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# Comparative Predation on Naturally Occurring Gypsy Moth (Lepidoptera: Lymantriidae) Pupae and Deployed Freeze-Dried Pupae

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9 Schauber and Jones: Predation on Natural vs. Freeze-dried *L. dispar* Pupae

10 Population Ecology

11

12 **Comparative predation on naturally occurring gypsy moth (*Lepidoptera: Lymantriidae*)**

13 **pupae and deployed freeze-dried pupae**

14

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21

22 ABSTRACT Predation is an important factor in the dynamics of gypsy moth (*Lymantria dispar*  
23 L.) populations, yet predation rates can be difficult to estimate accurately in the field. Biased  
24 estimates can result from spatial heterogeneity in risk or from artifacts associated with deploying  
25 prey. Here, we compare predation rates on freeze-dried gypsy moth pupae affixed with beeswax  
26 to pieces of burlap with predation rates on naturally occurring live pupae in the same sites. Daily  
27 predation rates, primarily by small mammals, were two to eight times greater for freeze-dried  
28 deployed pupae than natural pupae, depending on the year. These results indicate apparent  
29 predation rates can be substantially biased by artifacts associated with deployed prey, such as  
30 human scent, artificial substrates, or freeze-drying. Results from studies using similar methods  
31 may provide qualitative comparisons of relative predation risk, but their estimates of absolute  
32 predation rates should be interpreted with caution, and attempts made to quantify and correct for  
33 any resulting bias.

34

35 Key words: *Lymantria dispar*, predation, bias, estimation

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38 Predation on gypsy moth (*Lymantria dispar* L.) pupae, particularly by small mammals, is  
39 an important but highly variable factor affecting gypsy moth population dynamics in the  
40 northeastern United States (Bess et al. 1947, Elkinton et al. 1996, Jones et al. 1998, Liebhold et  
41 al. 2000). Unbiased estimates of predation rates are necessary to quantitatively analyze how  
42 predation affects gypsy moth population dynamics (Tanhuanpää et al. 1999). Obtaining  
43 unbiased estimates of predation is, however, a particularly vexing problem for field studies. One  
44 approach is to measure predation rates on naturally occurring pupae (Campbell et al. 1975, Cook  
45 et al. 1994). However, this approach may not provide sufficient sample sizes in low-density  
46 gypsy moth populations. Furthermore, predation risk can vary substantially over small spatial  
47 scales (Manson 2000), and pupae in sites of highest risk are likely to be underrepresented in the  
48 set of pupae that remain uneaten long enough to be discovered by researchers. Therefore,  
49 naturally occurring pupae found by researchers necessarily represent a biased subset of the  
50 population, leading to underestimation of true predation rates (Zens and Peart 2003).

51 Another approach is to deploy pupae in a representative selection of sites and measure  
52 subsequent predation (Smith 1985, Liebhold et al. 1998, Grushecky et al. 1998, Hastings et al.  
53 2002, Gschwantner et al. 2002, Schaubert et al. 2004, Elkinton et al. 2004). This potentially  
54 removes location bias, but deployed food items can carry human or other foreign scents,  
55 potentially altering consumer behavior (Wenny 2002, Duncan et al. 2002). A common practice  
56 is to embed gypsy moth pupae in beeswax on pieces of burlap (Smith and Lautenschlager 1981,  
57 Smith 1985). The burlap can be secured to a substrate of choice, preventing the pupa from being  
58 carried off, and predators can often be identified by toothmarks left in the wax. Freeze-dried  
59 pupae are often deployed (Cook et al. 1995, Ostfeld et al. 1996, Hastings et al. 2002) to avoid

60 potential augmentation of existing populations and to prevent creation of new populations by  
61 moths eclosing from deployed live pupae.

62         How these practices bias estimates of predation rate is unknown, because comparable  
63 measurements of predation rates on deployed and naturally occurring pupae are not available  
64 from the current literature. Our objective was to quantify the effect of one pupal deployment  
65 practice (use of freeze-dried pupae affixed with beeswax to burlap) on apparent predation rates.  
66 Throughout, we will use the acronym FDD to indicate freeze-dried pupae that we deployed in  
67 this manner. Although the magnitude and direction of bias might differ for other deployment  
68 practices (e.g., live deployed pupae, pupae affixed to other substrates or irradiated live pupae),  
69 our intent is to point out that such bias can be substantial and needs to be quantified for each  
70 deployment practice.

71

## 72 **Materials and Methods**

73         We compared predation rates on freeze-dried pupae waxed to burlap and deployed under  
74 burlap bands 1.5 m high on tree boles with predation on gypsy moths that naturally pupated  
75 under the same bands. Restricting the analysis to pupae found under the same bands removed  
76 the bias resulting from spatial heterogeneity in predation risk.

77         Pupal predation was monitored on six 2.25-ha, oak-dominated forest plots at the Institute  
78 of Ecosystem Studies, Millbrook, New York, USA, from 1994 to 1998. The plots were arranged  
79 in 3 pairs  $\geq 1$  km apart, with each pair composed of one control and one experimental plot. Data  
80 on natural and FDD pupae were collected from only two plots, both controls, in 1994. In 1995,  
81 1997, and 1998, mammal populations on the three experimental plots were altered by trapping  
82 and removing white-footed mice (1997), eastern chipmunks (*Tamias striatus*, 1998), or both

83 (1995). Mammal populations were not manipulated in 1996. Each plot was overlaid with a 10 ×  
84 10 ( $n = 5$  plots) or 9 × 11 ( $n = 1$  plot) grid of 15 × 15-m cells. In each plot, 20 or 21 cells were  
85 selected for burlap banding (selection of cells detailed in Jones et al. 1998): within each selected  
86 cell, two oak (*Quercus rubra*, *Q. velutina*, *Q. alba*, or *Q. prinus*) trees > 7 cm diameter at breast  
87 height were each banded with a strip of burlap (30 cm wide, folded once lengthwise, with slits  
88 cut to allow access for monitoring) at ca. 1.3 m above the ground. Bands were replaced each  
89 year. From late June through July each year, the bands were monitored every 1-3 days for the  
90 presence of gypsy moth larvae and pupae.

91       Once naturally occurring pupae were observed, freeze-dried pupae were deployed under  
92 the burlap band on one of the two banded oak trees in each selected cell. Female gypsy moth  
93 pupae were freeze-dried and affixed with purified beeswax in groups of five to panels of burlap  
94 (20 × 15 cm). Pupae were monitored every 1-3 days for approximately 20 days for signs of  
95 predation. Predators were identified as vertebrates or invertebrates on the basis of tooth marks,  
96 feces left on the burlap, and the pattern of damage to pupae (Smith 1985).

97       **Statistical Analyses.** We tested for a difference in total predation rates (by all predators)  
98 between natural and FDD pupae in each year using survival analysis (PROC LIFEREG; SAS  
99 Institute, Cary, North Carolina, USA), assuming a Weibull distribution of survival times. The  
100 Weibull distribution allows for the predation risk experienced by a pupa to change over time  
101 after it pupated or was deployed (Allison 1995), and we expected risk to increase over time as  
102 found by Schauber et al. (2004). Explanatory variables were tree ID, to account for tree-to-tree  
103 differences in predation risk, and pupa type (natural or FDD). The LIFEREG procedure can  
104 accommodate data that are right-censored (e.g., natural pupae that eclosed or FDD pupae that  
105 remained intact at the end of monitoring) or interval-censored (e.g., pupae attacked between

106 monitoring visits). Model coefficients were converted into the format of a hazard (instantaneous  
107 daily predation rate) function for ease of interpretation.

## 108 **Results**

109 A total of 152 natural pupae were found under a total of 96 bands with FDD pupae, with  
110 a maximum of six pupae found under the same band. Attack rates were especially high on  
111 control plots in 1995 and 1997, when unmanipulated mouse densities were high (Ostfeld et al.  
112 2001), but attack rates were low on experimental plots in years when mice were removed (1995  
113 and 1997). Predation on FDD pupae was significantly greater (all  $P < 0.05$ ) than predation on  
114 natural pupae in all years (Table 1), with estimated FDD:natural hazard ratios ranging from 2.0  
115 in 1998 to 8.1 in 1994. The 95% confidence interval for the Weibull scale parameter ( $\sigma$ ) was 0.5  
116 S 1.0 for all years except 1996, when  $\sigma$  was not significantly different from 1.0; therefore,  
117 estimated predation rates tended to increase over time after pupation or pupal deployment in four  
118 out of five years.

119

## 120 **Discussion**

121 Obtaining reliable estimates of predation rates is critical to understanding how predation  
122 affects prey population dynamics. However, predation rates are difficult to measure without bias  
123 due to spatial heterogeneity in risk (Zens and Peart 2003) or human artifacts. We have shown  
124 that predators attacked freeze-dried gypsy moth pupae affixed with beeswax at rates two to eight  
125 times greater than attacks on natural pupae on the same banded trees. Therefore, experimentally  
126 deploying pupae may provide useful measures of relative risk across time or space, but the  
127 resulting estimates should not be expected to accurately reflect absolute predation rates

128 experienced by naturally occurring gypsy moth pupae unless bias is quantified and accounted  
129 for.

130         Artifacts associated with deploying prey items can be major sources of bias in predation  
131 studies, as has recently been documented for studies of predation on natural vs. artificial bird  
132 nests (Thompson and Burhans 2004, Moore and Robinson 2004). At least three artifacts could  
133 account for the disparity we observed in predation rates between natural and FDD pupae. First,  
134 freeze-dried pupae were used rather than live pupae, which alone might conceivably account for  
135 our observed pattern. For example, Liebhold et al. (2005) reported considerably lower predation  
136 rates on live deployed gypsy moth pupae than freeze-dried deployed pupae, although no data  
137 from the freeze-dried pupae were provided to support this conclusion. However, the existence of  
138 a freeze-drying effect does not preclude the possibility of other artifactual effects on observed  
139 predation rates. For example, the pupae were affixed with beeswax to burlap, and these ancillary  
140 materials might have provided stimuli that predators such as small mammals learned to associate  
141 with food. Finally, human handling of pupae on burlap could have contaminated them with  
142 scent, which has been shown to increase predation by small mammals on seeds (Wenny 2002,  
143 Duncan et al. 2002).

144         Even after accounting for bias associated with deployment artifacts, unmeasured biases  
145 likely remain because the burlap banded trees may not have been a representative sample of  
146 gypsy moth pupation sites. Gypsy moth larvae seek sheltered refugia in which to pupate  
147 (Campbell et al. 1975, Campbell and Sloan 1977), so predation on even natural pupae under our  
148 burlap bands may be an overestimate of overall predation on all natural pupae. However, gypsy  
149 moths also often pupate in leaf litter (Campbell and Sloan 1976) and even in the burrows or nests  
150 of predatory small mammals (Schauber, pers. obs.), where their risk of predation is higher than



151 that of pupae above ground on tree boles (Smith and Lautenschlager 1981, Smith 1985, Cook et  
152 al. 1995, Schauber et al. 2004). Therefore, the direction and magnitude of bias associated with  
153 failure to sample a representative selection of pupation sites is unknown. Measuring the overall  
154 bias for a particular deployment method would require comparisons of observed predation rates  
155 on deployed pupae with observed predation rates in all naturally occurring pupae -- a difficult  
156 task at best. Elkinton et al. (1996) provide data on the relationship between white-footed mouse  
157 density and predation rates on live deployed pupae, and also provide a regression model relating  
158 mouse density and the proportional change in densities of naturally occurring gypsy moth egg  
159 masses. However, the model is on a log-log scale, which does not allow for the calculation of  
160 per mouse impact in any straightforward way.

161         Our findings encourage caution in the interpretation of predation rate estimates derived  
162 from deployed prey, such as pupae. Such estimates may provide useful indices of relative risk  
163 for making qualitative comparisons among sites or years. For example, Jones et al. (1998) found  
164 the reduction in attacks on FDD pupae due to removal of small mammals was reflected in greatly  
165 increased survival of naturally occurring gypsy moths from late-larval instars to oviposition. We  
166 acknowledge that our results cannot be extrapolated directly to other deployment methods.  
167 However, our findings highlight the more general need to acknowledge and quantify estimation  
168 bias due to deployment artifacts (including freeze-drying, human handling, and ancillary  
169 materials), spatial heterogeneity in risk, and non-representative sampling of sites in order to  
170 extract reliable estimates of absolute predation rates.

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258 Table 1. Results of survival analysis comparing freeze-dried deployed (FDD) and naturally  
 259 occurring pupae on banded trees at the Insitute of Ecosystem Studies, Millbrook, New York.

Year	$\hat{\sigma} \pm SE^1$	Mean hazard		Hazard ratio <sup>3</sup>	$\chi^2_1$ for pupa type	P-value for pupa type
		FDD <sup>2</sup>	Natural			
1994	$0.67 \pm 0.10$	0.040	0.005	8.1	14.8	0.0001
1995	$0.76 \pm 0.05$	0.130	0.047	2.8	20.8	<0.0001
1996	$1.07 \pm 0.09$	0.147	0.037	4.0	17.0	<0.0001
1997	$0.71 \pm 0.10$	0.058	0.015	3.8	7.1	0.008
1998	$0.78 \pm 0.07$	0.124	0.062	2.0	4.0	0.046

260

261 <sup>1</sup>Estimated scale parameter for the Weibull distribution of hazard, which indicates the change in  
 262 daily predation rate over time after deployment or pupation. Values of  $0.5 < \sigma < 1$  indicate  
 263 hazard increasing over time at a decreasing rate,  $\sigma = 1$  indicates constant hazard, and  $\sigma > 1$   
 264 indicates hazard decreasing over time.

265 <sup>2</sup>Estimated mean instantaneous daily predation rate on FDD or natural pupae just after  
 266 deployment or pupation, calculated by averaging  $\exp[-(\text{intercept} + \text{tree effect}) / \hat{\sigma}]$  over all trees  
 267 in a year for FDD pupae and averaging  $\exp[-(\text{intercept} + \text{tree effect} + \text{pupa-type effect}) / \hat{\sigma}]$  for  
 268 natural pupae.

269 <sup>3</sup>Hazard ratio for FDD:natural pupae, calculated by:  $\exp[(\text{pupa-type effect}) / \hat{\sigma}]$

270