

USE OF TRACK PLATES TO QUANTIFY PREDATION RISK AT SMALL SPATIAL SCALES

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Spatial heterogeneity in risk is a critical component of predator-prey interactions. However, at small spatial scales, it is difficult to quantify predation risk without altering it. We used track plates to measure local predation risk created by white-footed mouse (*Peromyscus leucopus*) foraging activity on oak-forest plots in Millbrook, New York. Live gypsy moth pupae (*Lymantria dispar*) were placed at 2 heights on trees and monitored for predation. Pupae deployed on trees visited by mice were more likely to be eaten than those on trees not visited. Logistic regression indicated that predation rates on gypsy moth pupae were positively correlated with track activity, indicating that areas of concentrated mouse activity were areas of heightened risk for gypsy moths. Survival of individual oat grains placed on and 50 cm from track plates were not statistically different, indicating that mice exhibited no detectable behavioral reaction toward track plates. We conclude that track plates offer an economical and reliable means of quantifying local risk of attack by terrestrial mammals without substantially altering the spatial distribution of risk.

Key words: *Peromyscus leucopus*, predation risk, spatial heterogeneity, track plates, white-footed mouse

Spatial heterogeneity in predation risk resulting from spatial variation in local density and foraging activity of predators can promote coexistence of prey and predator (Hassell et al. 1991; Hastings 1977; Hilborn 1975; Huffaker 1958). Areas of high predation risk may exist around frequently used travel routes, nesting sites, and preferred microhabitat of the predator. Conversely, areas that predators avoid or are excluded from because of vulnerability to their own predators, gaps between territories, alternate food supplies, or physical impediments (Brown 1988; Lewis and Murray 1993; Schmidt et al. 2001) will create patches of low predation risk or prey refugia.

White-footed mice (*Peromyscus leucopus*) are abundant generalist predators (Wolff et al. 1985) in northeastern forests of the United States that often consume gypsy moth (*Lymantria dispar*) pupae while foraging for more abundant, primary prey (Bess et al. 1947; Smith 1985; Smith and Lautenschlager 1981). Gypsy moths are an introduced pest species that can cause

severe defoliation to host trees, which leads to reduced growth and survival rates of trees (Baker 1941; Davidson et al. 1999; Kegg 1973). Gypsy moths pupate for about 2 weeks in mid-summer on or near the bases of trees (Campbell et al. 1975), where they are vulnerable to attack by white-footed mice. Both pupal survival and growth rates of low-density gypsy moth populations are negatively related to mouse densities (Elkinton et al. 1996; Jones et al. 1998; Ostfeld et al. 1996), and chronically dense mouse populations can potentially drive gypsy moths to local extinction (Schauer et al. 2004). Similarly, ground-based songbird nests are too sparse to attract directed searches by mice, but are attacked when incidentally encountered by mice (Schmidt and Ostfeld 2003). Empirically based, spatially explicit simulation models indicate that spatial heterogeneity in predation risk contributes to the persistence of incidental prey, such as the gypsy moth (Goodwin et al., in press).

Quantifying predation risk at small spatial scales without altering it is difficult. Deploying food items in sufficient amounts to measure local risk could attract predators or otherwise alter their local foraging intensity. Predator space use can be quantified by using radiotelemetry (Douglass 1989); however, this only provides information about the particular individuals being tracked, whereas estimating risk experienced

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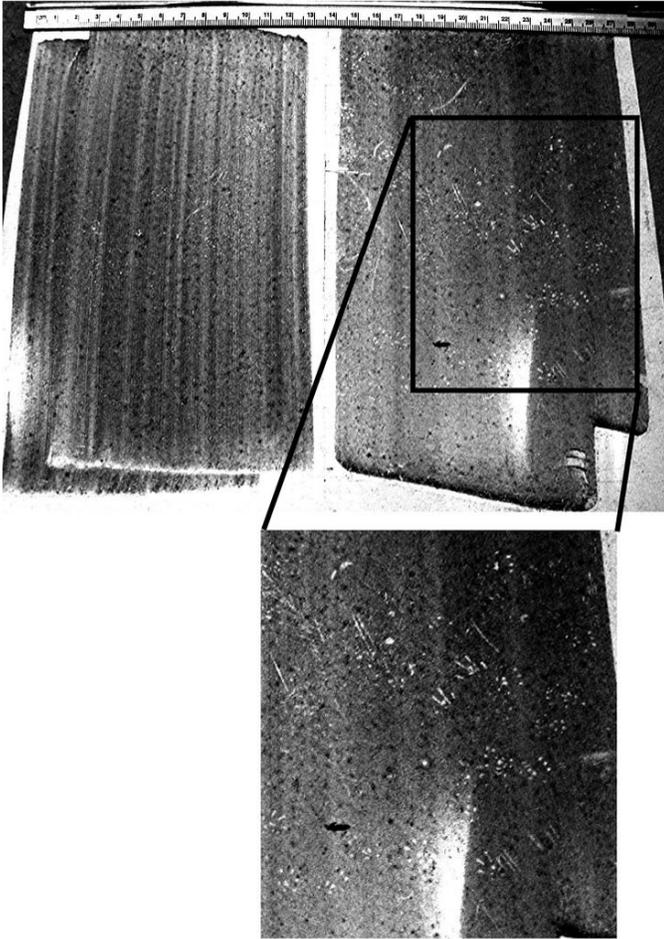


FIG. 1.—Track plates with a ruler (top) showing scale in centimeters. The plate on the left has been held under running water for 30 s, demonstrating water resistance. The plate on the right was used at a sample tree for 2 track nights and shows tracks of *Peromyscus leucopus* (see enlarged box).

by prey requires integrating foraging activities of all predators using an area. Track plates (Justice 1961; Mayer 1957; Sheppe 1965) offer an efficient method of quantifying small-scale activity of vertebrate predators. Track plates are economical to produce and can integrate activities of all predators using an area. Our goal was to develop a less intrusive method of quantifying risk at small spatial scales by measuring local predator activity by using track plates.

MATERIALS AND METHODS

We used track plates to measure white-footed mouse activity around individual trees during the summers of 2002, 2003, and 2004, comparing track activity to predation rates on gypsy moth pupae deployed on the same trees. The behavioral response of mice to track plates was evaluated by comparing rates at which oat grains placed on and near track plates were consumed.

Other studies have recorded tracks of small mammals by using sand (Bider 1968), smoked kymograph paper (Justice 1961; Mayer 1957; Sheppe 1965, 1967), talc-coated plates (Brown 1969), ink-coated tiles (Lord et al. 1970), carpenter's chalk (Drennan et al. 1998), ink and

contact paper (Glennon et al. 2002), and a carbon black and mineral oil mixture (Nams and Gillis 2003) as tracking media. This study used acetate sheets with a graphite, alcohol, and oil coating that had superior water-resistance and utility relative to previous methods. Track plates were constructed of 14 × 22-cm acetate sheets. A suspension of graphite powder in an ethanol and mineral oil mixture (80% denatured anhydrous ethyl alcohol, 15% powdered graphite, and 2.5% light-grade mineral oil by volume) was applied with a foam paintbrush to the acetate sheet, leaving a thin, waterproof layer of graphite upon which tracks were recorded (Fig. 1). Track plates were then affixed with paper clips to pieces of aluminum flashing to provide rigid backing. A single track plate (acetate, graphite, alcohol, and oil) was produced for less than US\$0.10 each plus a one-time cost of about US\$0.14 per piece of aluminum flashing. We were able to produce approximately 200 track plates in 30 min of work.

Study area.—All field studies were conducted on oak-dominated forest plots (about 2 ha) at the Institute of Ecosystem Studies, Millbrook, New York. Plots were dominated by red oak (*Quercus rubra*), black oak (*Q. velutina*), white oak (*Q. alba*), chestnut oak (*Q. prinus*), and sugar maple (*Acer saccharum*). Shagbark hickory (*Carya ovata*), pignut hickory (*C. glabra*), black birch (*Betula lenta*), and eastern white pine (*Pinus strobus*) also were present on the study plots. The understory was dominated by oak and maple seedlings and saplings, witch hazel (*Hamamelis virginiana*), maple-leaved viburnum (*Viburnum acerifolium*), and blueberry (*Vaccinium*). In 14 years of livetrapping by one of us (RSO), the white-footed mouse has been the most frequently trapped small mammal on our plots, but shrews (*Blarina brevicauda* and *Sorex*), eastern chipmunks (*Tamias striatus*), and southern flying squirrels (*Glaucomys volans*) also were captured. Footprints from these species are readily distinguished from those of white-footed mice. White-footed mouse prints may be confused with those of southern red-backed voles (*Clethrionomys gapperi*) or meadow voles (*Microtus pennsylvanicus*) but these species have rarely been captured on the plots.

Study design.—In July and August 2002, 5 track plates were placed in a circle 20 cm from the base of each of 5 randomly selected sample trees >20 cm diameter at breast height (dbh) on each of 2 plots (Cary Drive and Field Lab). Mouse activity at each tree was recorded in 3 ways: total number of footprints recorded on tracking plates; mean daily proportion of plates with mouse tracks (arcsine transformed); and a categorical presence or absence variable indicating whether any of the 5 plates was marked daily by mice at a sample tree. Aluminum flashing used as backing for track plates was placed around sample trees a least 1 week before the study so mice could become accustomed to the track plates. To quantify predation pressure, we monitored predation on 5 live gypsy moth pupae affixed with beeswax onto individual burlap squares (7 cm²—Smith 1985), which were deployed at a height of 1.5 m on the bole of each sample tree. We reared late-stage gypsy moth larvae (United States Department of Agriculture Animal and Plant Health Inspection Service, Otis Plant Protection Laboratory, Otis Air National Guard Base, Massachusetts) 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. Track plates and pupae were monitored daily for 6 days and plates with tracks (hereafter “tracked”) and depredated pupae were replaced. Attacks on pupae were attributed to white-footed mice or invertebrate (e.g., ant or slug) predators based on patterns of damage, tooth marks, and feces (Smith and Lautenschlager 1981). Daily predation rates for deployed gypsy moth pupae at each tree (number of attacks/30 pupa-nights) were estimated by using the Mayfield method (Mayfield 1975), which accounts for the number of days of exposure.

Results from the 2002 study indicated that the mean arcsine-transformed daily proportion of plates tracked was the best predictor of predation risk. Therefore, the experiment was repeated in 2003 and 2004 recording only the proportion of track plates marked at sampled trees, with an increased sample size, and with a smaller dbh requirement (<7 cm) to include mouse use of smaller trees for travel and foraging (Graves et al. 1988). In each year, 15 sample trees > 7 cm dbh were selected at random on each of 3 plots (Green, Henry, and Tea; $n = 45$ trees). Different sample trees were selected for each year. Three track plates were placed in a circle around the base of each sample tree, and 5 live gypsy moth pupae affixed with beeswax to individual squares of burlap (7 cm²) were attached to the tree. Pupae were attached to the base of the tree in 2003 and 1.5 m high on the tree bole in 2004. Most gypsy moths pupate at ground level, but some also pupate on tree boles under bark flaps (Campbell et al. 1975) and mice are known to frequently use tree boles for travel and nesting (Barry and Francq 1980; Graves et al. 1988). Pupae were placed at 2 different heights among years to quantify any vertical variability in predation risk. Time constraints and a shortage of pupae prevented us from simultaneously placing pupae at both heights in the same year. The aluminum flashing used as backing for track plates was again placed around sample trees at least 1 week before each study.

Track plates and pupae on each grid were monitored daily for 7 days during 15–23 July 2003 and 21–28 July 2004. In 2004, track plates were deployed on 13–14 June, 7 days before pupae were deployed. Plates were monitored every 1–3 days until pupal deployment, and then pupae and plates were monitored daily for 7 days. Tracked plates and depredated pupae were replaced daily. For our study, individual sample trees were the experimental units and mouse track activity at each tree was measured by using an arcsine transformation of the mean daily proportion of plates tracked over the 7-day experiment. Pupal predation was measured as the mean daily proportion of pupae consumed at each sample tree over the 7-day experiment (number of attacks/35 pupa-nights). For each year, we used logistic regression ($\alpha = 0.05$ —SAS Institute Inc. 1999) to test whether pupal predation at a tree was positively related to track activity. We also used logistic regression to test whether the relationship between track activity and pupal predation differed among study plots (plot \times tracks interaction) in 2003 and 2004.

Livetrapping data collected during a concurrent study were used to calculate the minimum number known alive (MNKA—Krebs 1966; Table 1) as an index of white-footed mouse abundance on each plot each year from June to August. Each plot was overlaid with an 11 \times 11 grid of livetrapping stations with 15-m spacing and 2 Sherman live traps (7.6 \times 8.9 \times 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) per station. Traps were covered with a square of wood to shield them from rain. Traps on each plot were opened for 2 consecutive nights at least once per month between early May and mid-November. Traps were baited with oats, opened approximately 2 h before sunset, and closed 2 h after sunrise. Each captured mouse or chipmunk was marked with a numbered ear tag. We then compared MNKA with the mean track activity for each plot and year.

Behavioral response to track plates.—We measured removal of individual oat grains to ascertain if white-footed mice were attracted to or deterred by track plates. Oats were affixed with beeswax to burlap squares (5 cm²) and placed on a 10 \times 10 grid of track plate stations with 7-m spacing and a single track plate at each station. At each station, a burlap square with a single oat was attached to a track plate with a paper clip and another such square was staked to the ground by using a wooden skewer within 50 cm of the same track plate. Track plates and oats were monitored daily for 4 days without replacement from 6 to 9 June 2004. We used the Cox proportional hazard model

TABLE 1.—Average white-footed mouse abundance (minimum number known alive [MNKA]), activity data from track plates, and predation rates on deployed pupae in oak-dominated forest plots at the Institute of Ecosystem Studies, Millbrook, New York.

Study plot	MNKA (June– August)	Range ^a	\bar{X} daily proportion of plates tracked	Range ^b	\bar{X} daily proportion of pupae eaten	Range ^b
2002						
Cary Drive	58.8	54–65	0.27	0.03–0.50	0.13	0.00–0.47
Field Lab	53.8	43–69	0.18	0.10–0.27	0.14	0.00–0.33
2003						
Green	79.5	61–92	0.54	0.33–0.86	0.90	0.51–1.00
Henry	59.0	51–65	0.63	0.14–0.90	0.92	0.51–1.00
Tea	58.5	41–78	0.55	0.28–0.86	0.92	0.66–1.00
2004						
Green	138.5	124–150	0.53	0.21–0.75	0.82	0.35–1.00
Henry	66.5	62–76	0.38	0.21–0.75	0.50	0.13–0.83
Tea	56.0	45–71	0.43	0.10–0.62	0.44	0.14–0.86

^a Minimum and maximum MNKA values from June to August on the plot.

^b Minimum and maximum values from individual trees on the plot.

(PROC PHREG—Cox and Oakes 1984; SAS Institute Inc. 1999) including station as a stratum variable to test the null hypothesis that oats were consumed equally on versus off track plates. Although we cannot be certain that oats did not motivate mice to approach track plates, mice have abundant alternate food sources during summer (Wolff 1996; Wolff et al. 1985) and it is unlikely that a single oat grain would be desirable enough to alter normal foraging patterns. Ultimately, our objective was not to test whether mouse behavior is affected by the oat grain, but to test whether mouse behavior is affected by the track plate.

The procedures used in this study were in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

RESULTS

Data were collected over 250 track-nights in 2002. An average of 23% of track plates were tracked per day and daily pupal predation rates averaged 13% (Table 1). Pupae on trees visited by mice had a greater probability of predation than trees with no recorded visits by mice ($\chi^2 = 3.9$, $d.f. = 1$, $P < 0.05$). The number of mouse footprints at a tree also was a predictor of pupal predation rate (Wald $\chi^2 = 10.2$, $P = 0.0014$), but the transformed proportion of plates tracked by mice was the strongest predictor (Wald $\chi^2 = 14.0$, $P = 0.0002$; Fig. 2A).

Data in 2003 were collected over 924 track-nights. One sample tree was excluded because of hornet activity. An average of 57% of track plates were tracked per tree per day and daily pupal predation rates averaged 91% (Table 1). However, even at locations where mouse track activity was low, depredated pupae showed evidence of attack by white-footed mice. Based on toothmarks and other evidence, white-footed mice were responsible for 95% of all attacks on pupae. Transformed track activity was again a strong predictor of pupal predation rates (Wald $\chi^2 = 46.6$, $P < 0.0001$; Fig. 2B).

Data in 2004 were collected over 945 track-nights. An average of 45% of track plates was tracked per tree per day.

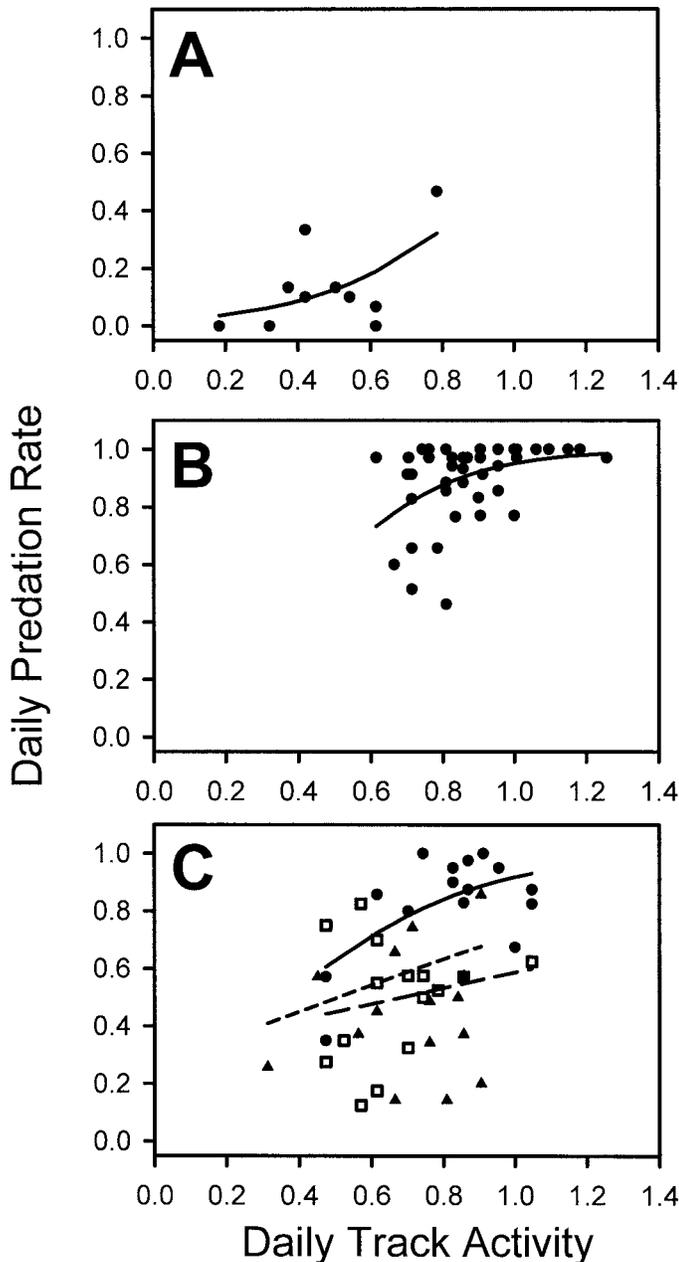


FIG. 2.—Observed (●) and predicted (—) values of predation risk to pupae of *Lymantria dispar* as a function of arcsine-transformed track activity of *Peromyscus leucopus* for A) the 6-day experiment in 2002 with pupae 1.5 m high on trees, and B) the 7-day experiment in 2003 with pupae at the base of the tree. C) Observed (at sites Green ●, Henry □, and Tea ▲) and predicted values of predation risk (at sites Green —, Henry - - -, and Tea - - - -) as a function of arcsine-transformed track activity of *P. leucopus* for each plot during the 7-day experiment in 2004 with pupae 1.5 m high on trees.

Daily pupal predation rates averaged 59% (Table 1), with 95% of the attacks being attributable to white-footed mice. Once again, transformed track activity was a strong predictor of pupal predation rates (Wald $\chi^2 = 86.0$, $P < 0.0001$), but the relationship between predation and track activity differed significantly among plots (Wald $\chi^2 = 15.7$, $P = 0.0004$; Fig. 2C). The interaction with plot probably resulted from the

substantially higher mouse densities on Green plot in that year (Table 1). We compared the mean activity levels before and after pupal deployment in 2004 with a paired t -test and found a significant increase (1-tailed $P = 0.01$) in mouse activity at sample trees after deployment of pupae.

Mice showed no detectable difference in their predation rates on oats located on or off track plates, after accounting for variation among stations ($\chi^2 = 0.95$, $P = 0.33$). Survival times for oats on and off plates ($\bar{X} \pm SE$ were 1.63 ± 0.08 days and 1.55 ± 0.09 days, respectively, yielding a hazard ratio of 0.85 (0.62–1.17, 95% confidence interval).

DISCUSSION

The proportion of plates tracked by mice was a successful predictor of white-footed mouse predation risk to deployed gypsy moth pupae. We found no strong evidence that track plates had any impact on mouse foraging activity, although the hazard ratio for oat grains placed on and near track plates had a wide confidence interval.

Our results show that track plates offer an economical and efficient method for measuring predation risk at small spatial scales. Live traps are commonly used to measure the spatial distribution of small mammal populations. Price (1977) reported an increase in capture frequency of rodents in areas where they foraged, indicating that live traps can provide information about spatial foraging activity. However, traps may not accurately represent how small mammals use space (Douglass 1989) because they impede movement until release, can cause positive (access to food) or negative (forced confinement) behavioral reactions, and may kill the animal (Justice 1961). Sheppe (1967) reported irregular movement patterns by mice for several nights after being trapped, including travel far outside of usual home ranges and some permanent shifts in range. Track plates avoid these problems, and allow increased collection of activity data because movements are not impeded (Sheppe 1965).

An alternative strategy for quantifying predation risk is to deploy food items at a sufficient sample size to measure local risk. However, similar or substitutable food types are not always available, and not all food can be attached to burlap with wax to attribute an attack to a specific predator. Also, predators may respond behaviorally or demographically to such concentrations of food, thereby increasing predation risk in the vicinity (Cooper and Ginnett 2000; Doonan and Slade 1995; Taitt 1981). For example, Yunger (2002) provided supplemental food for white-footed mice and documented an increase in mouse densities due to immigration. We also observed an increase in mouse activity after we deployed pupae at the scale of individual trees. Track plates are a superior choice for measuring predation risk at small scales because predator space use and identity can be determined without the use of an attractant or bait that could influence immigration and foraging behavior in a patch.

We recognize that our methods of measuring predation risk were not foolproof. First, pupae in our study may have acted like bait and attracted mice to our sample trees. However, our objective was to test whether track plate data provide a reliable

measure of local predation risk, not to demonstrate that mice do not respond to clumps of food. In fact, the increase in local mouse activity at our sample trees after deployment of pupae in 2004 demonstrates that track plates are sensitive indicators of local mouse activity (and thus risk to prey). Second, predation rates on pupae waxed to burlap may not truly correspond with predation rates on natural pupae, as studies have found with artificial nests and real nests (Ortega et al. 1998; Sloan et al. 1998) and our classification of damage to pupae as invertebrate or vertebrate is not flawless. It is possible that late invertebrate damage masked any sign of previous vertebrate attack or that more conspicuous vertebrate attacks concealed any initial invertebrate predation. However, because several studies have documented a positive correlation between mouse densities and pupal predation (Elkinton et al. 1996; Jones et al. 1998; Ostfeld et al. 1996) and pupae were monitored daily, which minimized the time allowed for multiple attacks, we feel that our methods provide a reliable index of predation risk that natural pupae would experience.

Earlier tracking studies that used sand (Bider 1968), smoked kymograph paper (Justice 1961; Mayer 1957; Sheppe 1965, 1967), talc-coated plates (Brown 1969), ink (Lord et al. 1970; Nams and Gillis 2003), and carpenter's chalk (Drennan et al. 1998) suffered from one or more of the following drawbacks: they required frequent maintenance, were odorous, were impossible to prepare ahead of time, and were difficult or impossible to archive. Our graphite, alcohol, and oil medium is less odorous, coated acetate sheets can be prepared in bulk before field studies and stacked without damage (Fig. 3), tracked sheets are easily replaced with fresh sheets, and sheets can be archived for later examination. Several previous tracking designs also required protection from the elements. Plastic tubes (Nams and Gillis 2003), plastic rain gutters (Drennan et al. 1998; Glennon et al. 2002), juice or milk cartons (Justice 1961; Sheppe 1965), and polyethylene canopies (Bider 1968) were used to protect track media from rain in these studies, but these shelters add to the cost and bulk of materials, add to the labor involved, and also may alter the behavior of target mammals in the vicinity by providing cover and protection from predation. Our track plates do not require shelters and were water resistant (Fig. 1) to moderate rainfall (<24 mm/day).

Most gypsy moths pupate in the forest litter on or near the base of trees (Campbell et al. 1975), and these pupae are more susceptible to predation by white-footed mice than are pupae on tree boles above the ground (Campbell et al. 1975; Campbell and Sloan 1976; Cook et al. 1994). Our results reflect this pattern, in that predation rate at a given level of track activity was higher in 2003, when pupae were placed at ground level (Fig. 2B), than in 2002 (Fig. 2A) and 2004 (Fig. 2C) when pupae were placed at 1.5-m height.

Variability in the use of space by predators has been correlated with heterogeneity in attack rates on incidental prey, such as songbird nests (Schmidt and Ostfeld 2003). Examination of our data indicates that areas of concentrated mouse activity are areas of high risk for gypsy moths. Therefore, locales ignored by or inaccessible to mice because of physical impediments, increased predation risk, or low alternate food



FIG. 3.—Two hundred track plates stacked (with a clean acetate sheet on top), clipped together, and ready for transport to study plots or for storage until needed. Plates that have recorded tracks can be archived in the same manner.

supplies (Brown 1988; Lewis and Murray 1993; Schmidt et al. 2001) create spatial refugia from risk that may aid in the persistence of gypsy moth populations (Goodwin et al., in press). We successfully used track plates to quantify risk to gypsy moth populations.

We conclude that track plates can provide an economical and reliable measurement of predation risk without substantially altering the spatial distribution of risk itself. Track plates (and estimates of local predation risk inferred from them) have promising applications in research involving the spatial distribution of activity by mammalian predators.

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