Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae)

N.E. Stamp[1] **and M.D. Bowers**[2]
[1] Department of Biological Sciences, State University of New York, Binghamton, NY 13901, USA
[2] Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

Summary. We examined how predation by vespid wasps, *Polistes dominulus* and *P. fuscatus*, affected the behavior, growth rate and survivorship of aggregated caterpillars of *Hemileuca lucina* (Saturniidae). Although these larvae can exhibit a variety of defense and escape behaviors, in general larvae reacted to wasp attacks by clinging to the hostplant. Neighboring larvae in the aggregation responded by leaving the feeding site and moving to the interior or base of the plant. To determine whether wasp attack affected the behavior and growth of the caterpillars that escaped, a field experiment was conducted with treatments of: 1) larvae exposed to wasps, 2) larvae protected from wasps, and 3) larvae protected from wasps but with the attack of wasps simulated (= harassment). Over just one instar, protected larvae gained significantly more weight than the harassed larvae, which in turn weighed significantly more than the larvae that escaped the wasps. The behavior of attacked and harassed larvae differed from that of the protected larvae; the disturbed larvae often fed in smaller groups and in shaded portions of the plant where only mature leaves were available. A laboratory experiment showed that at 35° C (daytime temperature) larvae had significantly higher relative growth rates and significantly shorter instar duration than larvae reared at 25° C. Our results suggest that wasps, in addition to killing caterpillars, indirectly affect larval fitness by slowing larval growth, at least in part by forcing larvae into cooler microhabitats where leaves are of lower quality.

Key words: Escape behavior – Food quality – Larval development – Natural enemies – Suboptimal microhabitats

Foraging patterns of caterpillars reflect the need to both find food and avoid predators, which may interfere with feeding and hence reduce growth rates (Heinrich 1979). One foraging pattern of particular interest is that of gregarious, unpalatable larvae because they are conspicuous due to their aggregation and warning coloration. Such larvae often bask in exposed locations (Capinera et al. 1980; Porter 1982), thereby increasing their body temperature, ingestion rate and thus growth rate (Sherman and Watt 1973; Casey 1976; Rawlins and Lederhouse 1981; Grossmueller and Lederhouse 1985; Knapp and Casey 1986). However, such behavior combined with aggregation and conspicuous col-

oration, render such larvae particularly susceptible to natural enemies that are undeterred by their defenses.

Predatory wasps are often important predators of caterpillars (Roush and Akre 1978; Akre 1982; Evans 1987). The social paper wasps (Vespidae), in particular *Polistes*, harvest caterpillars, which are masticated and then fed to developing larvae at the nest (Evans and West Eberhard 1970). However, the interactions of caterpillars and such predators have rarely been studied, except in agricultural situations (Rabb and Lawson 1957; Nakasuji et al. 1976; Gillaspy 1979; Gould and Jeanne 1984).

In this study, we examined the effect of predatory vespid wasps on the foraging and defensive behavior of the gregarious larvae of *Hemileuca lucina* Hy. Edw. (Saturniidae). Specifically, we used field experiments to determine the effect of larval group size on vulnerability to the wasps and the effect of wasp attack and harassment on larval behavior, growth and survivorship. In a laboratory experiment, we compared the growth rate of larvae at temperatures and diets representative of those that undisturbed and attacked *H. lucina* caterpillars are likely to encounter.

Methods

Background on prey and predators

Hemileuca lucina is univoltine, with flight and oviposition occurring in late September in Massachusetts. The egg masses are laid around the stem of the hostplant, *Spiraea latifolia* (Ait.) Borkh. (Rosaceae), and range in size from 42–235 eggs ($\bar{x} = 146$, $n = 176$ masses; Bowers and Stamp 1987). The larvae hatch in May and feed through June. In the first five instars, the larvae are black and consequently the aggregations are extremely conspicuous. In the fifth instar, larvae may live either in groups or alone, whereas sixth instar larvae are solitary. The larvae pupate in the soil where they aestivate until eclosion in the fall.

On 3 June 1985, we placed 619 newly-molted second instar *H. lucina* larvae in an experimental garden (Cambridge, Mass.) with regularly-spaced *S. latifolia* hostplants to examine survivorship relative to group size. Much to our surprise, 24 h later only 16 larvae (2.6%) were found alive, and most of these were at the base of plants where no leaves occurred.

Numerous wasps (primarily *Polistes dominulus* Christ but also *P. fuscatus* Fabricius: Vespidae) were searching the plants and attacking the remaining larvae. The biology

of the wasps *P. fuscatus* and *P. dominulus* (previously *P. gallicus*) is similar (West Eberhard 1969). *Polistes dominulus* is a European species recently introduced into the Boston area (Hathaway 1981), where it is now abundant. Already that species has spread to southern New Jersey (M. Raveret-Richter, pers. comm.).

Level of predation

In response to the observed wasp predation on *H. lucina* larvae, we set up an experiment using *S. latifolia* plants to determine the effect of larval group size on predation rate by these wasps. We tested group sizes of 5 and 10 in instars II, III, and IV and solitary larvae of instar VI. Although the mean size of egg masses was 146 eggs, larval aggregations found in the field were often much smaller. Aggregations of instar I were composed sometimes of fewer than 20 individuals, and the mean number of larvae per group was 12.9 ($\pm$5.4 SD, n=11) for instar IV and 10.3 larvae ($\pm$4.2 SD, n=18) for instar V. The group sizes of 5 and 10 were within the range of group sizes found in field situations and could be censused quickly and accurately.

Because the larvae curled up and tended to drop from the plants when handled, they were placed on the plants using paper cones (diameter of 4 cm, depth of 4 cm) attached to the top of a stem about 1 m in height. Within 15 min, larvae moved out of the cones and began feeding. There were 8 replicates of each group size. Each plant had one group of larvae, alternatively 5 or 10 larvae per group.

Larvae were censused every 10 min for the first hour and again at the end of the second hour. Instar II larvae were tested on sunny afternoons (4 and 11 June 1985) with temperatures ranging from 21° to 26° C. Instar III larvae were tested on 15 June and 1 July 1985, instar IV larvae on 19 June 1985 and instar VI larvae on 20 June 1985 under similar conditions.

Effect of wasp attack on larvae

Often, while a wasp attacked one member of a group, the other larvae moved from a feeding site on new leaves in full sunlight to a shady portion of the interior of the plant where only mature laeves were available. In some cases, larvae even moved off the plant altogether. To determine the effects of wasp attack on larval behavior, growth and survival, we set up an experiment that made use of both wasp attack and simulated wasp harassment. On 29 May 1986, 5 groups of 25 newly-molted instar III *H. lucina* were alloted to each of three treatments: 1) Control, 2) Predation and 3) Harassment. Each treatment had 5 replicates. Initial larval weights among the assigned treatments were similar (one-way ANOVA; df=2,12; P>0.50; average weight per larva=0.040 g). Each larval group was placed on a plant; the plants were 1 m apart in a 3 × 5 array in the experimental garden. The treatments were assigned sequentially to the plants to ensure adequate interspersion. Control larvae were protected by a screen cage (mesh of 1.5 mm^2). The cages were 75 cm in diameter and 120 cm in height with the bottom 15 cm buried in the ground and held in place by 15 cm high aluminum barriers. In the Predation treatment, the groups of caterpillars were placed on plants without cages, allowing the wasps free access to the caterpillars. Tanglefoot on aluminum barriers (15 cm high) around the plants prevented the larvae from leaving.

Because we did not know how many larvae would survive the Predation treatment, we set up a third treatment, Harassment, to ensure that at the end of the experiment we would have caterpillars that had been exposed to representative wasp harassment. We could then compare growth rates between undisturbed and attacked (i.e. harassed) caterpillars. Larval groups assigned to the Harassment treatment were placed on caged plants like the Control larvae; however, these larvae were harassed by simulating wasp attack, by using forceps to grasp the caterpillars. This was done by opening windows on the cages and harassing the larvae at 30-min intervals from 1000 to 1400 h for two consecutive days (29–30 May). Each harassment period lasted 10 min, and during that time, each group was disturbed about 5 times. That was accomplished by disturbing the first group for 5 s, then the second group for 5 s and so forth for a total of 10 min. All caterpillars on the plants were harassed; larvae on the ground were left alone. This procedure of harassment, including timing and frequency, was based on our observations of *P. dominulus* attacking *H. lucina* in May-June 1985.

For the first two days of the experiment, we checked the Control and Predation groups hourly to determine: 1) the number of subgroups, 2) whether they were feeding and, if so, on mature or new leaves, and 3) whether they were in sunlight or shade. We defined new leaves as those on unlignified stems; mature leaves were those on new stems that had already lignified that spring. The Harassment groups were observed immediately before harassment and 20 min afterwards during the first two days. For the remaining 9 days, all larvae were checked every other day. The larvae were collected on 9 June after they had molted to the next instar.

Growth rate of Hemileuca lucina larvae

Preliminary observations indicated that, in the absence of wasps, larvae usually fed on new leaves on branch tips and basked there as well. In contrast, larvae exposed to wasps were more likely to wander from the main group and find themselves on the mature leaves that were abundant in the sheltered and shaded interior of the plant. Furthermore, larvae feeding in the interior of a plant faced quite a different microclimate than larvae feeding at the tips of branches. Larval body temperatures reached only about 25° C, which is the mean maximal temperature in June in our study areas in Massachusetts (Natl. Climatic Data Center 1983), rather than approaching 35° C, that could be obtained by caterpillars basking in full sunlight (Stamp and Bowers, unpubl. data). We suspected that wasp harassment was reducing larval growth by forcing caterpillars to feed under suboptimal conditions.

Therefore, we examined the effect of new and mature foliage diets and daytime temperatures of 25° and 35° C on the growth rate of *H. lucina* larvae. To determine the effect of these different conditions on larval growth rates, we placed 15 caterpillars in each of 4 treatments: 1) new leaves and 25° C day:15° C night, 2) new leaves and 35° C day:15° C night, 3) mature leaves and 25° C day:15° C night, and 4) mature leaves and 35° C day:15° C night. These larvae were obtained in the first instar and were from a single egg mass. They were reared on new leaves in a growth chamber at 25° C day:15° C night with 16 h day:8 h night. When the caterpillars began molting to in-

Table 1. Effect of group size of larvae on predation by wasps. Heterogeneity test of 2×2 contingency table (as described by Zar 1974) indicated that replicates from day 1 and day 2 could be pooled ($P > 0.10$). Chi square analysis (with Yates correction for continuity) of the pooled data yielded a significant difference between group sizes in number of instar II larvae surviving attack by wasps after 2 h ($\chi^2 = 8.229$, df = 1, $P < 0.005$). No significant differences between group sizes were found in number of larvae surviving for instar III and IV larvae ($\chi^2 = 0.030$, df = 1, $P > 0.75$; $\chi^2 = 1.321$, df = 1, $P > 0.25$, respectively)

Instar	Percent larvae surviving	
	# Larvae per group	
	5	10
II	1.2%	13.7%
III	21.2%	19.4%
IV	22.5%	12.5%

Fig. 1. Rate of predation by wasps on instar II *H. lucina*. Mean number of larvae killed ± 1 SE is shown. Numbers above histogram bars indicate number of wasps at larval aggregations during each census period. **A** 4 June 1985, **B** 11 June 1985

star IV, they were isolated without food. When they completed molting, larvae were weighed and placed individually in 0.5 l containers with leaves in aquapics. The larvae were checked twice a day and given additional food as needed. When the larvae began to molt, the food was removed. The newly-molted, unfed larvae were weighed, frozen, and dried at 50° C for 5 days to achieve constant weight. Relative growth rate (RGR) was calculated on a dry weight basic, using the methods of Waldbauer (1968).

Results

Level of predation

Group size affected vulnerability to wasp predation when caterpillars were small but not when they were large. For instar II larvae, survival was affected by group size (Table 1): groups of 5 larvae were depleted more rapidly than groups of 10 (Fig. 1). In contrast, survival was independent of group size for instar III and IV larvae (Table 1). Whereas instar II larvae were found and killed by the wasps before they were able to move very far down the host plant, instar III and IV larvae moved more quickly and some even reached the ground. None of the 16 instar VI larvae that were placed individually on plants were killed.

When the wasps found a larval aggregation, they flew or walked up to the larvae, and then attacked the first larva encountered by biting it repeatedly, usually in the thoracic and mid-dorsum regions. They did not sting the caterpillars. They manipulated instar II larvae into balls and caried them off, whereas larvae of instars III and IV were torn to pieces and then carried away. The remains were either left or fell to the ground. Often, more than one wasp was seen at an aggregation and several times wasps fought over caterpillars. The wasps followed the caterpillars down the host plant, palpating with their antennae along silk trails, eaten leaves and frass.

Escape behavior and large larval size seemed to be effective against predation by wasps. The wasps had more difficulty, handling larvae of instars III and IV due to their large size (mean wet weight = 0.192 g ± 0.035 SD, $n = 36$ larvae and mean weight = 0.332 g ± 0.070 SD, $n = 40$, respectively), compared to the smaller instar II larvae (mean
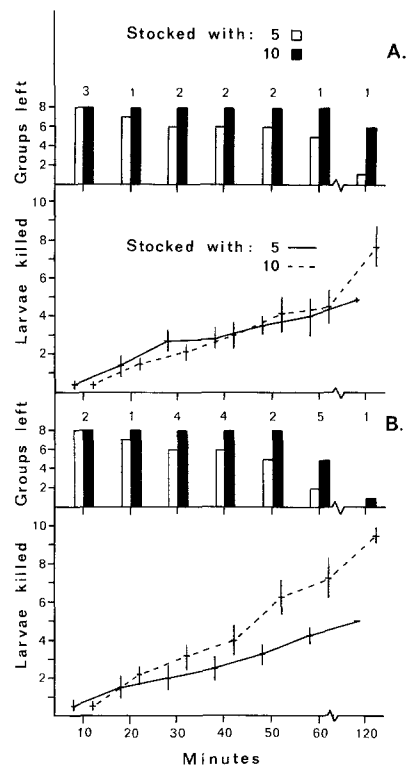
weight of 0.027 g ± 0.006 SD, $n = 20$). Ability to escape also increased as the larvae developed, mainly because the larger larvae moved faster and were more likely to drop off the plant. For example, of 48 instar III larvae alive at the end of the tests, 69% escaped by reaching the ground and, of 19 instar IV larvae alive at the end of a 2-h test, 95% reached the ground. Excluding those that dropped to the ground, instar III larvae traveled 23.2 cm per h (± 22.6 SD, $n = 98$) and instar IV larvae moved 16.0 cm per h (± 30.5 SD, $n = 12$). The wasps located instar VI larvae (mean weight = 1.586 g ± 0.272 SD, $n = 16$) and occasionally tried to bite them, but never with any success. However, by harassing those large caterpillars (instar VI), the wasps caused them either to migrate down the stem into the center of the plant, or to drop off the plant. All of the instar VI larvae moved at least half way down the plant (i.e. 24 cm or more) in reponse to the wasps. Of 16 instar VI caterpillars, 44% dropped off the plant when investigated by the wasps.

Effect of wasp attack on larvae

Larval survivorship was significantly lower in the Predation treatment than in the others (one-way ANOVA on square-root transformations followed by multiple comparisons; $F = 10.85$, df = 2,12, $P = 0.002$). The mean number of larvae surviving per plant was 15.8 (± 0.6 SE) for the Control; 15.8 (± 2.0 SE) for the Harassment; and 6.4 (± 1.5 SE), for Predation. Larvae in the Predation treatment were not caged and, based on our observations, attacks by wasps probably account for most of the missing larvae in that treatment.
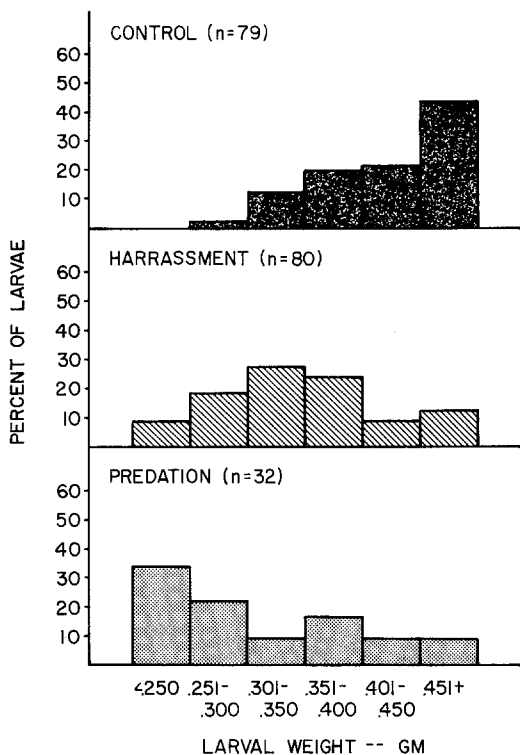
Fig. 2. Comparison of wet weights of *H. lucina* larvae after the Predation-Harassment experiment

Table 2. Behavior of larval groups in the Predation-Harassment experiment. Numbers of observations are indicated in parentheses

	Control	Predation	Harassment
Feeding – Day 1:			
Some eating	54% (27)	80% (40)	42% (21)
None eating	46% (23)	20% (10)	58% (29)
Feeding – both days:			
Some eating	65% (55)	85% (72)	59% (50)
None eating	35% (30)	15% (13)	41% (35)
Leaves being used – Day 1:			
New	89% (41)	83% (39)	53% (20)
Mature or both	11% (5)	17% (8)	47% (18)
Leaves used – both days:			
New	65% (52)	65% (52)	50% (37)
Mature	19% (15)	16% (13)	19% (14)
Both	16% (13)	19% (15)	31% (23)
Environment – both days:			
In full sunlight	54% (46)	62% (53)	13% (11)
In full shade	20% (17)	8% (7)	35% (30)
In both	26% (22)	30% (25)	52% (44)

Heterogeneity chi-square analyses on larval weights among the replicates for each treatment indicated that pooling the replicates for overall analysis was justified ($P > 0.10$ in each case). Chi square contingency table analyses indicated that the Control larvae weighed more than the disturbed (Harassment and Predation) larvae ($P < 0.001$; Fig. 2). The Predation larvae weighed less than the Harassment larvae ($P < 0.025$). The mean larval weights were 0.439 g (± 0.010 SE), 0.346 (± 0.009 SE), and 0.310 (± 0.015 SE) for the Control, Harassment and Predation larvae, respectively. Thus, over just one instar, harassment by predatory wasps had a significant negative impact on larval weight.

Monitoring of wasp attack and larval behavior during the first two days of the field experiment showed that there were few wasps attacking the uncaged larvae (i.e. 1 wasp killed a larva on the first day, and 7 larvae were killed by wasps on the second day). Thus overall, larval behavior in the Control and Predation treatments should not have been and, for the most part, was not significantly different during those days. The behavior of larvae in the Harassment treatment, however, was quite different. On the first day, larvae of the Control and Predation treatments frequently ate new leaves exclusively, whereas larvae of the Harassment treatment ate new leaves less often (χ^2 test followed by subdivision analyses, $\chi^2 = 14.85$, df = 1, $P < 0.001$, Table 2). Although by the end of the observations on the second day, no difference in the type of leaves being eaten was apparent among the treatments ($\chi^2 = 6.48$, df = 4, $P > 0.10$). Larvae in the Harassment treatment spent less time in full sunlight than unharassed larvae (Control and Predation treatments; χ^2 analyses including subdivision, $\chi^2 = 48.18$, df = 2, $P < 0.001$, Table 2).

Observations of group size among larvae in the three treatments showed patterns similar to those described above: larval subgroup size in the Control and Predation treatments were equivalent and greater than that of larvae in the Harassment treatment (one-way ANOVA on square-root transformations, followed by Newman-Keuls multiple range test; $F = 13.27$, df = 2,12, $P < 0.001$). The Predation treatment, without substantial wasp activity on the first two days, had a mean of 21 larvae per subgroup (± 1 SE); the Control treatment, a mean of 19 larvae per subgroup (± 3 SE); and in contrast, the Harassment treatment, a mean of 8 larvae (± 1 SE). However, subsequent periodic observations during the 11-day experiment showed that wasp predation increased, and that the behavior of larvae in the Predation treatment more closely paralleled that of larvae in the Harassment treatment. Larvae in these two treatments often left their groups, either by walking away or by dropping off the plant, and thereafter often occurred in small subgroups.

Growth rate of Hemileuca lucina larvae

At the start of the laboratory experiment, larval weights were similar among the 4 treatments (one-way ANOVA, $F = 0.68$, df = 3,56; $P > 0.50$). Both a day temperature of 35° C and a diet of new leaves yielded higher relative growth rates (RGR) than a day temperature of 25° C and a diet of mature leaves (Table 3). The difference in RGR between temperature treatments reflects both number of days that a larva needed to complete the instar and biomass gained. On average, larvae at the day temperature of 25° C required 2 more days to get through that instar than larvae at 35° C (Table 3). Larvae reared at 35° C were significantly larger than those reared at 25° C. The difference in RGR for those fed young and mature leaves was due to the extra half day required by larvae fed mature leaves to each the fifth instar compared to larvae fed new leaves. There was no

Table 3. Relative growth rate (RGR), days from molt-to-molt (test days) and biomass gained by instar IV larvae. Night-time temperature was 15° C in all treatments. Means (± 1 SE) are shown. Results of 2-way ANOVA are indicated with F ratio and significance level (P)

A. Larval growth

Day temperature	Leaf diet	RGR	Instar duration in days	Biomass gained in mg	n
25° C	mature	0.143 (+0.003)	8.3 (+0.1)	58.9 (+2.0)	15
25° C	new	0.155 (+0.001)	7.9 (+0.1)	60.6 (+2.5)	15
35° C	mature	0.197 (+0.008)	6.3 (+0.2)	63.7 (+2.4)	15
35° C	new	0.221 (+0.006)	5.7 (+0.2)	65.1 (+2.0)	14

B. Anova

Factor	RGR		Duration		Biomass	
	F	P	F	P	F	P
Temperature (T)	139.66	<0.001	186.91	<0.001	4.41	<0.05
Diet (D)	11.86	<0.002	10.88	<0.002	0.46	>0.50
Interaction (T × D)	1.40	>0.20	0.84	>0.20	0.00	>0.95

difference in biomass gained on the diets of new and mature leaves. Thus, both temperature and diet affected the growth rate of the caterpillars, with the higher temperature contributing to faster growth and bigger larvae and a diet of new leaves contributing to faster growth.

Discussion

Our observations of *H. lucina* aggregations showed that wasp attack not only killed some larvae but also modified larval behavior. Typically, *H. lucina* larvae exhibit a variety of defense and escape behaviors, which are used against tachinid flies and pentatomid bugs (Stamp and Bowers, unpubl. data). Thus, the changes in behavior were striking because the caterpillars displayed little of their usual repertoire of defense and escape behaviors (e.g. thrashing, regurgitating, biting, dropping from the plant; Cornell et al. 1987). Instead, attacked individuals responded to wasps by clinging to the plant with both thoracic legs and prolegs, precluding any overt defensive behavior, while other group members responded by leaving the feeding and basking sites and moving to the interor or base of the plant.

Large group size may contribute to effective defense by some gregarious insects (Tostowaryk 1972; Damman 1987). However, we found that only in instar II were *H. lucina* individuals in larger groups more likely to survive attack by wasps than those in smaller groups. The instar II larvae were less likely to escape by moving to the base of the hostplant. Thus, large group size, by simply decreasing the likelihood that an individual will be attacked, may be necessary for survival in this less mobile instar. Group size may be more important for group defense in response to tachinid flies and pentatomid bugs, where a variety of defense and escape behaviors are displayed (Cornell et al. 1987; Stamp and Bowers, unpubl. data).

The field experiment showed that attack and harassment by wasps reduced the growth of surviving *H. lucina* larvae, therefore prolonging larval development time, relative to those that were protected and undisturbed. Reduced growth may result from one or more of the following factors: 1)

more time spent in suboptimal thermal conditions, such as shade; 2) increased use of a suboptimal diet, such as mature leaves; and 3) increased stress due to physical harassment (by the wasps or us). The growth of larvae in the laboratory experiment showed that both thermal and dietary conditions were important in determining larval growth rates. However, caterpillars are unable to achieve an elevated body temperature 10° C above ambient (i.e. 35° C in our test) for the full 16 h of daylight under field conditions because radiation levels are too low in early morning and late afternoon and the caterpillars may be partially shaded some of the time. Consequently, the effect of temperature on growth of undisturbed larvae and harassed larvae under field conditions is unlikely to show as dramatic a difference as that demonstrated in the laboratory experiment. It may be that under natural conditions reduction in growth due to shading approaches that of larvae feeding on mature leaves.

The effects of stress on larval growth are difficult to evaluate separately but may also reduce growth rates. Caterpillars expend energy moving from a site of wasp attack, and considerably so when they must relocate a hostplant after dropping off one. Gregarious larvae, when isolated, tend to wander and seldom eat until they locate conspecifics (Bowers and Stamp, pers. observ.). Both behaviors would result in shorter or fewer feeding bouts and thus lower consumption rates and, in turn, reduce growth rates.

Prolonged larval development time may increase susceptibility to predators and parasitoids (Feeny 1976; Moran and Hamilton 1980; Price et al. 1980). Although two studies suggest that such may not always be the case (Clancy and Price 1987; Damman 1987), those studies examined systems quite different from ours and from many other herbivorous insects. In those systems, the prey were protected either by galls (Clancy and Price 1987) or leaf-shelters (Damman 1987). But in the case of exposed herbivores, such as *H. lucina*, prolonged larval development may often be an outcome of predator harassment and thus is likely to facilitate eventual discovery by other predators. Particularly with predatory wasps, which exhibit area specific search and may

increase substantially in numbers throughout the season as new individuals emerge, prolonged prey development may significantly reduce the individual fitness of prey. Both lower pupal weights, which in general are correlated with lower fecundity (Slansky 1982 and references therein), and prolonged development would affect the population size and dynamics of the prey species.

Because predatory wasps can be especially effective predators of caterpillars (Morris 1972; Gould and Jeanne 1984; Damman 1986, 1987; Evans 1987), as we found with *Polistes* attacking *H. lucina*, they have been investigated as potential agents of biological control. But such studies have yielded mixed results (Lawson et al. 1961; Gillaspy 1979; Gould and Jeanne 1984). Our study suggests an unrecognized mechanism by which wasps are effective biological control agents: predatory wasps alter foraging behavior of their prey. Attacked or harassed larvae may leave the hostplant or retreat to its base, thus temporarily escaping wasp predators, but at the same time abandoning preferred foraging sites. As shown in our study, such changes in caterpillar behavior may increase larval developmental time and thus potentially their susceptibility to disease and natural enemies. Hence, indirect effects of harassment (as well as outright killing) may contribute to decreases in pest caterpillar populations. Such altered foraging behavior of prey caterpillars may hinder accurate assessment of caterpillar density on crop plants because larvae are not present at typical feeding sites (and may be hiding at the base of the plant or not on the plant at all) and thus difficult or impossible to census. Therefore, any attempts to use wasps as agents of biological control should take into account these significant indirect effects of wasp predation.

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