Dispersal Tendencies of Neonate Larvae of *Lymantria mathura* and the Asian Form of *Lymantria dispar* (Lepidoptera: Lymantriidae)

MARINA A. ZLOTINA,1 VICTOR C. MASTRO,2 JOSEPH S. ELKINTON,1 AND DAVID E. LEONARD2

USDA–APHIS–PPQ, Otis Plant Protection Center, Building 1398, Otis ANGB, MA 02542–5008


**ABSTRACT** Recently, Asian gypsy moth, *Lymantria dispar* (L.), infestations have been found in Oregon, Washington, and British Columbia. In at least 1 case, circumstantial evidence suggests that the introduction occurred through airborne dispersal of neonates from grain ships that had been infested in the Far Eastern ports of Russia. Egg masses of Asian gypsy moth and another lymantriid, *Lymantria mathura* Moore, have been intercepted on the same ships. Both species are polyphagous defoliators of trees and could easily achieve pest status if established in North America. Neonate larvae of both species are capable of airborne dispersal, although there is no information on dispersal rates, or, for *L. mathura*, on settling velocities. We studied dispersal rates, settling velocities and diel periodicity of dispersal for both lymantriids, so this information could be incorporated into models that predict probable extent of neonate dispersal. Dispersal rates for *L. mathura* exceed those of Asian and North American gypsy moths. Neonates of *L. mathura* weigh less and have a slower settling velocity than Asian or North American gypsy moths, which allows them to be dispersed by wind for greater distances.

**KEY WORDS** *Lymantria mathura*, Asian gypsy moth, larval dispersal, settling velocity, diel periodicity.

**INFESTATIONS OF THE** Asian form of the gypsy moth, *Lymantria dispar* (L.), have been detected in the Pacific Northwest (port facilities of Vancouver, BC; Tacoma and Seattle, WA; Portland, OR, in the mouth of the Columbia River), and on the East Coast ports Sunny Point, NC, and Charleston, SC. Asian gypsy moth is a polyphagous defoliator of >500 species of plants in Asia, including conifers, such as larch (Gibbons 1992). The special threat of the Asian gypsy moth is the capability of adult females for sustained long-distance flight, whereas females of the North American strain do not fly. By estimations, if the Asian race becomes established, it would spread 4–5 times faster than North American strain (Wallner 1993). Some evidence suggests that one of the pathways of infestation could be egg masses with hatching larvae on ships from infested ports, because ballooning neonates blowing toward shore were observed in Vancouver, BC (Watler 1991, Gibbons 1992, Mudge and Johnson 1992, Bogdanowicz et al. 1993). Another pathway of Asian gypsy moth introduction (Tacoma, Sunny Point, Charleston) is possibly via different life stages on military cargo from infested areas of Germany (Garcia 1993, Bell 1994, Prasher and Mastro 1994).

Egg masses of another lymantriid, *L. mathura* Moore, were also found on Russian grain ships (Mudge and Johnson 1992, Wallner 1993, Mastro 1995), but no putative infestations have been detected. However, a sensitive survey tool such as a pheromone-baited trap for this species is not available.

There is little information in the literature about dispersal behavior in *L. mathura*. Females have been reported to oviposit on nonhost trees such as conifers (Nishigaya 1918) and on buildings and telephone poles (Anonymous 1992). Kozhanchikov (1950) mentions that larvae are capable of producing silk threads and are dispersed by ballooning in wind currents. This suggests that *L. mathura* possesses a mechanism for larval dispersal, similar to that demonstrated by other species of lymantriids.

Larval dispersal of neonates of the North American strain of the gypsy moth has been studied extensively (Leonard 1971; McManus 1973; Capinera and Barbosa 1976; Lance and Barbosa 1981; Weseloh 1985, 1997; Liebhold and McManus 1991; Diss et al. 1996). Different simulations of dispersal based on a 3-dimensional wind model, settling velocities of neonates, and length of silken threads have been developed to predict direction and distance traveled (Mason and McManus 1981, McManus and Mason 1983, Fosberg and Peterson 1986). Recently, a series of models was used to test the hypothesis that neonates of Asian gypsy moth dispersed from infested ships at the port of Tacoma to establish an infestation in the adjacent area. Historic on-site wind records and estimated settling velocities (McManus and Mason 1983) were used to...
Here, we studied the dispersal potential of neonates of *L. mathura* and the Asian form of *L. dispar* in a wind tunnel and measured settling velocities for larvae of both species. These data, incorporated into dispersal models, can provide estimates of the pattern and extent of larval dispersal that could be used to design delimiting survey and control programs. The information can also be used to provide minimum safe distances that potentially infested ships should remain from land during quarantine inspection.

**Materials and Methods**

**Rearing of Larvae.** We conducted experiments in the spring of 1994 on cultures of Asian gypsy moth originating from the egg masses collected on Russian ships in port areas of the Pacific Northwest, and on egg masses of *L. mathura* collected in the Kavalerovo, Primorsky Region of the Russian Far East. Asian gypsy moth larvae were reared at 24°C, ~40% RH, and a photoperiod of 16:8 (L:D) h on artificial diet (Bell et al. 1981) for 1 generation in a USDA–APHIS quarantine facility at the Plant Protection Center, Otis, MA. Egg masses of *L. mathura* were collected in the field during the summer of 1993 and maintained in cold treatment (5–7°C).

We removed egg masses of both species from cold treatment after 150 d and placed them in a rearing room to hatch under conditions described for rearing. We held egg masses separately in 120-ml (4-oz) covered plastic cups with a moistened cotton wick to maintain humidity. We collected newly hatched larvae daily and transferred 10 of each to covered 120-ml (4-oz) plastic cups with moistened wicks. We held larvae in these cups for 2 d before testing.

**Dispersal Studies.** The larval dispersal studies were conducted in a wind tunnel consisting of a square Plexiglas tube (120 by 25 by 25 cm), similar to one described by Diss et al. (1996). A squirrel cage fan with a rheostat was used to provide variable wind velocities. Air current passed through a 10-cm honeycomb baffle and was considered during each 1-h interval (i.e., between 0800 and 1700 hours DST). After tests were completed, we weighed a cohort of 30–40 larvae from each egg mass using a CAHN electronic balance (CAHN Instruments, Ceritos, CA).

**Measurement of Settling Velocity.** We measured the settling velocity for 25 larvae from each of 4 Asian gypsy moth and 6 *L. mathura* egg masses. We used a protocol for determining settling velocity similar to that described by McManus and Mason (1983). Individual 2-d-old neonates trailing silk were dropped inside (to avoid effects of air movement) a square Plexiglas tower (180 by 30 by 30 cm) that was position vertically on the floor. For testing, we removed larvae from the holding cups with a fine sable brush and placed them at the top of the tower. Jarring the brush caused larvae to drop on a thread of silk. We cut the silk with scissors ~1 cm from its attachment to the larvae, and timed the duration between release and when the larvae reached the floor with a stop watch measuring to 1/100 s. We calculated the settling velocity as the ratio of the length of travel (height of the tower) and travel time.

**Diel Periodicity of Dispersal.** Dispersal activity during the day for *L. mathura* and Asian *L. dispar* larvae was studied in wind tunnel experiments using the methods presented above.

We measured diel activity between 0800 and 1900 hours for 5 d. Ten larvae (1 replicate) were tested for dispersal. Data on a total of at least 20 larvae were considered during each 1-h interval (i.e., between 0800 and 0900 hours, 0900 and 1000 hours, and so on). The average percent of larvae dispersed from the platforms was plotted against time to obtain a diel curve of dispersal tendencies for *L. mathura* and Asian *L. dispar*.

**Data Analysis.** Although mean percents of actual numbers dispersed are presented in the tables, we used data transformations to satisfy the assumptions of analysis of variance (ANOVA) and achieve normal distributions. We transformed data on larval dispersal as a square root of (x + 0.5) where x is the actual number of larvae dispersed in each replicate. We used one-way ANOVA and the Scheffe option for comparison of means in Statistix (1992) to compare differences between larval dispersal of the 2 species. To compare differences in settling velocity of insects among various egg masses, we used ANOVA and Scheffe comparison of means with untransformed data.

We used the Kruskal–Wallis nonparametric one-way ANOVA and comparisons of mean ranks to test differences in larval weight because unequal variances were detected in Bartlett’s test (P < 0.01) (Statistix...
We used a linear regression procedure in Statistica (1992) to analyze the relations between weight of larvae from different egg masses and the tendency of these larvae to disperse.

Results

Larval Weight. Neonate larvae of Asian *L. dispar* were significantly heavier than larvae of *L. mathura* (Kruskal–Wallis statistic *H* = 213.64; *P* < 0.01, using *χ²* approximation, parametric AOV applied to ranks: *F* = 396.56; df = 1, 461; *P* < 0.01) (Table 1).

There were significant differences among replicates in the weights of neonate larvae within each species (for Asian gypsy moth, *H* = 68.96; *P* < 0.01; for *L. mathura*, *H* = 95.79; *P* < 0.01). Mean ± SD weights of larvae from 6 egg masses of Asian gypsy moth ranged from 0.57 ± 0.09 mg (n = 31 larvae) to 0.74 ± 0.08 mg (n = 31 larvae). Larval weights from 9 egg masses of *L. mathura* ranged from 0.46 ± 0.03 mg (n = 30 larvae) to 0.57 ± 0.07 mg (n = 30 larvae).

Settling Velocity. Mean ± SD settling velocity of larvae of Asian *L. dispar* was 0.96 ± 0.11 m/s, which is significantly higher than 0.88 ± 0.09 m/s for larvae of *L. mathura* (*F* = 35.50; df = 1, 248; *P* < 0.01). There were significant differences in settling velocities (*P* < 0.01) among replicates within each species.

Larval Dispersal. We found no significant differences in dispersal tendencies of larvae among different Asian gypsy moth egg masses (*F* = 0.42; df = 5, 70; *P* = 0.83) or for larvae from different *L. mathura* egg masses (*F* = 1.90; df = 9, 193; *P* = 0.05). *L. mathura* larvae demonstrated a higher tendency to disperse than did Asian gypsy moth larvae (*F* = 28.01; df = 1, 277; *P* < 0.01) (Table 1; Fig. 1).

Diel Periodicity of Dispersal. Larvae of both species demonstrated a similar pattern of daily dispersal activity. In the morning, between 0800 and 1100 hours (DST), dispersal rates were the lowest, ranging from 2 to 10% for *L. mathura* and from 5 to 13% for Asian gypsy moth (Fig. 2). From 1200 to 1700 hours, larvae of both species showed a gradual increase in dispersal to 20–53% for *L. mathura* and a less dramatic increase, to 5–28%, for *L. dispar*. At 1800 hours, dispersal of both species declined to 30% for *L. mathura* and 22% for Asian *L. dispar*.

Discussion

Dispersal of Asian gypsy moth neonates could have occurred from ships because larvae hatched on board and ballooned in wind to the abundant host plants on shore (Watler 1991, Mudge and Johnson 1992, Bogdanowicz et al. 1993). At the time when 1st infestations were reported, ships were not thought of as a definitive pathway of introduction of the species. Currently, USDA–APHIS, Plant Protection and Quarantine (PPQ) considers it possible that ballooning larvae could be introduced from ships. Vessels from high risk ports arriving in the United States during the hatching period of the Asian gypsy moth are allowed to move to the berth if no gypsy moth life stages are found by PPQ officers inspecting the vessels. These vessels are monitored daily during the early morning for ballooning larvae (Levy 1994).

The discovery of *L. mathura* egg masses on several grain ships has highlighted the possibility that other *Lymantria* species, including *L. monacha* (L.), could use the same route for entering North America. In assessing the risk for any exotic species, the probability of introduction and establishment must be considered. It is assumed that *L. mathura* has not yet established in North America, but there are no adequate means of detecting it at this time.

Both larvae of *L. dispar* and *L. mathura* were capable of dispersing by wind in our wind tunnel tests. An average of 15% of neonates of Asian gypsy moth ballooned compared with 32% for *L. mathura* (Table 1).

Table 1. Comparison of dispersal, weight and settling velocity for neonates of *L. mathura* and Asian *L. dispar*

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameter</th>
<th>Number</th>
<th>Mean</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. mathura</em></td>
<td>Dispersal, %</td>
<td>203</td>
<td>32.22</td>
<td>25.74–35.69</td>
</tr>
<tr>
<td></td>
<td>Weight, mg</td>
<td>277</td>
<td>0.51</td>
<td>0.50–0.52</td>
</tr>
<tr>
<td></td>
<td>Settling velocity, m/s</td>
<td>150</td>
<td>0.88</td>
<td>0.86–0.89</td>
</tr>
<tr>
<td>Asian <em>L. dispar</em></td>
<td>Dispersal, %</td>
<td>76</td>
<td>15.53</td>
<td>11.73–19.32</td>
</tr>
<tr>
<td></td>
<td>Weight, mg</td>
<td>186</td>
<td>0.65</td>
<td>0.63–0.66</td>
</tr>
<tr>
<td></td>
<td>Settling velocity, m/s</td>
<td>100</td>
<td>0.96</td>
<td>0.94–0.98</td>
</tr>
</tbody>
</table>

Replicates, 10 larvae per replicate; larvae, number of larvae.
1). Experiments conducted by Diss et al. (1996) using similar protocols with North American L. dispar, recorded 26% of neonates ballooning in the wind tunnel. The percent of larvae dispersing in a wind tunnel, however, is lower than observed in the field (McManus 1973). In the wind tunnel experiments, we did not provide the larvae with a tree (or any other vertical object) on which they could ascend and move up toward the light, while trailing silk. This natural behavior of larvae reaching top branches of the tree appears to enhance the probability of dispersal (McManus 1973). Another possible explanation is that the time of exposure to wind in the tunnel (6 min) was shorter than the time spent for observations in the field, where data were collected hourly (McManus 1973). Although McManus (1973) indicated that in the field all newly hatched gypsy moth larvae are predisposed to disperse, he suggested that within any egg mass, a percentage of the progeny may be more prone to dispersal than others. Later, McManus and Mason (1983) hypothesized that the predisposition of larvae to disperse is insignificant compared with the importance of environmental conditions in determining dispersal.

The potential for dispersal is considered the product of the tendency of larvae to balloon and the length of the period in which dispersal can take place (Diss et al. 1996). The higher percent of ballooning larvae in the wind tunnel experiment suggests that L. mathura has a greater potential for dispersal than North American or Asian gypsy moth larvae under the same environmental conditions.

Both Asian L. dispar and L. mathura larvae display diel rhythms in their dispersal, which is common for North American gypsy moth neonates. The most dispersal in our wind tunnel occurred in the early afternoon, between 1300 and 1700 hours DST (Fig. 2). The highest rate of dispersal for North American gypsy moth larvae in the field has been noted between 1200 and 1400 hours (McManus 1973). Although Leonard (1971) found that the peak of larval dispersal occurred between 0845 and 1000 hours, he did recover larvae between 1200 and 1600 hours. We believe that time of maximum dispersal activity for L. mathura and Asian L. dispar should be considered by PPQ programs when monitoring high risk vessels in American ports.

The mean settling velocity rate of L. mathura (0.88 m/s) and Asian gypsy moth (0.96 m/s) differed (Table 1). Slower settling velocity rates for L. mathura larvae indicate that under the same travel time and wind velocities, these larvae would travel longer distances than Asian L. dispar larvae. Both L. mathura and Asian L. dispar larval settling velocities fall within the range of the settling velocity of North American gypsy moth 0.41–1.17 m/s (McManus and Mason 1983). Thus, both L. mathura and Asian gypsy moth neonates would likely disperse as far or further than North American gypsy moth. Probability of larval establishment is dependent on several factors, including wind direction and velocity, proximity of the ship to the land, availability and quality of hosts, time of the year, mortality factors, and so on.

The controversy about relationships between egg size and larval dispersal still remains unsolved. In the early 1970s, Leonard (1970, 1971) suggested that smaller larvae were more likely to disperse because most of these larvae were from dense populations and had a longer prefeeding period and a higher activity level. Later, it was considered that small larvae were less likely to disperse because of reduced photoperiodism (Barbosa et al. 1981) and a lower tendency to descend on silk when acceptable hosts were available (Capinera and Barbosa 1976, Lance and Barbosa 1981). Recent research by Diss et al. (1996) showed that the average weight of eggs from a mass was not

![Fig. 2. Diel periodicity of dispersal for L. mathura and Asian L. dispar. Numbers above each bar indicate number of replicates of 10 larvae.](https://academic.oup.com/ee/article-abstract/28/2/240/486264)
correlated with the tendency of larvae from that egg mass to balloon.

Our results indicate that neonate Asian L. dispar have higher mean weights and lower dispersal tendency, whereas L. mathura larvae have lower mean weight and higher dispersal (Table 1). When comparing average percent dispersal in each egg mass of Asian L. dispar and L. mathura, the same tendency is evident (Fig. 1), although regression slopes for each of the species are not significant.

To date, surveys to detect establishment of L. mathura in North America remain difficult. Some components of the pheromone of L. mathura were recently identified (M.A.Z. and V.C.M., unpublished data), but synthetic analogs have to be tested in the field. Searches for egg masses are troublesome because eggs are laid deep in crevices (Kozhanchikov 1950, Maslov et al. 1985). The number of egg masses laid in crevices on ships is unknown, but if high numbers of eggs are laid deep in crevices (Kozhanchikov 1950, field). Searches for egg masses are troublesome because eggs are laid deep in crevices (Kozhanchikov 1950, Maslov et al. 1985). The number of egg masses laid in crevices on ships is unknown, but if high numbers of eggs were transported, given our findings on dispersal potential of neonates, L. mathura’s introduction into North America is possible. After an introduction, subsequent establishment of this polyphagous species is likely because L. mathura larvae feed readily on a broad range of potential North American hosts in the family Fagaceae and are able to survive and develop on hosts from Oleaceae, Juglandaceae, Betulaceae, and Pinaceae (Zlotina et al. 1998).

Acknowledgments

We thank M. McManus (USDA Forest Service, Handen, CT) for review of the manuscript, R. T. Cardé (University of California, River Side) for suggestions to incorporate a test on settling velocity in our study, J. R. Tardif (USDA–APHIS, Otis, MA) for constructing the wind tunnel, and Nancy Elison (USDA–APHIS, Otis, MA) for help with maintenance of insect cultures. We also thank 2 anonymous reviewers whose suggestions substantially improved our manuscript. This research was funded by a USDA–APHIS Cooperative Agreement and was done as a partial requirement of M.A.Z. for the degree of Ph.D. at the University of Massachusetts, Amherst.

References Cited


November 1992, Indianapolis, IN. The Indiana Department of Natural Resources, Indianapolis, IN.


Received for publication 2 June 1998; accepted 4 January 1999.