Behaviour of late-instar gypsy moth larvae in high and low density populations

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ABSTRACT. 1. Using scaffolding and night-vision equipment, we observed fifth and sixth instars of the gypsy moth, *Lymantria dispar* (L.), on *Quercus velutina* Lam. in the field.

2. In low-density populations, larvae fed at night and spent the day resting in sheltered sites away from the canopy. In high-density populations, larvae remained in the canopy throughout the day and night, and the amount of feeding during daylight hours increased with population density.

3. Larvae at all population densities used a similar sequence of behaviours and sampled a number of leaves when selecting feeding sites, but larvae in high-density populations switched feeding sites more frequently and fed continuously for shorter periods.

4. Larvae seldom interfered with each other's feeding in any of the populations.

5. When fifth instars were collected from the field and held for 24 h in an electronic feeding monitor, they maintained feeding rhythms that were characteristic of their source populations. Larvae spent more time crawling and less time feeding when offered foliage from high-density rather than low-density populations.

Key words. *Lymantria dispar* (L.), Lepidoptera, *Quercus*, herbivory, feeding rhythms, population quality, microhabitat, insect–plant interactions, feeding monitor, defoliation.

Introduction

In his studies on *Malacosoma pluviale* Dyar, Wellington (1957, 1965) demonstrated that population dynamics of forest pests may be associated with interpopulation variation in the

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behaviour, development, and viability of individual insects (also see Papaj & Rausher, 1983). These factors, collectively termed population quality, have been implicated in the initiation and collapse of outbreaks of the gypsy moth, *Lymantria dispar* (L.) (Barbosa & Capinera, 1978; Wallner & Walton, 1979).

Population quality in the gypsy moth is associated with several factors, including population

density (Campbell, 1978). In the field, increases in population density are accompanied by decreases in fecundity, pupal size, and larval development time (Campbell, 1978). In high-density populations, late instars remain in the canopy and are active during the day; in low-density populations, late instars spend the day in relatively protected sites near the ground (e.g. under bark flaps or in the litter). Unfortunately, aside from descriptions of this shift in micro-habitat, there are few published reports on the behaviour of late-instar gypsy moths in popula-tions of different densities. We therefore con-ducted a study of the behaviour of late instars from high- and low-density populations in 1982 and 1983.

Materials and Methods

All study sites were located on Cape Cod, Massachusetts, in wooded areas dominated by 7–11 m high oak: red (*Quercus rubra* L.), black (*Q. velutina* Lam.), scarlet (*Q. coccinea* Muenchh.), and white (*Q. alba* L.), with various proportions of pitch pine (*Pinus rigida* Mill.). The 1982 high-density population was in Cotuit, Massachusetts. Hardwoods at the site were defoliated 100% prior to pupation, although defoliation was only 50–90% during the observa-tion period (defoliation was estimated subjec-tively). In 1983 the high-density site was located within Otis Air National Guard Base; final defoliation of oaks was 70–80%. During both years a wooded site in the Ashumet area of Falmouth, Massachusetts, served as the low-density plot, with little noticeable defoliation occurring in either year. To gain access to the canopy we surrounded one to three black oaks (7–9 m high) at each site with an observation tower (4×4×8 m high) of 5 cm diameter pipe.

At all sites we made two sets of observations on larvae that appeared to be beyond the fourth stadium. First, we recorded activities of individual larvae over extended periods (>20 min), paying particular attention to interactions between larvae and to sequences of behaviours that larvae used to locate feeding sites. Second, we assessed daily patterns of feeding, resting and locomotion. At each high-density site we observed a group of larvae every other hour throughout two 24 h periods (hourly during cre-puscular periods); groups consisted of all larvae on the terminal c. 2 m of three (1982) or five (1983) branches (40–110 larvae per observation period). This method was impractical in low-density populations, so we observed individual larvae every 10 min throughout their feeding period. In low-density populations we noted whether larvae were fifth instars (penultimate instar females and ultimate instar males) or (noticeably larger) sixth instars. In high-density populations, size of larvae and number of stadia are highly variable (Leonard, 1974) and we did not attempt to quantify instar.

Night observations were made with light-amplifying image intensifiers (either ITT model ANPBS–5A night-vision goggles or a Javelin night-vision scope fitted with a no. 3 close-up lens). This equipment was not available for the 1982 high-density site. Instead, we illuminated larvae with a portable red light (the 12 V tungsten source on a model MS-47 light, Ultra-violet Products Inc., covered by the deep red acetate filter from Cokin Creative Filter set no. B-375). Because some larvae appeared to 'pull back' from this light, we did not attempt to make observations from 23.00 to 04.00 hours.

In the laboratory we used an electronic feed-ing detector (Lance *et al.*, 1986a) to monitor feeding rhythms of field-collected larvae. The detector was attached to a strip-chart recorder with a 15 cm/h chart speed. Feeding activity pro-duced clusters of short (0–10 cm), overlapping spikes, and time spent feeding was determined by measuring the lengths of these clusters. Crawling created patterns of spikes that were taller (up to 20 cm) and more widely spaced. We quantified crawling activity by counting individual spikes that occurred outside of feed-ing periods. Between 13.00 and 14.00 hours, we collected a larva, placed it in the monitor, and provided it with a red oak leaf. Each test ran for 24 h at 25°C and 50–60% relative humidity, with photophase from 05.00 to 21.00 hours. Data were discarded if a larva did little or no feeding during the test period and did not feed when we subsequently offered it a red oak leaf from a low-density site. Successful tests were run on twenty fifth instars from low-density sites, and on twenty comparably sized larvae from high-den-sity sites. Half of the larvae in each group were offered a leaf from a low-density site, and half were offered a leaf from a high-density site.

Results and Discussion

Food-seeking behaviour

Larvae in high- and low-density populations used the same general sequence of behaviours to locate feeding sites. Initially, a larva crawled along a twig until it came to a leaf cluster. Then, it normally went through a behaviour we call 'petiole-sampling': the larva held the twig with its prolegs and moved its head back and forth, grasping individual leaf petioles one or more times with its mouthparts and thoracic legs. Larvae touched a mean of 2.8 ± 1.2(SD) petioles per cluster ($52 \pm 18\%$ of the petioles in the clusters; $N=36$), spending c. 0.5–3 s in contact with each. Petiole-sampling was somewhat more common in low-density populations than in high-density sites (Table 1). It appeared to be a means of rapidly assessing leaf quality, although it may have provided larvae with some other type of information, e.g. whether silk was present.

Larvae went through a further series of behaviours before feeding extensively on a particular leaf: (1) crawling out at least partially onto the leaf, (2) bite-testing the leaf, (3) initiating feeding, and (4) feeding for an extended period. Larvae often stopped at some point in this sequence and searched elsewhere for food. The frequencies with which they stopped after each step did not differ significantly between high- and low-density sites (Table 1). Quality of foliage in forest trees can vary from leaf to leaf (Schultz, 1983), and variation in foliage quality affects survival and fecundity of gypsy moths

(Barbosa & Greenblatt, 1979; Valentine *et al.*, 1983). Larvae that we observed appeared 'choosey' when selecting feeding sites. Gypsy moths perhaps benefit by selecting high quality leaves from within individual trees.

Daily patterns of feeding

In the low-density population, larvae spent the day resting in the litter or in fissures in the bark of boles and large limbs. They left these sites around the time of sunset (20.15–20.50 hours Eastern Daylight Time) and began searching for food when they reached the canopy. Sixth instars ($n=18$) fed throughout $\bar{x}=89 \pm 9\%$ (SD) of the night (32% of the 24 h day; Fig. 1A); fifth instars ($n=7$) spent significantly less time eating ($\bar{x}=46 \pm 20\%$ of the night or 27% of 24 h; with arcsine-transformed data, $F=40.3$, $P<0.001$). With sixth instars, feeding occurred in continuous periods of $\bar{x}=71 \pm 86$ min ($n=68$). Fifth instars fed continuously for shorter periods ($\bar{x}=35 \pm 34$ min, $n=27$; $P=0.031$, Mann-Whitney test). Between feeding episodes, larvae occasionally switched feeding sites, but they typically fed on three or fewer leaves during a single night. Between 04.30 and 06.30 hours, larvae left the foliage and returned to daytime resting sites.

At high-density sites, larvae remained in the canopy and fed occasionally during the day. At the 1982 site (100% defoliated), there was a sharp peak of feeding between 07.00 and 08.00 hours and a broad peak in the late after-

TABLE 1. Frequencies with which late-instar gypsy moths exhibited various behavioural transitions while selecting feeding sites.

Behavioural transition (A → B)	Percentage of larvae making transition (no. of observations)		χ^2
	Low-density population	High-density population	
A. Larva approaches leaf cluster B. Samples petioles	96% (57)	68% (38)	12.15*
A. Larva samples petioles B. Accepts cluster (crawls onto leaf)	71% (55)	65% (26)	0.06
A. Larva on leaf B. Bite-tests leaf	77% (52)	81% (100)	0.14
A. Larva bite-tests leaf B. Initiates feeding	55% (40)	62% (81)	0.26
A. Larva initiates feeding B. Feeds continuously for >1 min	50% (22)	32% (50)	1.41

* χ^2 significant at $P<0.005$; for all other values of χ^2, $P>0.05$.
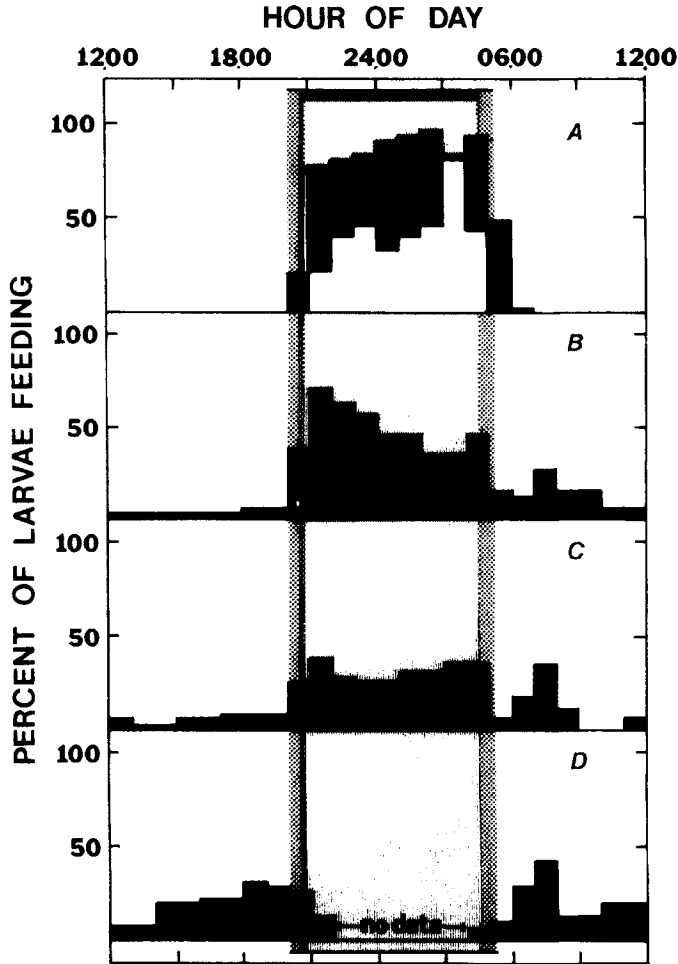
HOUR OF DAY

FIG. 1. Feeding rhythms of late instar gypsy moth larvae in the field. (A) Sixth instars in a low-density population (Ashumet area of Falmouth, Massachusetts), where there was little noticeable defoliation (white area denotes feeding of fifth instars). (B) All larvae past the fourth stadium, in a population resulting in 30–40% defoliation (data from Leonard, 1970). (C) In a population experiencing 70–80% defoliation (Otis ANG Base, Massachusetts). (D) In an area that was totally defoliated (Cotuit, Massachusetts; no data from 23.00–04.00 hours). Shaded area denotes night with twilight at either end.

noon and evening (Fig. 1D). Although observations were not made during most of the night, low levels of feeding at either end of scotophase suggest that there was less nocturnal feeding in this population than in the others. During the period in which observations were made, larvae spent c. 18% of their time feeding.

At the 1983 high-density site, feeding occurred primarily at night but continued at low levels throughout the day (Fig. 1C). Despite this, larvae did not leave the canopy during the day – between 15.00 and 17.00 hours on 25 June, we found five larvae in eight 1 m² plots in the litter, but counted 224 larvae (none below 3 m) in one of our study trees (area of interception=c. 10 m²). Larvae at the 1983 site fed c. 17% of the 24 h day. Again, there was a peak of feeding between 07.00 and 08.00 hours; Leonard (1970) observed a similar peak in a site that was only 30–40% defoliated (Fig. 1B).

Larvae in high-density populations fed continuously for periods of only $\bar{x}=7.8\pm6.9$ min (this does not include periods of <1 min) and fed on $x=2.3$ leaves per hour during 30 h of observation of individual larvae. These data, however, were taken during mid-day; duration of continuous feeding may have been longer during peak feeding periods.
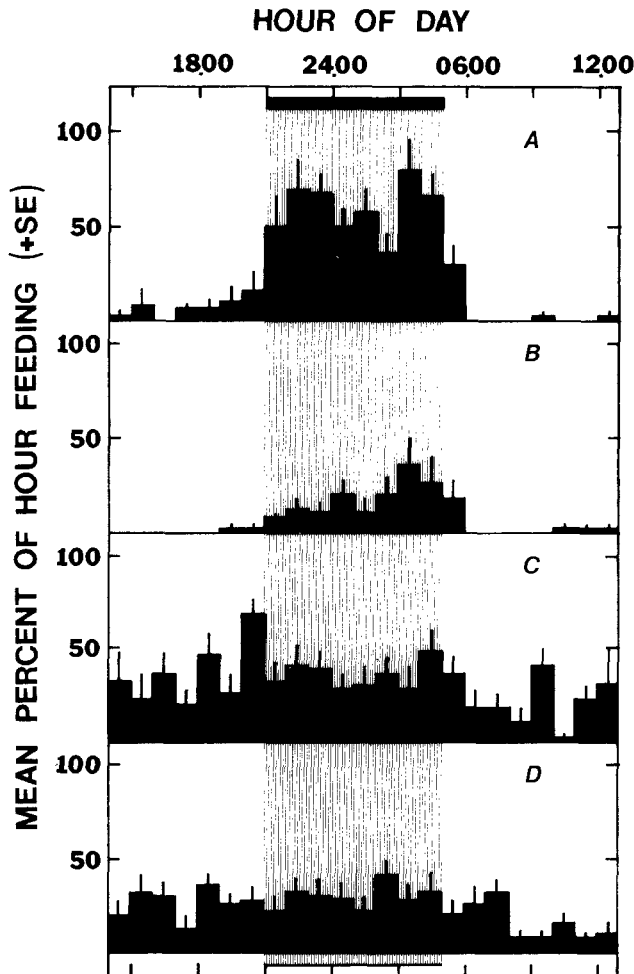
HOUR OF DAY

FIG. 2. Feeding rhythms of field-collected fifth instar gypsy moth larvae in the laboratory. (A) Larvae from a low-density population when offered leaves from a low-density site. (B) Larvae from a low-density population when offered leaves from an outbreak site. (C) Larvae from an outbreak when offered leaves from a low-density site. (D) Larvae from an outbreak when offered foliage from an outbreak site. Shaded area denotes scotophase.

Feeding monitor tests

In laboratory tests, larvae exhibited feeding rhythms that were characteristic of their source populations. Larvae from low-density populations conducted $\bar{x}=87\%$ of their feeding during scotophase when offered foliage from a low-density site, and $\bar{x}=77\%$ when offered foliage from a high-density site (Fig. 2, A and B). For larvae from high-density populations, $\bar{x}=40\%$ and $\bar{x}=43\%$ of feeding occurred during scotophase when the insects were offered leaves from low-density and high-density sites, respec-

tively (Fig. 2, C and D; $P<0.005$ for each of the four interpopulation comparisons with the different types of food; Mann-Whitney test).

Source of foliage affected both crawling activity and total amount of feeding. Larvae from low-density populations fed for $\bar{x}=168\pm76$ min per 24 h (11.7% of the 24 h day) when offered leaves from low-density sites, but fed on foliage from high-density sites for only $x=48\pm40$ min (3.3% of 24 h; after square root transformation, $F=19.5$ with 1, 18 d.f.; $P<0.001$). Larvae from high-density populations fed for $\bar{x}=227\pm63$ min (15.7% of 24 h) on

leaves from low-density sites and $\bar{x}=170\pm65$ min (11.8%) on leaves from outbreak sites; this difference was not significant ($F=4.04$; $0.05<P<0.1$). When offered foliage from outbreak sites, larvae from high- and low-density populations produced $\bar{x}=93\pm61$ and $\bar{x}=209\pm147$ activity spikes per day, respectively. With leaves from low-density sites, they produced $\bar{x}=66\pm27$ (outbreak larvae) and $\bar{x}=68\pm47$ (low-density larvae) activity spikes. In a two-way ANOVA of logarithmically transformed data, source of foliage had a significant effect on activity of larvae ($F=9.57$ with 1,36 d.f.; $P<0.01$). Source of larvae and the interaction term were not significant ($F=1.75$ and 3.51, respectively).

Causes of density-related shifts in behaviour

Several authors have proposed that interactions among conspecifics can cause lepidopterous larvae to change their behaviour when population density increases (e.g. Klomp, 1966; Corbet, 1971; Rafes & Gninenko, 1973). Leonard (1967) postulated that feeding rhythms of gypsy moths are influenced by 'hunger' (and 'hunger-induced wandering') that occurs when larvae in dense populations interfere with each others' feeding. In our observations, however, larvae that were feeding or resting on leaves were rarely touched by other larvae; even at high-density sites this occurred only twice during 30 h of observation on individuals. When touched by other larvae the insects twitched their heads or abdomens once or twice, paused for several seconds, and then resumed their previous activity. Mutual feeding interference is probably not the direct cause of the observed variation in feeding rhythms.

Klomp (1966) suggested that occasional physical contact with conspecifics might, in itself, place stress on larvae of forest defoliators; such a mechanism could trigger density-related changes in larval quality even in moderately low-level populations (also see Campbell, 1978). Lance et al. (1986b), however, found that crowding per se had little or no effect on feeding rhythms of gypsy moth larvae.

Wallner & Walton (1979) suggested that food quality may be an important determinant of density-related differences in the behaviour and development of gypsy moth larvae. Quality of oak leaves declines in response to defoliation (Wallner & Walton, 1979; Schultz & Baldwin, 1982; Valentine et al., 1983). Indeed, in 1983 laboratory studies, mean pupal weights of females were reduced 12–42% when we reared larvae on leaves from our high-density sites rather than our low-density sites (Lance, 1985). Results of the feeding monitor tests indicate that differences in leaf quality also may be partially responsible for the increased rates of leaf- and tree-switching that occur in high-density populations. Furthermore, when Lance et al. (1986c) reared larvae from the third instar onward on poor quality food, the insects exhibited feeding rhythms characteristic of larvae in high-density populations. As was the case with field-collected larvae, these changes were not reversed by short-term (i.e. 24 h) exposure to a high quality diet. Changes in food quality appear to be the primary cause of density-related variation in the behaviour of gypsy moth larvae.

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