Appetitive Flight Behavior of Male Gypsy Moths1 (Lepidoptera: Lymantridae)2

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ABSTRACT The flight direction of male gypsy moths across an observation area (10 by 10 m) at three sites representing high, intermediate, and low population densities was not preferentially crosswind, upwind, or downwind, nor was it correlated with any cardinal direction. Horizontal flight and tree-oriented vertical flight were the predominant behaviors observed at both low- and high-density sites. Males spent more time in tree-oriented vertical flight in the high-density site, although even at low density it was a predominant behavior in the virtual absence of females and, presumably, pheromone. Similarly, more males were captured at sticky traps unbaited with pheromone stapled to tree trunks than at traps hung in the air > 2 m from large trees. Most males flew at heights < 2 m above ground at both sites, although more time was spent flying above 2 m at the high density sites. Similarly, more males were captured on unbaited sticky traps on trees at 0 m than at 2, 4, or 6 m at both sites. On unbaited sticky traps suspended in air > 2 m from large trees, most males were captured at 0 m at the low-density site, but trap catch was evenly distributed at all heights in the high-density site.

Most of the research on the mate-finding behavior of male Lepidoptera has focused on the pheromone-mediated, anemotactic flight and the close-range behaviors culminating in copulation. An important but little-studied component of mate finding is the "appetitive" flight that presumably occurs before the males enter a pheromone plume of sufficient concentration to elicit upwind flight. In this study we examine the hypothesis that male gypsy moths fly preferentially crosswind (Carde 1981), hence maximizing their chances of contact with a pheromone-active space. We also study the amount of time allocated to flying male gypsy moths to various behavioral modes such as tree-oriented vertical flight at locations with high and low population density. We attempted to relate the vertical distribution of male flight to the capture of males at unbaited sticky traps at different heights above ground.

Materials and Methods

Location of Research Sites

Male appetitive flight behavior was observed in July 1980 at two locations in Centre County, Pa., separated by ca. 40 km and at a third location in Hampshire County, Mass., in July 1982. The first location, on a mountainside at an altitude of 442 m near Lemont, Pa., had a low-density, innocuous gypsy moth population with no detectable defoliation. The second location, on a ridge top near Port Matilda, Pa., (altitude 646 m), had a high-density outbreak population (Table 1) with nearly complete defoliation. The third location, in Blandford, Mass., (altitude 400 m) had an intermediate population density with partial defoliation. The two sites in Pennsylvania had a similar forest composition, dominated by Quercus rubra, Q. prinus, Q. alba, Acer rubrum, and saplings of Castanea dentata. The site in Blandford, Mass., was dominated by Acer rubrum, Fagus grandifolia, Quercus rubra, Betula papyrifera, and Pinus strobus. As an indicator of the relative density of gypsy moth populations at the three observation sites, the number of gypsy moth life stages on all trees within a 50-m2 section of the grid (10 by 10 m) described below, as well as the number and dbh of the trees were recorded (Table 1).

In each location a square grid of strings (10 by 10 m) was staked out at a height of 1 m parallel to the cardinal directions. The strings intersected at 2-m intervals, and each intersection was assigned a coordinate number. Several trees within the grid were marked with brown masking tape every 1 m to a height of 4 m. Continuous verbal observations of males that flew above or below the grid of strings were recorded on audiotape. Observations were conducted between 13:20 and 16:30 h at the low-density site, between 13:30 and 15:47 h at the high density site in Pennsylvania, and between 15:04 and 16:55 h in Massachusetts. We recorded the coordinate to which the moth was nearest at each moment, the male's height above ground, and the behavior exhibited. The types of behavior consisted of horizontal flight, positive anemotactic "zig-zag" flight, tree-oriented vertical flight (up or down flight within ca. 1 m of a tree bole frequently contacting it), hovering flight at ground level (below 1 m), hovering flight above 1 m away from trees, walking and wing-fanning on a tree, landing and quiescence on a tree, and landing and quiescence on the ground. The observations were transcribed for analysis of the direction, speed, and height of male flight and the time spent in each behavior category. At Blandford, Mass., we focused our attention exclusively on direction of horizontal flight to verify the observations pertaining to flight direction obtained at the sites in Pennsylvania. Consequently, the analyses presented on the type of behavior observed were conducted on the observations from Pennsylvania and not from Massachusetts. The observations were made from a step ladder (ca. 2 m above ground) outside the grid perimeter. Moths were chosen for observation sequentially as they passed into the field of view of the observer. To reduce observer-caused directional bias, the observer

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periodically moved to a different edge of the grid so that one-fourth of the moth observations in each grid were taken with the observer facing in each of the cardinal directions. The time to the nearest second was read from a wrist watch and recorded on tape. The time of each behavior (±3 sec) was subsequently determined when the tapes were transcribed by running a stop watch concurrently with the playback of the tape. The tape-recorded times were used to check that the playback speed and stop watch accurately measured actual time elapsed during the experiment.

Weather data

The wind direction, wind speed, air temperature, relative humidity, and time were recorded and stored every 10 sec with a Campbell Scientific CR21 weather station data logger with a 024A wind direction sensor and a 014A anemometer located at the edge of the grid. The timer on the data logger was synchronized with the watch used to record the time of the observed moth behavior. The wind vane and anemometer were positioned at a height of 2.5 m and had a stall speed of 0.4 m/sec.

Analysis of Flight Direction

Those moths that exhibited "straight-line flight paths" were analyzed for flight directions in relation to the wind. A straight-line flight path was defined as one which covered at least 4 m at a speed of at least 0.4 m/sec, during which the direction changed by less than 90°, as determined from the spatial coordinates of the moth in the grid at each moment. The overall direction of flight was equated to the direction between the beginning and end of the straight-line path.

Unbaited Sticky Traps

To further monitor flight behavior, 10 unbaited sticky traps were hung at both sites in Pennsylvania. Five of these traps were hung from branches in the canopy so that the panels were suspended at least 2 m from the nearest tree. The remaining traps were hung so that panels were positioned against the bole of a large tree (>0.5 m dbh). Each trap consisted of four sticky panels positioned at 0, 2, 4, and 6 m above ground. The panels were made from the bottom half of Pherocon IC traps (Zoecon Corp., Palo Alto, Calif.) and coated on one side with Tanglefoot (Tanglefoot Co., Grand Rapids, Mich.). The traps were put in place on 20 July 1980, between 14:00 and 19:00 h at the low-density site and between 13:30 and 17:00 h on 23 July 1980 at the high-density site.

Results

Flight Direction

There was no significant tendency for moths engaged in horizontal flight to fly crosswind, upwind, or downwind (Fig. 1) at any of the three sites (P > 0.05, chi-square, goodness of fit test). Upwind and downwind flight were arbitrarily defined as flight within ±30° of the respective upwind and downwind directions. With this definition, we would expect one-sixth of all flight paths to be upwind, one-sixth downwind, and two-thirds crosswind, under the null hypothesis of equal probability of flying in all directions.

The wind direction at each site varied continuously over ca. 120° during the observation periods, with the average direction from the NW and the WSW at the high- and low-density sites in Pennsylvania, respectively, and SW at the site in Massachusetts. The flight direction of males in reference to the fixed cardinal directions did not differ significantly from random at all three sites (chi-square goodness of fit test, P > 0.05). The mean wind speed was 0.82 m/sec (±0.27 SD) at the low-density site and 1.16 m/sec (±0.32) at the high-density site in Pennsylvania and 0.94 m/sec (±0.24) at the site in Massachusetts.

Time Allocation to Different Behaviors

At both sites in Pennsylvania, male gypsy moths spent more time in tree-oriented vertical flight than in any other behavioral mode (Fig. 2a). This result is consistent with the significantly higher trap catch at trees than away from trees at corresponding heights (See Table 2, Wilcoxon signed ranks test, P < 0.05). A relatively large amount of time at both sites was also spent in hovering flight just above ground level in apparent orientation to objects on the ground. Only 1 of the 277 moths observed hovered above 1 m at a distance of greater than 2 m from a tree.

Tree-oriented vertical flight most commonly commenced at the base of the tree (comprising 71 and 86% of all such flights at the high- and low-density sites,
respectively). The moths either hovered near the tree and then flew horizontally near ground level out of the grid (78 and 88% of the tree-oriented flights, respectively, at high- and low-density sites) or moved up the tree and flew into the canopy (10 and 3% of such flights at high- and low-density sites). Many males moved up and down the tree repeatedly before dispersing. These males flew slowly up the tree bole, making occasional contact with it, and then dropped quickly down to the base before coming up again.

Horizontal flight was the second major behavior in terms of mean time spent. It was the principal behavior in terms of proportion of the time spent (Fig. 2b), comprising 61 and 44% of the flight time at the low- and high-density sites, respectively. The difference between these two measures is caused by the fact that a large proportion of moths traversed the grid quickly, contributing little to the mean time spent but scoring 100% in the proportion of time spent in horizontal flight. In contrast, moths that engaged in tree-oriented vertical flight remained in the grid for lengthy periods, contributing disproportionately to the average amount of time spent in this behavior category.

The mean proportion of time spent in horizontal flight was greater (Wilcoxon rank-sum test, *P* < 0.01) at the low-density site than at the high-density site. There was correspondingly more time spent in tree-oriented vertical flight and hovering flight at ground level at the high-density site. Apparent differences between the two sites in the mean proportion of time spent in these two behavioral categories were not statistically significant.

Very little time at either site was invested by males in walking and wing-fanning on trees, or in quiescence on the ground or on trees. Of course, the observations recorded only the frequency of quiescence initiation by flying males, as opposed to the frequency of quiescence behavior of all males. A greater proportion of time was allocated to walking and wing-fanning on trees at the high- than at the low-density site. (Wilcoxon rank-sum test, *P* < 0.05). No males at either site were observed engaging in anemotactic zigzag flight in response to pheromone. Such behavior occurs when virgin females are present (Cardé and Hagaman 1983). Nor were males at either site observed to initiate mating with females. Virtually all observed females had already mated and were laying eggs (Table 1).

**Height of Flight**

The males at both sites in Pennsylvania flew below 1 m an average of 45% of the time (Fig. 3a). They flew

Fig. 1. Direction of horizontal "straight-line" flight of male gypsy moths in relation to the wind direction at sites with low population density in Lemont, Pa., 20 July 1980; intermediate population density near Blandford, Mass., 27 July 1982; and high population density near Port Matilda, Pa., 23 July 1980.

Fig. 2. Mean number of seconds spent (a) and mean proportion of time spent (b) by male gypsy moths in horizontal flight, hovering flight at ground level, tree-oriented vertical flight, walking and wing-fanning on a tree, quiescence on a tree, or quiescence on the ground after entry into the observation grids (10 by 10 m) at sites on high- and low-density population sites in Pennsylvania, 1980. *n* indicates number of males observed in a particular behavioral category.
Discussion

The large amount of time invested by males in tree-oriented flight and the relatively high catch at unbaited sticky traps suggests that this behavior is an important component of the mate-seeking behavior of male gypsy moths. These results are consistent with the observations of Carde and Hagaman (1983) and the results of Richerson et al. (1976a), who found that released male gypsy moths were trapped in higher
Table 2. Number of male gypsy moths captured at unbaited sticky traps at different heights in an area with low population density, 20 July 1980, Lemont, Pa., and an area with high population density, 23 July 1980, Port Matilda, Pa.

<table>
<thead>
<tr>
<th>Trap location</th>
<th>Trap no.</th>
<th>Height above ground</th>
<th>Low-density site</th>
<th>High-density site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0 m</td>
<td>2 m</td>
<td>4 m</td>
</tr>
<tr>
<td>≥2 m from trees</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
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<td></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>15</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>8</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>29</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Stapled to trees</td>
<td>6</td>
<td>27</td>
<td>8</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>6</td>
<td>24</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>33</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>28</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>28</td>
<td>7</td>
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</tr>
<tr>
<td>Total</td>
<td></td>
<td>122</td>
<td>62</td>
<td>82</td>
</tr>
</tbody>
</table>

Vertical Distribution of Male Activity

Previous studies have shown that the number of male gypsy moths captured in traps baited with females, female tip extracts, or synthetic pheromone is generally highest at traps located near the ground (Forbush and Fernald 1896, Stevens and Beroza 1972, Granett 1974, Cardé et al. 1975). However, with pheromone traps, the effects on trap catch of the vertical distribution of male flight activity is compounded by the vertical distribution of pheromone downwind of a source. Several theoretical treatments of pheromone dispersion (Sutton 1953, Miksad and Kittredge 1979) predict that concentrations of pheromone downwind from an elevated source are highest at ground level. These predictions, however, are not supported by recent experimental evidence (Elkinton et al., unpublished data). With gypsy moth wing-fanning behavior as an assay for pheromone concentration 20 m downwind of the source, lower concentrations appeared to occur at ground level than at the height of the source (1.6 m). Nevertheless, anemotactic flight in response to pheromone may occur near ground level because of the requirement for visual cues for close-range successful optomotor upwind navigation (Kennedy 1940).

Weseloh (1972) found that male catch was highest with unbaited traps at 11 m vs. 8, 4, and 0.6 m. He hypothesized that this result as compared with earlier studies with pheromone traps was due to the fact that "males oriented to strong pheromone sources are active at different levels of the forest than are those not so orienting and presumably flying randomly." In contrast, Richerson et al. (1976a) trapped males released at ground level preferentially at 2 m compared with 4 and 6 m in unbaited traps attached to trees. In similar plots treated with microencapsulated (±)-disparlure, trap catch was distributed equally at all three heights. Our results are consistent with those of Richerson et al. (1976a,b), in that trap catch and flight behavior occurred preferentially at ground level, with a shift to the more uniform distribution at all heights at the high-density sites, perhaps because of elevated "background" levels of pheromone, as the study of Richerson et al. (1976b) suggests. However, the differences we observed in male behavior between the two sites may be caused by other density-related factors, such as increased sunlight on the forest floor due to defoliation at the high-density site or, perhaps, factors unrelated to density.

Our results may not be inconsistent with those of Weseloh (1972). Neither we, nor Richerson et al. (1976a,b), nor any of the previously cited authors who used pheromone traps, except for Granett (1974), placed any traps above 6 m. A large and unknown proportion of males may be active in the canopy above this height (ODell and Mastro 1980). However, Granett (1974) caught fewer moths [with a (±)-disparlure bait] at 10 m than at ground level. Differences between these studies may be due to
differences in the height of the canopy. In our results there was an indication from two traps where the panels at 6 m were close to canopy foliage (traps 1 and 5 at the low density sites, Table 2) that trap catch increased again in the canopy. This hypothesis requires further testing. Alternatively, Weseloh’s studies may have been conducted at a site where densities were sufficient to cause the male activity to shift to greater heights.

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