisier” than that of most functional response data generated under laboratory conditions where predator density is known and held constant. For example, one of the two plots with 50 sunflower seeds had 98% predation whereas the other plot had 34%. This difference is likely due to patchiness in small mammal occurrence on the plots.

There were mouse feces on about 50% of the burlap squares from which pupae or seeds had been removed (Table 3), and a smaller percentage had tooth marks in the beeswax. These percentages were fairly consistent across seed or pupal densities. While we do not know what animal species consumed each seed and pupa, these observations suggest that white-footed mice (*P. leucopus*) were the dominant consumers of both of these prey items. We observed no cases of feces produced by other small mammals. These findings are consistent with previous work which has shown that *P. leucopus* is the most abundant small mammal in the forests surrounding this study area (DeGraaf et al. 1989). The congeneric *P. maniculatus* that co-occurs with *P. leucopus* in many forests in eastern USA, does not occur in these forests. We observed two sunflower burlaps with bird feces.

### Experiment 3: effect of the availability of alternative prey items

Results shown in Table 4 indicate that the rate of predation by small mammals on gypsy moth pupae was significantly lower in stands where sunflower seeds were distributed than in control stands. This indicated that

**Fig. 1A, B** Observed proportions of **A** gypsy moth pupae and **B** sunflower seeds consumed by predators during a 1-day test period on 20 m×20 m test plots at the Quabbin Reservoir in western Massachusetts (Experiment 2). Plots vary density from one to 400 pupae or seeds per plot. *Dashed lines* represent cubic logistic regression models fit to the data; *solid line* is the best-fit type II functional response model (Holling 1959b disc equation) for pupae or a type III model (Hassell 1978) for sunflower seeds



**Table 2** Parameter values of best-fit logistic regression models and functional response models of proportion of sunflower seeds or pupae consumed by predators in plots with different numbers of seeds or pupae in Experiment 3

| Parameter  | Pupae                |                      |                           | Sunflower seeds       |                      |                           |
|--|----------------------|----------------------|---------------------------|-----------------------|----------------------|---------------------------|
|  | Estimate             | SE                   | Probability of > $\chi^2$ | Estimate              | SE                   | Probability of > $\chi^2$ |
| <b>Logistic regression cubic model<sup>a</sup></b> |                      |                      |                           |                       |                      |                           |
| Intercept ( $b_0$ )                                | -1.19                | 0.265                | 0.001                     | 0.118                 | 0.223                | 0.59                      |
| $b_1$  | 0.0062               | 0.0081               | 0.441                     | 0.0029                | 0.0061               | 0.24                      |
| $b_2$  | -0.00014             | $5.7 \times 10^{-5}$ | 0.017                     | -0.00050              | $3.9 \times 10^{-5}$ | 0.17                      |
| $b_3$  | $2.7 \times 10^{-7}$ | $9.8 \times 10^{-8}$ | 0.005                     | $1.86 \times 10^{-7}$ | $6.5 \times 10^{-8}$ | 0.0042                    |
| <b>Functional response model<sup>b</sup></b>       |                      |                      |                           |                       |                      |                           |
| $T_h$  | 0.054                | 0.016                |                           | 0                     | 0                    |                           |
| $a$  | 0.404                | 0.302                |                           | -                     | -                    |                           |
| $b$  | -                    | -                    |                           | 0.097                 | 0.033                |                           |
| $c$  | -                    | -                    |                           | 0                     | 0.030                |                           |
| $d$  | -                    | -                    |                           | 0.0022                | 0.041                |                           |

<sup>a</sup>Logit( $p$ ) =  $b_0 + b_1x + b_2x^2 + b_3x^3$  where  $p$  is predicted proportion consumed and  $x$  is number of pupae or seeds per plot  
<sup>b</sup>For pupae the model is the Holling (1959b) disc equation (type II response) whereas for sunflower seeds the model is from Hassell (1978) for a type III functional response. See text for model details

predation on gypsy moth pupae was significantly decreased by the availability of a more highly preferred alternative prey item such as sunflower seeds. In con-

trast, predation was significantly higher than controls in stands where the diet of small mammals was supplemented during the winter.

**Table 3** Percentage of sunflower seeds and pupae that were consumed by predators and percentages of consumed pupae and seeds that had mouse feces left on the burlap square or tooth marks left in the bees wax

| Number per plot | Pupae     |           |                 | Sunflower seeds |           |                 |
|-----------------|-----------|-----------|-----------------|-----------------|-----------|-----------------|
|                 | Eaten (%) | Feces (%) | Teeth marks (%) | Eaten (%)       | Feces (%) | Teeth marks (%) |
| 1               | 34.0      | 60.0      | 20.0            | 27.5            | 50.0      | 45.8            |
| 6               | 22.9      | 68.2      | 13.6            | 43.7            | 75.0      | 31.3            |
| 12              | 22.9      | 68.0      | 20.0            | 70.8            | 68.2      | 43.2            |
| 25              | 36.0      | 50.0      | 0.0             | 74.0            | 61.5      | 57.7            |
| 50              | 8.7       | 36.0      | 0.0             | 19.0            | 26.9      | 46.2            |
| 100             | 19.5      | 51.9      | 3.7             | 56.3            | 50.0      | 23.5            |
| 200             | 3.5       | 47.4      | 0.0             | 50.5            | 38.1      | 9.4             |
| 400             | 5.0       | 50.0      | 20.0            | 99.0            | 24.5      | 13.0            |
| Mean            | 19.06     | 53.93     | 9.67            | 55.10           | 49.28     | 33.75           |

**Table 4** Pupal predation (percentage consumed) caused by vertebrate predators under control (unaltered) conditions, experimental winter-feeding of supplemental food (mouse chow), and summer distribution of alternate food items (sunflower seeds). Each of the three treatments were paired at each stand ( $n=8$ )

| Variable        | Mean percentage predation | SE  | $T^a$ | Probability of $> T $ |
|-----------------|---------------------------|-----|-------|-----------------------|
| Control         | 14.8                      | 4.8 |       |                       |
| Sunflower seeds | 3.4                       | 1.2 | 2.52  | 0.012                 |
| Mouse chow      | 33.4                      | 8.0 | 2.15  | 0.030                 |

<sup>a</sup> $T$  statistic testing the null hypothesis that each treatment is not significantly different from the control (two-tailed Wilcoxon signed-ranks test)

## Discussion

The results of this study suggest a somewhat different type of interaction between a generalist predator and herbivore populations than that conceived by Holling (1959a, 1965). Holling studied what superficially appears to be a very similar system: predation by populations of the white-footed mouse, *P. leucopus*, on the foliage-feeding sawfly, *N. sertifer*. In that system, Holling found that predation rates increased positively with sawfly density and this positive density dependent mortality regulated populations. Holling differentiated this type of predation as a type III functional response from a type II functional response. In a type II functional response, per capita predation rates decreased monotonically with host density, and predation levels could be explained completely based on predators randomly encountering prey items. In contrast, Holling concluded that the type III functional response is caused by learning or a change in predator searching behavior in response to changes in prey density. Holling (1965) conducted experiments with mice preying on varying densities of sawfly cocoons in arenas in which alternative prey items were available that were either highly preferred (sunflower seeds) or less preferred (dog biscuits). In both cases, the functional response of mice to sawfly cocoons was sigmoid (type III), but when sawflies were presented with less-preferred cocoons along with the more preferred sunflower seeds, the functional response to the cocoons was barely sigmoid and close to a type II response. Research by Murdoch (1969) and Murdoch and Oaten (1975) demonstrated that type III functional responses often arise when predators switch from one prey species to another

as their relative abundance changes, and that the response is affected by the relative preference for the prey. Switching was very likely a component of our experiments, since the mice would have fed on the seeds or pupae we gave them in lieu of whatever else they were feeding on when our experiment was run. It seems likely that prey switching or learning will be more pronounced, and therefore type III responses more likely, with preferred compared to non-preferred prey items, so we suspect that our findings represent a general phenomenon characteristic of the functional response of many predators. However, we have found few other studies which could be used to verify our hypothesis.

Results presented here (Table 1) indicate that gypsy moth pupae are of relatively low palatability to predators. These results are confirmed by choice experiments in arenas with small mammals and various naturally occurring prey items that showed small mammals almost always choose prey items other than gypsy moth pupae (Smith and Lautenschlager 1981). The relatively low preference of small mammals for gypsy moth pupae suggests that predators do not seek them out and this would result in a type II functional response as predicted by a random search model (Holling 1959b; Murdoch 1973).

Most of the studies to date in both experimentally manipulated (including this study) and in naturally occurring gypsy moth populations, indicate that the functional response of predation to gypsy moth densities is inversely density dependent, as under a type II response (Elkinton et al. 1989, 1996; Grushecky et al. 1998). However, in all of these studies, it is likely that alternative prey items were naturally occurring and

available to predators; the availability of more palatable prey items may have resulted in the type II response. It is conceivable that in some situations these alternative items may not exist, and the response to gypsy moth pupae would be a type III response. However, this situation may rarely or never occur in nature based upon the consistency of past studies.

The results of the experimental elevation of alternative prey (sunflower seeds) indicated that this action caused a substantial (77%) reduction in levels of predation on gypsy moth pupae (Table 4). This manipulation demonstrated that the availability of alternative prey items may drastically reduce predation rates. This conclusion is also supported by studies of relationships between naturally occurring (not manipulated) alternative prey and gypsy moth populations. Smith and Lautenschlager (1981) reported that predation by *P. leucopus* on gypsy moth populations in New Lisbon, NJ, USA greatly decreased in years when cankerworms were abundant. Also, Smith (1989) analyzed gut contents of *P. leucopus* at various intervals during the spring and summer and found that as berries became more abundant during the summer, they were more frequently found in gut contents, while arthropods in their guts decreased in their presence. Smith concluded that predation on gypsy moth life stages would be affected by the abundance of berries.

Smith and Lautenschlager (1981) demonstrated that supplementation of food supplies using artificial food (mouse chow) caused an increase in small mammal populations. Jones et al. (1998) reported that winter-feeding using acorns also resulted in an increase in small mammal density the next spring. However, the data shown in Table 3 are the first results demonstrating that supplemental winter-feeding may increase rates of predation on gypsy moth pupae. Several other studies (e.g., Elkinton et al. 1989, 1996; Grushecky et al. 1998) have shown a close correlation between small mammal densities and rates of predation on gypsy moth pupae in natural populations. Thus, the most likely explanation for the elevated rates of predation in stands receiving supplemental feeding was that this feeding increased winter survival of small mammals, thereby elevating their population densities and consequently their rate of attack on pupae. These results support the theory that growth of low-density gypsy moth populations is indirectly linked to the availability of overwintering food sources (e.g., mast) of small mammal predators (Elkinton et al. 1996; Jones et al. 1998; Liebhold et al. 2000)

Here we demonstrate that gypsy moth pupae are not highly preferred by small mammal predators, and consequently, that the availability of alternative prey may influence the functional response of predators to gypsy moth abundance as well as the over-all magnitude of predation. In previous work we (Elkinton et al. 1996; Liebhold et al. 2000) and others (Jones et al. 1998) have proposed that gypsy moth outbreaks are initiated by failure of the acorn mast crop, a key overwintering food source for mice. Low densities of mice the following

summer result in low predation and thus lead to gypsy moth population increases. The results reported here indicate that availability of mast is not the only factor affecting predation by small mammals on gypsy moths. Our experimental supplementation of the winter diet of small mammals demonstrated that predation by mammal populations is influenced by winter food availability. This result is in agreement with the conclusion by Jones et al. (1998) and Elkinton et al. (1996) that mast abundance influences small mammal densities, which in turn influence predation on gypsy moth populations. However, our results suggest a more complex web of interactions that may be associated with the onset of gypsy moth outbreaks. Gypsy moth outbreaks may also result from an increased abundance of alternative food items during the same period that gypsy moths exist as late larval instars and pupae in the field. These alternative food items could be other insect species or seeds or both.

**Acknowledgments** The authors thank Alexei Sharov and David Williams and an anonymous reviewer for helpful comments on earlier drafts of this manuscript. We also acknowledge assistance provided in the field by Jeff Boettner, David Feicht, Gloria Witkus and Regis Young, and statistical advice provided by Thomas Jacob and John Buonaccorsi. This research was funded in part by the USDA Forest Service Northeastern Research Station, the USDA Competitive Research Grants Program (Grant# 89-337250-4684) and a MacIntyre-Stennis grant to the Massachusetts Agricultural Experiment Station (ms no. 3335). All experiments reported in this paper conformed with local state and federal laws governing the treatment of animal subjects.

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