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Effects of Intertrap Distance and Wind Direction on the Interaction of Gypsy Moth (Lepidoptera: Lymantriidae) Pheromone-Baited Traps

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ABSTRACT More male gypsy moths, Lymantria dispar L., were captured in traps at the perimeter compared with traps at the center of a 6-x-6 grid of pheromone traps spaced every 80 m. Additional tests demonstrated suppression of catch at the center of hexagonal arrays of traps with intertrap distances ranging from 2.5 to 40 m. In a hexagonal array of traps spaced every 20 m and monitored every 1-3 h, more males were captured in upwind and downwind traps than in crosswind or central traps.

KEY WORDS Insecta, pheromone, trap interaction, Lymantria dispar

In previous studies, we examined the efficiency of gypsy moth (Lymantria dispar L.) pheromone-baited traps and the various factors that affect trap catch (Elkinton & Cardé 1980, Elkinton & Childs 1983, Elkinton & Cardé 1984). These studies used arrays of traps deployed at a variety of intertrap distances. Because male gypsy moths detect (+)-disparlure from dispensers that are commonly used in such pheromone-baited traps (release rate of approximately 200 ng/h) at a distance of at least 80 m (Elkinton et al. 1984), it seems likely that the number of males captured at one pheromone trap may be influenced by the presence of other traps when the intertrap distances are less than 80 m. Such trap interaction has been demonstrated for other Lepidoptera (Wall 1984a,b). In this study, we report a series of experiments that describe the effects of intertrap distance and wind direction on the distribution of gypsy moth captures in arrays of pheromone traps.

Materials and Methods

All experiments used USDA milk carton traps (Schwalbe 1981) baited with 500 μg of (+)-disparlure in plastic laminated Hercon wicks (3 by 25 mm). The experiments were conducted in forests dominated by oak (Quercus spp.) with moderate-to-high density gypsy moth populations during the period when adult male gypsy moths were flying.

In Experiment 1, traps were deployed in a 6-x-6 grid with an intertrap distance of 80 m (Fig. 1A) as part of a previously reported mark-recapture study of released males (Elkinton & Cardé 1984). The traps were attached to the boles of large trees (>25 cm diameter at breast height [dbh]) at a height of 1 m. Males were removed from the traps and counted each morning. The experiment was conducted on the Prescott Peninsula of the Quabbin Reservoir, Mass., in July 1981.

The second experiment consisted of groups of seven traps deployed in a hexagonal array (Fig. 1B) with intertrap distances of 2.5, 5, 10, 20, 40, and 80 m. The traps were hung from branches or small saplings at a height of 1 m and sampled daily during the period of male flight in July 1984. Six such hexagonal arrays (one for each distance) were deployed at each of three sites: one near Windsor Dam in Ware, Mass., and two in Brimfield State Forest in Brimfield, Mass., they were sampled daily for 9 d for a total of 27 replicates. Each hexagonal array was deployed at least 200 m from the nearest adjacent hexagonal array.

Experiment 3 was designed to evaluate the effect of wind direction on the distribution of catch in an array of traps. A hexagonal array with an intertrap distance of 20 m was positioned at various locations near Otis Air Base, Mass., between 19 July and 10 August 1985. Traps were hung at a height of 1.5 m from steel posts driven into the ground at positions at least 2 m from the nearest overstory trees. Samples were taken every hour during the period of peak flight in early afternoon or every 2-3 h during the morning or late afternoon so that the numbers of males captured during each sample period were comparable. Periods during which <10 males were captured in all seven traps were discarded from the analysis. A total of 43 sample periods was conducted over 12 d. After each period, the males were removed and counted, then the traps were assigned positions at random and repositioned on the posts. Horizontal wind speed and direction were monitored with an SA-200 ultrasonic anemometer (Kaijo Denki Company, Tokyo) positioned at a height of 2 m and 2-3 m from the center trap. An ultrasonic anemometer was used because it was capable of measuring the very
light wind speeds (often <30 cm/s) that are common beneath a forest canopy and that are below the stall speed of most propeller anemometers. The wind speed and direction were recorded instantaneously every 10 s on a CR 21 data logger (Campbell Scientific, Logan, Utah), and the mean wind speed and vector-average direction were recorded on a paper tape printer for each 1- and 2-h period. On each trial, the vector average wind direction would fall between two of the six perimeter traps from a point of reference at the center of the grid (Fig. 1B). Thus, these two traps were considered the upwind traps for that trial.

In Experiment 1, we compared the daily proportion of males captured per trap in the 20 perimeter traps, the 4 innermost traps, and the 12 traps in between (Fig. 1) using Wilcoxon’s matched-pairs signed-ranks test and Sidak’s inequality (Sokal & Rohlf 1981, 242) to maintain experimentwise P < 0.05. The same statistical procedure was used in Experiment 2 to compare the mean number of males caught per day at the central trap with the mean of the six perimeter traps or the mean proportion caught per trap in upwind, downwind, crosswind, and central traps in Experiment 3.

To determine if there was a correlation between successive trials in the probability of catching more males in upwind traps, we used a version of the sign test (Sokal & Rohlf 1981, 449). The proportion caught in the upwind trap was compared with the proportion caught on the immediately preceding trial and rated as (+) if both trials were greater than or less than the mean proportion for upwind traps across all trials, and (−) if one was greater and one was less than this proportion. Only trials conducted on the same day were compared in this manner. Under the null hypothesis of no correlation between successive trials, one would expect an equal proportion of (+) and (−) ratings. An identical procedure was used to test the correlation between trials of catching more moths in downwind traps. We used Spearman’s rank correlation procedure (Sokal & Rohlf 1981, 607) to see if the proportion captured in the upwind traps was correlated with wind speed or the standard deviation in wind direction recorded during each trial.

Results

The number of males captured per trap was higher in traps around the perimeter of the 6-x-6 grid of traps with an intertrap distance of 80 m (Table 1) compared with traps at the center. The four innermost traps caught fewer per trap than the 12 traps between the perimeter and the innermost four traps (Fig. 1A).

In the hexagonal arrays with a variety of intertrap distances, we found that at all distances tested (except 80 m), the center trap caught significantly fewer moths than the mean catch among the six traps on the perimeter (Table 2). As in the first experiment, there was less than a two-fold difference in trap catch between the inner and outer traps at all distances tested.

In Experiment 3, the upwind traps in a hexagonal array usually captured the most moths (Table 3), which supports the findings of Wall & Perry (1978) with the pea moth, Cydia nigricana F., although in our tests the difference in catches between upwind and downwind traps was not statistically significant. There was a significant difference between catches in crosswind and upwind traps and between those in the central trap and both upwind and downwind traps. However, the differences observed were not very large, and the variability in trap catch in relation to the wind direction was high (Fig. 2). The differences in catch observed between upwind or downwind traps and
the central trap appear to be smaller than that reported by Wall & Perry (1980, 1981) for C. nigriciana. On some days, the downwind traps appeared to catch consistently more moths than the upwind traps. There was a significant correlation between successive trials in the occurrence of proportions captured in upwind and downwind traps that were more than or less than the average proportion captured across all trials (P < 0.05, sign test, Sokal & Rohlf 1981, 449). Similar findings over much shorter sampling intervals were reported by Perry & Wall (1984a). However, there was no significant correlation (P > 0.05, Spearman's rank correlation, Sokal & Rohlf 1981, 607) between the wind speed or standard deviation of the wind direction (an indication of the width of the time-average plume) and the proportion captured in the upwind traps.

**Discussion**

The most intuitively obvious explanation for traps on the perimeter of an array capturing the most moths is that these traps were the first ones encountered by moths approaching from outside the array. Some of these moths would be captured in the perimeter traps, leaving a smaller number available to be captured by the inner traps. In relatively small arrays of traps as used in this experiment, it seems likely that the vast majority of captured moths originate from outside the array.

**Table 2. Mean number of male gypsy moths captured per trap per day at six perimeter traps and a central trap in hexagonal arrays of pheromone traps with different intertrap distances**

<table>
<thead>
<tr>
<th>Intertrap distance (m)</th>
<th>Mean no. &amp;d # per trap per d</th>
<th>Central trap</th>
<th>Six perimeter traps</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5</td>
<td>18.4</td>
<td>17.8</td>
<td>22.4</td>
</tr>
<tr>
<td>5.0</td>
<td>13.9</td>
<td>13.5</td>
<td>19.4</td>
</tr>
<tr>
<td>10.0</td>
<td>10.8</td>
<td>11.4</td>
<td>17.1</td>
</tr>
<tr>
<td>20.0</td>
<td>15.4</td>
<td>14.8</td>
<td>23.5</td>
</tr>
<tr>
<td>40.0</td>
<td>17.3</td>
<td>17.2</td>
<td>26.9</td>
</tr>
<tr>
<td>80.0</td>
<td>29.2</td>
<td>29.0</td>
<td>45.4</td>
</tr>
</tbody>
</table>

* Central trap catch significantly less than mean for perimeter traps at experiment-wise P ≤ 0.05 (Wilcoxon's matched-pairs signed-ranks test and Sidak's inequality [Sokal & Rohlf 1981]); n = 27.

Because male gypsy moths can detect pheromone emanating from such traps at a distance of at least 80 m (Elkinton et al. 1984), it seems likely that most of the males entering the array do so by detecting pheromone and initiating upwind flight at some distance downwind of the array. Consequently, one might expect that more males would be captured on the downwind than the upwind edge of the array.

On the contrary, experiments with the pea moth in English wheat fields have demonstrated that it is usually the upwind traps in an array that capture the most males (Wall & Perry 1978). The original explanation of this phenomenon, suggested by Wall & Perry (1978), was that moths flying in a pheromone plume will bypass the downwind traps because the boundary of the downwind plume is masked by the plume from traps farther upwind. Consequently, the moths will continue upwind until they encounter a plume boundary in the vicinity of the upwind trap, whereupon they follow the boundary to the upwind trap. Subsequent experiments demonstrated that the proportion of moths was sometimes greater in the downwind traps than upwind traps but that central traps always captured the fewest moths (Perry & Wall 1984a,b). An updated explanation of this phenomenon is contained within a simulation model (Perry & Wall 1984b) of moths flying in a pheromone plume. The simulation predicted patterns of trap catch similar to those observed in the field. The model assumed that moths fly in random directions outside of the “active space” of the pheromone, upwind within the active space, and in casting flight crosswind as described by David et al. (1982, 1983) when they cross a plume boundary. The model further assumes that at distances greater than 10 m downwind of a pheromone source, the pheromone plume assumes the form of a homogeneous cloud within which the moths are continually exposed to a level of pheromone concentration above the threshold for upwind flight (Perry & Wall 1984b, 1985).

Such homogeneous plumes may exist in a wheat field, but our previous experiments with gypsy moth wing-fanning assays in a forest (Elkinton et al. 1984) demonstrated that beneath a forest canopy, ho-
Fig. 2. Proportion of the total number of males captured per trap in the two upwind traps, two downwind traps, and the central trap over a series of 43 trials at four sites between 17 July and 3 August 1984 in a hexagonal array of traps (intertrap distance 20 m). The horizontal dotted line represents the proportion expected (0.143) if males were distributed equally among the seven traps; lines between points connect trials conducted consecutively on the same day.

Homogeneous plumes do not exist. Instead, the pheromone plume consists of filaments of pheromone-laden air interspersed with clean air, so that moths flying within them are continually encountering plume boundaries. In those experiments, male gypsy moths held in wire mesh cages at various distances (20–80 m) downwind of a pheromone source repeatedly initiated and stopped wing fanning over 15-min test periods, illustrating the discontinuous nature of the pheromone plume. Murlis & Jones (1981) drew similar conclusions from ion tracer experiments conducted at shorter distances in open fields.

The apparent difference in pheromone plume structure between our experimental conditions and those of Wall & Perry may be due in part to the effects of vegetation on pheromone dispersal (Wall & Perry 1986). A continuous layer of wheat stems, compared with the widely spaced tree boles and lack of understory vegetation at our experimental sites, would probably cause much higher mechanical turbulence (thus more rapid disruption of the plume filaments [Elkinton & Cardé 1984]) as well as a much greater surface area for adsorption and re-elution of pheromone. Another important difference between the two experimental conditions may be in the pheromone release rate (relative to the release rate of females and male sensory thresholds). In our experiments, the limit of detection was approximately 100 m; we have observed few wing-fanning responses at this distance. On the other hand, Perry & Wall (1984b) believe pea moths respond at 500 m. Furthermore, in field tests of different trap designs and lures (e.g., Cardé et al. 1977), we have never observed any obvious pheromonal contamination of vegetation such as reported by Wall & Perry (1983) at levels sufficient to cause significant numbers of males to be attracted to positions from which baited traps have been recently removed. We would expect to observe such an effect because disparlure is readily adsorbed onto surfaces (e.g., Charlton & Cardé 1982), but perhaps it is apparent only at higher pheromone release rates than we typically use. These contrasts suggest that Wall & Perry may have worked with pheromone lures that released at rates much higher than the rate that we used of 10- to 100-fold greater than that of females (Charlton & Cardé 1982). On the contrary, however, Wall & Perry (C. Wall, personal communication) used lures...
that released approximately 30 ng/h, which they believe is comparable with that of natural females.

The explanation of Wall & Perry (1978) can be reformulated in a way that is consistent with the filamentous structure of the plume that persists many meters downwind of its source in a forest. In our view, the most straightforward explanation for our results is that most males probably enter the array from the downwind direction and are more likely to approach traps first on the downwind edge, which accounts for the relatively high catch at these traps. However, even if males approach within 1 m and orient to a particular trap, only a fraction (approximately 21%) are captured (Elkinton & Childs 1983). Thus, many males may approach and leave several traps in succession and gradually progress through the array to the upwind edge. However, once they have flown beyond the upwind edge, they are in a region where above-threshold levels of pheromone are very infrequent, thus substantial further upwind flight is much less likely. Instead, such males are likely to engage in crosswind casting flight (David et al. 1982, 1983) or tree-oriented vertical flight (Elkinton & Cardé 1983), thus they may re-enter the grid in the vicinity of the upwind traps. Such moths would increase catch in the upwind traps relative to traps in the center of the grid. We also have observed moths that have flown into a region upwind of a pheromone source flying downwind where they reencounter pheromone-laden air (Perry & Wall 1985). These moths also are likely to be captured in the upwind traps.

This explanation is similar to those of Wall & Perry (1978) and Perry & Wall (1984b), but it avoids invoking the notion of a wide homogeneous plume or suggesting that moths locate upwind traps by following plume boundaries. We think it is best to define the boundary of a time-average plume in probabilistic terms as the region in which encounters with above-threshold concentrations of pheromone changes from frequent to infrequent. The result is a change in the frequency of upwind flight relative to either crosswind casting flight or flight that is oriented at random to the wind direction.

An alternative explanation for the higher catch in the upwind traps might be as follows: males that approach the grid from downwind have a nearly equal chance of being captured in any trap, with only a slightly higher probability in favor of the downwind traps. However, males that fly into the grid from the upwind or crosswind directions can be attracted only toward traps that are farther upwind, and it is these males that constitute the additional numbers captured in upwind traps. However, this hypothesis does not explain why catch in the crosswind traps was less than in the upwind traps. The hypothesis would be more appealing if male gypsy moths engaged preferentially in crosswind flight before encountering pheromone-laden air, but previous studies (Elkinton & Cardé 1983) did not reveal evidence of such crosswind flight. Furthermore, even in a grid only 5 m across (intertrap spacing 2.5 m, Experiment 2), the number of males captured in the central trap was lower than the mean for the perimeter traps. In such a grid, the diameter of the grid relative to the length of the active space that extends downwind of the grid is extremely small, so we might expect a correspondingly small proportion of moths entering the grid from crosswind as opposed to the downwind direction. Detailed records of male flight behavior in the vicinity of several pheromone-baited traps would be required to verify either of these hypotheses.

Neither of these hypotheses explains why there were systematic variations or positive correlations between successive trials in the proportions captured in upwind or downwind traps. In their simulation model, Perry & Wall (1984b) produced such variation by changing parameters that regulated the behavior of flying moths. We think it is likely that parameters relating to the wind and the shape, structure, or alignment of pheromone plumes account for these results. However, neither we nor Perry & Wall (1984a) were able to find any relationship between the proportion captured in the upwind traps and wind speed or standard deviation of wind direction. The latter is an indication of the width of the time-average plume (Elkinton et al. 1984), but these measures are but crude indicators of plume shape or structure. There was no obvious relationship between trap position or site of the test and the proportion captured in the upwind traps. For instance, at site A on 17 and 18 July, more moths were captured in the upwind traps (Fig. 2). However, on 19 July at the same site, more moths were captured in the downwind traps, representing a different position in the hexagon. It is possible that particular combinations of trap position and wind direction, perhaps in relation to nearby trees, caused certain traps to catch more moths.

The results of these experiments have implications for the use of pheromone traps for monitoring population density and for field tests conducted to evaluate different pheromone lures or trap designs. Such tests are commonly done with intertrap distances of approximately 20 m. The higher catch at perimeter traps in such tests is a major source of variability that may obscure true differences between treatments. This confounding factor can be eliminated by deploying unsampled traps outside the perimeter of the array of traps used in the experiment (Cardé & Elkinton 1984) and with Latin square designs (Perry et al. 1980). When traps are used for population monitoring, the numbers captured in single isolated traps will not be comparable with the numbers captured per trap when several traps are deployed in close proximity.

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