

*Journal of the Lepidopterists' Society*  
60(3), 2006, 156–160

## FOREST TENT CATERPILLAR: MATING, OVIPOSITION, AND ADULT CONGREGATION AT TOWN LIGHTS DURING A NORTHERN MINNESOTA OUTBREAK

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**ABSTRACT.** Mating and oviposition of the forest tent caterpillar, *Malacosoma disstria* (Hübner) (Lasiocampidae), were studied in two sites  $\approx 2$  ha each at levels 1–5 m above the ground, and adult congregation at lights was studied in brightly lit town districts. The observations were made near or at Ely, St. Louis Co., Minnesota, in the latter years of an outbreak peaking during 1999–2003. Descent of the nomadic larvae from the forest canopy to less defoliated vegetative strata for feeding and cocooning later enabled mating to be observed conveniently from the ground. Adult activity began or intensified at  $\approx 5:30$  pm CDT, when males vigorously sought mates in foliage harboring cocoons. Mating pairs were captured and caged in jars containing a host branchlet for oviposition; mean duration of copulation was 202 min. Captive mated females always oviposited the morning after mating; mean duration of oviposition was 88 min. Dispersal behavior always preceded oviposition. Five new oviposition hosts were recorded. Naturally deposited egg rings were found most often on branchlets oriented nearer horizontal than vertical. Females congregating in brightly lit districts were usually gravid, but seldom oviposited.

**Additional key words:** *Malacosoma disstria*, Lasiocampidae, defoliation.

In northern Minnesota and elsewhere, the forest tent caterpillar, *Malacosoma disstria* (Hübner) (Lasiocampidae), builds up periodically to outbreak densities (Witter 1979). During Minnesota outbreaks, quaking aspen, *Populus tremuloides* Michx. (Salicaceae), and most other broad-leaved trees and shrubs except red maple, *Acer rubrum* L. (Aceraceae), are severely defoliated. Red maple contains an antifeedant (Nicol *et al.* 1997), but the nomadic larvae readily spin cocoons among its leaves. The forest tent caterpillar is univoltine, and the larvae hatch in spring at host bud-break (Batzer and Morris 1971).

Many thousands of hectares of forest, primarily quaking aspen, were defoliated in the outbreak that peaked during 1999–2003 in northern Minnesota when this study was done (Minnesota Dept. of Nat. Res. For. Ins. Disease Newsletter 1999–2004). Although defoliation seldom kills trees, it reduces their wood-volume growth, and the larvae are considered a nuisance by landowners and outdoor recreationists (Duncan *et al.* 1956). The eastern tent caterpillar, *Malacosoma americanum* (Fabricius), also occurs in Minnesota (Stehr and Cook 1968), but mostly in the eastern part of the State, and it was not seen in the outbreak area. Fitzgerald (1995) provides an exhaustive compendium of information for all *Malacosoma*.

At low, nonoutbreak densities, forest tent caterpillar adults mate high above the ground in the forest canopy; during outbreaks they mate on lower, understory vegetation. Mating nearer the ground occurs because larvae descend to less defoliated strata to find food and cocooning sites (Batzer *et al.* 1995), and males concentrate their search for mates where female cocoons occur. The larvae require angled surfaces for

cocooning, and they commonly create cocoon structures by drawing and spinning leaves together (illustrated by Batzer and Morris 1971 and Fitzgerald 1995, p. 60). In this study, many cocoons were spun on herbaceous plants of the ground stratum as well as shrubs. The downward shifting later enabled mating to be conveniently observed from the ground.

Previous reports touch on topics treated here. Bieman and Witter (1983) described field mating behavior at low and high levels of mate competition, reflecting low and high population densities. Stehr and Cook (1968) noted that forest tent caterpillar oviposition proceeds helically and in a layer one egg deep. Shepherd (1979) reported daily rhythms of male and female activity. Hodson (1941) noted adult congregation at town lights. As elaborated in the discussion section, the present study supplies more or different details about these and related topics.

### MATERIALS AND METHODS

This study was conducted near and in the town of Ely, St. Louis Co., Minnesota. Mating and oviposition were observed in two multilayered stands  $\approx 40$  yr old. Overstories in these stands were dominated by quaking aspen, but scattered examples of other tree species were present, in descending order of abundance, balsam poplar, *Populus balsamifera* L. (Salicaceae); red pine, *Pinus resinosa* Ait.; jack pine, *P. banksiana* Lamb.; eastern white pine, *P. strobus* L. (Pinaceae); white birch, *Betula papyrifera* Marsh. (Betulaceae); and balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae). The understories were dominated by willow, *Salix* sp. (Salicaceae), but contained scattered examples of other species, in descending order of abundance, red-osier dogwood,

*Cornus stolonifera* Michx. (Cornaceae); speckled alder, *Alnus rugosa* (Du Roi) Spreng (Betulaceae); pin cherry, *Prunus pennsylvanica* L. (Rosaceae); beaked hazel, *Corylus cornuta* (Marsh.) (Betulaceae); and American cranberrybush, *Viburnum trilobum* Marsh. (Caprifoliaceae). The vertical range of observation was 1–5 m above ground, and the sites were each  $\approx$ 2 ha.

Copulating pairs captured in late afternoon were caged in wide-mouthed, 1-liter glass jars with gauze-covered tops containing an aspen or willow branchlet 3–6 mm in diameter. Cages were moved in the evening to a darkened basement with temperatures constantly at 17–19°C, which approximated cool, outdoor evening temperatures. Cages were returned in the morning to shaded outdoor spaces where temperatures ranged 19–26°C. Observations of copulation and oviposition durations were made at  $\leq$ 30-min intervals.

Gender identification of adults was based on antennal rami, which are  $\geq$ 2 $\times$  longer in males than in females. Males also are noticeably smaller than females (sample measurements given later). Early in the study, active males were netted and released after their gender was confirmed ( $n > 20$ ). Females were dissected for verification of their gravid or spent condition. Egg fertility was determined by the presence of embryos.

Egg numbers/ring were estimated as described by Witter and Kulman (1969), and spumaline—the frothy substance that covers egg rings—was removed as these authors recommended by brushing with a discarded toothbrush. Forewings were removed for accurate length measurement. Angles of egg-bearing branchlets in the field were referenced to horizontal and were estimated with a large protractor. All clock hours refer to Central Daylight Time. Statistics were computed with SYSTAT (1992) software, except for  $G_{adj}$ , which was computed according to Sokal and Rohlf (1981). The abbreviation SD refers to standard deviation.

Mean daily temperatures during the late larval stage were computed from daily maxima and minima recorded at the Winton meteorological station  $\leq$ 5 km from Ely (Minnesota State Climatology Office 2005).

## RESULTS

*Mating.* The first adults of the flight season were males, as the species is protandrous. Throughout daily adult activity, starting or intensifying typically  $\approx$ 5:30 pm, males visible by the hundreds in any directional view flew vigorously and constantly in vegetative strata containing cocoons. They flew mainly in a zone within <0.5 m of tree and shrub canopies, circling, zigzagging, alighting and crawling along branchlets before taking flight again if they did not find an opportunity to copulate. The number of active, searching males around

foliage that contained cocoons was  $\approx$ 4 $\times$  that around foliage that contained no cocoons. On windy evenings, males confined their activity closer to canopies. During two cool, rainy, late afternoons with ambient temperatures <15°C, only a small fraction of the males known to be present were active.

Many female pupae appeared to emit their calling pheromone (Struble 1970) before they completed eclosion, as up to 6 males often concentrated activity around a single cocoon until the female eclosed. Males copulated with such females within 1–2 sec after the tip of the female abdomen cleared the cocoon. The wings of such females inflated during copulation. Most mating pairs were found within 10 cm of a cocoon structure presumed to be that of the female, and meconium was often seen on such structures. Some copulating females walked several cm as they were being observed before capture, and because of their larger size pulled the smaller males along. None of the females observed in this study attempted to fly during copulation. Females did not always begin calling before completing eclosion. The locations of two such females found resting quietly on cocoon structures were marked for continuing observation during the evening. At first, captured males released within centimeters of these females flew away. However, by onset of darkness both females were in copula, apparently having eventually emitted their calling pheromone. The sexes were always positioned end to end during copulation.

A total of 69 pairs were seen in copula during this study, of which 48 were successfully caged for further observation. Some copulating pairs separated on capture, presumably because copulation had just begun or was nearly completed. Copulating pairs were seen in the field as soon as daily male activity commenced and pairs known to be newly copulating were captured as late as 9:30 pm. Neither active males nor mating pairs were seen during early dawn hours, presumably because of too cool temperatures. Caged pairs remained in copula following capture for 150–255 min, averaging 202 min ( $n = 10$ ), but it should be noted that beginning and ending of copulation was not always precisely timed, and that some durations are subject to an error of  $\pm$ 30 min. Copulating pairs occurred on all the trees and shrubs named earlier, including the conifers. None of the conifers had been fed on, but they provided cocooning sites under conditions of extensive foodplant defoliation. Based on forewing lengths—a proxy for body size—there was a statistically significant relation between gender body sizes of naturally mating pairs: forewing length averaged  $16.8 \pm$  SD 1.42 mm for females, and  $12.4 \pm$  SD 1.05 mm for their mates (Pearson's  $r = 0.49$ ,  $df = 23$ ,  $P = 0.013$ ).

*Oviposition.* As in other species of *Malacosoma*, the forest tent caterpillar deposits its eggs in one batch during one oviposition event unless disturbed during the process. Of the 48 captive mated pairs, 88% of the females began ovipositing the day after copulation, most starting in early morning. The earliest an oviposition was completed was 7:05 am. Other females began ovipositing later, the latest at noon. If not ovipositing the day after copulation, captive females failed to do so entirely. Duration of individual oviposition in captivity monitored during daily hours of observation, which began at 7:00 am, ranged 65–134 min, averaging 88 min ( $n = 11$ ). Shorter and longer oviposition durations were associated with smaller and larger egg rings, which imply smaller and larger females and cooler and warmer ambient temperatures.

Just before beginning to oviposit, captive females always exhibited dispersal behavior. For 5–15 min they flew upward and around inside their cages. Further, naturally deposited egg rings were never observed near cocoon structures ( $n = 74$ ). After attempting to disperse, females became quiet, positioning themselves more or less diagonally on the caged branchlet head up with wings partly spread, and extended abdominal tips around the branchlet nearly 180° before starting to oviposit. As they oviposited, they gradually moved around and down the branchlet, coating eggs and the egg ring surface with spumaline. The second turn of the egg ring was aligned with the first so that the top margin of rings seldom had gaps (Fig. 1d). By the completion of oviposition, several turns of the egg ring had been deposited and the females were standing on the egg ring surface. Directions of female progression around branchlets during oviposition were clockwise in 12 cases (60%) and counterclockwise in 8 (40%), with only 3 reversals during the process, 2 from clockwise to

counterclockwise, and 1 the opposite. Within minutes of completing oviposition females flew vigorously again as before oviposition.

Whether termed 'mass' or 'ring', eggs were deposited as a continuous helical band each turn of which was tightly fitted with the previous turn, the width of the band generally diminishing downward (Fig. 1). When egg ring deposition was observed closely in captivity, seams in the spumaline covering between turns of the band were usually faintly evident as slight depressions, sometimes as ridges. Depending on female size, number of eggs, and branchlet diameter, rings consisted of up to five turns (Fig. 1a, c). After spumaline removal, margins between turns were not evident. After two days of rainy, windy weather, an increase in irregularly deposited eggs was evident in field egg rings presumably because oviposition had been interrupted by such weather (Fig. 1e). Spumaline was more or less clear when dispensed, but darkened after  $\approx 24$  h.

For egg rings deposited in captivity, number of eggs/ring averaged  $285 \pm \text{SD } 112$  and for those deposited naturally,  $246 \pm \text{SD } 66$ , and the difference was not significant (Student's  $t = 1.20$ ,  $df = 13.8$ , separate variances,  $P = 0.25$ ). Based on 5–39 eggs/ring dissected in late July and early August, 94% of rings contained fertile eggs, with an average of 94% of dissected eggs/ring fertile ( $n = 14$ ). Corresponding values for eggs collected in the field were 100 and 98% ( $n = 39$ ). These differences between captive and field eggs were close and inferred to be nonsignificant statistically.

Species on which naturally deposited egg rings were found included quaking aspen (76%), willow (12%), with the remainder (12%) on red osier dogwood, balsam poplar, beaked hazel, speckled alder, pin cherry, and American cranberrybush ( $n = 72$ ).

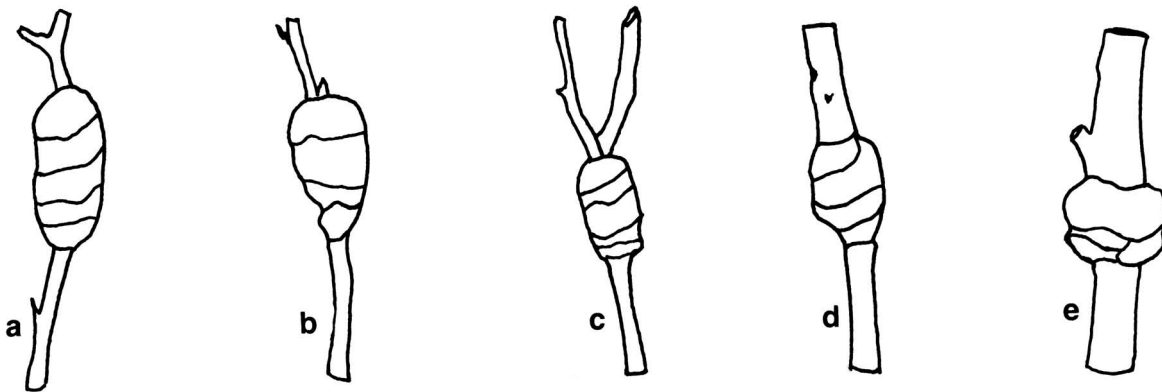


FIG. 1. Delineated margins of the band or bands of eggs in egg rings of the forest tent caterpillar on aspen branchlets. Delineation is based on seams in corresponding spumaline deposition. In the absence of female disturbance, oviposition proceeds in a downward helical manner.

Branchlets on which egg rings were found in the field ranged 2–6 mm in diam. Orientation of egg-bearing branchlets in the field tended to be nearer horizontal than vertical. All 5 samples of 28–74 branchlets containing naturally deposited egg rings in late July and early August were distributed similarly in each sample among three equally progressing angle classes. When pooled, 50% were on branchlets angled 0–30° relative to horizontal, 18% on those 30–60°, and 32% on those 60–90° ( $n = 291$ ), with departure from a no-preference distribution highly significant ( $G_{\text{adj}} = 42.9$ ,  $df = 2$ ,  $P < 0.001$ ). The distribution through 0–90° thus was backward-J-shaped.

*Adult congregation at lights.* Like many moths, forest tent caterpillar adults are photopositive. During flight periods, thousands of adults congregated near streetlights and on brightly lit exterior walls of buildings in towns in the outbreak area. In Ely, a few congregated males had frayed wings, indicating much flight history, but the females showed little or no wing wear. The source was almost certainly infested quaking aspen that were  $\leq 1$  km distant. Once congregated, the adults remained notably inactive, and seemed to be present night and day until dying or becoming prey of birds and bats. Both genders seemed equally represented, but copulating pairs were seldom seen. Eggs were sometimes seen on building walls, but were scarce relative to the numbers of females present.

Congregated females collected at various times of day for close examination came from the 400–600 and 900 blocks of Sheridan Street in downtown Ely. Their yearly forewing lengths during 2000–2003 averaged 20.0, 18.9, 19.1, and 18.9 mm, respectively, and appeared to indicate temporally decreasing body size ( $F = 13.5$ ,  $df = 3$ , 166;  $P < 0.001$ ). Corresponding percentages that were fully gravid were 96, 90, 97 and 58.

#### DISCUSSION

*Mating and oviposition.* The present study indicates strongly that the vegetative stratum in which most mating occurs is the one containing the most cocoons. The high frequency with which males were observed to copulate with females at the moment of female eclosion is more likely to occur at high than at low population densities, and was observed earlier in Minnesota (Hodson 1941, Bieman and Witter 1983). Female calling pheromone doubtless stimulated such intense male activity. Bieman and Witter (1983) also reported that some males lingered near empty or parasitized cocoons, as well as brown objects, which suggests they also use visual cues.

Typically, females eclosed and copulated in late afternoon and evening, and oviposited early the next

day. The absence of early morning flight activity in this study is not surprising for northern forest tent caterpillar populations. Shepherd (1979) also reported little or no male activity near dawn in Alberta and British Columbia, and found that males ceased flying at  $< 11^\circ\text{C}$ . Such temperatures were common near dawn in the present study. Daily patterns of male activity, female eclosion, and evening female calling closely match those reported by Shepherd.

Shepherd (1979) and Bieman and Witter (1983) also reported attempted dispersal by newly mated captive females. Lack of proximity between naturally deposited egg rings and cocoon structures is further evidence of preoviposition dispersal.

Positive and significant correlation between gender body sizes of mating pairs indicates that the sexes do not mate randomly with respect to size. Reasons for this are unknown, but one might speculate that larger males out-compete smaller ones to mate with larger females. The mean duration of copulation observed in captivity, 202 min, is near the mean duration of 197 min extracted from Table 1 in Bieman and Witter (1983) for their high population density.

Highly variable numbers of eggs/ring averaging 285 in captivity did not seem to differ significantly from the similarly variable mean of 246 observed in the field, nor did the apparent fertility means of 94% in captivity differ significantly from the corresponding 100 and 98% observed in the field. Both higher and lower fertilities were recorded earlier in Minnesota (Witter and Kulman 1972). After close observation confirmed the helical pattern of oviposition reported by Stehr and Cook (1968) and revealed corresponding seams in spumaline deposition, it became possible to reconstruct the course of oviposition in detail (Fig. 1).

Of naturally deposited egg rings found at study sites, 88% were on quaking aspen and willow. The remaining 12% were on 6 lesser utilized oviposition species, of which 5—red-osier dogwood, speckled alder, balsam poplar, beaked hazel, and American cranberrybush—were absent from Fitzgerald's (1995) foodplant tabulation for the forest tent caterpillar and other *Malacosoma*. (Flowering dogwood, *Cornus florida* L., an occasional foodplant of southern populations [Goyer *et al.* 1987], was presumably omitted accidentally from the tabulation.) The new oviposition host records reported here involved no more than 2 egg rings/host, and they are probably explainable by the presence of these plants in areas of high forest tent caterpillar population density.

The backward-J-shaped distribution of angles of branchlets bearing naturally deposited egg rings 1–5 m above the ground is reported here for the first time. Its



significance, if any, is unclear. One possibility is that branchlets nearer horizontal than vertical—where most egg rings were deposited—may be more abundant in midcrowns especially of the overstory and thus provide larvae easier access to the larger foliage volumes at midcrown.

*Adult congregation at lights.* Hodson (1941) earlier reported adult congregation at town lights where the nearest source infestations were several kilometers distant. In the present study, sources were  $\leq 1$  km distant. Such short-range attraction to lights at high population densities does not seem surprising. Female movement to lit areas probably occurred during the evening after late-afternoon eclosion and mating. Most congregated females were gravid, and while their status with respect to mating is unknown, they seem likely to have already mated because of the generally assiduous male pursuit. Congregation results in little reproduction because females do not appear to return to foodplants. The paucity of eggs at lights may result from lack of suitable oviposition sites (branchlets). The decreasing yearly body sizes of congregated females during 2000–2003 may be explainable by either or both of two effects: decreasing diet quality with repeated foodplant defoliation, and the generally inverse relation between body size and direction of temperature difference during late larval development (Miller 2005). During late larval development, 10–19 June, in 2000, when female forewing length was greatest, daily mean temperature averaged a cool 12.4°C, whereas in 2001–2003, when female forewing length decreased, daily mean temperature was higher by an average of 4.4°C. Less common than adult congregation at lights is convective transport of adults in the turbulent air of cold fronts for hundreds of kilometers in a few hours as Brown (1965) reported in Alberta and elsewhere. The population dynamics significance of convective transport is unclear as the gravid and mated statuses of transported females have not been reported.

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Received for publication 20 May 2005; revised and accepted 18 July 2006