

## Developmental change in aggregation, defense and escape behavior of buckmoth caterpillars, *Hemileuca lucina* (Saturniidae)

Jennifer C. Cornell<sup>1</sup>, Nancy E. Stamp<sup>2</sup>, and M. Deane Bowers<sup>1</sup>

<sup>1</sup> Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

<sup>2</sup> Department of Biological Sciences, State University of New York, Binghamton, NY 13901, USA

Received June 18, 1986 / Accepted February 6, 1987

**Summary.** Changes in response to attack and the tendency to aggregate were examined in the six larval instars of the buckmoth, *Hemileuca lucina* (Saturniidae). In response to simulation of attack by a parasitoid and of biting by a predator, early instars (I, II, and III) exhibited defensive behavior much more often than escape behaviors, whereas late instar larvae (IV, V, and VI) usually resorted to escape rather than defend themselves. The situations in which attacked larvae were most likely to stimulate other group members to respond were: second and third instar larvae thrashing in response to simulation of a parasitoid or headrearing in response to simulation of a biting predator; and fourth, fifth and sixth instar larvae dropping in response to either stimulus. An index of reaggregation indicated that first instar larvae had difficulty reaggregating; second, third and fourth instar larvae reaggregated quickly; and fifth and sixth larvae dispersed. As larvae developed, the change from predominantly defense to escape behaviors paralleled the decline in tendency to aggregate.

caterpillars also have a variety of defense and escape behaviors, such as thrashing, biting, regurgitating, and dropping to the ground or spinning down on a silk strand (Stamp 1986 and references therein). In addition, they may either rid feeding sites of cues that predators may use to locate them or move some distance between feeding sites (Heinrich 1979; Stamp 1984b).

Gregarious, unpalatable larvae are particularly interesting because their unpalatability suggests that they may be immune from attack by most vertebrate predators. Such caterpillars advertise their unpalatability by warning coloration and reinforce that message by aggregation. In some cases, unpalatability may deter invertebrate predators (Berenbaum 1984; Ferguson and Metcalf 1985). Aggregation and group coordinated responses may aid and enhance such defenses (Tostowaryk 1971, 1972; Stamp 1982). Thus, gregarious, unpalatable larvae would seem to be well protected against their natural enemies. However, field observations indicate that often such caterpillars are subject to high levels of predation and parasitism (e.g. Stamp 1984a). In addition, larval response to natural enemies and aggregation behavior may change as larvae develop (Suzuki et al. 1980), potentially altering their susceptibility to predators.

Several factors may contribute to a pattern of change in response to enemies and tendency to aggregate. (1) The effectiveness of defense and escape behaviors may depend on the size (developmental stage) of the caterpillar relative to the attacker and on the changing set of natural enemies during the larval period (Morris 1963; Stamp 1984a, 1986). For example, fifth instar tent caterpillars (*Malacosoma californicum*, Lasiocampidae) were generally aggressive enough to ward off predatory pentatomids, whereas smaller instars were not (Iwao and Wellington 1970). (2) Climatic conditions may

### Introduction

Caterpillars are well known for a diversity of defenses against predators and parasitoids. For example, they may have stinging hairs or bristles, they may have defensive glands such as osmeteria (Eisner 1971; Honda 1981), they may be unpalatable due to chemicals sequestered from their host-plants and advertise that by conspicuous coloration (Blum 1981), they may build webs or roll leaves into which they retreat when disturbed or attacked (Fitzgerald 1980; Stamp 1984a), or they may be cryptically-colored (Heinrich 1979). Many

change over the larval period and thus alter the costs and benefits of aggregation. For instance, in early spring, tent caterpillars (*Malacosoma* sp.) may benefit from a communal web because it ameliorates temperature fluctuations, in particular quick frosts, and provides an environment with higher humidity; but in late spring, frost is less likely, relative humidity of the air is higher, and internal web temperatures are often too warm for the larvae (Sullivan and Wellington 1953; Heinrich 1981; Segerra-Carmona and Barbosa 1983). (3) Availability of the hostplant, especially high quality leaves, relative to the changing mobility of larvae may also alter the costs and benefits of aggregation. For example, Tsubaki and Shiotsu (1982) suggested that gregarious larvae may utilize food more economically by feeding in larval groups in early instars, but that for late instars, the frequency and distance of travel to food may become prohibitive for large groups, thus leading to dispersal and individual foraging.

Our objectives in this study were to document changes in larval aggregation, defense and escape behavior. We used larvae of the buckmoth, *Hemileuca lucina* Hy. Edw. (Saturniidae). These larvae are gregarious, black with urticating spines, and, by such behavior and coloration, quite conspicuous. A series of laboratory experiments addressed these specific questions: (1) What behaviors do these larvae exhibit in response to being attacked and how do those behaviors change with instar? (2) Does the array of responses differ when the type of attacker (stimulus) differs? (3) Does the tendency of larvae to aggregate change as larvae develop, and, if so, is that related to changes in larval responses to attack?

## Methods

*Hemileuca lucina* is univoltine with adult flight and oviposition occurring in mid to late September. Egg masses are laid in rings around the base of stems of the hostplant, *Spiraea latifolia* Ait. (Borkh.) (Rosaceae). The eggs over-winter and hatch in May in Massachusetts. The mean weight of an unfed larva at hatching is 1.17 mg ( $n=265$ ). Mean weights of larvae in the first five instars, four days after molt were: Instar I,  $\bar{x}=5.15$  mg ( $n=172$ ); Instar II,  $\bar{x}=12.66$  mg ( $n=152$ ); Instar III,  $\bar{x}=38.24$  mg ( $n=134$ ); Instar IV,  $\bar{x}=89.63$  ( $n=127$ ); Instar V,  $\bar{x}=249.66$  ( $n=111$ ). The larvae are gregarious during the first five instars, but the number of larvae per group decreases during the fourth and fifth instars and occasionally solitary individuals are found. Changes in group size during that period reflect both mortality and subdivision of the aggregations. The sixth instars are solitary, and may disperse from the hostplant and feed on other species of rosaceous plants (Stamp and Bowers, unpublished data). Larvae pupate in late June in the soil, and aestivate through the remainder of the summer.

## Larval response to attack

In late May 1984, five egg masses of *H. lucina* were collected in Dover, Massachusetts. A group of 50 larvae from each mass was reared in the laboratory on leaves of *S. latifolia*. Larvae were reared at ambient temperatures in the laboratory (about 22° C) and seasonal photoperiod provided through a large window. At the mid-point of each instar, 25 randomly-chosen larvae from each group were stimulated with one of two artificial stimuli designed to simulate the attack of naturally occurring predators and parasitoids (Stamp 1986). A small, two-haired brush was used to simulate the touch of a parasitoid and a pinch with forceps was used to simulate the attack of a predator such as a bird or predaceous invertebrate. Each stimulus was applied three times to the posterior of an individual larva at five second intervals, unless the larva responded sooner; then a second larva in the group was tested, and so on. Each group of 25 larvae was tested first with the forceps, allowed to rest and feed undisturbed for 24 h, and then tested with the two-haired brush.

The larval behaviors exhibited in response to these two stimuli were categorized as:

1. *Headrear*: the head and anterior portion of the body reached backwards towards the posterior part of the caterpillar.
2. *Thrash*: the head and anterior portion of the body swung from side to side.
3. *Bite*: the mandibles opened and closed.
4. *Regurgitate*: larva produced a drop of dark brown fluid, probably from the foregut. If it did not contact any resistance, the drop was re-imbibed by the caterpillar.
5. *Drop*: larva writhed, released its hold on the twig or other substrate, fell to the ground, and then moved off rapidly.
6. *Curl*: head and posterior were tucked under the body causing larva to fall from the twig or other substrate. Larva remained still when it reached the ground.
7. *Cringe*: larva contracted lengthwise with head and posterior slightly elevated, and released hold of twig or other substrate. Larva remained still when it reached the ground.
8. *No response*: larva did not respond to the stimulus.

Individuals were tested while in their group with the larvae resting or feeding on a sprig of *S. latifolia* in water. If the group became agitated during the experiment, testing was suspended for three minutes, which was sufficient time for the larvae to resume their previous activities.

Where appropriate, chi-square contingency tables were used for analysis. When  $df=1$ , Yate's correction for continuity was applied and is denoted  $\chi_c^2$ . Subdivision of contingency tables was performed as described in Zar (1984).

## Larval aggregation

Aggregation behavior was measured in each of the six instars and for group sizes of 5, 10, and 20, with five replicates of each. The larvae used for these experiments were from the five groups used for the defensive behavior experiments. Each set of 5, 10, and 20 larvae were taken from a single sibling group, so that comparisons among different group sizes could be made on larvae from a single egg mass.

To measure aggregation tendency, individuals from a sibling group were placed in an arena, at a pre-determined distance from each other, and then monitored for tendency to reaggregate. Larvae were initially placed in a ring on a sheet of white paper, with five body lengths between each individual. The body lengths used to separate larvae were calculated by measuring larvae in each instar, and they were: Instar I – 6.4 mm ( $\pm 0.5$  SE,  $n=220$ ); Instar II – 10.2 mm ( $\pm 0.3$  SE,  $n=196$ ); Instar III – 13.9 mm ( $\pm 0.2$  SE,  $n=154$ ); Instar IV – 24.1 mm ( $\pm 0.4$  SE,  $n=144$ ); Instar V – 43.2 mm ( $\pm 1.3$  SE,  $n=$

110); Instar VI – 67.3 mm ( $\pm 2.0$  SE,  $n=103$ ). For the test, larvae were allowed to move freely for 10 min, during which time nearest-neighbor distances were measured for each larva every 2 min. The distance between each individual and its nearest neighbor was measured using calipers in Instars I–III and a tape measure in Instars IV–VI. We developed an index of reaggregation for the group, which was calculated for each trial with each group at every 2-min interval, as follows:

$$\frac{(\text{original distance separated}) - (\text{mean nearest neighbor distance})}{(\text{original distance separated})} \times 100$$

The mean nearest neighbor distance was calculated from the mean of all nearest neighbor distances measured in each trial. To eliminate any cues left by the silken trails produced by the larvae, a clean sheet of paper was used for each test.

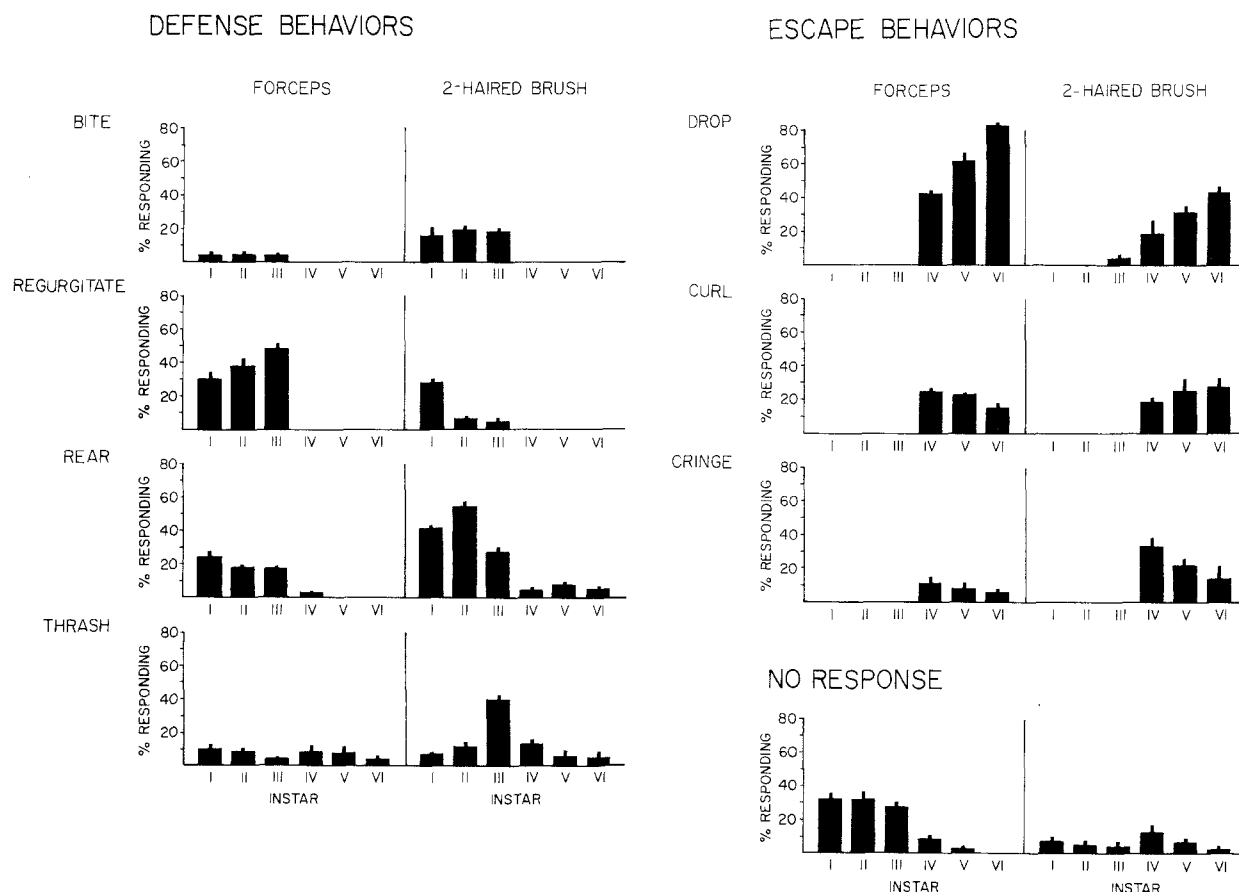
## Results

### Larval response to attack

In general, larval behavior changed with instar; as larvae grew, new behaviors were observed, while others disappeared. The behaviors elicited by the two-haired brush and the forceps can be divided

into two general categories: defense and escape (Fig. 1). Defense behaviors included headrearing, thrashing, biting, and regurgitating. These behaviors may function to deter or deflect attack, and in doing so, individuals need not leave the group. In contrast, escape behaviors, defined as dropping, cringing, and curling, disrupted the group as larvae fell to the ground.

The distribution of behaviors exhibited by larvae showed a significant change between early (I, II, and III) and late (IV, V, and VI) instars. Early instars were more likely to defend themselves, whereas late instars were more likely to try to escape (Fig. 1; Table 1). Chi-square analysis of Defense versus Escape behaviors (Table 1) showed that there was a significant difference in the distribution of these behaviors over instars for both stimuli (forceps –  $\chi^2 = 729.40$ ,  $df = 5$ ,  $P < 0.001$ ; brush –  $\chi^2 = 786.62$ ,  $df = 5$ ,  $P < 0.001$ ). Subdivision of the contingency table showed that this difference was due to a reversal in the incidence of Defense versus Escape behaviors between the early (I, II, and III) and late (IV, V, and VI) instars (forceps –  $\chi^2 =$



**Fig. 1.** Distribution of larval behaviors of *H. lucina* shown in response to stimulation by pinching with forceps or touching with a two-haired brush. The behaviors are expressed as the percentage of the total responses to each of these stimuli in each instar. Means with standard error bars are shown

**Table 1.** Total number of defense and escape behaviors exhibited by *H. lucina* larvae in response to stimulation by brush and forceps. These numbers are the totals for all five groups of larvae

	Instar					
	I	II	III	IV	V	VI
<b>Brush</b>						
Defense	193	210	210	36	27	22
Escape	0	0	5	117	133	152
No Response	11	10	9	18	6	4
<b>Total</b>	<b>204</b>	<b>220</b>	<b>224</b>	<b>171</b>	<b>166</b>	<b>178</b>
<b>Forceps</b>						
Defense	118	129	131	22	17	5
Escape	0	0	2	153	172	147
No Response	57	63	50	13	3	0
<b>Total</b>	<b>175</b>	<b>192</b>	<b>183</b>	<b>188</b>	<b>192</b>	<b>152</b>

778.60,  $df=1$ ,  $P<0.001$ , brush -  $\chi^2_c=722.83$ ,  $df=1$ ,  $P<0.001$ ) (Fig. 1; Table 1).

For three of the behaviors, headrearing, thrashing, and dropping, the response of the tested individual often stimulated neighboring individuals to react similarly (Table 2). Such group behaviors lasted as much as 30 min.

The larvae responded to the two-haired brush and forceps somewhat differently. Early instar larvae (I, II, and III) were much more responsive to the two-haired brush, simulating a parasitoid, than to the forceps, simulating a biting predator (Response vs No Response,  $\chi^2_c=145.85$ ,  $P<0.001$ ). In contrast, in the late instars (Instars IV, V, VI), larvae were equally responsive to the two stimuli ( $\chi^2_c=3.26$ ,  $P>0.05$ ).

### Larval aggregation behavior

Larval instar had a significant effect on tendency to reaggregate (ANOVA after arcsine transforma-

tion,  $F=378.93$ ,  $df=5,72$ ,  $P<0.001$ ) (Fig. 2). First instar larvae seldom reaggregated, probably due to their low mobility relative to other instars. Fifth and sixth instars also showed little reaggregation, and tended to disperse. Instars II, III, and IV became increasingly aggregated with time, and after 10 min, were usually massed together. Group size had no effect on the tendency to aggregate (ANOVA after arcsine transformation,  $F=0.976$ ,  $df=2,72$ ,  $P>0.50$ ), nor was there an interaction effect of group size and instar (ANOVA after arcsine transformation,  $F=1.31$ ,  $df=10,72$ ,  $P>0.10$ ).

### Discussion

In *Hemileuca lucina*, both response to attack and tendency to aggregate changed greatly between early and late instars. Defensive behaviors exhibited by the early instars (biting, regurgitating, headrearing and thrashing) promoted group cohesion, by the larvae staying in place to defend themselves, during the same period when tendency to aggregate by these larvae was high. It was also in the early instars that the group-coordinated defenses of thrashing and headrearing occurred. Those behaviors were observed in both field and laboratory aggregations in response to natural predators (predatory hemipterans) and parasitoids (tachinid flies), with aggregations responding defensively for up to 30 min (Cornell, personal observation; Bowers and Stamp, unpublished data).

Even though first instar larvae showed little reaggregation in the laboratory test, they apparently have a strong tendency to aggregate but had some difficulty doing so, probably due to their small size. In the field, newly-hatched *H. lucina* caterpillars aggregated on their egg masses for 12–36 h before moving up into the foliage of their hostplant rather than moving immediately after hatching. That phenomenon may be important in ensuring a sufficiently dense silk trail for larvae

**Table 2.** Percent of total responses of a particular behavior (total number of those behaviors is in parentheses), where neighboring larvae responded to stimulation by brush or forceps in the same way as the initially stimulated larva. Thus 5.9% of 17 thrashing responses elicited thrashing by other larvae in the group. These are totals for all five groups of larvae

Behavior	Stimulus	Instar					
		I	II	III	IV	V	VI
Thrash	Brush	5.9 (17)	70.0 (26)	43.0 (93)	3.6 (28)	8.3 (12)	0.0 (12)
	Forceps	5.6 (18)	7.7 (13)	40.0 (6)	0.0 (19)	0.0 (17)	0.0 (5)
Headrear	Brush	3.7 (66)	18.3 (120)	8.2 (62)	0.0 (8)	0.0 (13)	0.0 (10)
	Forceps	14.3 (42)	42.1 (38)	5.9 (34)	0.0 (4)	—	—
Drop	Brush	—	—	0.0 (5)	20.5 (30)	13.5 (50)	27.0 (78)
	Forceps	—	—	0.0 (2)	32.1 (81)	22.9 (109)	28.1 (114)

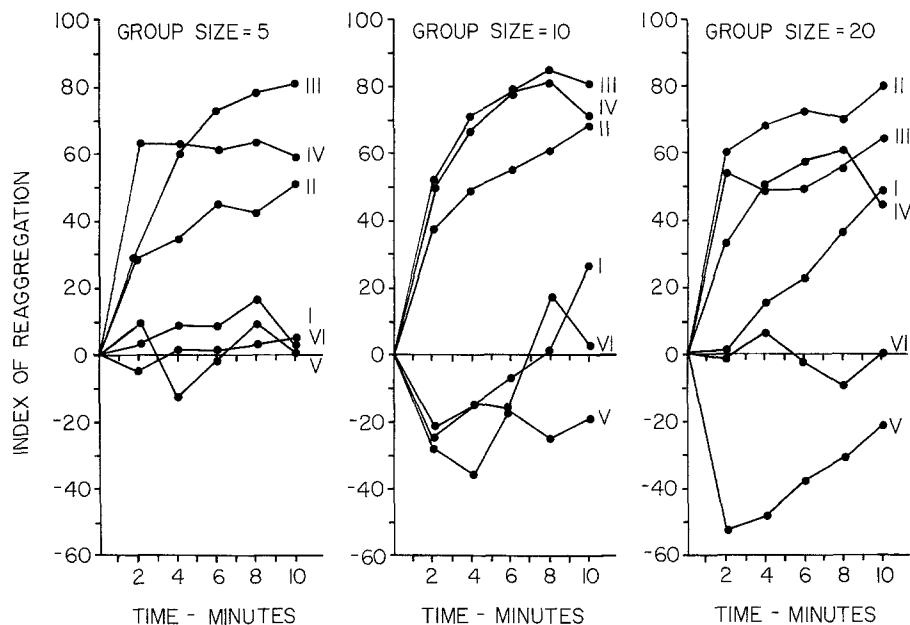


Fig. 2. Reagggregation behavior of *H. lucina* larvae. An index of 100 represents complete reagggregation; 0 represents individuals remaining at or returning to original test distances from each other; negative numbers indicate that individuals are farther apart than initial test distances

to follow and thus end up reagggregated at a feeding site (Fitzgerald 1980), and in providing a fresh trail of pheromone (Capinera 1980). The presence of an aggregation of a certain minimum size appears to be important for the survival of first instar larvae. For example, survivorship of *H. lucina* larvae in groups of 20 was 88%, while that of larvae in groups of 5 was only 35% (Bowers and Stamp, unpublished data). Those larvae in small groups ate little and wandered around the container most of the time, apparently seeking an aggregation.

In contrast to the pattern for early instars, the escape behaviors shown by the late instar larvae contributed to subdivision of the aggregations and eventual scattering of individuals. Similarly, the results of the reagggregation tests showed that larvae in Instars V and VI tended to disperse rather than aggregate. Field observations support the results of the laboratory experiments. Group size of individual aggregations declined steadily with larval instar and all Instar VI larvae were solitary (Stamp and Bowers, unpublished data). When aggregations of late instar larvae were disturbed in the field, either accidentally by us or by tachinid flies trying to parasitize them, with the result that a larva dropped from the hostplant, we frequently saw most or all group members following suit within a few seconds. Those larvae on the ground often reagggregated with each other, but usually did not rejoin the larvae remaining on the hostplant. This behavior would contribute to subdivision of the aggregations despite a tendency to aggregate, as we found for Instar IV larvae (Figs. 1 and 2). Other factors that may contribute to group size

declining steadily over the larval period include larvae blown from the aggregation by gusty wind, larvae wandering after defoliating the hostplant, and larvae disturbed or killed by predators (Stamp, personal observation).

One pattern then, is that early instar larvae defend themselves and tend to stay with their group, indicating that the risks associated with escape are great, the advantages of being in a group are significant, or both. Some of the risks involved in resorting to escape (in particular by leaving the hostplant) are those of being found by ground predators, becoming desiccated, and spending time and energy in locating a hostplant (Dethier 1959; Rausher 1979). Some of the advantages of remaining within the group may be that groups facilitate finding high quality food, quick travel to such sites, and overwhelming hostplant defenses (Ghent 1960; Fitzgerald 1976; Schultz 1983). In addition, aggregated larvae may be better able to thermoregulate behaviorally (Seymour 1974), reduce water loss (Stamp and Bowers, unpublished data) and provide effective defense against natural enemies (Tostowaryk 1971, 1972).

When larvae switch to escape behaviors, it suggests that the risks associated with escape are reduced, the advantages of being in a group have declined, or both. By the fourth instar, *Hemileuca lucina* larvae are about 24 mm in length, weigh about 100 mg, and are likely to be the same size or larger than most invertebrate predators and parasitoids. They are thus better able to defend themselves than smaller caterpillars, on a one-to-one predator-prey basis (Stamp 1986). Larger larvae

are also better able to thermoregulate behaviorally than smaller larvae (Casey and Hegel 1981), to avoid desiccation (Stamp and Bowers, unpublished data), and to locate a hostplant (Rausher 1979). Therefore, it is not surprising that across instars, an increase in size and a declining tendency to aggregate parallels an increased likelihood of an escape response. That same pattern has been observed in *Hyphantria cunea* (Suzuki et al. 1980, and refs. therein).

Instar IV appears to be pivotal for *Hemileuca lucina*. The change at that point in responses to enemies and tendency to aggregate probably reflects a summation of factors, such as the changing body-size ratio of larvae to their enemies and possibly the kinds of natural enemies they encounter, changing abiotic conditions (from relatively cool spring temperatures to warmer in early summer), and declining leaf quality in hostplants (Stamp and Bowers, unpublished data) coupled with the tendency of these caterpillars to defoliate their hostplants. Since these factors may vary in expression among other species of gregarious caterpillars, that pivotal instar may vary as well.

*Acknowledgements.* We thank T.D. Fitzgerald and D.M. Gordon for comments on the manuscript. J. Cornell and D. Bowers were supported by the Clark Fund of Harvard University and NSF grant BSR-8307353 to D. Bowers, and N. Stamp by a post-doctoral fellowship from the University of California at Davis.

## References

- Berenbaum MR (1984) Mantids and milkweed bugs: Efficacy of aposematic coloration against invertebrate predators. *Am Midl Nat* 111:64–68
- Blum MS (1981) *Arthropod Defenses*. Academic Press, New York, p 562
- Capinera JL (1980) A trail pheromone from silk produced by larvae of the range caterpillar, *Hemileuca oliviae* (Lepidoptera: Saturniidae), and observations on aggregation behavior. *J Chem Ecol* 6:655–664
- Casey TM, Hegel JR (1981) Caterpillar setae: insulation for an ectotherm. *Science* 214:1131–1133
- Dethier VG (1959) Food-plant distribution and density and larval dispersal as factors affecting insect populations. *Can Entomol* 112:731–738
- Eisner T (1971) Chemical defense against predation in arthropods. In: Sondheimer E, Simeone JB (eds) *Chemical ecology*. Academic Press, New York, pp 157–217
- Ferguson JE, Metcalf RL (1985) Cucurbitacins: plant-derived defensive compounds for diabetocites (Coleoptera: Chrysomelidae). *J Chem Ecol* 11:311–318
- Fitzgerald TD (1976) Trail marking by larvae of the eastern tent caterpillar. *Science* 194:961–963
- Fitzgerald TD (1980) An analysis of daily foraging patterns of laboratory colonies of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae), recorded photoelectrically. *Can Entomol* 112:731–738
- Ghent AW (1960) A study of the group-feeding behavior of larvae of the Jack Pine Sawfly, *Neodiprion pratti banksianae* Roh. *Behaviour* 16:110–148
- Heinrich B (1979) Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. *Oecologia* (Berlin) 42:325–337
- Heinrich B (1981) Ecological and evolutionary perspectives. In: Heinrich B (ed) *Insect thermoregulation*. Wiley, New York, pp 235–302
- Honda K (1981) Larval osmeterial secretions of the swallowtails (*Papilio*). *J Chem Ecol* 7:1089–1113
- Iwao S, Wellington WG (1970) The influence of behavioral differences among tent-caterpillar larvae on predation by a pentatomid bug. *Can J Zool* 48:896–898
- Morris RF (1963) The effect of predator age and prey defense on the functional response of *Podisus maculiventris* Say to the density of *Hyphantria cunea*. *Can Entomol* 99:24–33
- Rausher MD (1979) Egg recognition: its advantage to a butterfly. *Anim Behav* 27:1034–1040
- Schultz JC (1983) Habitat selection and foraging tactics of caterpillars in heterogeneous trees. In: Denno RF, McClure MS (eds) *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, pp 61–90
- Segerra-Carmona A, Barbosa P (1983) Nutrient content of four rosaceous hosts and their effects on development and fecundity of the eastern tent caterpillar, *Malacosoma americanum* (Fab.) (Lepidoptera: Lasiocampidae). *Can J Zool* 61:2868–2872
- Seymour RS (1974) Convective and evaporative cooling in sawfly larvae. *J Insect Physiol* 20:2447–2457
- Stamp NE (1982) Behavioral interactions of parasitoids and Baltimore checkerspot caterpillars, *Euphydryas phaeton*. *Environ Entomol* 11:100–104
- Stamp NE (1984a) Interactions of parasitoids and checkerspot caterpillars, *Euphydryas* spp. (Nymphalidae). *J Res Lepid* 23:2–18
- Stamp NE (1984b) Foraging behavior of tawny emperor caterpillars (Nymphalidae: *Asterocampa clyton*). *J Lepid Soc* 38:186–191
- Stamp NE (1986) Physical constraints of defense and response to invertebrate predators by pipevine caterpillars (*Battus philenor*: Papilionidae). *J Lepid Soc* 40:191–205
- Sullivan CR, Wellington WG (1953) The light reactions of larvae of the tent caterpillars, *Malacosoma disstria* Hbn., *M. americanum* (Fab.), and *M. pluviale* (Dyar) (Lepidoptera: Lasiocampidae). *Can Entomol* 85:297–310
- Suzuki N, Junimi Y, Uematsu S, Kobayashi K (1980) Changes in spatial distribution pattern during the larval stage of the fall webworm, *Hyphantria cunea* Drury (Lepidoptera: Arctiidae). *Res Popul Ecol* 22:273–283
- Tostowaryk W (1971) Relationship between parasitism and predation of diprionid sawflies. *Ann Entomol Soc Am* 64:1424–1427
- Tostowaryk W (1972) The effect of prey defense of the functional response of *Podisus modestus* (Hemiptera: Pentatomidae) to densities of the sawflies *Neodiprion swainei* and *N. pratti banksianae* (Hymenoptera: Neodiprionidae). *Can Entomol* 104:61–69
- Tsubaki Y, Shiotsu Y (1982) Group feeding as a strategy for exploiting food resources in the burnet moth *Pryeria sinica*. *Oecologia* (Berlin) 55:12–20
- Zar JH (1984) *Biostatistical analysis*, 2nd ed. Prentice-Hall, New Jersey, p 718