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

Population Ecology

Comparative predation on naturally occurring gypsy moth (Lepidoptera: Lymantriidae) pupae and deployed freeze-dried pupae

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

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

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

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

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

Materials and Methods

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

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

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

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

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

Results

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

Discussion

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

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

Even after accounting for bias associated with deployment artifacts, unmeasured biases likely remain because the burlap banded trees may not have been a representative sample of gypsy moth pupation sites. Gypsy moth larvae seek sheltered refugia in which to pupate (Campbell et al. 1975, Campbell and Sloan 1977), so predation on even natural pupae under our burlap bands may be an overestimate of overall predation on all natural pupae. However, gypsy moths also often pupate in leaf litter (Campbell and Sloan 1976) and even in the burrows or nests of predatory small mammals (Schauber, pers. obs.), where their risk of predation is higher than that of pupae above ground on tree boles (Smith and Lautenschlager 1981, Smith 1985, Cook et al. 1995, Schauber et al. 2004). Therefore, the direction and magnitude of bias associated with failure to sample a representative selection of pupation sites is unknown. Measuring the overall bias for a particular deployment method would require comparisons of observed predation rates on deployed pupae with observed predation rates in all naturally occurring pupae -- a difficult task at best. Elkinton et al. (1996) provide data on the relationship between white-footed mouse density and predation rates on live deployed pupae, and also provide a regression model relating mouse density and the proportional change in densities of naturally occurring gypsy moth egg masses. However, the model is on a log-log scale, which does not allow for the calculation of per mouse impact in any straightforward way.

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

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

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

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

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

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