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Distribution, Dispersal, and Apparent Survival of Male Gypsy Moths\textsuperscript{1} as Determined by Capture in Pheromone-Baited Traps\textsuperscript{2}

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ABSTRACT


An average of 3.9\% of laboratory-reared, marked male gypsy moths (Lymantria dispar L.) released uniformly across a 0.64 km\(^2\) area were captured in pheromone-baited traps set out 800 m apart in a 64 km\(^2\) grid. In contrast, an average of 0.9\% of males released simultaneously from a single point at the center of the grid (566 m from the nearest trap) were captured. The 4.0\% recapture can be used to estimate the average density and the 0.9\% recapture to estimate the maximal density of a population of feral moths, based on the numbers caught in a trapping grid of the same trap density, if we assume that the feral and laboratory-reared moths behave similarly. Approximately 97\% of the recaptured males from the uniform release and 80\% from the grid center release were captured within 800 m of the release site and no moths were recaptured beyond 1600 m. An average of 18\% of males released from the center of a smaller (0.64 km\(^2\)) grid of higher trap density (80 m spacing) were recaptured. Once again, recaptures occurred predominantly in traps near the center of the grid. The proportion recaptured was highest on the warmer days. Males were released 1, 2 and 3 days after eclosion to assess the effects of adult age, and mortality plus emigration upon trap catch. A higher proportion of older moths (2- and 3-days-old) were captured than one-day-old moths. The apparent average rate of mortality plus emigration between the first and second day after release was 96\%, an estimate that may be influenced by individual differences in responsiveness of males to a pheromone source.

Introduction

There is widespread use of pheromone-baited traps for detection and delimitation of gypsy moth populations in Michigan and elsewhere in the United States (ca. 95,000 in 1979). Little information is deduced from trap catch data beyond the fact that moths are present or that they are more prevalent in some areas than in others. There has been little research attempting to relate pheromone trap catch to actual population density and dispersion. Indeed, the utilization of pheromone trap catch information to determine the spatial distribution of populations has been hindered by a lack of a definitive methodology (Cardé 1979, Croft 1979). In this study, we have measured what proportion of marked male gypsy moths released into a survey grid of pheromone...
traps will be recaptured. If we assumed that we would catch a similar proportion of the wild males present in the area, then we could estimate population density from the numbers caught in traps. However, before we can use such estimates with confidence, we must determine how trap catch varies not only with different trap densities but also with population density, habitat, and weather-related variables such as temperature and wind speed.

In this study we investigated the relationship between population and trap catch at a trap density of one per 0.65 km², a widely used survey trap density in Michigan and elsewhere. Previous research using marked male gypsy moths released into a grid of traps at this density, (Schwalbe, 1980) has shown that approximately 1% of the released males would be recaptured. However, in that study all males were released from a single point at the center of the grid of traps, so that the minimal distance between the site of release and the nearest trap was 566 m. In nature, wild males may originate anywhere within such a grid of traps and the distance between a male and the nearest trap may vary from 0-566 m. Undoubtedly males are more likely to be caught if they originate near the traps, and thus such single point release data would lead to underestimates of the proportion of wild males in a trapping grid of that density.

To test this hypothesis we released males uniformly at 100 equally spaced points within a 0.64 km² block which was bounded at each corner by a pheromone trap and situated at the center of a 64 km² grid of such traps. The release area thus represents a "typical" 0.64 km² producing male gypsy moths of which a certain proportion will be captured at various distances from the site of release.

We also released marked males in a pheromone-trapping grid of much higher density (400/2.6 km²) to investigate the distance of dispersal, survival, effect of moth age, trap efficiency and the effects of the marking procedure on the probability of male recapture.

Materials and Methods

Design of Experiments

Experiment 1.—The research area was an 8 x 8 km (5 x 5 mi) block of deciduous forest in central Michigan (Midland Co.), with scattered fields and clearings comprising about 15% of the total area as determined from aerial photographs. The center 1.6 x 1.6 km was a continuous block of deciduous forest. One hundred pheromone traps were evenly distributed approximately 800 m apart (4 per mi²). Marked male gypsy moths were released from an 800 x 800 m block (1/4 mi²) at the center of the 64 km² (25 mi²) study plot (Fig. 1). In one release strategy marked males were released from a single point at the center of the release area. In the second strategy, males marked with another color were released in equal numbers from each of 100 points spaced evenly 80 m apart throughout the release area.

In this experiment the 4 traps at the corners of the release area were sampled once in the morning before release and once in the afternoon. The 36 traps within 1.6 km of the release area were sampled once a day and the remaining traps near the perimeter of the 64 km² study site were sampled once a week.

Experiment 2.—An additional 100 traps were placed 80 m apart in the release area at the center of the 64 km² block (Fig. 2). Males in this experiment were released in equal numbers from 25 points within an 80 x 80 m block at the center of the release area. This experiment thus represents a 10-fold reduction in the inter-trap distance and the release pattern compared to the first experiment. Moths emerging on a given day were divided into 3 equal groups which were released on the first, second and third day, respectively, after emergence (Fig. 3). The moths not released were held in emergence cages where they were subject to the same temperature and light conditions as released males. Thus, on any day we released from one to 3 groups of males, each of a different age and marked a different color. The com-

![GRID CENTER RELEASE](image1)
![UNIFORM RELEASE](image2)

**Fig. 1.**—Spatial distribution of capture of male gypsy moths released from a single point and uniformly from 100 points in the 800 x 800 m block at the center of a 8 x 8 km grid of pheromone traps.
parative recapture rates of males of a given age that differed only in how many days they had been flying in the forest gave an estimate of the rates of mortality and emigration.

In this experiment all 100 traps in the release area were sampled in the morning before release of the moths. The traps near the center surrounding the site of release were sampled again in the afternoon. The 36 traps within 1.6 km of the release area from the first experiment were sampled once a week.

Experiment 3.—In the first 2 experiments we used Pherocon 1C traps instead of the smaller Delta trap (Mastro et al. 1977) currently used by the USDA for gypsy moth surveys, because we wanted a trap that would be effective after 10 or more males were trapped. The Pherocon 1C traps in all 3 experiments were hung from branches or small saplings > 2 m away from trees > 0.5 m trunk diam, so that the pheromone could disperse unimpeded in all directions. In the third experiment we compared the efficiency of the two traps by replacing every other Pherocon trap in the 800 × 800 m grid of Experiment 2 with a Delta trap. The Delta traps were stapled at a height of approximately 1.5 m to the trunks of trees at least 0.5 m in diam. Traps were positioned at random on the N, S, E or W side of the trees. The moths were released in equal numbers from each of 90 points, 80 m apart, halfway between the nearest pheromone traps.

In this experiment we also examined the effects of marking on the probability of recapturing males by releasing at each point an equal number of marked and unmarked males. Both groups were the same age and handled in the same way except for the mark. This experiment was conducted in September after the flight of wild males had ended.

Rearing and Marking Procedures

Male gypsy moths were reared in laboratory culture at the APHIS Gypsy Moth Methods Development Laboratory, Otis Air Base, Massachusetts. They were sexed and shipped to Michigan as pupae in paper cups. The cups were opened and placed in wire mesh emergence cages.

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**Figure 2.**—Daily spatial distribution of captured male gypsy moths released in an 80 × 80 m block in the center of an 800 × 800 m grid of pheromone traps.

**Figure 3.**—Daily release pattern for gypsy moths in the experiment to assess mortality and emigration.
cages which we placed inside a walk-in screen cage several km from the study area. The cups with pupae were transferred each afternoon to empty cages so that all adult males in any cage would be the same age. Males were released on the day following emergence except in the second experiment when 2 and 3-day-old males were also released. Before release the males were confined inside paper cups (8 cm diam, 11 cm high) whose inside surface had been coated with a very small amount of fluorescent powder (Dayglo Corp., Cleveland, OH). The males became marked with powder as they fanned their wings against the sides of the cups. The use of red, orange, yellow, blue and green powders alone and in various combinations gave 9 discernible colors. After recapture, color determinations were conducted under a UV light. In all experiments a period of at least one week elapsed between releases of moths of a given color. Generally, moths were released between 10:00 and 12:00 hr, which is before the period of peak flight (Cardé et al. 1974). Moths were released by opening the cups and launching the moths into the air, thereby assuring that they were capable of flight. Individuals that did not fly (<5%) were killed and replaced.

**Pheromone Source Trap Design and Temperature Data**

The pheromone source in these experiments was 300 μg of (+)-disparlure (Farnum et al. 1977, Cardé et al. 1978) dispensed in 100 μl of petroleum ether onto a cotton wick, pinned to a cork and stuck in the inside surface of the traps. The wicks were prepared and set outside more than 100 km from the research area for 3 days prior to placement in traps. Pheromone wicks were replaced in each trap once a week.

The Pherocon IC traps (Zoecon Corp., Palo Alto, CA) used in this study were set up according to manufacturer’s specifications except that the inside surface of both top and bottom halves were coated with a thick layer of Tanglefoot (Tanglefoot Co., Grand Rapids, MI). The opening between the two halves was increased to 7 cm (Miller et al. 1977). The total trapping surface was ca. 1150 cm² compared to ca. 225 cm² for the Delta traps. The traps were replaced as they filled with gypsy moths or other insects. A continuous chart of the ambient temperature beneath the canopy at 0.3 m above the ground was recorded on a Mechanical Weather Station, Model 1071, (Meteorology Research Inc., Altadena, CA).

**Calculation of Daily Survival**

The rate of first day survival (S₁) was estimated according to a method developed for fish (Ricker 1975). The rate of survival is defined as the proportion of those released on the first day that survive (or are available for recapture) at the time of release on the second day. The number of first day releases available for recapture on the second day is estimated from the following:

\[
\frac{R_{12}}{R_{12} + M_{12}} = \frac{R_{22}}{M_2}
\]

where

- \(R_{12}\) = the number released on the first day and recaptured the second day.
- \(R_{22}\) = the number released on the second day and recaptured the second day.
- \(M_{12}\) = the number of first day releases still available for recapture the second day.
- \(M_2\) = the number released on the second day.

Dividing \(M_{12}\) by the number released on the first day \(M_1\) we have \(S_1 = \frac{R_{12} M_2}{R_{22} M_1}\) (Ricker 1975, p. 123). For small numbers of recapture, an unbiased estimate of \(S_1\) is given by \(S_1 = \frac{R_{12} M_2}{M_1 (R_{22} + 1)}\) (Ricker 1975, p. 124). The rate of mortality (including emigration) on the first day \(D_1\) is equal to \(1 - S_1\). Similar arguments lead to the following equations for \(S_2\), the rate of survival between the times of release on the second day and third day and \(S_{12}\), the total rate of survival between the first and third days release:

\[
S_2 = \frac{R_{22} M_3}{(R_{33} + 1) M_2}
\]
\[
S_{12} = \frac{R_{13} M_3}{(R_{33} + 1) M_1} \text{ with } R_{13}, R_{33} \text{ and } M_3 \text{ defined as above.}
\]

The rate of mortality over the first and second days combined \(D_{12}\) should equal \((D_1 + D_2)\). The rate of mortality on any given day is comprised of 2 components: 1) mortality caused by capture in traps \((D_t)\) and 2) all natural causes of mortality plus emigration \((D_n)\). Since trap mortality is known, we can calculate the rate of natural mortality from our estimates of total mortality. On the first day of release \(D_1 = R_{11}/M_1\).

The variance estimates for the survival rate for each day (Table 6) are derived from Seber (1972):

\[
V(S_i) = S_i^2 \left( \frac{1}{R_{12}} + \frac{1}{R_{22}} - \frac{1}{M_1} - \frac{1}{M_2} \right)
\]

(Ricker 1975, p. 123).

**Estimation of Confidence Intervals**

A 95% confidence interval about the mean percent recaptured \((100 \times \bar{p})\) for the uniform release and the grid center release was based on a width of \(K\sigma_p\) from the Chebyshev inequality: \(P(\bar{p} - p < K\sigma_p) \leq 1/k^2 = 0.05\) where \(\sigma_p\) is the mean daily proportion recaptured, \((p)\) is the “true” mean and \(\sigma_p\) is the standard deviation of \((\bar{p})\). The confidence interval was calculated using an unbiased estimate \(S_p^2\) for \(\sigma^2_p\) equal to the sum of the variances of the daily binomial proportions \((p_i)\) recovered:

\[
S_p^2 = \frac{1}{121} \sum_{i=1}^{11} \frac{n_i (1 - p_i)}{n_i - 1} \text{ for the uniform release}
\]
\[
S_p^2 = \frac{1}{49} \sum_{i=1}^{7} \frac{n_i (1 - p_i)}{n_i - 1} \text{ for the grid center release}
\]

where \(n_i\) is the number released on each day. This method of calculating a confidence interval avoids any assumption about the distribution of \((\bar{p})\), in contrast to
more common methods based on the t-distribution, and avoids any assumption that all \((p_i)\) are identically distributed, as required for a binomial confidence interval about the total proportion recaptured over the entire experiment.

**Results**

**Percent Recaptured**

An average of 4.0% of the males released uniformly from 100 points in the release area were recaptured, compared to 0.9% of the males released at grid center (Table 1), a difference significant at \(P < 0.05\) (Wilcoxon rank sum test). The recapture of males released at grid center corresponds exactly to the 0.9% recapture from an earlier study with same trap density (Schwalbe 1980). A 95% confidence interval for the mean percent recaptured was 3.1%–4.8% for the uniform release and 0.38%–1.4% for the grid center release (Chebyshev inequality).

At the higher trap density (400 traps/2.6 km\(^2\)) recaptures averaged 18% of the moths released, with a 95% confidence interval of 13.7%–21.4% (t-distribution, \(n = 36\)). The proportion recaptured was high on days of warm ambient temperature (Fig. 4) during the period of peak flight (12:00–15:00 h). There was a correlation of \(r = .75\), significant at \(P < 0.05\), between the temperature and the proportion \((p_i)\) recaptured transformed to arcsin \((\sqrt{p_i})\).

**Distributions of Trap Catch in Space**

In the first experiment 96.7% of the recaptures from the uniform release strategy and 87.5% from the grid center release occurred in the traps at the 4 corners of the release area (Fig. 2). The few remaining recaptures occurred in the surrounding traps within 800 m of the release area, with the exception of one recapture in a trap at a distance of 1600 m (1 mi). There were no recaptures in any other trap near the perimeter of the 64 km\(^2\) grid of pheromone traps.

Similarly, the great majority of males recaptured in the second experiment (trap spacing 80 m) were caught in the 4 traps at the corners of the release site (Fig. 2). Most of the remaining recaptures occurred in other traps near the center of the grid. Few recaptures occurred in traps near the perimeter. The clustering of recaptures in the 4 corner traps was particularly evident on the first day after release. Second day recaptures were also concentrated near the center of the grid but were no more likely to occur in the 4 corner traps than at any of the other 12 traps near the center (\(P < 0.05\), Pearson's \(X^2\) test). Only 3 moths were recaptured more than 2 days after release and 2 of these were in the 4 corner traps.

Most of the moths captured in the 4 traps at the corners of the release area were caught on the first day after release (Table 2). In contrast, the majority of moths caught in peripheral traps were taken on the second day after release.

**Age Effects**

In the second experiment, significantly higher proportions of males released 2 days after emergence were captured than one-day-old moths (Table 3, \(P < 0.05\), Wilcoxon ranked-sign test for matched pairs). Higher proportions of 3-day-old males were captured than one or 2-day-old males, although the difference was not statistically significant.

**Mortality and Emigration Estimates**

In Table 4 we compare the proportions captured of males that emerged on the same day but were released one, 2 and 3 days after emergence. On the third day after emergence there are 3 groups of males of the same age in the forest that have all been subject to the same weather conditions. The only difference among the groups is the length of time that they have been in the forest for one, 2 or 3 days. If there were no mortality or emigration, we would expect to recapture similar proportions of all 3 groups, assuming that all moths of a given age are equally likely to be caught in traps. The proportion of males recaptured after the second and third day in the forest are calculated as the number caught/ (number released – number caught on previous days), thus taking account of those males already captured.

**Table 1.**—Percent recapture of male gypsy moths released uniformly from 100 points within an 800 × 800 m area and from a single point at the center of a 64 km\(^2\) grid of pheromone traps (4 traps per 2.6 km\(^2\)).

<table>
<thead>
<tr>
<th>Date</th>
<th>Uniform Release</th>
<th>Grid Center Release</th>
<th>Uniform Release</th>
<th>Grid Center Release</th>
</tr>
</thead>
<tbody>
<tr>
<td>7/16/79</td>
<td>380</td>
<td>4.8%</td>
<td>30</td>
<td>2.0%</td>
</tr>
<tr>
<td>7/17/79</td>
<td>400</td>
<td>7.0%</td>
<td>30</td>
<td>2.0%</td>
</tr>
<tr>
<td>7/18/79</td>
<td>200</td>
<td>4.5%</td>
<td>30</td>
<td>2.0%</td>
</tr>
<tr>
<td>7/23/79</td>
<td>300</td>
<td>4.7%</td>
<td>30</td>
<td>2.0%</td>
</tr>
<tr>
<td>7/24/79</td>
<td>200</td>
<td>4.0%</td>
<td>30</td>
<td>2.0%</td>
</tr>
<tr>
<td>7/25/79</td>
<td>200</td>
<td>1.0%</td>
<td>30</td>
<td>0.7%</td>
</tr>
<tr>
<td>7/30/79</td>
<td>300</td>
<td>5.0%</td>
<td>30</td>
<td>0.7%</td>
</tr>
<tr>
<td>7/31/79</td>
<td>300</td>
<td>4.3%</td>
<td>100</td>
<td>3.0%</td>
</tr>
<tr>
<td>8/1/79</td>
<td>300</td>
<td>1.7%</td>
<td>30</td>
<td>1.0%</td>
</tr>
<tr>
<td>8/6/79</td>
<td>200</td>
<td>4.0%</td>
<td>30</td>
<td>0.5%</td>
</tr>
<tr>
<td>8/7/79</td>
<td>200</td>
<td>4.0%</td>
<td>150</td>
<td>1.3%</td>
</tr>
<tr>
<td>8/8/79</td>
<td>100</td>
<td>3.0%</td>
<td>150</td>
<td>0.9%</td>
</tr>
<tr>
<td>Total</td>
<td>2880</td>
<td>3.9%</td>
<td>1550</td>
<td>0.9%</td>
</tr>
</tbody>
</table>

**Fig. 4.**—Correlation of mean temperature during period of peak flight (12:00–15:00 h) with percent recapture of male gypsy moths on the same day of release.
Table 2.—Number of males recaptured from one to 3 or more days after release at the 4 traps at the corners of the release area and at peripheral traps.

<table>
<thead>
<tr>
<th>No. of days elapsed before recapture</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Four corner traps</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uniform release</td>
<td>74</td>
<td>34</td>
<td>9</td>
</tr>
<tr>
<td>Grid center release</td>
<td>8</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>82</td>
<td>39</td>
<td>10</td>
</tr>
<tr>
<td>Peripheral traps^</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uniform release</td>
<td>1</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Grid center release</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>1</td>
<td>5</td>
<td>0</td>
</tr>
</tbody>
</table>

^ All peripheral trap captures were within 1600 m of release area.

The results indicate that there is heavy mortality and/or emigration and that very few moths are caught after the first day. Using the first day recapture as the expected value for recapture assuming no mortality and emigration, we estimated the daily rate of survival and mortality (Table 5) between the time of release on first day and time of release on the second day (Ricker 1975). The numbers caught after the second day after release were too small to yield estimates of the rate of survival beyond the first day after release.

Comparison of Trap Types and Effects of Marking

The capture of moths in Pherocon IC traps was significantly greater than in the smaller Delta traps (P < 0.05, Wilcoxon ranked-signs test for matched pairs), although the difference does not appear to be very great (Table 6). There was no difference in capture rate of marked and unmarked individuals.

Discussion

The consistently higher trap catch generated by the uniform as opposed to the grid center releases indicates that single point source releases cannot be used to estimate the average proportion of wild males that will be recovered in a grid of traps, particularly if the "typical dispersal distance" is much less than the spacing between traps. The 4.0% (95% C.I. of 3.1–4.8%) recovery from uniform releases is an estimate of what trap catch represents in a grid of traps spaced 800 m apart. Thus, if there was an average of 3 males/trap in a survey grid of this density, our data would suggest that the average population of males in the grid was in the range of 250–387 males per 2.6 km² or 1 mi² (4 traps per 2.6 km² × 3 males per trap/.031, .048). This population density estimate applies to the average condition. At any particular site the males may be clustered nearer or farther away than the average. The maximum possible clustering away from the traps is represented by the grid center release. Assuming that the probability of recapture for a male decreases with increasing distance from the nearest trap, we might use the estimates from the grid center release (0.38–1.4%) to put an upper limit on male density in any given 2.6 km². For instance, if we captured one male in one of the 4 traps in a given 2.6 km², we would estimate a maximum population of 263 males in that 2.6 km² (4 traps per 2.6 km² × 0.25 males per trap/.003). To maximize the number of males using the average estimate. By similar arguments zero trap catch in a given 2.6 km² implies a population of less than 263 males/2.6 km².

Table 3.—Percent of males released from one to 3 days after eclosion recaptured on the first day after release (age = days after eclosion).

<table>
<thead>
<tr>
<th>Date</th>
<th>Number released</th>
<th>Percent recaptured</th>
</tr>
</thead>
<tbody>
<tr>
<td>8/15/79</td>
<td>92</td>
<td>10.9%</td>
</tr>
<tr>
<td>8/16/79</td>
<td>220</td>
<td>8.3%</td>
</tr>
<tr>
<td>8/17/79</td>
<td>300</td>
<td>3.0%</td>
</tr>
<tr>
<td>8/22/79</td>
<td>300</td>
<td>48.7%</td>
</tr>
<tr>
<td>8/23/79</td>
<td>300</td>
<td>13.0%</td>
</tr>
<tr>
<td>8/24/79</td>
<td>300</td>
<td>7.0%</td>
</tr>
<tr>
<td>8/29/79</td>
<td>700</td>
<td>19.5%</td>
</tr>
<tr>
<td>8/30/79</td>
<td>275</td>
<td>17.3%</td>
</tr>
<tr>
<td>8/31/79</td>
<td>275</td>
<td>22.0%</td>
</tr>
<tr>
<td>9/5/79</td>
<td>525</td>
<td>33.1%</td>
</tr>
<tr>
<td>9/6/79</td>
<td>200</td>
<td>25.3%</td>
</tr>
<tr>
<td>9/7/79</td>
<td>375</td>
<td>4.8%</td>
</tr>
<tr>
<td>Totals</td>
<td>4262</td>
<td>19.7%</td>
</tr>
</tbody>
</table>

Table 4.—Percent of same age males recaptured one, 2, and 3 days after release.

<table>
<thead>
<tr>
<th>Date of recapture</th>
<th>Number released</th>
<th>1 day</th>
<th>2 days</th>
<th>3 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>8/15/79</td>
<td>292</td>
<td>10.9%</td>
<td>2.0%</td>
<td>3.1%</td>
</tr>
<tr>
<td>8/16/79</td>
<td>220</td>
<td>8.3%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/17/79</td>
<td>300</td>
<td>3.0%</td>
<td>2.2%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/22/79</td>
<td>300</td>
<td>48.7%</td>
<td>3.6%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/23/79</td>
<td>300</td>
<td>13.0%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/24/79</td>
<td>300</td>
<td>7.0%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/29/79</td>
<td>700</td>
<td>19.5%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/30/79</td>
<td>275</td>
<td>17.3%</td>
<td>0.0%</td>
<td>0.0%</td>
</tr>
<tr>
<td>8/31/79</td>
<td>275</td>
<td>22.0%</td>
<td>1.2%</td>
<td>0.0%</td>
</tr>
<tr>
<td>9/5/79</td>
<td>525</td>
<td>33.1%</td>
<td>0.7%</td>
<td>0.0%</td>
</tr>
<tr>
<td>9/6/79</td>
<td>200</td>
<td>25.3%</td>
<td>22.1%</td>
<td>0.0%</td>
</tr>
<tr>
<td>9/7/79</td>
<td>375</td>
<td>4.8%</td>
<td>1.1%</td>
<td>0.0%</td>
</tr>
<tr>
<td>Totals</td>
<td>4262</td>
<td>19.7%</td>
<td>0.9%</td>
<td>0.2%</td>
</tr>
</tbody>
</table>
Table 5.—Estimates of the first day rate of apparent survival and mortality of marked male gypsy moths released in a grid of pheromone traps 80 m apart.¹

<table>
<thead>
<tr>
<th>Date of 1st Release</th>
<th>Daily Rate of Survival ($S_0$)</th>
<th>S.D. of Survival Rate</th>
<th>Daily Rate of Mortality² ($D_0$)</th>
<th>Mortality Rate due to Traps ($D_m$)</th>
<th>Apparent Natural Mortality Rate² ($D_m$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>8/13/79</td>
<td>0</td>
<td>—</td>
<td>1.0</td>
<td>.04</td>
<td>.96</td>
</tr>
<tr>
<td>8/14/79</td>
<td>0</td>
<td>—</td>
<td>1.0</td>
<td>.03</td>
<td>.97</td>
</tr>
<tr>
<td>8/15/79</td>
<td>.05</td>
<td>.05</td>
<td>.95</td>
<td>.06</td>
<td>.89</td>
</tr>
<tr>
<td>8/21/79</td>
<td>.03</td>
<td>.03</td>
<td>.97</td>
<td>.13</td>
<td>.84</td>
</tr>
<tr>
<td>8/22/79</td>
<td>.07</td>
<td>.07</td>
<td>.93</td>
<td>.29</td>
<td>.64</td>
</tr>
<tr>
<td>8/27/79</td>
<td>0</td>
<td>—</td>
<td>1.0</td>
<td>.06</td>
<td>.94</td>
</tr>
<tr>
<td>8/28/79</td>
<td>0</td>
<td>—</td>
<td>1.0</td>
<td>.06</td>
<td>.94</td>
</tr>
<tr>
<td>8/29/79</td>
<td>.05</td>
<td>.05</td>
<td>.95</td>
<td>.12</td>
<td>.83</td>
</tr>
<tr>
<td>9/3/79</td>
<td>.11</td>
<td>.07</td>
<td>.89</td>
<td>.26</td>
<td>.63</td>
</tr>
<tr>
<td>9/4/79</td>
<td>0</td>
<td>—</td>
<td>1.0</td>
<td>.20</td>
<td>.80</td>
</tr>
<tr>
<td>9/5/79</td>
<td>.03</td>
<td>.03</td>
<td>.97</td>
<td>.25</td>
<td>.72</td>
</tr>
<tr>
<td>Total</td>
<td>.06</td>
<td>.02</td>
<td>.94</td>
<td>.13</td>
<td>.81</td>
</tr>
</tbody>
</table>

¹ Estimates assume that all moths were equally responsive to pheromone source. Response heterogeneity may also explain high apparent mortality. See text.
² Includes emigration.

All of these estimates are tentative and only apply when trap capacity is not a limiting factor. The estimated confidence intervals are derived from the release experiment and not from the capture of feral males in a survey situation. We do not know if the proportion recaptured would be different in heterogeneous habitats such as the widely scattered woodlots that are typical of much of lower Michigan. Furthermore we do not know the effect of gypsy moth population density on the proportion of males caught in traps. There is some evidence with other moths that the proportion of males trapped decreases as the number of females competing with traps increases (reviewed by Cardé 1979). Also we do not know if the difference between time of day of male release in this experiment and the eclosion rhythm of feral males would cause a difference in the proportion recovered.

Another unknown in this study is the effect of the initial dispersion pattern of feral male gypsy moths on the proportion captured in traps. Gypsy moths in nature are unlikely to be distributed uniformly in space. The dispersion is undoubtedly clumped, especially because of the minimal dispersal abilities of females and the clumped distributions of preferred host trees and trees with favorable larval resting sites. Therefore, one might argue that recapture estimates based on a uniform release are no more representative of recapture rates of wild males than those based on single point source releases. However, the average distance between individual males and the nearest pheromone traps will be the same for a uniform and a clumped distribution, provided traps are not placed in some systematic fashion relative to population centers. Therefore, averaged over many sites, the recapture probability for the clumped and the uniformly distributed males will be the same if we assume that the distance between a male and the nearest trap is the major determinant of its probability of capture. The effects of gypsy moth dispersion and effects of females on trap catch may compound one another because in a clumped population a male is more likely to emerge closer to a female than to the nearest pheromone trap.

Another implicit assumption of our study is that laboratory-reared males are behaviorally equivalent to their wild counterparts. Potentially, differences in laboratory-reared strains may arise through numerous factors, including genetic selection and the effects of conditions experienced during mass production. The New Jersey Standard Strain (NJSS), now in mass production at the APHIS Gypsy Moth Methods Development Laboratory, Otis Air Base, Mass., and utilized in these studies, was first colonized at Otis in 1967. Behavioral differences between NJSS and wild-collected Pennsylvania adults were observed by Richerson and Cameron (1974). They reported that compared to wild females, laboratory-reared females emitted substantially less pheromone and lacked an emission rhythmicity. In laboratory and field cage bioassay trials, they also found significant differences between wild and laboratory-reared males in several responses to virgin females, including the likelihood of contacting a female. However, rearing procedures for the NJSS have been improved since those tests. Several subsequent studies comparing wild and laboratory-reared (NJSS) males have demonstrated comparable behavior in tethered flight duration (ODell, unpublished), initial moth dispersal after eclosion (ODell and Mastro 1980), marked and unmarked male response to wild and laboratory-reared females in release-recapture field tests (Mastro and ODell 1977, 1978), preflight and in-flight response to (+)-disparlure in a wind tunnel (Waldvogel 1980) and in field release-recapture trials (Mastro and ODell 1977, 1978). ODell et al. (1980) reported differences between laboratory-reared and wild males in their

Table 6.—Number of marked and unmarked male gypsy moths captured in Delta and Pherocon 1C traps.

<table>
<thead>
<tr>
<th>Pherocon traps</th>
<th>Marked (No. released No. = 585)</th>
<th>Unmarked (No. released = 585)</th>
<th>Total captures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delta traps</td>
<td>66</td>
<td>55</td>
<td>121</td>
</tr>
<tr>
<td>Total</td>
<td>108</td>
<td>101</td>
<td>209</td>
</tr>
</tbody>
</table>
periodicities of response to females; i.e., peak capture of 1-day-old laboratory-reared males generally occurred 1 or 2 hours later in the day than wild males of similar age. However, such differences may not occur with our eclosion-holding procedure and would probably not affect the results of our study. Thus, recent studies suggest that laboratory-reared and wild males are behaviorally equivalent.

The distribution of trap catch about the site of release in both the first and second experiments suggests that gypsy moth males do not fly very far. Dispersal beyond 800 m is rare unless there are certain individuals that disperse instead of responding to pheromone traps. It will be important to determine the degree to which the ***rogue*** individuals, or those which have the greatest dispersive tendencies, contribute to trap catch in a survey situation. Assuming that a population of feral males would behave in the same manner as the males used in the uniform release experiment, we would estimate that 95.7% (92.0–99.3%, binomial confidence interval, \( \alpha = 0.05 \)) of all moths captured in a grid of one pheromone trap per 0.64 km² will originate from less than 800 m from the site of capture. This estimate applies to the trapping grid as a whole. At any given site, a large number of the captured moths may represent the small proportion of moths that disperse several km from a very large infestation, a condition that should be apparent from the catch in traps nearer the site of infestation. On the basis of parallel experiments, Schwalbe (1980) draws similar conclusions.

The distance flown before capture in traps is dependent on trap density. In the first experiment with traps spaced every 800 m, 6/4430 were captured in traps at a distance of at least 800 m from the site of release. In the second experiment with traps spaced every 80 m, 0/4262 were caught at this distance. This difference does not necessarily imply that males are more likely to disperse when the density of traps or pheromone sources is low. A parsimonious explanation is that at the higher trap density males are trapped before they fly as far. The close correlation between the proportion recaptured and the ambient temperature (Fig. 4) is consistent with the temperature dependence of the latency of wing fanning behavior of male gypsy moths exposed to (+)-disparlure in a wind tunnel (Cardé and Hagaman, unpublished data) and spontaneous wing fanning activity of caged males in the field (Elkinton and Cardé, unpublished data).

The finding that 2-day-old males are more likely to be captured than one-day-old males is not unprecedented. Mark-recapture experiments with this insect in previous years have shown the same trend (Cardé, unpublished). The effects of age on recapture rate in traps may arise in any number of ways, such as differences in either dispersal or appetitive flight, in addition to response to pheromone.

The results of the second experiment imply that there is a heavy rate of mortality and emigration, such that few individuals remain to be captured beyond the second day. The estimates of natural loss (Table 5), which is the estimated total loss minus the known mortality in traps, are underestimated because some of the moths caught in traps would have otherwise died or emigrated. The clustering of trap catch near the site of release even on the second and third days following release suggests that emigration does not contribute much to the rapid depletion of males. During the release of males we observed numerous episodes of predation by birds. We do not know whether such predation was enhanced by the initial high concentration of moths at the site of release or whether the birds learned to follow us as we released moths.

A critical assumption in our survival estimates is that all moths of a given age have the same probability of responding to pheromone and being captured in traps. An alternative explanation of the rapid decline in recaptures after the first day is that the released moths vary in the degree of responsiveness as expressed by trap catch. On the first day perhaps many of the more responsive males were caught, leaving a larger proportion of less responsive males, only a few of which were caught on subsequent days. There is individual variability in the response latency to wing fanning and in the ground speed of flying moths to a given dose of pheromone presented in a wind tunnel (Cardé and Hagaman 1979). It is not known, however, how constant these differences remain over time or precisely how they relate to trap catch. A release-recapture test conducted by Schwalbe and Paszek (1978) in Massachusetts suggests that natural, daily loss of adult males may be considerably lower than the apparent rate of 78 to 81% observed in our study. When 408 laboratory-reared males were released into a forest and (+)-disparlure-baited traps were deployed in a 127 m grid spacing 48 hr later, 37% of these males were recaptured over the next 72 h, with 92% of the captures occurring within 600 m of the release site. Although their test involved only a single release of males, it does indicate that variability in the many behaviors that culminate in trap catch, rather than roughly a natural rate of 80% daily male mortality, is a factor in determining the likelihood of capture in a trap.

The differences between Pherocon and Delta trap recapture indicates that we cannot directly apply estimates of capture probabilities derived from Pherocon traps to a survey situation using Delta traps. However, the differences in trap catch are not substantial. Furthermore, such differences may be enhanced when the two trap types are presented in competition with one another. If the moths have no choice between the two types, there may be no difference in the numbers captured in each. We do not know to what extent the small differences observed were caused by differences in the trap size and the shape, the physical structure of the pheromone plume, or by the presence of a large tree next to the Delta traps.

The failure to observe any effects of marking on the proportion of males recaptured enhances our confidence in this technique as an invaluable tool for studying the flight behavior and the population dynamics of adult male gypsy moths. More experiments will be required to establish whether there is a difference in behavior or recapture probability between wild and laboratory-reared males.
Conclusion

The use of uniform and point source releases of marked individuals over a specific area offers a valuable technique to estimate the relationship between actual population levels and catch in pheromone-baited traps deployed in a survey or monitoring pattern. The uniform release is especially valuable in situations where the distance between traps is typically much greater than the average distance of dispersal. The techniques may also be used to estimate the distance of dispersal. Finally, the release of marked individuals of different age classes allows assessment of age-related response differences, adult mortality and emigration. These procedures have particular usefulness in supplying absolute population estimates for monitoring or survey situations where density is below a level that can be reliably measured by more traditional techniques, such as an egg mass census. These relative estimates can be used to calibrate trap catch.

Acknowledgment

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