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PHYSICAL CONSTRAINTS OF DEFENSE AND RESPONSE TO INVERTEBRATE PREDATORS BY PIPEVINE CATERPILLARS (*BATTUS PHILENOR*: PAPILIONIDAE)

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ABSTRACT. The responses of pipevine swallowtail caterpillars (*Battus philenor*: Papilionidae) to simulated attacks of invertebrate enemies and to actual attack by coccinellid larvae (*Hippodamia convergens*: Coccinellidae) were examined. The caterpillars were more reactive to the simulated attack of a biting predator than to the simulated touch by an insect enemy. Active fifth instars reached around to the posterior or walked away in response to stimuli, whereas prepupal fifth instars were more likely to extrude the osmeterium and never moved away from the stimuli. Caterpillars that were larger than the coccinellid predators were attacked but seldom eaten. In contrast, larvae that were the same size or smaller than the coccinellids were killed more frequently. When the caterpillars were attacked posteriorly, they defended a limited area by reaching around while the prolegs remained attached. The area defended depends on cuticular stretch, number of attached prolegs, current physiological state, and type and degree of stimulation.

A common view of insects as prey is that behaviorally they are rather defenseless. Dixon (1973) stated, "The general impression conveyed by the literature is that aphids and related small insects are helpless, sedentary and thin-skinned creatures that invite the attention of any predator that comes along." Generally, that same view is held for caterpillars and other immature insects. Yet caterpillars can and will defend themselves under certain circumstances, such as when attacked by insect predators and parasitoids. However, as I show here, pipevine swallowtail caterpillars (*Battus philenor* (L.): Papilionidae) have important constraints that limit the effectiveness of defensive behavior.

Most six-legged insects can turn up to 360° in their own defense. For instance, aphids can move forward or backward rapidly, and they can kick their adversaries (Banks 1957). Aphids can escape just before contact or immediately afterward by simply moving away quickly; many invertebrate predators must be within a centimeter of, or bump into, prey before detecting them (Russel 1972). Furthermore, before or after contact by predators, aphids can swivel on their stylets up to 180° and thus continue feeding while avoiding their enemies (Russel 1972, Brown 1974). In contrast, caterpillars have a cylindrical body with short thoracic legs anteriorly and short prolegs posteriorly. This means that they differ greatly in their maneuverability from six-legged insects, especially aphids which are pear-shaped with relatively long legs. As a consequence of the mobility of six-legged insects, most invertebrate predators are more mobile than caterpillars and can outmaneuver them.

Thus, caterpillars may benefit by escape, often dropping off their host plant (Myers & Campbell 1976). However, leaving the host plant can be risky. Caterpillars (and other soft-bodied insects) may starve before they locate a host plant, or die from desiccation or ground predation (Dethier 1959, Roitberg & Myers 1978, Rausher 1979). Larvae may drop on a thread of silk, which they can later climb, returning safely and quickly to their host plant (Dempster 1971). But predatory ants may climb down silk threads to capture larvae (Allen et al. 1970).

Some caterpillars feed in hiding, a strategy that appears to be especially effective for early instars (Allen et al. 1970, Lopez et al. 1976). Web-making caterpillars may disappear into their webs when disturbed (Fitzgerald 1980). But webs do not deter some wasps and pentatomids from pursuing caterpillars within (Morris 1972, Schaefer 1977). Carabid beetles may tear open webs (Langston 1957). Chrysopid larvae with their long, sicklelike mandibles, and pentatomid and reduviid bugs with their long beaks, can attack prey through cloth and webbing (Fleschner 1950, Bornemissza 1966, Allen et al. 1970, Berisford & Tsao 1975). Furthermore, some predatory pentatomids and spiders live in webs of caterpillars (Morris 1972, E. W. Evans, pers. comm.).

Therefore, caterpillars may benefit by vigorous defense when escape is less effective or more risky, such as when an insect predator initiates contact but cannot overwhelm the caterpillar. Typically, a defensive caterpillar attaches firmly to the substrate with the prolegs, lifts the thoracic legs and swings the anterior of the body toward the attacker, especially when approached from the side or rear by a predator. Caterpillars may use their bodies to hit and their mandibles to grasp an attacker (Morris 1963, McFadden 1968, Iwao & Wellington 1970, Frank 1971, Heinrich 1979, Suzuki et al. 1980, Stamp 1982). Unlike vertebrates and adult insects, caterpillars do not use their legs defensively. Instead, they may regurgitate or wipe offensive glands on attackers (Eisner & Meinwald 1965, Feltwell 1982).

The questions posed in this study were: 1) when does a caterpillar opt to escape or for defense? 2) how does it defend itself? and 3) how effective is it in defending itself, or when are insect enemies successful in countering a caterpillar's defense?

METHODS

Pipevine swallowtail caterpillars were used because of their variety of defensive responses: thrashing with the front half of the body, grasping with the mandibles, regurgitating, and extruding the osmeterium and wiping it on attackers. On 16 May 1983, eggs were collected at Rancho Cordova, California, along with Dutchman's pipevine (*Aristolochia californica* Torr.), the host plant. Caterpillars were reared in

the laboratory at room temperature in plastic boxes with the host plant stems in aquapics.

Response to Simulated Attack

To examine the responses by swallowtail caterpillars, I used two stimuli. On first, second, third, and fifth instars, a two-haired brush simulated the touch of an insect predator (palpitating antennae or beak of predatory hemipteran) or parasitoid (palpitating antennae or probing ovipositor). The stimulus was applied three consecutive times to the posterior of each caterpillar at 15 sec intervals for up to 6 trials. For the fifth instar, a pinch with forceps on a fleshy tubercle at the rear end at 15 sec intervals simulated the bite of an insect predator, such as an ant. Responses were recorded with a video camera. Thrashing with the front half of the body, biting with the mandibles, extruding the osmeterium, and regurgitating were classified as stationary defense. Walking away and wriggling (rolling around with no legs attached) were classified as escape behaviors. For Chi-square analyses, the Yates correction for continuity was used when $v = 1$, and is denoted by χ_c^2 (Zar 1974). The power of tests (probability of not committing a type II error, $1 - \beta$) was calculated as described by Cohen (1977).

To compare active and inactive larvae, the stimuli were applied in the same manner as above to two sets of final instars: feeding and prepupal (no longer feeding and residing on a silk mat).

Tests with Invertebrate Predator

To determine how effective swallowtail caterpillars were in defending themselves, they were tested with coccinellid larvae (*Hippodamia convergens* Guerin-Meneville). Coccinellid larvae are voracious predators of eggs and small insects (Banks 1957, Brown 1974). I observed a third instar *H. convergens* feeding on a second instar *B. philenor* in a riparian area in Rancho Cordova; it is thus reasonable to assume that the coccinellids are natural predators of these swallowtail caterpillars. Fourteen third instar coccinellids were collected on 23 May 1983 at Rancho Cordova, California, in a large field that had no *Battus philenor* caterpillars or host plants. Thus, the predators would not have had any prior contact with pipevine swallowtail caterpillars.

Each coccinellid was kept in a Petri dish with a source of water but no food for 24 h. Using a paintbrush, I placed each coccinellid in a Petri dish with a swallowtail caterpillar on a leaf of the host plant. Caterpillars were used only if they were actively feeding. Fluon (polytetrafluoroethylene from Imperial Ltd., England) was painted on the sides and bottom of the dish to prevent the coccinellids from searching there. The interactions of each coccinellid and caterpillar were moni-

tored for 10 min. Only those trials where the coccinellids exhibited foraging behavior were used for analysis. Some coccinellids were used more than once but only at 24-h intervals. To determine the body-size ratio (BSR), body length of caterpillars was measured in mm when they were eating and when the dorsal midline (anterior to posterior) was straight. Body length of the coccinellids was measured when they were between foraging bouts and thus motionless.

Modelling Defensive Space

The area defended by swallowtail caterpillars was determined by using a video camera to record the path of the head in response to stimuli (two-haired brush or forceps) applied to the posterior. Measurements were made from tracings of body length at the start, and how close the head came to the posterior during defense. Using a map meter, measurements were also made of body length (down the midline) when the caterpillar reached around to defend itself. Body extension was estimated by maximal body length during defense divided by body length at the start. Only the recordings where the head moved laterally rather than over the back were analyzed. While the camera recorded body movement, I recorded the number of prolegs detached immediately after the stimulus.

RESULTS

Response to Simulated Attack

In response to the two-haired brush (simulating the touch of an invertebrate predator or parasitoid), all of the tested instars exhibited escape and defensive behaviors (Fig. 1). With repeated stimulation, the larvae were more likely to exhibit escape behaviors, except for the fifth instar where the escape response declined. Defensive responses decreased with the sequence of stimuli. The fifth instar appeared to become more tolerant of the stimuli in that both defense and escape responses declined with the sequence of stimuli (Fig. 1).

Comparing responses of the fifth instar to the two stimuli showed that they were more reactive, by exhibiting responses, to pinching than to touching by the brush (χ^2_c, $P < 0.025$). But the larvae responded with escape and defensive behaviors in similar proportions (escape, defense or no response; χ^2 test, $v = 2$, $P > 0.10$, $1 - \beta = 0.58$ for $\alpha = 0.05$, $n = 58$). They were more likely to reach backward in response to the forceps than to the brush (χ^2_c, $P < 0.025$). The caterpillars also walked farther away in response to pinching than to touching by the brush (moving more than 2 cm within 15 sec or not, χ^2_c, $P < 0.05$).

Comparisons were made of behavior of active (still feeding) and

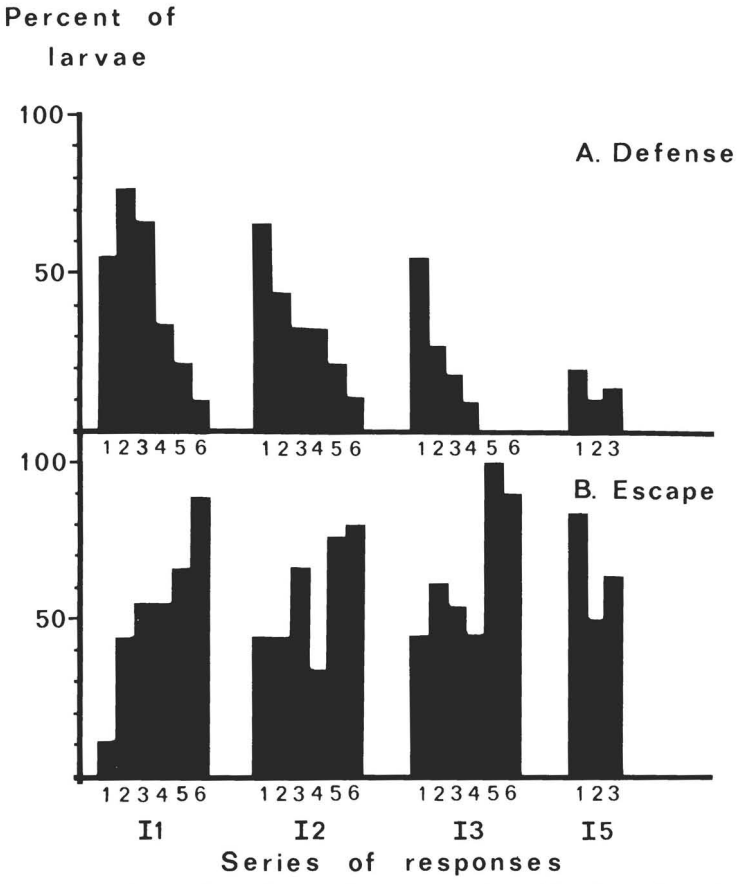

FIG. 1. Reaction by swallowtail caterpillars to a two-haired brush touching the posterior at intervals of 15 sec (indicated by the series of numbers on the x-axis). Sample sizes were n = 9 for the first and second instars (I1, I2), n = 11 for the third instar (I3) and n = 30 for the fifth instar (I5). Responses were classified as defense or escape. Some larvae exhibited both types of response at a single trial. A. Defensive responses. B. Escape behaviors.

inactive (prepupal and no longer feeding) fifth instars. In contrast to active larvae, prepupal caterpillars exhibited no escape behavior. They responded defensively to the brush in the same proportion as caterpillars still feeding (χ^2_c, $P > 0.50$, $1 - \beta = 0.12$ for $\alpha = 0.05$, Fig. 2). However, prepupal larvae were more likely to extrude the osmeterium than feeding caterpillars (χ^2_c, $P < 0.025$). Although both the active (feeding) and inactive (prepupal) larvae reached around or thrashed, the active larvae were able to reach to their posterior or to walk away, whereas the prepupal caterpillars were much less mobile and never walked away.

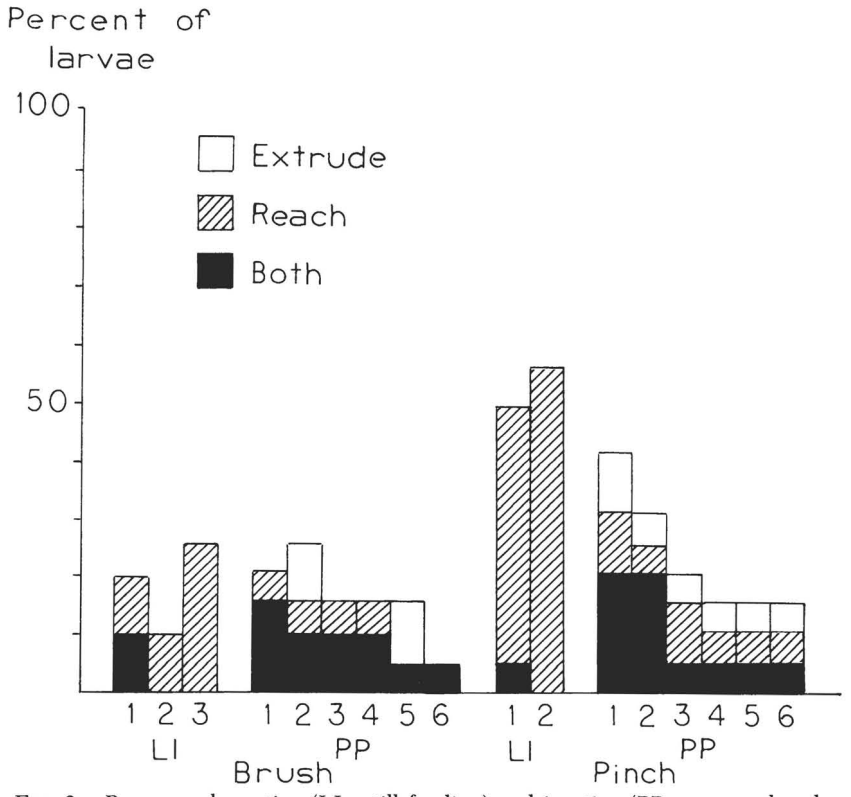

FIG. 2. Responses by active (LI—still feeding) and inactive (PP—prepupal and no longer feeding) final instar swallowtails to either a brush or forceps. Numbers on the x-axis represent the sequence of stimuli applied at intervals of 15 sec. Sample sizes were 30 and 28 for the active larvae stimulated by brush and forceps, respectively, and 35 for the prepupal larvae. Extrude—osmeterium extruded, with an attempt by the caterpillar to wipe them on the brush or forceps. Reach—caterpillar reached with head backwards toward stimulus.

Tests with Coccinellid Predators

To examine effectiveness of defense, caterpillars were monitored in response to invertebrate predators (coccinellid larvae). When the caterpillars were the same size or smaller than the predators (n = 16), 43.8% of the caterpillars were eaten. In contrast, when the caterpillars were larger than the predators (n = 16), only 6.3% were eaten. The frequencies of eaten and uneaten caterpillars were significantly different (χ^2_c, $P < 0.05$). Examination of the behavior of these caterpillars showed that large caterpillars (body-size ratio of prey to predator greater than 1) were more likely to thrash in response to the coccinellids, and small caterpillars (relative to the predators) were more likely to

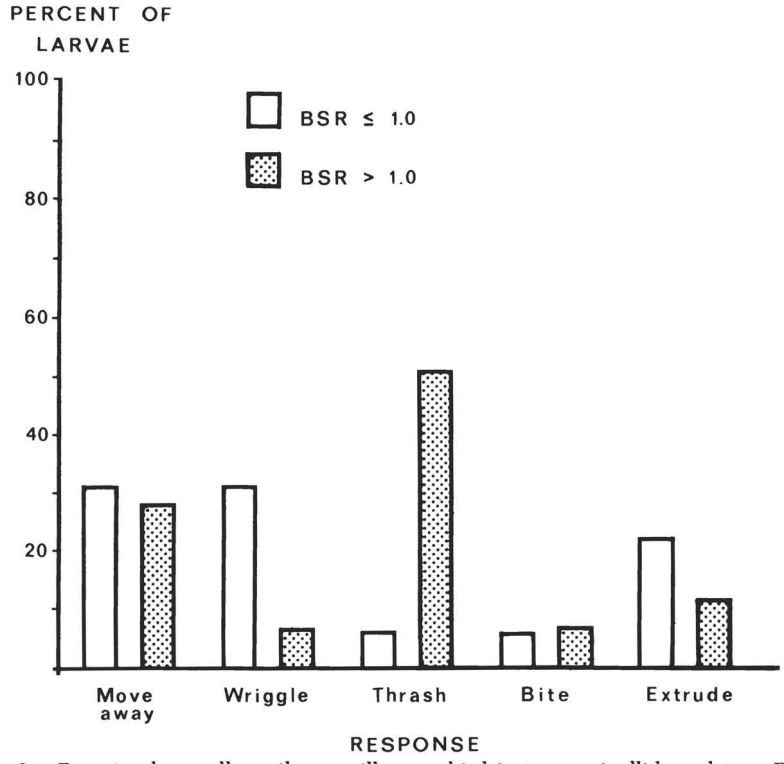

FIG. 3. Reaction by swallowtail caterpillars to third instar coccinellid predators. Responses are divided into those where body-size ratio (BSR) of caterpillar to predator was greater than 1, or less than or equal to 1.

wriggle (no legs attached) (χ^2 tests, $P < 0.001$, Fig. 3). In this experiment, body size ratio had no effect on escape, biting, or on extruding the osmeterium (Fig. 3).

Third instar coccinellids had little difficulty subduing first instar swallowtails, which were smaller than the predators. For example, after a coccinellid touched one of six first instars feeding together, the touched caterpillar extruded its osmeterium. The predator backed off, then approached and bit the larva behind its head. The other larvae had been feeding and moving around. After the first caterpillar was attacked, the rest remained motionless for 11 min. Only after the coccinellid backed into one of them did the rest leave the area. Although it took up to 15 min for a coccinellid to consume a first instar, these predators ate as many as three caterpillars consecutively. All of the coccinellids that ate pipevine swallowtail caterpillars survived and pupated, which suggests that these caterpillars are appropriate prey for the coccinellids.

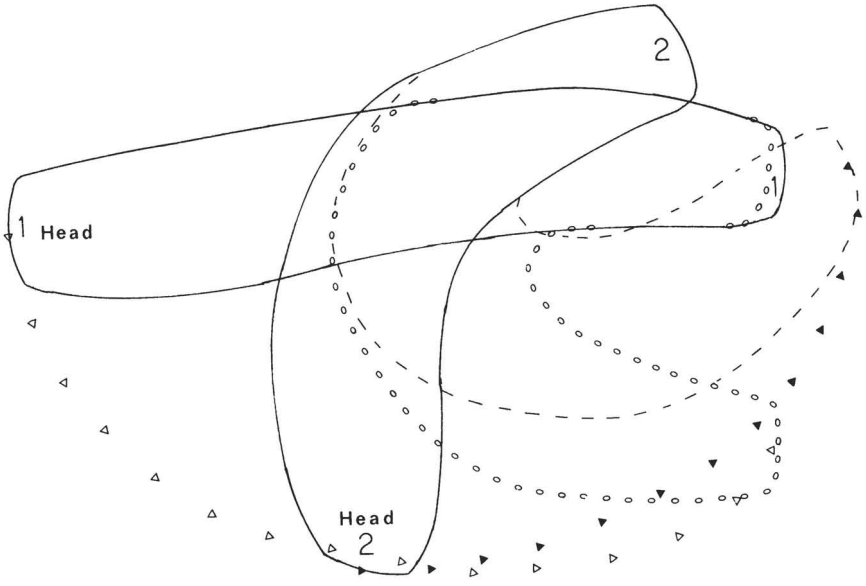

FIG. 4. Example of typical movement of a final instar swallowtail larva in response to pinching stimuli (applied at right), based on tracing body movement from a video record. 1—position of head just before first stimulus on posterior. Open triangles show path of head after first stimulus. 2—position just before second stimulus, applied 15 sec after the first. Dark triangles indicate path of head after second stimulus.

When predator and caterpillar were of similar size, caterpillars were usually successful in defending themselves. For instance, after contact by a coccinellid, one caterpillar thrashed vigorously. The predator grabbed it. The caterpillar responded by biting the legs of the coccinellid but did not use its osmeterium. The coccinellid released the caterpillar, moved away, and began grooming.

Modelling Defensive Space

To determine how capable larvae were at defending their posteriors, the path of the head was traced using video recordings of larval response. As shown in Figs. 4 and 5, the caterpillars defended a limited, circular area around themselves. This was a consequence of their head-to-rear defense, where they did not turn around and place their posterior away from the stimulus as most animals do. Both stimuli elicited the head-to-rear response. Although some caterpillars may feed while attached to a branch, and consequently are restricted in their ability to turn around, many caterpillars are free to move around on the leaves on which they reside. Those in this study were unrestricted also. Thus,

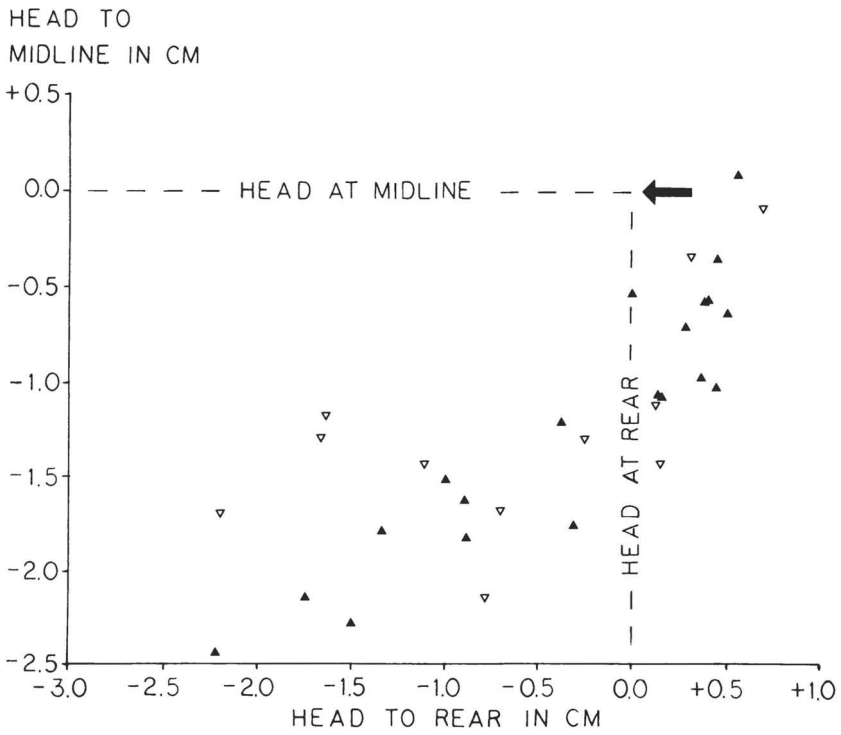

FIG. 5. Response by fifth instar swallowtails to either the two-haired brush or forceps applied to the posterior (arrow). Caterpillar's head always began at the top left and moved to the side (down and to the right). The farthest point of the head back toward the posterior is shown. Open triangles indicate response to the brush by 11 caterpillars, dark triangles the response to the forceps by 20 caterpillars.

these caterpillars exhibited a head-to-rear defense even when they could have turned around completely to face attack.

Of 31 fifth instars, 48% responded by reaching to or beyond the posterior. That so many did so was due to two factors: body extension, and detaching some prolegs. In response to the brush, body extension (beyond the original length) was 30% (±4.0 SE, n = 11). Extension was 33% (±4.5 SE, n = 20) in response to the forceps, with no significant difference between the two stimuli (arcsin transformation, two-sample t-test, $P > 0.50$, df = 1,29, $1 - \beta = 0.46$ for $\alpha = 0.05$). These caterpillars have five pairs of prolegs but may detach up to four of the anterior pairs in defending themselves. The mean number of attached pairs after brush stimulation was 4 (±0.3 SE, n = 11), and after pinching, 4 (±0.1 SE, n = 20, square-root transformation, two-sample t-test, $P > 0.20$, df = 1,29, $1 - \beta = 0.46$ for $\alpha = 0.05$).

DISCUSSION

Response to Attacks

Defensive and escape behaviors varied with instar and physiological state (active versus prepupal larvae). For example, the prepupal larvae were more likely to extrude the osmeterium than active caterpillars (those still feeding). The active larvae were mobile and thus could escape, whereas the prepupal larvae were not mobile, were slow to respond, and thus had no escape options and few defensive ones. Correspondingly, invertebrate predators and parasitoids may be more successful when attacking relatively defenseless (inactive or small) insects than when attacking active and larger ones (Dixon 1959, Evans 1976, Cate et al. 1977, Tilman 1978). For example, Rabb and Lawson (1957) stated that "an appreciable number" of tobacco hornworms captured by *Polistes* wasps were molting, and often those wasps approached but left alone fifth stage (large) larvae. Iwao and Wellington (1970) found that tent caterpillars differed in their behavior, with inactive types being less defensive and more often parasitized. Similarly, in this study coccinellid predators were more successful in their attacks when *B. philenor* caterpillars were smaller than they were.

The caterpillars defended themselves by biting the coccinellids, particularly on their legs, by extruding the osmeterium and wiping it on the coccinellids, and occasionally by thrashing and regurgitating. The caterpillars were more reactive to pinching than to touch by the brush. Probably pinching provided a clear signal of attack, whereas the brush stimulus may be received as a more general signal and not clearly different from the touch of a leaf moved by the wind. Relatively large caterpillars thrashed in response to the coccinellids; most of the time the coccinellids responded by backing off and eventually leaving the caterpillars alone. In contrast, the small larvae often wriggled when touched by the coccinellids. By wriggling, the caterpillars moved erratically, which may have made it difficult for the predators to respond effectively to the prey (Humphries & Driver 1967); some caterpillars rolled off the leaf and escaped from predators.

Physical Constraints of Defense

The premise here is that by moving only the front half of the body, the typical caterpillar defends a limited space around itself (to either side and over its back, Fig. 6). Variables that affect the maximal defendable area are: L, the length of the moving (defending) portion of the body; D, the diameter of the body; and M, the length of the moving portion of the body after maximal cuticular stretch. To estimate M, the cuticle was extended by 25% (a reasonable estimate based on Hep-

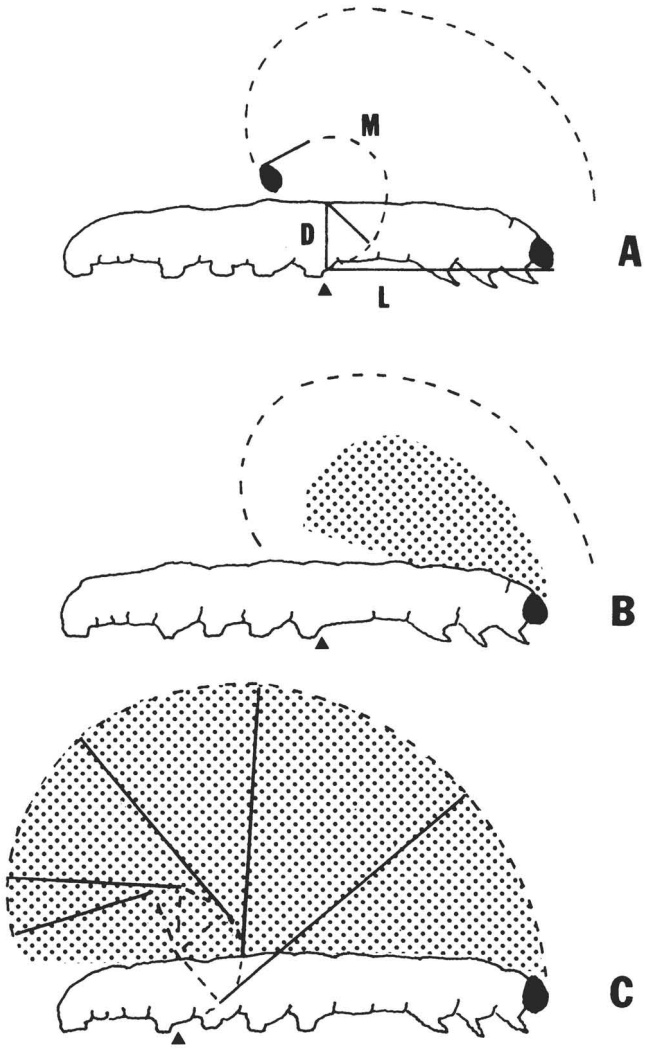

FIG. 6. A. Defendable area of a typical caterpillar when arching the head over its back. B. Shaded portion shows maximal defendable area when there is no cuticular stretch, dashed line when there is cuticular stretch. C. With only two pairs of prolegs attached, a caterpillar can defend a much larger area than depicted in A.

burn & Levy 1975, Wolfgang & Riddiford 1981, Fig. 6B). Cuticular stretch lengthens the outer bending side and thus accommodates the body volume. The effect of cuticular stretch is to increase the reach and, consequently, maximal defendable area of the caterpillar. The illustrations (Figs. 4, 5 & 6) indicate where caterpillars may be most

vulnerable to attack by insect enemies that cannot simply overwhelm them. That area is some portion of the rear end. With some prolegs detached, a caterpillar can defend a larger area and reach beyond the posterior than when five sets of prolegs are attached (Fig. 6A & C). Thus, the maximal defendable area of a particular caterpillar should affect: 1) type of defensive behavior employed by the caterpillar; 2) attack behavior of enemies, especially specialist parasitoids; 3) the sequence of attack-defense behaviors exhibited during enemy-caterpillar interactions; and 4) outcome of the event.

Using measurements of body diameter and the moving (defending) portion of a caterpillar relative to total body length, the maximal defendable space can be estimated (Fig. 6). When the ratio of the moving portion relative to total body length is high, or when diameter of the body is small, the caterpillar can reach its posterior easily (Fig. 6C). A slender geometrid caterpillar that has two pairs of prolegs uses this increased maneuverability to its advantage by preying on small insects that touch its posterior (Montgomery 1982). Cuticular elongation may also affect maximal defendable space because it allows cuticular adjustment (stretch of the outer bending surface) to accommodate a body volume that is more or less compressible, depending on how close the caterpillar is to molting to the next instar (Fig. 6B).

Most invertebrate predators rely on tactile and chemical cues more than visual ones to detect prey (chrysopid larvae, coccinellid larvae and adults, predatory wasps, pentatomid bugs; Banks 1957, Klingauf 1967, Fleschner 1950, Storch 1976, Steiner 1974, Hicks 1931, Evans 1982). Usually, such predators encounter their prey physically before they attack (Banks 1957, Dixon 1959, Swynnerton 1915, Allen et al. 1970, Myers & Campbell 1976). Consequently, predators may benefit by attacking whatever part of the prey they encounter and thus prevent the victim's escape (Brown 1974, Evans 1982).

But invertebrate predators and parasitoids often attack prey and hosts cautiously. For instance, predatory pentatomids (*Perillus circumcinctus*) tested most potential prey (chrysomelid larvae) by extending the beak and then retreating when the prey defended themselves (E. W. Evans, pers. comm.). After contact is made and prey defense is initiated, invertebrate predators may best respond to a prey's defense by attacking the most vulnerable part of the prey. For example, aphids are more likely to be caught by predators when approached from the rear (Dixon 1958, Klingauf 1967). For caterpillar-shaped animals, the posterior may be the most vulnerable location also (sawfly larvae, Morrow et al. 1976). Parasitoids that attack Baltimore checkerspot caterpillars outside the communal webs maneuver carefully toward the hind end of the defensive hosts (Stamp 1982). Consequently, the proportion

of successful assaults may be greater on the posterior than near the head.

In conclusion, when a caterpillar is smaller than the predator, the caterpillar is less likely to defend itself successfully. In this case, escape may be a more appropriate response. In contrast, when the body-size ratio of the caterpillar to the insect predator is large enough, a caterpillar's defense may be fairly effective. But caterpillars can defend only a limited space around themselves due to the particular stance they take. The maximal defendable space of caterpillars should change with body diameter, length of the moving (defending) portion of the body relative to total length, cuticular stretch, and physiological state. Insect enemies that cannot overwhelm a caterpillar may respond to the maximal defendable space by orienting to and attacking the more vulnerable (less defended) portion of the caterpillar's body.

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