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USING 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,

USA. Live gypsy moth pupae (*Lymantria dispar*) were placed at 2 heights on trees and

monitored for predation. Pupae deployed on trees visited by mice had a higher of

predation than those on trees not visited. Logistic regression indicated that predation

rates on gypsy moth pupae were positively correlated to 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 near 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.

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 (Smith 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 and Lautenschlager 1981). Gypsy moths are an introduced pest species that can cause severe defoliation to host trees which leads to reduced forest growth and increased tree mortality (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; Ostfeld et al. 1996; Jones et al. 1998), and chronically dense mouse populations can potentially drive gypsy moths to local extinction (Schauber 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 alter their local foraging intensity. Predator space use can be quantified using radio-

telemetry (Douglas 1989); however, this only provides information about the particular animals tracked, whereas estimating risk experienced 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 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 consumption rates on oat grains placed on and near track plates.

Other studies have recorded tracks of small mammals 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), and carpenter's chalk (Drennan et al. 1998) as tracking media. This study used acetate sheets with a graphite/alcohol/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/mineral oil mixture (3 parts graphite: 6 parts alcohol: 1 part 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

was produced for less than $1.50 and approximately 200 track plates were produced in 30 minutes of work.

Study area.—All field studies were conducted on ca. 2-ha oak-dominated forest plots at the Institute of Ecosystem Studies (IES), Millbrook, New York, USA. 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*) were also 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 spp*.). In 14 years of live-trapping (R. S. Ostfeld, unpublished data), the white-footed mouse has been the most frequently trapped small mammal on our plots, but shrews (*Blarina brevicauda* and *Sorex* spp.), 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: (1) total number of footprints recorded; (2) mean daily proportion of plates with mouse tracks (arcsine-square root transformed); and (3) a categorical presence/absence variable indicating whether any of the 5 plates were 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 cm^2), which were deployed at a height of 1.5 m on the bole of each sample tree (Smith 1985). ~~Track plates were monitored for 12 days, and pupae were deployed on the sixth day. Track plates and pupae were examined daily~~ 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 were estimated 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-square root 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 (Sherri 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 an intermittent circle around the base of each sample tree, and a group of 5 live gypsy moth pupae affixed with beeswax to individual squares of burlap (7 cm^2) 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 in the leaf litter, 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 on the bole and at the

base of sample trees within the same year. The aluminum flashing used to support the

coated acetate sheets 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 from 21 – 28 July, 2004. 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 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 (# attacks/35 pupa-nights). For each year, we used logistic regression

(SAS Institute 1999; $\alpha = 0.05$) to test whether the mortality rate of pupae at a tree was

positively related to track activity.

Live-trapping data collected during a concurrent study were used to calculate the

minimum number known alive (MNA; Krebs 1966) as an index of white-footed mouse

abundance on each tracking plot each year from June to August. We then compared

MNA with the mean track activity for each plot and year. THIS NEEDS TO BE

EXPANDED SOMEWHAT: GRID SIZE, WHAT TRAPS WERE USED, TRAP

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 cm^2) and placed on a 10×10 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 paperclip and another such square was staked to the ground 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 (Cox and Oakes 1984) 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 et al. 1985; Wolff 1996) 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.

RESULTS

Data were collected over 250 track-nights in 2002. An average of 23% (range = 3 – 50%) of track plates were tracked per tree per day and daily pupal predation rates averaged 13% (range = 0 – 47%). Pupae on trees visited by mice had a greater probability of predation than trees with no recorded visits by mice ($X^2 = 3.9$, d.f. = 1, $P <$

0.05). The number of mouse footprints at a tree was also a predictor of pupal predation rate (Wald $X^2 = 10.2$, $P = 0.0014$), but the transformed proportion of plates tracked by mice was the strongest predictor (Wald $X^2 = 14.0$, $P = 0.0002$; Fig. 2A). Average white-footed mouse MNA from June − August 2002 was 58.8 (range = 54 − 65) on Cary Drive and 53.8 (range = 43 − 69) on Field Lab.

REPORTING MNAS ADDS VERY LITTLE INFO, UNLESS WE COMPARE THEM TO THE TRACK & PREDATION DATA. I KNOW THE EDITOR SUGGESTED THAT TABLE 1 SHOULD BE REMOVED, BUT I DISAGREE AND I THINK WE CAN ARGUE SUCCESSFULLY FOR KEEPING IT. I SUGGEST GETTING RID OF REDUNDANCIES (I.E., NO MENTION OF PUPAE # AND HEIGHT IN THE TABLE, NO MENTION OF MNA'S IN RESULTS TEXT). THE OTHER DATA (GRID LEVEL TRACK ACTIVITY AND PREDATION RATES) ARE NOT CURRENTLY IN TEXT OR FIGURES, AND THEREFORE NOT REDUNDANT. ALSO, REPORT TRACK ACTIVITY & PREDATION RATES TO 2 DECIMAL PLACES.

Data in 2003 were collected over 924 track-nights. One sample tree was excluded due to hornet activity. An average of 57% (range = 28 − 90%) of track plates were tracked per tree per day and daily pupal predation rates averaged 91% (range = 51 − 100%). 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 depredated an average of 66% (range = 82 − 90%) of pupae daily, whereas invertebrates depredated an average of 4% (range = 2 − 6%) of pupae daily (all other pupae were uneaten). ARE THESE MOUSE VS. INVERT DATA AVERAGED OVER THE GRID OR THE TREE? Transformed track activity was again

a strong predictor of pupal predation rates (Wald $X^2 = 46.6$, $P < 0.0001$; Fig. 2B). Average white-footed mouse MNA values from June – August 2003 on Green, Henry, and Tea plots were 79.5 (range = 61 – 92), 59.0 (range = 51 – 60), and 58.5 (range = 41 – 78), respectively.

TEST FOR TRACK x GRID INTERACTION? DOES RELATIONSHIP BETWEEN PREDATION & TRACK ACTIVITY VARY AMONG GRIDS. THIS WOULD BE A QUICK ANALYSIS TO RUN.

Data in 2004 were collected over 945 track-nights. An average of 60% (range = 33 – 87%) of track plates were tracked per tree per day and daily pupal predation rates averaged 72% (range = 25 – 100%). White-footed mice depredated an average of 44% (range = 43 – 83%) of pupae daily, while invertebrates depredated an average of 2% (range = 1 – 5%) of pupae daily (all other pupae were uneaten). Once again, transformed track activity was a strong predictor of pupal predation rates (Wald $X^2 = 86.0$, $P < 0.0001$; Fig. 2C). Average white-footed mouse MNA values from June – August 2004 on Green, Henry, and Tea plots were 138.5 (range = 124 – 150), 66.5 (range = 62 – 76), and 56 (range = 45 – 71), respectively.

Mice showed no detectable difference in their predation rates on oats located on or off track plates, after accounting for variation among stations ($X^2 = 0.95$, $P = 0.33$). Mean (SE) survival times for oats on and off plates were 1.63 (0.08) and 1.55 (0.09) days, respectively, yielding a hazard ratio (95% CI) of 0.85 (0.62-1.17).

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 evidence that

track plates attracted or deterred mice that were foraging on oat grains placed on and near track plates. BUT, NOTICE THE WIDE CONFIDENCE INTERVAL ON THE HAZARD RATIO. THIS MEANS THAT THE DATA ARE CONSISTENT WITH THE RISK OF PREDATION HAVING BEEN AS MUCH AS 38% LOWER FOR OATS ON THE PLATE AS FOR OATS OFF THE PLATE. SINCE SUCH A BIG DIFFERENCE WOULD CERTAINLY BE BIOLOGICALLY SIGNIFICANT, SO WE CAN'T EXCLUDE AN EFFECT. BEST TO BE HONEST: ALTHOUGH THERE WAS SUGGESTIVE EVIDENCE, WE FOUND NO STRONG EVIDENCE OF AN IMPACT OF THE PLATE ON OAT ATTACK RATES.

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 (Douglas 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, not all food can be attached to burlap with wax to attribute an attack to a specific predator, and 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. Track plates are a superior choice for measuring predation risk 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. Pupae in our study may have acted like bait and attracted mice to our sample trees, although Schauber et al. (2004) found no evidence of an aggregative response of mice to clumps of pupae. Our objective, however, 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. Any increase in local mouse activity in response to the presence of pupae should be apparent in our track-plate data and contribute to the positive relationship between track activity and predation rate.

I THINK WE NEED TO SAY SOMETHING ABOUT THE WAX/BURLAP PROBLEM -- ACKNOWLEDGE THE ISSUE & POTENTIAL PROBLEMS, USE PREVIOUS STUDIES TO INDICATE THAT PREDATION ON WAXED/BURLAPPED PUPAE IS CORRELATED WITH POPULATION EFFECTS.

Earlier tracking studies 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), and carpenter's chalk (Drennan et al. 1998) suffered from one or more of these drawbacks: they required frequent maintenance, were odorous,

were impossible to prepare ahead of time, and were difficult or impossible to archive. Our graphite/oil/ alcohol medium is less odorous, coated acetate sheets can be prepared in bulk prior to field studies (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 1998), 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, 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 per 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.

Differences in the use of space by predators can be correlated with heterogeneity in attack rates on incidental prey, such as songbird nests (Schmidt and Ostfeld 2003). Our data indicate that areas of concentrated mouse activity are areas of high risk for gypsy moths. Therefore, locales ignored by or inaccessible to mice due to physical impediments, increased predation risk, or low alternate food supplies (Brown 1988; Lewis and Murray 1993; Schmidt et al. 2001) create spatial refugia from risk on a

~~horizontal plane~~ which 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.

<div align="center">

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FIGURE LEGENDS

FIG. 1. Track plates with a ruler showing scale in cm. The plate on the left has been held under running water for 30 seconds, 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 zoomed box).

FIG. 2.   Observed (circles) and predicted (lines) arcsine-square root transformed values of predation risk to *Lymantria dispar* pupae as a function of *Peromyscus leucopus* track activity for A) the 6-day experiment in 2002 with pupae 1.5 m high on trees, B) the 7-day experiment in 2003 with pupae at the base of the tree, and C) the 7-day experiment in 2004 with pupae 1.5 m high on trees.

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.
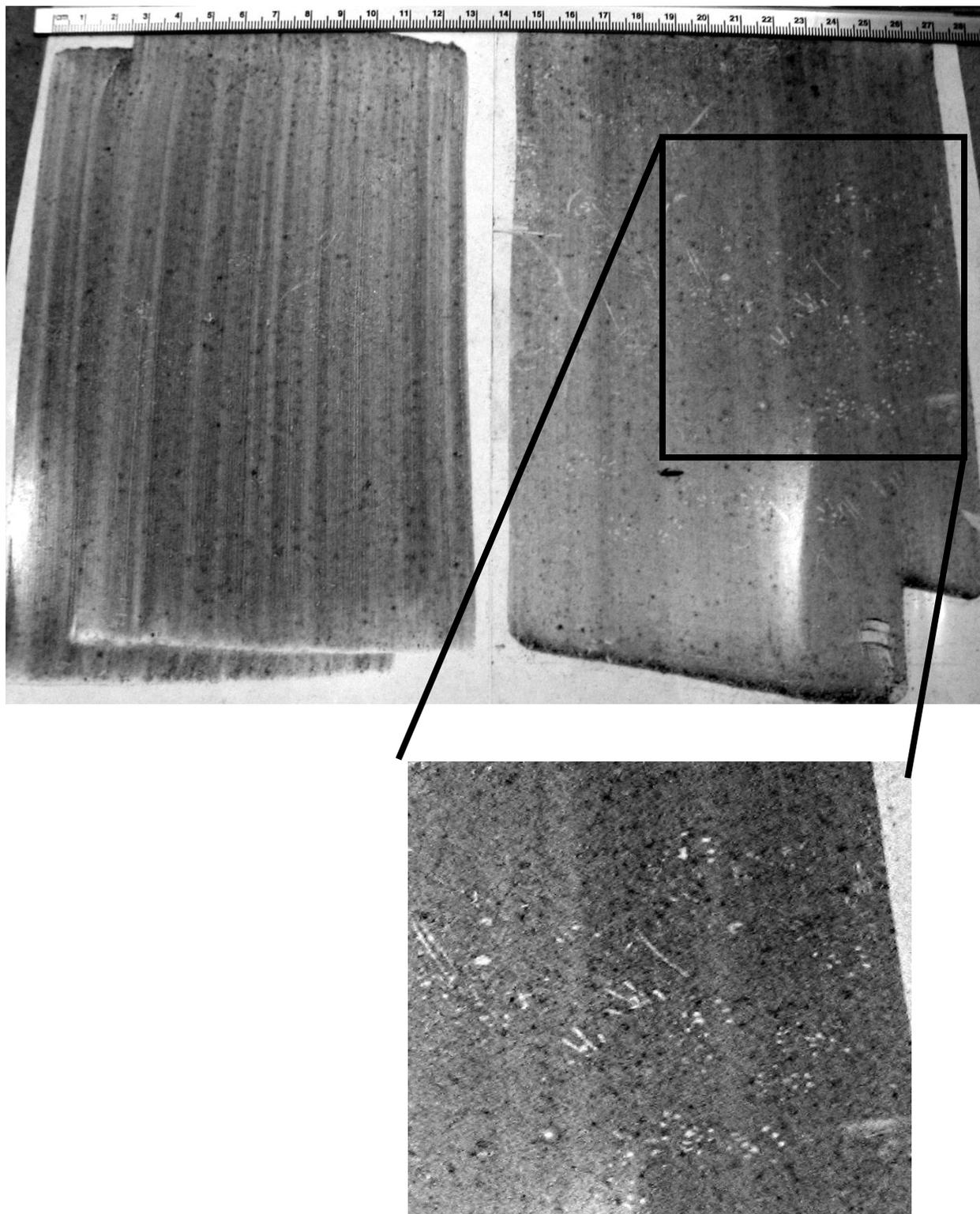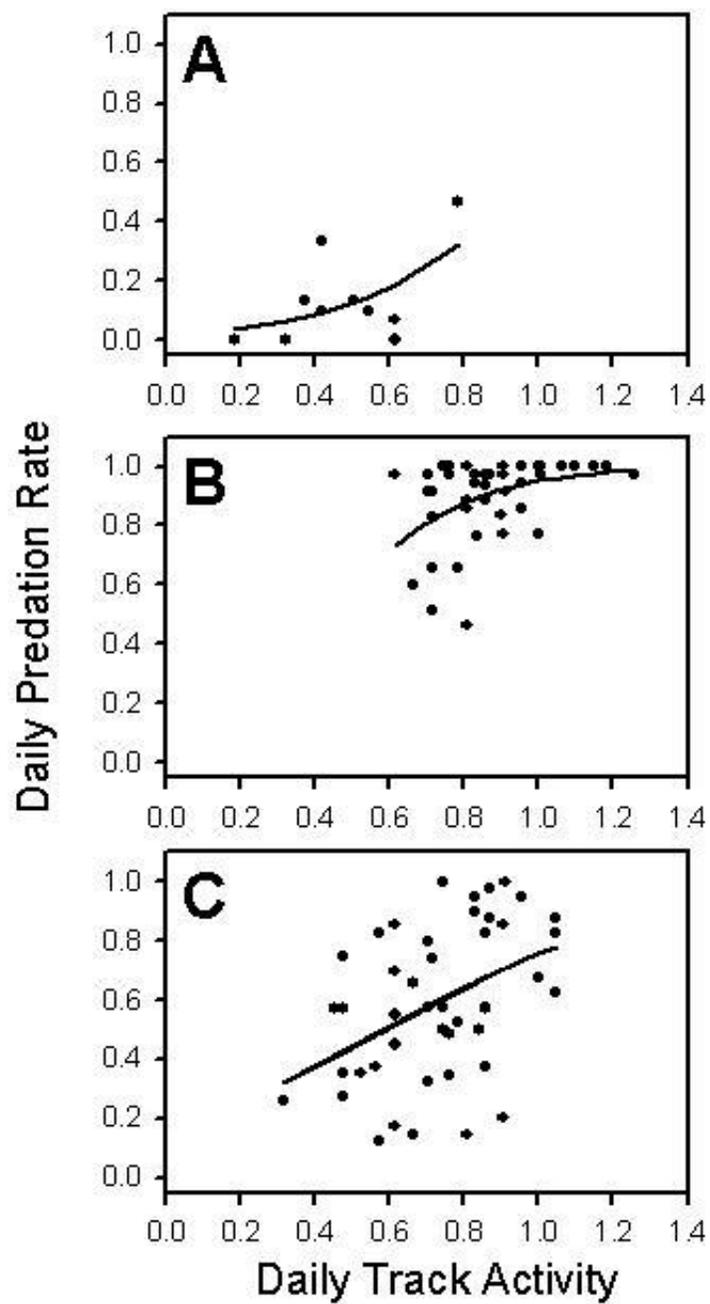
FIG. 1.

FIG. 2.

FIG. 3.