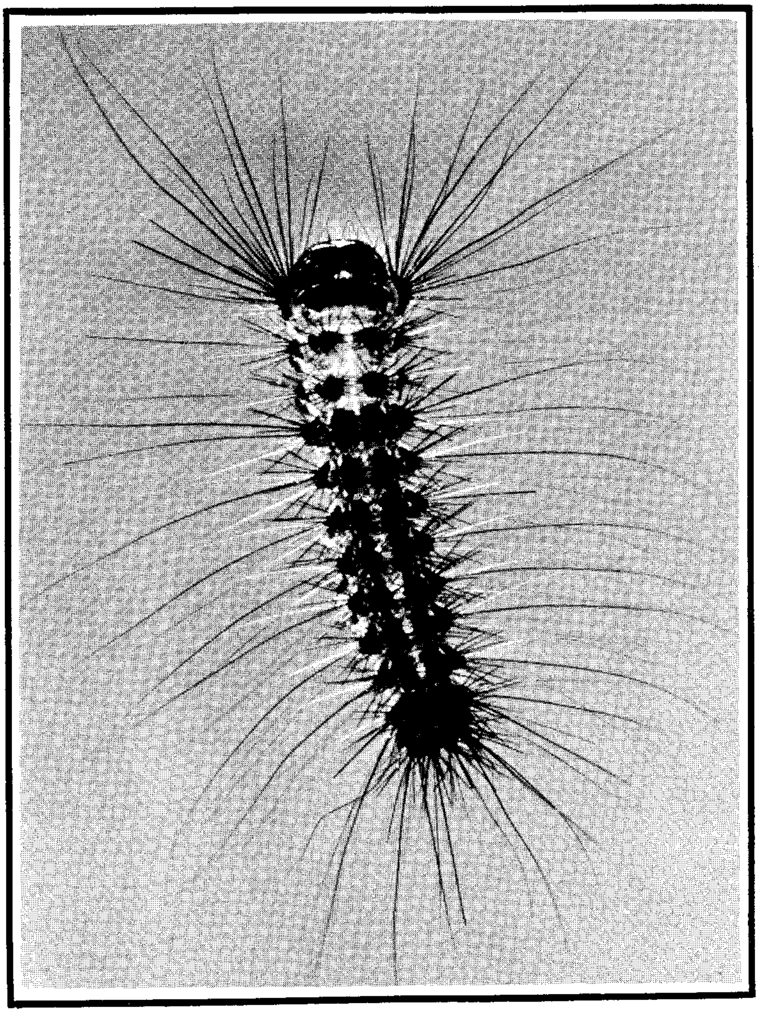
by Michael L. McManus

The *Role of Behavior* in the dispersal of *Newly Hatched Gypsy Moth Larvae*



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The *Role of Behavior* in the dispersal of *Newly Hatched Gypsy Moth Larvae*

ABSTRACT

Newly hatched gypsy moth larvae are morphologically and behaviorally adapted for airborne dispersal. The diel periodicity of both hatching and dispersal from the egg mass and photopositive behavior assure that larvae are in optimal position for dispersal when air turbulence is maximal at midday. The rate of larval activity depends upon ambient temperature and relative humidity ($R^2 = 0.77$). The larvae continually trailed silk and did not feed upon reaching the foliage. Rather the larvae appeared predisposed to disperse and were readily dislodged by slight winds.

THE GYPSY MOTH (*Porthetria dispar* L.) has been defoliating hardwoods in New England since its accidental introduction in 1896. It has become endemic in this region, and frequently it reaches locally epidemic levels. The range of this pest has extended steadily southward into central Virginia and westward into central Pennsylvania.

Unlike many lepidopterous pests that disperse actively in the adult stage, the gypsy moth spreads by the inadvertent transport of egg masses on vehicles and various other objects and by windblowing of newly hatched larvae.

The importance of larval dispersal in the spread of this insect was established through experiments conducted at the gypsy moth laboratory at Melrose Highlands, Massachusetts, from 1910 to 1932. It was shown conclusively that the newly hatched larvae could be blown a distance of 21 to 30 miles (*Collins 1917*) and recovered at an altitude of at least 2,000 feet (*Collins 1934*).

Despite the importance of larval spread, little is known about how the larvae respond to external environmental stimuli. This is a report on the importance of behavior in the natural process of dispersal of newly hatched gypsy moth larvae.

Our approach to obtaining this information was to separate the dispersal process into three distinct phases: (1) the period from hatching until the larvae move off the egg mass; (2) the initial distribution of the larvae in the tree crown; and (3) the subsequent moving of larvae from the foliage. Because these larvae are small (3.0 mm.) and difficult to observe on the bark of larger trees, we conducted most of our studies on two small caged trees where we could restrict the movements of the larvae.

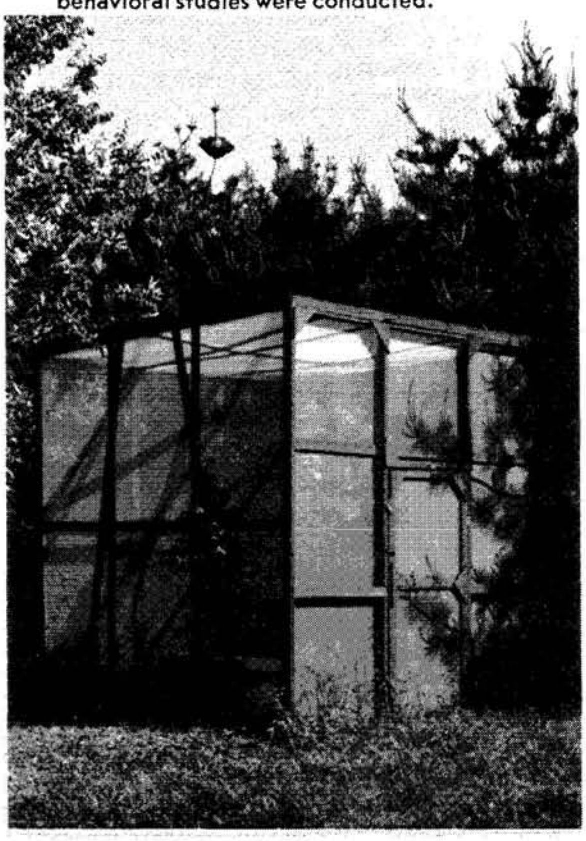
Methods and Procedures

General

The studies were conducted at Branford, Connecticut, in the summers of 1969 and 1970. The study trees were four black oaks (*Quercus velutina* Lam.), approximately 8 feet tall and 1 to 1½ inches d.b.h. (diameter breast high). Two of the trees were enclosed individually in 9 x 9-foot cages made of monofilament saran (fig. 1), and the other two were left uncaged. The trees were situated in an opening protected on three sides by stands of white pine (*Pinus strobus* L.) and mixed hardwoods.

The larvae we used in these studies came from egg masses collected from a sparse population near Oxford, Connecticut, in January of both years. These were refrigerated at 32°F. until used.

Figure 1.—The tree cage where most of the behavioral studies were conducted.



Dispersal of Larvae from the Egg Packet

Individual egg masses were enclosed within a saran mesh packet and then stapled to the tree 1 foot above ground. Observations were made on time of hatch, behavior of the larvae while on the packet, and behavior of the larvae as they ascended the tree. Temperatures were recorded continually at the packet surface with a copper-constantan thermocouple, and relative humidity was recorded periodically with a thermistor relative humidity gun. A hygrothermograph was maintained in the immediate area to provide comparative readings of temperature and relative humidity.

During early releases, we noticed that the larvae moved up the tree more rapidly under certain climatic conditions. On overcast days and before rainfall, they were sluggish. But under clear conditions, especially after the recent passage of a high-pressure front, they moved rapidly up the tree.

To quantify this, we determined the rate of ascent of more than 400 larvae from 12 different egg masses by measuring the time required for individuals to travel a 1-foot interval scribed on the bark. Individual larvae were chosen at random as they ascended, and the time of departure and ambient temperature were also recorded.

Distribution of Larvae in the Tree Crown

Every major branch on the study trees was tagged so that the exact locations of the larvae could be recorded. Total counts were made at 0900, 1200, and 1600 hours daily after larvae were released.

An additional test was designed to evaluate the effect of light on the initial distribution of larvae on the trees after their release. Because of variability in the duration of hatch of any gypsy moth egg mass, a different release procedure was utilized. Two egg masses were incubated together under field conditions. When hatching began, the egg masses were brought inside at room temperature (70°F.) until about 400 larvae were accumulated. An equal number of larvae were then placed in two small saran trays and stapled to the bases of the caged and uncaged trees. This gave us a known quantity of larvae of approximately the same age (12 to 24 hours).

Three light conditions were tested: (1) a normal exposed tree (uncaged); (2) incident light but no direct overhead light) and (3) a completely darkened tree. The latter two conditions were created by covering the cages in varying degrees with large canvas strips. Total counts were made 1 hour after release and then at the aforementioned intervals.

Dispersal of Larvae from Foliage

The effect of wind on dispersal was evaluated by releasing equal numbers of larvae (200) on both caged and uncaged trees and then periodically counting the remaining larvae. We were able to estimate the overall effect of the cage in reducing air flow by using a thermistor anemometer. The average maximum velocity both inside and outside the cage was estimated by recording the maximum inclination of the indicator needle at 15-second intervals for running periods of 2 minutes (8 readings). This was repeated at 5-minute intervals for a 30-minute period (total of 48 readings).

The dropping of individual larvae from the foliage was recorded on two occasions by making continuous observations of populations on the caged trees during the day.

Results

Hatching and Behavior on the Egg Mass

The period of hatching for an individual egg mass varied from 2 to 5 days. Although newly hatched individuals were recorded on the egg mass throughout the day, most larval emergence occurred early in the morning. Newly hatched larvae can be differentiated from the others because they are buff or tan upon hatching, but turn black in 2 to 4 hours.

After emerging, the larvae spent an indefinite length of time resting on the egg-mass surface before they began moving up the tree. In the spring of 1969, this time ranged from 1 to 49 hours for individual egg masses.

Although environmental conditions during this period obviously affected the larvae, there was no definitive relationship between ambient temperature or relative humidity and the initial movement of larvae off the egg mass. If the egg-mass temperature exceeded approximately 90°F., the larvae usually moved to the back side of the packet, where they were partially shaded. Thermocouple temperatures at the packet surface often exceeded 100°F. in direct sunlight, and many resting larvae withstood these high temperatures with no apparent adverse effects. Larvae normally did not ascend the tree when the ambient temperature exceeded 85°F.

Dispersal from the Egg Mass

Larvae usually began ascending the tree after 0800 hours. This activity reached a peak between 0900 and 1000 hours, declined at midday, and increased again between 1300 and 1400 hours (fig. 2). A few larvae that hatched in the early morning ascended the tree during the afternoon activity period, but the majority remained on the egg packet until the following morning.

The rate at which individual larvae ascended the tree was determined by the tem-

Figure 2.—The daily pattern of larvae leaving the egg mass and dropping from the foliage, summer 1969-70.

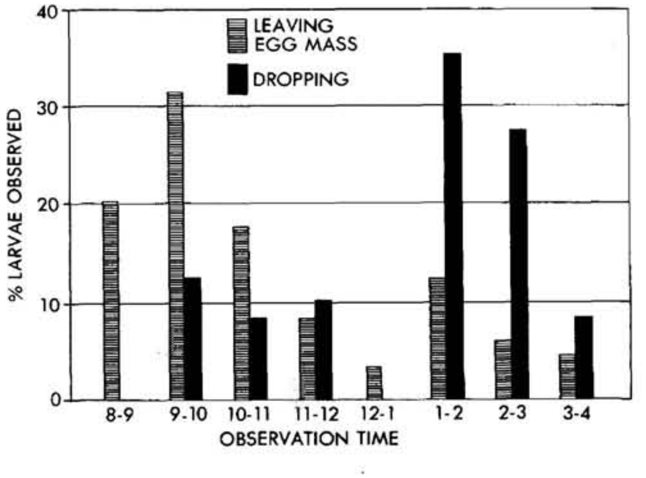


Table I.—Analyses of variance for the regression of rate of ascent ($\hat{R}$) of newly hatched larvae on temperature (T) and relative humidity (RH)

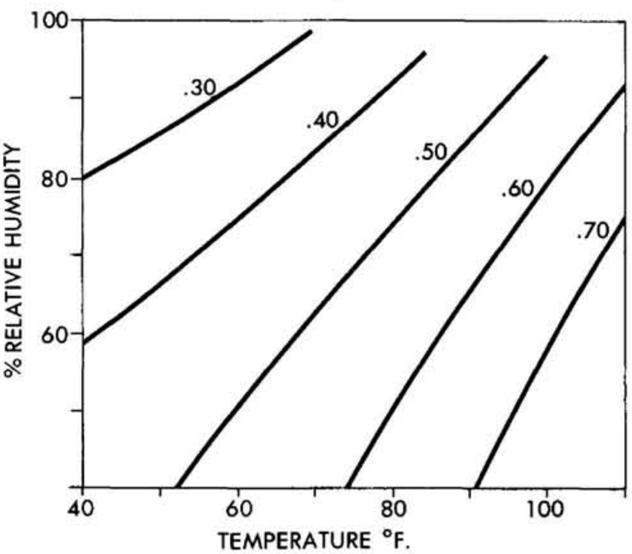
Source	DF	MS
T	1	0.01472*
RH	1	0.03223**
Error	15	0.00307

$\hat{R} = 0.4595 + .000036T - .000034RH$

perature and relative humidity at that time. Multiple-regression analysis showed that 77 percent of the variation in rate of ascent was accounted for by these two variables (table 1). The rate of movement was directly related to the combined effect of increasing temperature and decreasing relative humidity (fig. 3).

Although movement of larvae off the egg packet was periodic, larvae moved independently of one another; and no individual leader was evident. Larvae were observed trailing silk, and they tended to follow other silk trails. For example, an adventitious bud that protruded slightly from the side of one tree was repeatedly crossed by individual larvae, although it was somewhat of an obstacle. Accumulated silks could be seen readily at the

Figure 3.—A profile of the rate of ascent of newly hatched larvae (in feet per minute) under variable conditions of temperature and relative humidity.



point of contact both below and above the bud. By forcing a number of larvae to crawl onto a lower branch that they normally avoided, and lay down silk trails in the process, we were able to induce a number of other larvae onto that branch at a later hour of the same day.

Distribution on the Tree

Newly hatched larvae are strongly photopositive and ascend the tree in direct response to overhead light. On sunny days, the larvae

% DISTRIBUTION of LARVAE on CAGED OAK TREE

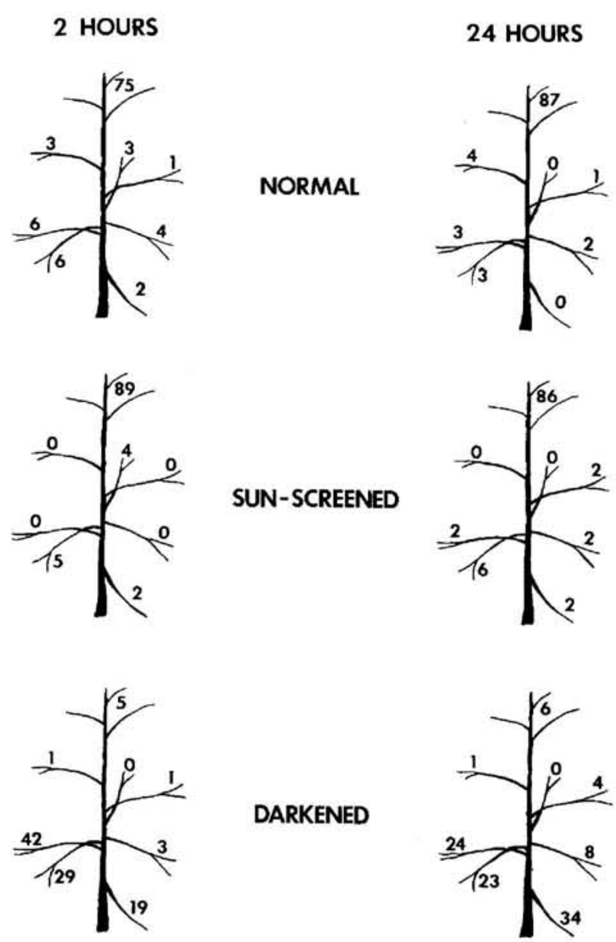


Figure 4.—The percentage distribution of newly hatched larvae after their release on caged oak trees under three conditions of light.

usually moved up that side of the stem that was exposed to the sun, and they accumulated at the highest point of the tree. The only exception to this was in the early morning, when the sun was near the horizon. Larvae initially accumulated at the highest point on the eastern side and then moved to the top branches as the sun moved overhead. On overcast days, they moved directly to the top branches, although their response to dull light was not as strong as their response to bright light (fig. 4).

The percentage distribution was similar on the normal and sun-screened trees at both 2 hours and 24 hours after release. However, on the darkened tree, few individuals moved above the lower tier of branches, and most of the larvae eventually dropped from the branches without feeding.

Dispersal from the Tree

A large egg mass was allowed to hatch normally under field conditions. Although this egg mass contained 600 to 700 viable eggs, only 140 larva were counted on the tree at any one time because of continual dispersal (fig. 5).

The duration of hatch was 6 days, and second-stage larvae appeared 8 days after emergence began. By this time, the population on the tree had stabilized.

Figure 5.—The change in numbers of larvae on a caged oak after normal hatching of a single egg mass, June 1969.

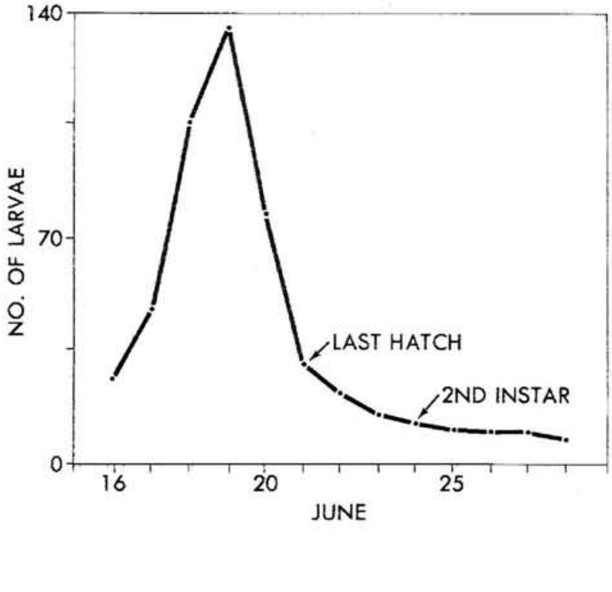


Figure 6.—A group of larvae suspended from an upper branch of a caged oak tree after being dislodged by a slight gust of wind.

When the newly hatched larvae aggregated at the top of the tree, they were continually active on the upper surface of the leaves and twigs and eventually formed a network of silk across the upper branches. They did not feed, although foliage was abundant at all times. A slight gust of wind was sufficient to dislodge them from the foliage and cause them to hang from the tree on silken threads (fig. 6).

Observation of populations on the caged trees revealed that, when winds were less than 2 m.p.h. the larvae dropped readily from the foliage on silken threads. Dropping of the larvae was most evident in the early afternoon between 1300 and 1500 hours (fig. 2); but a light peak occurred between 0900 and 1130 hours, shortly after the peak larval activity period for leaving the egg packet and ascending the tree.

When a larva was suspended on a silken thread, one of three things resulted. (1) The larva extended itself on the thread in response to additional wind until it contacted a surface such as the cage. Often the suspended larva was blown 360° around the tree and relocated on another branch. (2) The larva extended itself on the thread in response to wind until the thread broke. (3) The larva remained suspended on the silken thread until the wind subsided, then crawled back up the thread onto a leaf or branch. Larvae were seldom observed lowering themselves to the ground.

At a recorded wind velocity of 125 feet per minute (1.2 m.p.h.), a suspended larva was blown out to a position perpendicular to the tree. Any velocity in excess of this was sufficient to cause redistribution of the larvae on the tree. We did not determine the velocity of wind required to dislodge a larva from a leaf surface, or to fracture a silken thread.

Figure 7.—A comparison of the number of larvae dispersed when 225 newly hatched larvae were released at the base of both caged and uncaged oak trees at 1100 hours, June 1969.

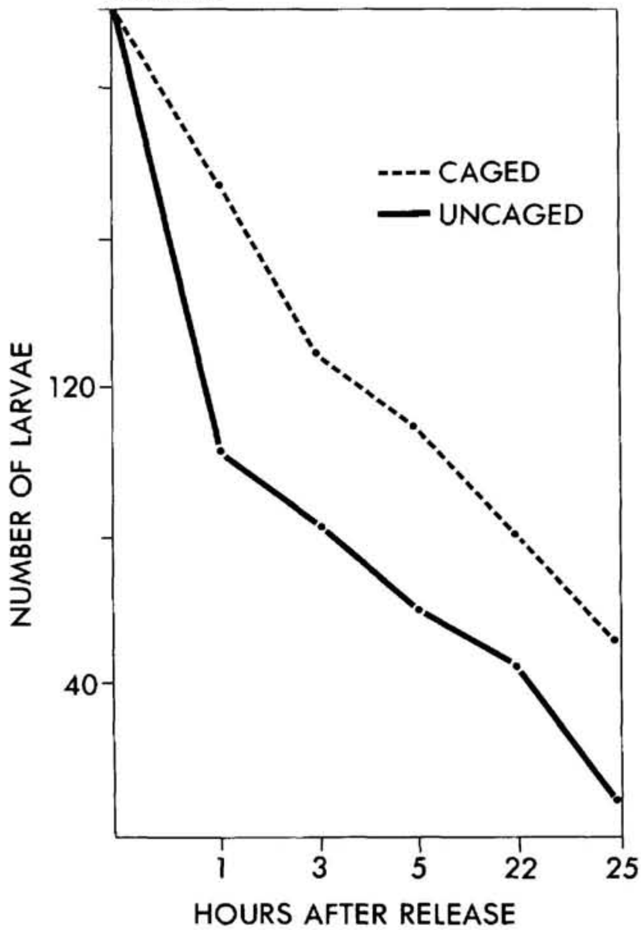
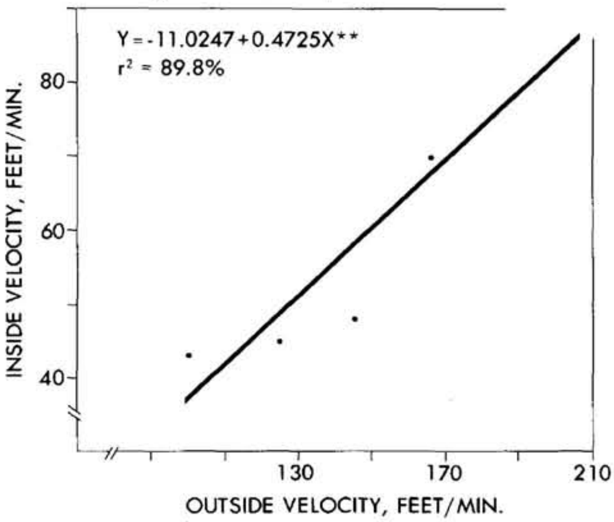


Figure 8.—Relationship of the average maximum wind velocity inside and outside the cage on five dates, summer 1969.



A progressive loss due to dispersal resulted when 225 newly hatched larvae were released at 1100 hours on both caged and uncaged trees (fig. 7). On the uncaged tree, more than 50 percent of the population dispersed within 1 hour of release. On the caged tree, a 15-percent reduction occurred within the same hour.

Releases of equal numbers of larvae on caged and uncaged trees demonstrated the impact of wind on dispersal and the complexity of the dispersal process. The saran cage effectively reduced the average maximum wind velocity by approximately 60 percent (fig. 8). The hourly rate of dispersal of the larvae varied with the time of initial release and the time of day. The dispersal rate 1 hour after release was highest when the larvae were released at 1100 hours (table 2). The difference

Table 2.—Dispersal rate of newly hatched larvae 1 hour after release, July 1969

Release time (hours)	Average dispersal rate	
	Caged tree	Uncaged tree
1100	[1]0.36	0.71
1400	.24	.41
1500	.37	.36

[1]Each figure represents an average for 2 release dates.

in dispersal rates between caged and uncaged trees was maximal for the 1100 releases and negligible for the 1500 releases. This reduction in dispersal coincided with diminishing air turbulence and reduced larval activity in the late afternoon hours.

The average hourly rates of dispersal were significantly higher the first hour after release than at any other time, (table 3) and are not equally representative for the other time intervals. The hourly rate of dispersal was always higher on the uncaged trees. But in the interval from 1600 to 0900 hours, dispersal was negligible on both the caged and uncaged trees. By 1200 hours of the second day, few larvae were left on the uncaged tree, and the numbers on both trees had stabilized.

Table 3.—Average hourly dispersal rates of newly hatched larvae from caged and uncaged trees within daily time intervals, for four release dates, summer 1969

Condition	Initial rate of dispersal (1st hour)	Average hourly dispersal rates within time intervals					
		Day I			Day II		
		0900-1200	1200-1600	1600-0900	0900-1200	1200-1600	1600-0900
Caged	0.33	—	0.179	0.009	0.092	0.158	0.024
Uncaged	.52	—	.325	.029	.281	.185	.021

Discussion

Early studies of the gypsy moth have shown that the newly hatched larvae are easily dispersed by wind. Our observations suggested that, although dispersal may often be passive, larval behavior and activity rhythms are highly adaptive for assuring dispersal in this species.

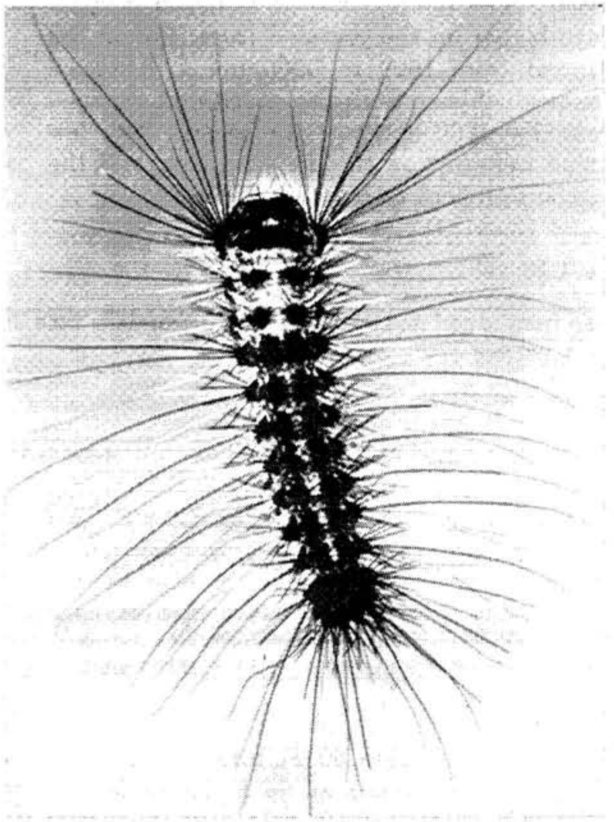
Upon hatching, gypsy moth larvae are well adapted for windblown dispersal (fig. 9). Burgess *(1913)* reported that the so-called aerostatic hairs on the dorsum of the larvae give them added buoyancy. However, the profuse acuminate lateral hairs are probably more effective in the dispersal process because they effectively increase the lateral surface area of the larvae by eight times.

Because the larvae turn black shortly after hatching, as "black bodies" they readily absorb solar radiation and are active at low ambient temperatures. Although 50°F. was the lowest temperature at which we observed larvae leaving the egg mass and ascending the tree, it is probably not a minimum temperature for this activity.

Leonard *(1970)* observed feeding activity of first-stage larvae at 45°F. Burgess *(1913)* reported from laboratory studies that larvae were not active below 60°F., and that few caterpillars moved about at 65°F. However, his observations were of glass battery jars that were artificially heated from below and therefore did not account for the effect of solar radiation. The internal body temperature of a dark-bodied insect may greatly exceed that recorded at the surface. Gara et al. *(1971)*, using blackened bead thermistors to stimulate insects in the field, found that the thermistors heated to 10 to 15°F. above the ambient air temperatures. This would explain why gypsy moth larvae are active at relatively low ambient temperatures.

According to Zanforlin *(1970)*, laboratory tests have shown that larvae of Lymantriidae (including the gypsy moth) express both negative geotaxis and positive phototaxis, although the geotaxis is much weaker. This was confirmed in our tests of the effect of light on the distribution of larvae in the tree crown. In the absence of light, the larvae did not ascend the tree and did not feed over a period of days. The strong response to overhead light placed the newly hatched larvae at the tops of the trees, whence they were most rapidly dispersed.

Figure 9.—Dorsal view of a newly hatched gypsy moth larvae, showing profuse acuminate lateral hairs.



It is difficult to equate our observations on silking behavior with those reported earlier by Leonard (*1967*). He concluded from laboratory tests that newly hatched larvae did not trail silk until starved. When this occurred, larvae underwent a phase of increased activity characterized by increased locomotion, irritability, and silking.

Our field studies revealed that newly hatched larvae always trailed silk when ascending the tree, and this was not affected by the length of time spent on the egg packet. The rate of larval ascent and general activity was related to the temperature and relative humidity at that time.

It is possible that, in the spring, all newly hatched larvae attain some level of starvation before they leave the egg mass and ascend the tree. But it would be difficult to ascertain when larvae are starved, because they would be influenced partially by the weather conditions at the time. Forbush and Fernald (*1896*) noted that newly hatched larvae can readily live for 4 days without food under field conditions. And Maksimovic (*1958*) reported that newly hatched larvae can survive up to 8 days without food under variable climatic conditions. Obviously the tolerance of the larvae to starvation is not completely understood.

The behavior of the larvae upon reaching the top branches of the tree also appears to enhance the probability of dispersal. The larvae continually move about and trail silk, but make no attempt to feed. They respond to gusts of wind by arching their bodies, thus increasing their susceptibility to being dislodged. After a period of time, they begin dropping from the foliage on threads of silk. This was more prevalent on the caged trees, where winds were often neglible. If suspended larvae did not contact another surface or become airborne, they immediately began crawling back up the silk to the leaf surface, thus again placing themselves in an opportune position for dispersal.

Foliage quality did not inhibit feeding. When larvae were released in the spring and in mid-July of 1969, succulent foliage was abundant and in July a second flush of growth was produced on the trees. Age of the foliage apparently was not limiting to the newly hatched larvae, because new populations were successfully established on the study trees in late August 1969.

There is a diel periodicity in many aspects of larval activity during the first instar. Hatching, the movement of larvae off the egg mass, and dropping of larvae on silken threads all occur at specific times in the diel cycle. These activity rhythms often have adaptive values.

Hatching began after sunrise and reached a peak between 0600 and 1000 hours. Edwards (*1965*) stated that the hatching of *Hemerocampa* larvae after sunrise allows them to remain active and feeding for some hours just after hatching, instead of remaining inactive for the first 10 to 12 hours, as would be the case if they hatched near sunset. Hatching at this time allows gypsy moth larvae to be exposed immediately to favorable conditions before the peak activity periods during the day.

The main exodus of larvae off the egg packet occurred between 0830 and 1030 hours. This placed the larvae at the tops of the trees before the daily cycle of maximum temperatures and wind. Both the surface wind speed, on which frictional mixing depends, and the intensity of convection have a maximum at midday and a minimum before sunrise (*Geiger 1965*).

The dropping of larvae on silken threads was also rhythmic and was most obvious on the caged trees, where winds were minimal. Although some dropping was evident in the late morning, the peak occurred in the early afternoon (1300 to 1500 hours) when environmental conditions favored dispersal. The loss of larvae from the trees was always highest during this same time.

My observations on the dispersal of larvae from individual trees indicated that two periods of dispersal occurred, the highest rates occurring in the afternoon between 1200 and 1400 hours on the day of release. Although limited to four separate release dates, our results compared favorably with earlier studies by Minott (*1922*) and Leonard (*1971*). They investigated the daily incidence of dispersal by trapping larvae on vertical screens located adjacent to infested woodlands. Minott reported two daily dispersion periods—0900 to 1200 hours and 1400 to 1700 hours, the greatest dispersal occurring during the afternoon period. Leonard found that the peak of larval dispersal occurred in the morning, the highest rate between 0845 and 1000 hours. However, he did recover larvae between 1200 and 1600 hours.

The rhythms exhibited by larvae of the gypsy moth for hatching, dropping, dispersal, and feeding are similar to those discussed by Edwards (*1965*) for the Douglas-fir tussock moth (*Hemerocampa pseudotsugata* McD.). In addition, larvae of both species are nocturnal in the later instars, at least in sparse populations. Adult emergence and flight of males also occur rhythmically in *H. pseudotsugata*, but have not been investigated for the gypsy moth.

Very little is known about qualitative differences among individuals in any gypsy moth egg mass. Leonard (*1970b*) suggested that smaller eggs that occur in *P. dispar* egg masses may be nutritively deficient and yield active larvae that are readily dispersed by wind. My measurements of the rate at which larvae ascended the trees indicated that individual larvae in any sample do move much more rapidly than others. And Leonard's suggestion may well explain these differences.

But the evidence presented here suggests that all newly hatched gypsy moth larvae are predisposed to disperse. However, within any egg mass, a proportionate number of the progeny may be more dispersible than others, or more capable of surviving the stresses created by prolonged or repeated dispersals. The morphology and behavioral responses of the larvae, and the adaptation of events to diel rhythms, indicate that a well-developed system exists to assure dispersal of the larvae from a point source. This may result in the long-range dispersal of gypsy moth larvae under certain optimal conditions, or in their redistribution within a forest stand or local geographical area.

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