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Influence of Host Behavior and Host Size on the Success of Oviposition of *Cotesia urabae* and *Dolichogenidea eucalypti* (Hymenoptera: Braconidae)

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Behavioral interactions among Cotesia urabae *Austin and Allen,* Dolichogenidea eucalypti *Austin and Allen (Hymenoptera: Braconidae), and their host* Uraba lugens *Walker, the gum leaf skeletonizer (Lepidoptera: Noctuidae), were observed at three host sizes over a 20-min period. These sizes were first instar (small, gregarious), fourth–fifth instar (mid, gregarious), sixth–seventh instar (large, solitary) larvae. Unlike* C. urabae, D. eucalypti *used its legs to hold small larvae before ovipositor insertion.* D. eucalypti *also visited patches of small larvae more frequently, proceeded less often through patches of mid larvae, and made significantly fewer ovipositions in mid and large larvae. Small larvae responded to both parasitoids by dispersing outward, while mid larvae responded to parasitoids by moving inward to form a denser group. Larvae reared or thrashed after each parasitoid visit, especially mid larvae, and some continued to do so for up to 2 h after parasitoid departure. Mid and large larvae occasionally injured parasitoids by biting their appendages. By rearing or thrashing immediately prior to an encounter with a parasitoid, mid and large larvae decreased the likelihood of being parasitized by up to 50%.*

KEY WORDS: *Cotesia urabae*; *Dolichogenidea eucalypti*; *Uraba lugens*; Braconidae; Noctuidae; parasitoid; gregariousness; host acceptance; host defense.

INTRODUCTION

Animal defense against predation or parasitism can be primary or secondary (Robinson, 1969). Primary defenses decrease the chance of an encounter with

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a predator (or parasitoid) and operate regardless of whether or not the predator is in the vicinity (Edmunds, 1974). These include crypsis, aposematism, batesian mimicry, and anachoresis. Secondary or direct defenses operate when the prey (or host) is encountered and increase the prey's chance of survival. The secondary defensive behaviors of caterpillars include biting, regurgitation, thrashing, rearing, and dropping on a silk thread (Awan, 1985; Stamp, 1986). Group defense may be classified as primary and/or secondary (Edmunds, 1974).

Host acceptance is the process whereby a parasitoid accepts or rejects a host for oviposition after contacting it (Weseloh, 1974). Host acceptance depends on the parasitoid detecting certain physical and chemical stimuli produced by the host (see Arthur, 1981). Despite detecting these stimuli, host acceptance may still be interrupted by the aggressive behavior of the host (Schmidt, 1974). The outcome of an encounter is often assumed to be due primarily to the action of the parasitoid, although some authors acknowledge that the behavior of the host may be a factor (Noble and Graham, 1966; Sullivan and Green, 1950; Taylor, 1988).

In this paper I investigate the behavioral interactions between the parasitoids *Cotesia urabae* and *Dolichogenidea eucalypti* and their host *Uraba lugens*. The specific aims were (1) to compare how the defensive behaviors of different sizes of *U. lugens* influence host acceptance and the host-parasitoid interaction and (2) to quantify and compare the oviposition behavior of *C. urabae* and *D. eucalypti* when attacking different sizes of hosts. These two parasitoids attack three sizes of *U. lugens* in the field: small (typically first instar), mid (fourth–fifth instar) and large (sixth–seventh instar) (Allen, 1990a). The majority of second to third instar *U. lugens* do not overlap with adult parasitoids in the field and therefore escape being parasitized (Allen, 1990a). This wide range of host sizes enabled testing of how the interactions differ between the different developmental stages of host. *U. lugens* is gregarious until about the fifth instar (Campbell, 1962; Morgan and Cobbinah, 1977), requiring that the effect of gregariousness on these defensive interactions also be quantified.

MATERIALS AND METHODS

Experimental Protocol

Thirty-six groups, of approximately 60 *U. lugens* each, were reared on cut *Eucalyptus leucoxylon* F. Muell. foliage in 20 × 20-cm cages at 20°C with a photoperiod of 12 : 12 L : D. At each of the three size classes tested (small, mid, large; see above), 12 groups were selected, and the numbers in each reduced to 40 larvae per group by removing excess larvae at random. Cut leaves, upon which larvae were feeding, along with the 40 larvae were placed in a 19 × 3-cm glass petri dish positioned under a color video camera for observations. The groups of large larvae were accompanied by six leaves, while the groups of small and mid larvae were each located entirely on one leaf.

Adult female *C. urabae* and *D. eucalypti* were collected as larvae in the field late in the host's summer generation, reared at 20°C, allowed to mate, and then stored at 12°C until use. Parasitoids for experiments were selected at random; their age (time in storage) varied from 1 to 19 days for *C. urabae* and from 4 to 22 days for *D. eucalypti*. Six *C. urabae* and six *D. eucalypti* were tested for each size class of *U. lugens*. Immediately prior to each experiment, each parasitoid was given 3 min "preexposure" in another petri dish with either small or mid *U. lugens*, during which time they were allowed to oviposit in larvae. This provided parasitoids with oviposition experience and demonstrated readiness to oviposit. After preexposure each parasitoid was released onto a leaf within the experimental petri dish containing *U. lugens*.

An event recorder program on a portable computer was used to record parasitoid oviposition and a voice tape recorder run to document both parasitoid and *U. lugens* behavior. Recording began when the parasitoid first made contact with a *U. lugens* in the petri dish and continued for 20 min, at the completion of which the parasitoid was removed. The number of *U. lugens* rearing or thrashing was recorded at 5 min intervals for 2 h after parasitoid departure. Subsequently all larvae were reared at 20°C until all parasitoids had emerged and the unparasitized *U. lugens* had pupated.

The video, synchronized voice recordings, and event recorder data were used to produce time recordings of the following parasitoid behaviors associated with oviposition.

(1) Visit. The time interval between patch entry and patch exit. A patch is defined as the group of small or mid larvae, whereas a single large larva was considered equivalent to one patch. The boundary of each patch for small and mid larvae was defined by connecting the outermost edge of each larva on the perimeter of the group of 40 larvae. For a large larva the patch boundary was defined as the outermost edge of that larva.

(2) Encounter. When a parasitoid contacted a *U. lugens* (for large larvae, encounter = visit). Three types of encounter were noted.

(a) Approach-retreat: parasitoid contacts a *U. lugens* but retreats.

(b) Attack-fail: parasitoid contacts a *U. lugens*, sets upon it, but fails to insert ovipositor.

(c) Attack-insertion: parasitoid contacts a *U. lugens*, sets upon it, and inserts ovipositor (whether or not an egg was actually deposited was not determined).

The defensive behavior of *U. lugens* was documented throughout each observation. The number of small *U. lugens* rearing or thrashing immediately after each visit by a parasitoid was voice recorded during the observation, but their size prevented any more detailed recordings of defensive behavior. For mid and large *U. lugens*, slow-motion video recordings were replayed to record the number rearing or thrashing immediately after each visit by a parasitoid, the position within the group of each *U. lugens* encountered, the frequency of encounter for each *U. lugens*, and whether larvae were rearing or thrashing prior to, during, and/or after each encounter. For the gregarious sizes (small and mid) patch area prior to commencing the experiment and immediately after parasitoid departure was outlined with a pen on the television monitor. The area of each patch was then calculated using an Apple Graphics Tablet® (Model A2M0029).

Analysis of Data

Variations in the success of parasitoids in attacking *U. lugens* were examined, depending on the type of data, by two methods. The overall frequencies of approach-retreat, attack-fail, and attack-insertion were first tested between replicates (parasitoids) and then pooled to test between size classes and species of parasitoid, using log-linear contingency table analysis (LLCTA) (Genstat, 1987). Number of visits and number of ovipositor insertions per parasitoid were compared between species of parasitoid and size classes of host using ANOVA and Student Newman–Keuls (SNK) ($P < 0.05$) procedures of SAS (1985).

The influence of mid and large larval behavior immediately prior to an encounter on the success of an attack by a parasitoid was examined by comparing the frequencies of attack-fail, approach-retreat, and attack-insertion to larvae that were either exhibiting rearing or thrashing behavior or not displaying these behaviors. Frequencies were pooled across replicates to overcome low expected cell frequencies and tested using LLCTA. Changes in patch area between that prior to parasitoid entry and after parasitoid departure from the petri dish were analyzed using paired *t* tests.

RESULTS

The behavior of parasitoids attacking *U. lugens* differed depending on the size of host larvae attacked. Parasitoids had legs of sufficient length to raise their bodies above the level of rearing small larvae (Fig. 1A) and thus could proceed unhindered in any direction within the patch. In contrast, parasitoids could not walk through patches of mid *U. lugens* but instead ran over the top of them. This action increased the risk of contact with fluid regurgitated by larvae and of being bitten by them. Large larvae were approached from varying directions by parasitoids, but it was apparent that their longer setae hindered the parasitoids ability to reach the exocuticle for insertion of the ovipositor. In preliminary tests mid and large larvae were occasionally seen to bite parasitoids,

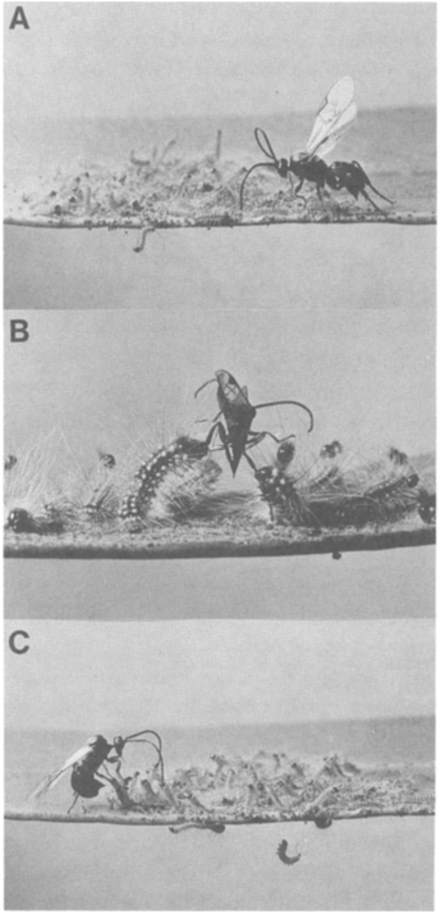

Fig. 1. Behavior of *U. lugens* and parasitoids of *U. lugens*: (A) *C. urabae* proceeding through a patch of small larvae where many individuals are rearing as a result of several visits by this parasitoid; (B) *C. urabae* bitten and held by the mandibles of two mid *U. lugens* while proceeding through the patch; (C) *D. eucalypti* utilizing its legs to hold a small larva during oviposition (note larva dropping by a silk thread underneath the leaf and the closed wings during oviposition of *D. eucalypti*).

frequently not releasing their mandibles until the appendage had been severed (Fig. 1B).

Both species of parasitoid always proceeded to move through patches of small larvae after entering them. In contrast, *C. urabae* entered and continued to move through patches of mid larvae for just 21% of visits, while *D. eucalypti* did so for only 1% of visits. In the remaining visits, parasitoids withdrew from the edge of the patch after an encounter. For those *C. urabae* seen to move through a patch of mid larvae, 51% had at least one further encounter with a larva during that visit. This behavior affected the distribution of parasitoid oviposition within patches of mid larvae. Thus every oviposition by *D. eucalypti* and 90% of ovipositions by *C. urabae* were with mid larvae on the edge of the patch.

Oviposition was very quick, lasting less than 1 s for both species of parasitoid. *C. urabae* typically moved around the patch and oviposited with its wings raised, while *D. eucalypti* typically kept its wings folded. While walking through a patch of small larvae both species jabbed their ovipositor up and down like the needle of a sewing machine (Fig. 1A). Such jabs frequently missed larvae and did not appear to be directed at specific individuals. Sometimes attacks were directed at small larvae by thrusting the ovipositor forward at an angle rather than from directly above. This frequently tended to displace the larva rather than penetrate its exocuticle. *D. eucalypti* often avoided such an outcome by using its front and/or mid pair of legs to hold small larvae when directing its ovipositor at a forward angle (Fig. 1C). Holding behavior was employed on rearing and nonrearing larva and occurred at least once in 26.7% of all patch visits made by *D. eucalypti*.

The total number of visits made by parasitoids declined with increasing larval size for both species of parasitoid but the only statistically significant decline was for *D. eucalypti* between the small and the mid and large larvae (Fig. 2). *D. eucalypti* made more visits than *C. urabae* to patches of small larvae but significantly fewer to mid and to large larvae.

When the outcome of each visist was considered, *C. urabae* was more frequently successful in ovipositing into hosts than *D. eucalypti*, and the success of both species declined with increasing larval size (Fig. 3). The frequencies of approach-retreat, attack-fail, and attack-insertion for visits by both species of parasitoid on the three sizes of larvae were all significantly different from each other (overall $\chi^2_{10} = 625.3$, $P < 0.0001$). The frequency of approach-retreat was greatest for both species of parasitoid when they attacked mid larvae. If the visit proceeded beyond the approach-retreat stage, large larvae were apparently more difficult to oviposit into than either small or mid larvae. This was particularly true for *D. eucalypti*, which failed to oviposit into large larvae. The greater size and longer setae of large larvae appeared to protect them from oviposition after a parasitoid had set upon it.

During the 20 min period, the most ovipositor insertions were made by parasitoids when attacking small larvae. The number of insertions or ovipositions when attacking mid larvae was next highest (Table I). More than one oviposition in a visit often occurred when parasitoids attacked the gregarious

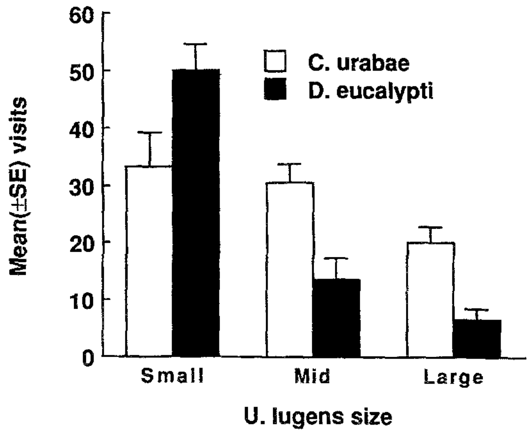

Fig. 2. The mean (±SE; $N = 6$) number of visits made by *C. urabae* and *D. eucalypti* to a patch of 40 small, 40 mid, and 40 large *U. lugens* over 20 min.

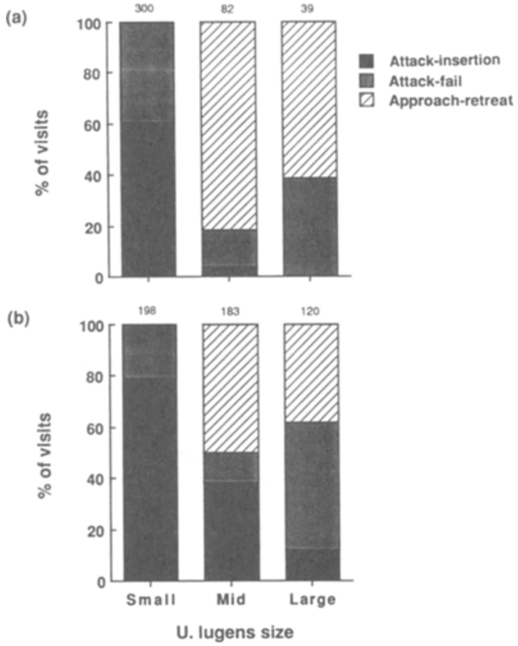

Fig. 3. The outcomes of all visits made to patches of 40 small, 40 mid, and 40 large *U. lugens* by (a) *D. eucalypti* and (b) *C. urabae*. Data from six parasitoids were pooled for each bar. Numbers above bars are the total number of visits made.

Table I. The Mean Number of Ovipositions (Ovipositor Insertions) per Parasitoid and Number of Ovipositions per Successful Visit (Visits Where at Least One Oviposition Occurred) for *C. urabae* and *D. eucalypti* Attacking Groups of 40 *U. lugens* of Three Different Sizes[a]

Species of parasitoid	Size of *U. lugens*	Mean No. of ovipositions per parasitoid	Total No. of ovipositions	Mean No. of ovipositions per successful visit	No. of successful visits
C. urabae	Small	49.5 ± 9.8[a] (22–84)	297	1.89 ± 0.11 (1–10)	157
C. urabae	Mid	13.7 ± 1.5[b] (8–17)	82	1.17 ± 0.06 (1–4)	70
C. urabae	Large	2.3 ± 0.8[b] (0–5)	14	1.00 (1)	14
D. eucalypti	Small	46.5 ± 7.5[a] (32–80)	279	1.54 ± 0.07 (1–6)	181
D. eucalypti	Mid	0.5 ± 0.2[b] (0–1)	3	1.00 (1)	3
D. eucalypti	Large	0[b]	0	0	0

[a] Values are mean ± SE. Range in parentheses. *N* is 6 for ovipositions per wasp. Differing superscript letters alongside means within a species of wasp indicate significant differences ($P \leq 0.05$) as determined by SNK tests.

sizes of larvae. Ovipositions in two or more larvae occurred in 34% of successful visits to a patch of small larvae for *D. eucalypti* and in 48% of successful visits to a patch of small larvae for *C. urabae*. Ovipositions in two or more larvae during successful visits to mid larvae occurred during 14% of such visits by *C. urabae* but did not occur for *D. eucalypti*.

The frequency of superparasitism, particularly in small larvae, can only be inferred. High rearing mortality, especially of small larvae, made it impossible to determine the total numbers of larvae successfully parasitized and hence to compare the number of observed ovipositor insertions with the number of parasitoids emerging. The number of ovipositor insertions exceeded the number of small larvae present in the petri dish for two *D. eucalypti* and four *C. urabae*, which seems to indicate a lack of discrimination before ovipositor insertion. Both parasitoids frequently had more than one encounter with a larva. Approximately 40% of mid larvae encountered by parasitoids were encountered more than once and 17–27% of large larvae were encountered more than once. Superparasitism of mid larvae by *C. urabae* may have occurred with five ovipositor insertions observed in one larva, three in another, and two in 7 of the 69 larvae in which parasitoids inserted their ovipositors.

U. lugens showed both defense and escape (locomotory) behavior during the 20 min observation period. Locomotory behavior significantly increased patch size for small larvae ($t = 6.03$, df $= 11$, $P < 0.0001$) but significantly decreased patch size for mid larvae as mid larvae moved toward each other ($t = 3.82$, df = 11, $P < 0.0001$) (Table II). The change in patch area did not significantly differ in relation to the species of parasitoid. Small larvae frequently released their legs or prolegs from the leaf after several visits by a parasitoid. This accentuated the increase in patch size because parasitoids occasionally "carried" small larvae which became temporarily impaled on their ovipositor. Random "sewing machine" movements of the ovipositor became less effective and angled ovipositor thrusts frequently just displaced small larvae as dispersal increased and more larvae released their legs and prolegs.

The incidence of rearing or thrashing was low initially but reached a higher level after several visits by parasitoids, remaining at or above that level thereafter. The majority of the 40 larvae did not rear or thrash after each visit by a parasitoid, although a greater number appeared to be doing so during, rather than after, each visit. Mid larvae exhibited the highest incidence of rearing or thrashing, particularly after visits by *C. urabae*. Thrashing, a behavior which typically follows rearing in *U. lugens* (Allen, 1989), was never observed with small larvae.

Rearing or thrashing behavior by all three sizes of larvae was continued by at least some larvae after the parasitoid departed the petri dish, but mid larvae continued to rear or thrash for the longest period of time. The mean ± SE (range) number of minutes that rearing or thrashing continued after *C. urabae* departed was as follows: small, 16 ± 7 (0–35); mid, 108 ± 7 (75–120); and large, 56 ± 16 (0–110). That after *D. eucalypti* departed was as follows: small, 15 ± 15 (0–90); mid, 68 ± 21 (0–120); and large, 30 ± 19 (0–100). Small larvae maintained a rearing posture after parasitoid departure, while sporadic thrashing was the more typical behavior of mid and large larvae.

Rearing or thrashing by a larva did not necessarily prevent a subsequent encounter with a parasitoid, but the outcome of an encounter differed if a larva was rearing or thrashing just prior to that encounter (Fig. 4). Ovipositor inser-

Table II. The Mean Patch Area Prior to and After Parasitoid Departure for *C. urabae* and *D. eucalypti* Attacking Patches of 40 Small and 40 Mid *U. lugens*[a]

Species of parasitoid	Size of *U. lugens*	Mean patch area prior to parasitoid entry (mm^2) (P)	Mean patch area after parasitoid departure (mm^2) (A)	Mean ratio A/P
C. urabae	Small	27 ± 4	69 ± 14	2.51
C. urabae	Mid	504 ± 74	407 ± 58	0.82
D. eucalypti	Small	35 ± 4	99 ± 14	2.83
D. eucalypti	Mid	663 ± 123	587 ± 115	0.89

[a] Values are means ± SE. *N* is 6 for each mean.

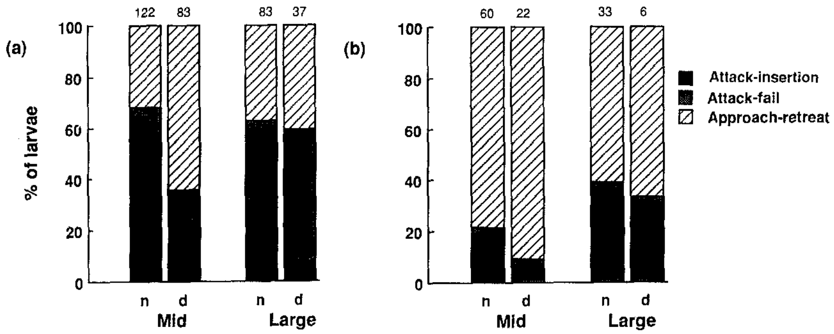

Fig. 4. The outcome of encounters between (a) *C. urabae*, (b) *D. eucalypti*, and the mid or large larvae of *U. lugens* when, immediately prior to the encounter, the larvae were either rearing or thrashing (d) or not rearing or thrashing (n). Data from six parasitoids were pooled for each bar. Figures above each bar indicate the number of encounters with larvae.

tion occurred less frequently in mid and large larvae that were rearing or thrashing immediately prior to an encounter with a parasitoid. These larvae typically elicited approach-retreat behavior by parasitoids. However, this trend was statistically significant only with *C. urabae* attacking mid larvae ($\chi^2_2 = 21.23$; $P < 0.001$); small sample sizes occurred in the other tests. Upon contact by a parasitoid, over 95% of mid and large larvae responded defensively, mostly by rearing; after the parasitoid had left, levels of defensive behavior remained high but were mostly expressed by thrashing. The behavior of larvae prior to the encounter did not influence these latter behaviors. Insufficient video resolution did not enable documentation of the effect of defensive behavior on the outcome of encounters with individual small larvae.

DISCUSSION

Gregariousness and the Defensive Behavior of *U. lugens*

Advantages of gregariousness in insects include aiding thermoregulation (Seymour, 1974; Sullivan and Wellington, 1953), facilitating feeding behavior, and helping overcome plant defenses (Ghent, 1960; Slansky and Panizzi, 1987; Risebrow and Dixon, 1987). Gregariousness may assist defense by (1) aiding in early predator detection, (2) benefiting the individual by placing conspecifics in the path of predator attack, (3) confusing predators by diverting predator focus, (4) diluting the predator's effect, and (5) in some instances, endangering the predator (Pulliam and Caraco, 1984). For aposematic insects, gregariousness may also help reinforce the warning value of aposematic coloration (Cott, 1940). Although defense may not necessarily be the primary function of the gregarious behavior of the younger instars of *U. lugens*, it is constructive to look at how it may enhance the defense of *U. lugens* against *D. eucalypti* and *C. urabae*.

Predator detection may be enhanced by gregariousness in *U. lugens*, because after the first visit by a parasitoid some individuals not directly encountered by the parasitoid began rearing, thrashing, or walking. These individuals may detect and then react to the defensive behavior of attacked conspecifics due to their close proximity to each other in the group and thus help reduce their vulnerability to parasitism. A similar behavior has been demonstrated in aggregations of the marine gerrid *Halobates robustus* Barber (Treherne and Foster, 1981). There was no evidence of detection of parasitoids by *U. lugens* prior to the first parasitoid visit, although this has been reported for the solitary caterpillars *Barathra brassicae* L. (Noctuidae) and *Malacosoma pluviale* (Dyar) (Lasiocampidae) which respond to an approaching parasitoid's wing vibration frequency (Myers and Smith, 1978; Tautz and Markl, 1978).

Gregariousness seems of little benefit in enhancing the defensive actions of small larvae. Although regurgitation and biting were observed, mandibular size and volume of regurgitate limited their effectiveness. Outward dispersal of larvae seemed the most effective response to reducing the success of parasitoid oviposition. Dispersal diluted the parasitoid's effectiveness and possibly diverted the parasitoid's focus, thereby countering the success rate possible had larvae remained in a tight group. Fujisaki (1975) concluded that the active breakup of colonies of first-instar winter cherry bug (*Acanthocoris sordidus* Thunberg) in response to predator attack enhanced instar survival. Neither *A. sordidus* nor small *U. lugens* disperse sufficiently to prevent subsequent reaggregation.

For mid larvae there were probably benefits of gregariousness for defense. Individuals residing in the center of the group were protected by their conspecifics because most encounters and ovipositions occurred with larvae on the group edge. Enhanced survival of insects located centrally within groups has also been demonstrated in the field with diprionid sawfly colonies (Tostowaryk, 1971, 1972). Mid larvae of *U. lugens* in the center of a group were protected by the tighter aggregation coupled with their longer setae, which had become at least as long as the parasitoid's body length. Additionally, moving over the top of a patch increased the likelihood of regurgitate contacting parasitoids and of parasitoid injury from biting *U. lugens*. Regurgitate appears to act as an irritant to the parasitoids, and in at least some insects, including grasshoppers (Eisner, 1970) and sawflies (Morrow *et al.*, 1976), it is protective against certain predators.

Individual mid *U. lugens*, by rearing or thrashing immediately prior to the encounter, were demonstrated to decrease their chance of being parasitized, but whether the chance of an encounter was also decreased was not ascertained. This was because parasitoids approaching a group of mid *U. lugens* have a choice of larvae and the reason why any particular larva was attacked was unclear. Decreased encounters in response to defensive behavior have been shown for *Aphidius rhopalosiphi* (DeStefani-Perez) attacking the cereal aphid *Metopolophium dirhodum* (Wlk.) (Gardner *et al.*, 1984). For *U. lugens* the combined effect of many mid larvae displaying defensive behavior may enhance any value of this defence.

Of the three sizes of larvae, large larvae, although not gregarious, were encountered by parasitoids least frequently and with least success. By this stage, however, the body size of *U. lugens* was much larger relative to that of the parasitoid. Large *U. lugens* had two or three head capsules stacked above their head (McFarland, 1978) and it was clear that these head capsules helped extend the ''area of defense'' (Stamp, 1986) to the *U. lugens* posterior during rearing behavior.

Thus as host development progresses, the behavioral responses of *U. lugens* to parasitoid attack change. Other insects also show changes with age in their responses to attack. *Heliothis punctiger* Wallengren, when attacked by the predator *Oechalia schellenbergii* Guerin-Méneville, changes the frequency of multiple defensive responses (Awan, 1985), and the aphid *Myzus persicae* (Sulzer) also increases its overall level of defensive behavior when attacked by the parasitoid *Ephedrus cerasicola* Stary (Hofsvang and Hågvar, 1986). Change of another kind is shown by *Hemileuca lucina* Hy. Edw. (Saturniidae), which is gregarious in early to mid larval instars and increases escape activity as it increases size (Cornell *et al.*, 1987). Cornell *et al.* (1987) hypothesized that with *H. lucina* defense was more effective when gregarious and escape more effective when solitary. *H. lucina* differs in this from *U. lugens*. When *U. lugens* becomes solitary it appears that individual defense is effective while escape occurs in early instars. This is an important difference that suggests a changing benefit of gregariousness to defense with age in *U. lugens*. For small larvae gregariousness is of little benefit to defense, while for mid larvae, which are larger relative to the parasitoid, it clearly helps defense. Obviously it would be constructive to test other possible reasons for gregariousness in order to understand more completely the evolutionary advantages of gregariousness in *U. lugens*.

Experimental Design, *U. lugens* Defensive Behavior, and Superparasitism

Unfortunately limitations on some potential host–parasitoid interactions were imposed by the experimental design. All encounters occurred with the leaf flush to the base of the petri dish so that larvae walking to the leaf edge could not escape by dropping on silk; nor could parasitoids oviposit in larvae from the opposite side of the leaf. The gregarious feeding by *U. lugens* causes skeletonizing of leaves, providing numerous holes through which a parasitoid could oviposit into the ventral surface of *U. lugens*. Furthermore, no tests were done with the larvae feeding underneath the leaf. In the field, *Eucalyptus* leaves are oriented at varying angles, while *U. lugens* eggs and larvae occur on both the upright and the underneath leaf surfaces (Campbell, 1962; Morgan and Cobbinah, 1977).

More than one ovipositor insertion was observed when either parasitoid attacked small larvae and when *C. urabae* attacked mid larvae; however, true superparasitism (multiple deposition of eggs) was not confirmed. The experimental design did not allow parasitoids to leave the petri dish, which may encourage superparasitism if insufficient hosts are present and parasitoids are unable to leave the patch (van Lenteren, 1981). Host numbers may have become limiting with small larvae but whether the petri dish provided sufficient area for the parasitoid to leave the patch (as perceived by the parasitoid) was unknown.

Superparasitism may also be affected by the continuation of defensive behavior by *U. lugens* for up to 2 h after parasitoid departure. Prolonged defensive behavior by *Euphydryas phaeton* Drury (Stamp, 1982) and the aphid *M. dirhodum* (Gardner *et al.*, 1984) decreases the frequency of further parasitoid encounters. Some parasitoids, however, such as *Cotesia plutellae* Kurdj. are attracted to moving hosts (Arthur, 1981; Lloyd, 1940) so that prolonged defensive behavior may also increase further encounters.

Host Acceptance and the Success of Oviposition of *C. urabae* and *D. eucalypti*

Host acceptance is the process whereby hosts are accepted or rejected for oviposition after contact has been made (Weseloh, 1974). Hopper and King (1984) defined parasitoid preference in terms of the difference between the relative frequency of host types parasitized and the relative frequency of host types available. Preference may arise because parasitoids find some hosts more easily than others or because, once found, some hosts are more likely to be parasitized than others (Hopper and King, 1984). True preference testing (simultaneous choice) was not undertaken in this experiment as neither parasitoid had the simultaneous choice of all three sizes of *U. lugens* in the field (Allen, 1990a). Nevertheless, many factors that may influence host acceptance and host preference were examined in this experiment, some determined by the parasitoid (i.e., frequency of visits) and some by the host (i.e, type of defense). However, the influence of the host's behavior is often ignored when determining a parasitoid species' levels of host acceptance and preference. It is also important to be aware that differences in the host habitat and the host finding ability of parasitoids (Vinson, 1975) will also influence parasitoid success in the field.

C. urabae was most successful attacking small larvae and least successful attacking large larvae but initiated an equivalent number of visits to all three sizes tested. This parasitoid species oviposited successfully and developed in all three larval sizes, although the degree of parasitoid mortality from internal host defenses was not determined. Its ability to handle all three larval sizes reflects its phenology since it encounters all three larval sizes in the field. During the summer generation of *U. lugens*, *C. urabae* oviposits into small larvae, emerges, then completes a second generation by ovipositing into mid larvae.

During the winter generation of *U. lugens*, *C. urabae* again oviposits into small larvae, emerges later, then completes a second generation by ovipositing into large larvae (Allen, 1990a). Nevertheless, the varying degree of success of oviposition in hosts of different size suggests less about its host preferences and degree of host acceptance than the behavioral interactions of parasite and host during oviposition. The increasing setal length, body size, and effectiveness of defensive behavior largely determined the outcome of encounters with successive size classes of host.

D. eucalypti made fewer visits to mid and large larvae than to small larvae and did not succeed in ovipositing in large larvae. This result also parallels the phenology of this species in the field. During the winter generation of *U. lugens*, *D. eucalypti* has only one generation, ovipositing into small larvae and emerging to pupate during pupation of that generation of the host. During the summer generation of *U. lugens*, *D. eucalypti* has two complete generations, first ovipositing into small larvae, emerging, then ovipositing into mid larvae (Allen, 1990a). Unlike *C. urabae*, *D. eucalypti* does not parasitize large larvae and is absent as an adult at the time large larvae occur in the field. *D. eucalypti* is able to ''avoid'' large larvae through a physiological delay to development whereby it remains within the host during the winter generation of *U. lugens* (Allen, 1990a). Once again as with *C. urabae*, the overall success of oviposition by this parasitoid was influenced by the size and effectiveness of defensive behavior of *U. lugens*.

The poor success of *D. eucalypti* when attacking mid larvae is apparently a limiting factor on the phenology of the parasitoid in the field. None of the three ovipositor insertions observed during the experiment resulted in emergence of an adult parasitoid. Although the stung *U. lugens* could have died during rearing, internal host defenses could well have killed the developing *D. eucalypti*. Hopper (1986) found a higher egg-larval mortality of *Microplitis croceipes* (Cresson) in older (fifth instar) *Heliothis virescens* (F.), as did Lewis and Vinson (1971) for *Cardiochiles nigriceps* Viereck in the fouth–fifth instars of the same host. Mid larvae of *U. lugens* may have more effective internal defenses than small larvae.

Even if *D. eucalypti* are presented with difficulties in relation to oviposition (and possibly development) in mid larvae, there are at least three ways in which the parasitoid may enhance its percentage parasitism in the field. First, it may exploit the range of *U. lugens* sizes present in the field (Allen, 1990b) by selectively foraging for patches of *U. lugens* with smaller host sizes. Second, *D. eucalypti* may attack some larvae from the opposite side of the leaf by inserting its ovipositor through the feeding holes. Finally, *D. eucalypti* may exploit patches of *U. lugens* when the larvae are molting (Allen, 1990b). *E. phaeton* is less responsive to attack when molting (Stamp, 1984) and this was also observed of *U. lugens* during preliminary experiments.

The varying success of *C. urabae* and *D. eucalypti* in attacking hosts of different sizes reflects their respective phenologies. *C. urabae* was the more ''general'' and more successful of the two parasitoids with all three larval sizes tested. Therefore, although it is important to understand the preference and host acceptance behavior of a parasitoid, it is equally important to account for the host's defensive behavior during oviposition to truly elucidate a parasitoid's oviposition success.

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