Aggregation as a cost-reducing strategy for lycaenid larvae

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If a mutualistic relationship entails providing services at a cost, selection will favor individuals that maximize the net benefits of the interaction and minimize the costs. Larvae of many species of lycaenid butterflies secrete nutritious food rewards to attending ants and, in return, receive protection against predators and parasitoids. Because ants typically recruit more workers to larger resources, by forming groups the larvae may ensure more reliable access to ants and thereby gain better protection. A further consequence of aggregating should be a change of the cost–benefit relationship for individual larvae. The larger the group, the smaller a single larva's influence will be on total ant density, which could lead to a smaller investment in secretion, thus reducing the per capita cost of cooperation. In this study, the influence of ant attendance, group size, and companion quality on larval investment was investigated. The interaction between the obligately ant-dependent lycaenid, *Jalmenus evagoras*, and its attendant *Iridomyrmex* ants was manipulated and the effect on larval secretion measured. As the level of ant attendance increased, the delivery of food rewards increased, both for solitary and for aggregated larvae. When aggregated, larvae provided less food rewards to ants than when solitary, and secretion rate decreased with increasing group size. Furthermore, larvae had lower secretion rates when paired with a bigger, more attractive larva than when paired with a smaller one. The considerable reduction in secretion rates for larvae in groups suggests that gaining protection at a lower secretion cost could be one factor that promotes aggregation in myrmecophilous lycaenids. *Key words:* aggregation, ants, butterflies, cooperation, cost–benefit relationship, food rewards, *Iridomyrmex, Jalmenus evagoras*, Lycaenidae, mutualism, protection, strategic behavior. *[Behav Ecol 9:109–115 (1998)]*

L arval aggregations occur in many insect species and may evolve as a means of defense against predation, either through a dilution effect, aposematism, or active group defense (see Vulinec, 1990, for a review). The size of an aggregation often influences larval survival, and group size is likely to vary in time and space. As the size of the aggregation changes, altering the conditions for group members, individual behavior is likely to be affected as well. The relationship between group size and behavioral time budgets, like the frequency of predator scanning versus foraging, is well studied in birds and ungulates (e.g., Elgar, 1989; Lima and Dill, 1990). A main theoretical perspective in these studies has been the effect of group size on individual cost–benefit relationships. For instance, an individually costly investment in defense against predators might benefit all group members, leading to a "tragedy of the commons" situation (Hardin, 1968). For insects, the relationship between group size and behavioral investment in defense has rarely been studied. In this study we examined the effect of group size on the behavior of aggregated larvae of the Australian lycaenid butterfly, *Jalmenus evagoras*, toward their attendant ants.

More than half of the species from the family Lycaenidae form associations with ants during their juvenile stages (Fiedler, 1991; Malicky, 1969; Pierce, 1987). The majority of these interactions seem to be mutualistic: ants protect larvae from parasitoids and predators in return for food rewards in the form of nutritious droplets produced by the larvae from specialized exocrine glands (Cottrell, 1984; Malicky, 1969). The lycaenid–ant interaction can be viewed as a trade of different kinds of services: food versus protection. If providing services to a partner is costly, and benefits only come from services provided in return, selection will favor individuals that maximize the benefits from the interaction and minimize the cost

of their own contribution. In a number of lycaenid species, individuals aggregate during some portion of their juvenile stages. With only one or two exceptions, species whose larvae and/or pupae aggregate are also tended by ants (Costa and Pierce, 1997; Kitching, 1981; Pierce and Elgar, 1985). It has been argued that aggregating could be a way for lycaenid larvae to enhance the benefits of ant protection and/or decrease the costs (Mathews, 1993; Pierce et al., 1987).

An ant colony's allocation of workers to a food source is often influenced by the profitability of the resource (e.g., Crawford and Rissing, 1983; Taylor, 1977), and hence larger aggregations of larvae should attract more workers. Juveniles of *J. evagoras* are dependent on ants for their survival and aggregate during all stages (Pierce et al., 1987). The tendency to aggregate is affected by ant attendance (Carper, 1989; Pierce et al., 1987); both younger instars and pupating older instars have a higher propensity to aggregate in the presence of ants (Pierce et al., 1987, 1991). Furthermore, when ants are present, a larva's decision to aggregate changes as the density of ants changes (Carper, 1989; Pierce et al., 1991). For *J. evagoras* in the field, the mean number of attendant ants per larva tends to increase with larval age, and larger groups attract larger total numbers of ants (Baylis, 1989; Nash, 1989; Pierce et al., 1987).

This ant response may benefit groups of larvae or pupae in several ways. First, by joining a group, an individual could receive increased protection. Even with a per capita decrease in attendance, larvae in groups will benefit if the degree of ant protection depends on total ant density more than on per capita attendance (Nash, 1989; Pierce et al., 1987). Second, the effect of aggregations on recruitment could reduce the cost of cooperation by reducing the amount of secretion necessary to recruit sufficient numbers of ants (Pierce et al., 1987). Release of food rewards to attendant ants is costly for *J. evagoras* (Pierce et al., 1987), and selection may favor adaptations leading to decreased secretion rates. Thus, aggre-

gating may enhance the benefits larvae receive from their mutualism with ants (increased protection) and reduce the costs (decreased secretion).

The aim of this study was to examine how aggregation affects secretion rates (i.e., the cost of cooperation) in *J. evagoras*. Aggregation could potentially affect the secretion rate at a given per capita attendance in three ways. First, secretion rate could be independent of group size if it is solely dependent on per capita attendance. Second, secretion rate could increase with group size if larvae compete for ants among themselves. Finally, secretion rate could decrease with group size if individual larvae are able to decrease their own contributions while the group as a whole nevertheless attracts sufficient ants for protection. Aggregation could then be a strategy to distribute the secretion costs over a greater number of individuals and thus lower the costs for each individual in the group. Furthermore, because larval attractiveness varies with larval age, it may be beneficial to aggregate with larger larvae. Individual larvae might therefore vary their responses according to the size of other larvae in the group.

This is the first study investigating whether lycaenid larvae change the amount of secretion in response to the presence of conspecific larvae and in response to the number and size of conspecific companions. Earlier studies have shown that lycaenids can be both flexible and strategic in their behavior toward the attendant ants (Axén et al., 1996; Fiedler and Hagemann, 1995; Leimar and Axén, 1993). Individuals vary the contribution they offer to the mutualistic partner according to both the partner's behavior and the need for the partner's services (Axén et al., 1996; Leimar and Axén, 1993). In the experiments reported here, we varied the aggregation conditions of *J. evagoras* larvae and observed their response. Both solitary and aggregated larvae were exposed to variation in ant attendance. Other larvae were subjected to different group sizes, either with ants having free access to the group or with a controlled number of ants tending each test larva. We also observed the reaction to the size of a companion larva.

METHODS

Study animals

Larvae of the lycaenid butterfly *Jalmenus evagoras* Donovan are tended and protected by several species of ants in the genus *Iridomyrmex* during both the larval and the pupal stages (Figure 1). The larvae feed on the leaves of 23 different species of *Acacia* (Hawkeswood, 1981; Nash, 1989). Females lay eggs in clusters and use ants as cues in oviposition (Pierce and Elgar, 1985). Plants commonly receive egg masses from more than one female. Larvae of mixed ages form dynamic aggregations throughout their larval life and finally pupate in groups on the host plant (Pierce et al., 1987).

The larvae of *J. evagoras*, like those of most other myrmecophilous lycaenids, possess a number of adaptations that allow them to associate with ants (Kitching, 1983). The dorsal nectar organ secretes food rewards upon solicitation by ants in the form of small droplets. In *J. evagoras*, these droplets contain various sugars and several different amino acids (Pierce, 1983), and the ants may receive substantial nutritional benefits from the secretions (Nash, 1989; Pierce et al., 1987). Many lycaenids have eversible tentacles flanking the dorsal nectar organ. The tentacles are believed to secrete volatile substances that alert and alarm ants (Fiedler and Maschwitz, 1987; Henning, 1983). Tentacular display may help to regulate the number of attending ants (Axén et al., 1996). In *J. evagoras*, the dorsal nectar organ and the eversible tentacles are present from the second instar (Kitching, 1983).

Figure 1
Fifth instar larva of *Jalmenus evagoras* tended by *Iridomyrmex* ants. (Illustration by Christopher Adams.)

Larvae of *J. evagoras* used in this study came from a population collected as eggs from Ebor, New South Wales, Australia (30°24′ S, 152°19′ E; altitude 1300 m), in January of 1995, and reared in a greenhouse on potted plants of two of their common host plants, *Acacia melanoxylon* and *A. filicifolia*. We used early fourth instar larvae in all experiments. In some experiments, larvae were marked individually with a dot of water-based Tipp-Ex fluid.

The ants used in the experiments belong to the *Iridomyrmex anceps* species group (sp. 25, Australian National Insect Collection). We kept a queenright colony in a plastic aquarium where the ants could nest inside test tubes. The test tubes were wrapped in foil and half-filled with water, tightly plugged with cotton, to keep the interior of the tubes humid and dark. The ants were provided with Bhatkar diet (Bhatkar and Whitcomb, 1970) and chopped crickets each day. We removed the food during experiments.

Experimental setup

All experiments had the same general setup. The ant colony was connected to one or several foraging arenas where the ants were fed and where the interactions with *J. evagoras* larvae took place. The ants could walk through plastic tubes between the colony and the foraging arenas. The number of ants in the arenas was controlled by constricting the tube with a clip.

Before the start of an experiment, we placed one or several fourth instar larvae in a foraging arena together with a leaf of the food plant. After 10–15 min, the ants were allowed to enter. We closed the entrance to the foraging arena when the desired number of ants had entered.

During a trial, we observed the interactions through a binocular microscope and recorded both droplet deliveries and
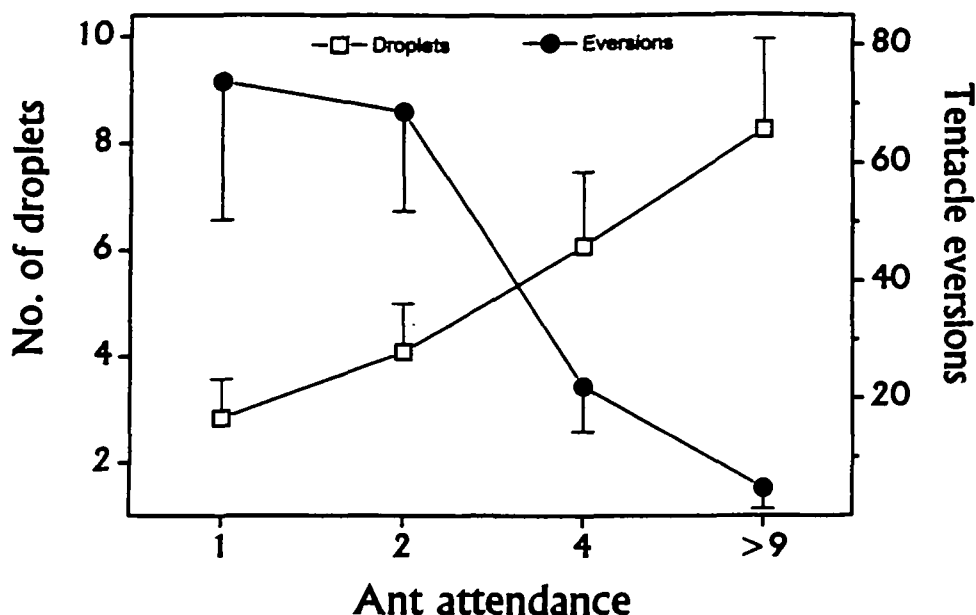
tentacle eversions. Only one larva was observed at a time. The number of ants tending the test larva was noted every 10 s.

Statistical analysis

All statistical comparisons were matched and performed with either the Friedman test or the Wilcoxon paired-sample test. Exact critical values of χ_r^2 for the Friedman test were used whenever available in Zar (1996); in other cases we used the large sample approximation (χ^2). For the Wilcoxon test, exact two-tailed critical values from Zar (1996) were used (discarding zero differences).

EXPERIMENTS

Larval response to ant attendance

Methods

To investigate how a solitary larva reacts to different levels of ant attendance, each of 12 larvae were subjected to 4 treatments with different levels of ant attendance: either 1, 2, 4, or more than 9 ants in the arena. We carried out all treatments for a given larva the same day and in a randomized order. The larva was placed in the arena, and after 10 min the ants were allowed to enter. After 10 min together with ants, we observed the interaction for 10 min. After the first observation period, the number of ants was changed, and the interaction was allowed to stabilize for 10 min before the start of the next observation period.

Results

The level of ant attendance affected the behavior of solitary larvae (Figure 2). As the actual number of tending ants increased (Friedman test, χ_r^2 = 36.00, a = 4, p < .001, n = 12), larvae increased the secretion rate (Friedman test, χ_r^2 = 16.54, a = 4, p < .001, n = 12). The rate of tentacle display changed in the opposite direction, with decreasing display with increasing attendance (Friedman test, χ_r^2 = 23.24, a = 4, p < .001, n = 12).

Larval response to group size

Methods

To assess larval response to different group sizes, we exposed 20 individually marked larvae to 5 treatments in which larval

group size was allowed to vary. Four different group sizes were created by adding unmarked larvae of similar size to the test larvae in combinations of 1, 2, 3, or 4. The test larva was placed either together with one of these groups or alone in a foraging arena. Each test larva was exposed to all 5 different group sizes, that is, alone, with one other larva, or with 2, 3, and 4 other larvae, and in a randomized order.

We tested four individually marked larvae successively in four different foraging arenas. All larvae were first placed in the foraging arenas. The ant colony was then given free access to all foraging arenas. After 15 min of interaction, the first observation period started in the first arena. We observed this interaction for 5 min before moving to the next arena. When all four test larvae had been observed, they were removed and placed in another arena with another group size. After 15 min, a new series of observations took place. When all four test larvae had gone through all five treatments, we terminated the experiment.

Results

Larval behavior was affected by group size (Figure 3), both with regard to secretion rate (Friedman test, χ^2 = 24.50, df = 4, p < .001, n = 20) and rate of tentacle display (Friedman test, χ^2 = 17.02, df = 4, p = .002, n = 20). The secretion rate was almost three times higher when a larva was alone than when it was in a group of three or more, and tentacle display followed a similar pattern of gradual decrease with increasing group size. With ants allowed free access to the arenas, the group size also affected ant attendance (Figure 3). The per capita attendance decreased with increased group size (Friedman test, χ^2 = 20.99, df = 4, p < .001, n = 20).

Larval response to group size at a constant level of ant attendance

Methods

The aim of this experiment was to investigate the possibility that the decrease in secretion observed in the previous experiment was due only to lower per capita attendance and not group size per se. To this end, we held per capita attendance constant while varying the group size. The test larva (n = 24) was either alone, with one other larva, or with three other larvae. An approximately constant per capita tending level was
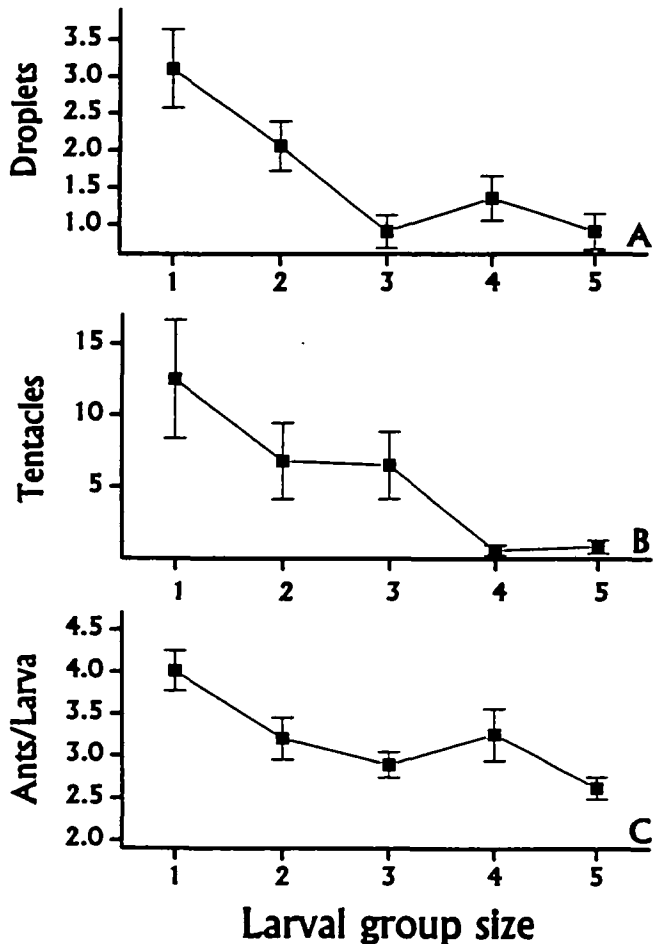
Figure 3
Larval response to group size when ants have free access to the caterpillars: number (mean±SE) of (A) secreted droplets, (B) tentacle eversions, and (C) per capita attendance during 5 min. Each larva (N=20) experienced five treatments and was either alone or in a group of two to five larvae.

Figure 4
Larval response to group size at a constant per capita level of attendance: number (mean±SE) of (A) secreted droplets, (B) tentacle eversions, and (C) per capita attendance during 5 min. Each larva (n = 24) experienced three treatments and was either alone or in a group of two or four larvae.

achieved by having two ants/larva in the arena, that is two, four, and eight ants. Other than these modifications, the experiment was performed in the same way as the previous one.

Results
In accordance with the experimental design, no difference in per capita level of attendance was found between treatments (Friedman test, $\chi^2 = 0.19$, df = 2, $p = .91$, $n = 24$; Figure 4). In spite of this, the effect of group size seen in the previous experiment remained (Figure 4). As the group size increased, individual larvae decreased their secretion rate (Friedman test, $\chi^2 = 17.61$, df = 2, $p < .001$, $n = 24$) and also the rate of tentacle display (Friedman test, $\chi^2 = 6.84$, df = 2, $p = .033$, $n = 24$). Thus, an increased group size affected both behaviors and in the same direction.

Larval response to level of ant attendance at a constant group size

Methods
In the first experiment, with solitary larvae reacting to different degrees of attendance, the rate of droplet delivery and tentacle eversions changed in opposite directions. In the experiments with larvae reacting to the size of the aggregation, on the other hand, the two behaviors changed more or less
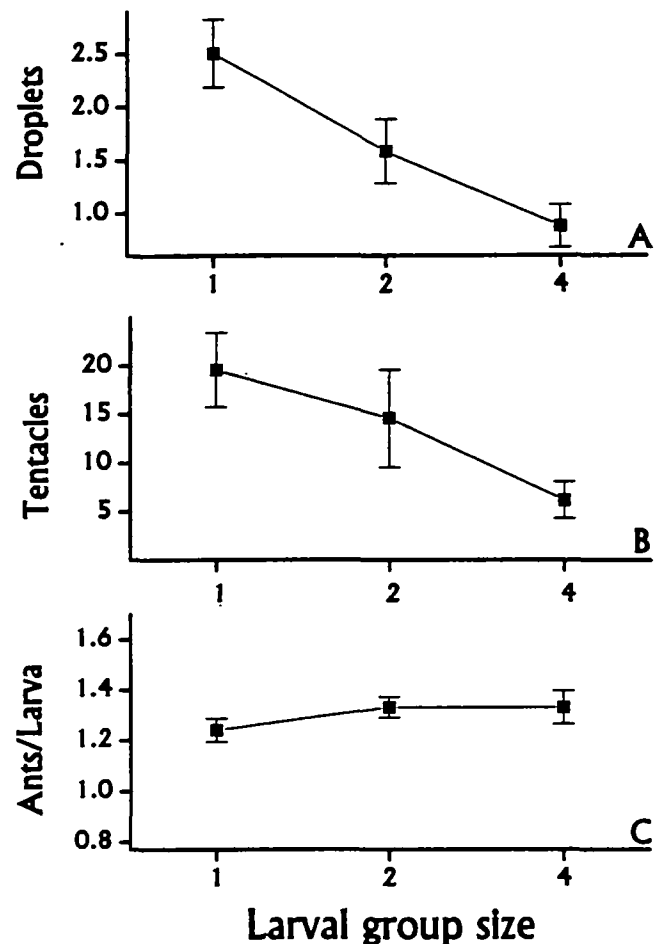
in parallel. To see if larvae in groups respond in the same way to variation in ant attendance as solitary larvae, we exposed individually marked larvae in groups of four to different numbers of ants.

We varied the number of ants by adding either 1, 2, or 4 ants per larva; that is, 4, 8, or 16 ants were allowed in the foraging arena. After 30 min with ants, all larvae were observed, one at a time, for 5 min. When all 4 larvae in the group had been observed, we changed the treatment by adding or taking away ants, and, after an additional 30 min of interaction, a new series of observations started. A total of 10 groups (40 larvae) were observed, and the different treatments for a group were performed in a randomized order. We used the mean value of the larval response in each group in the Friedman test.

Results
Larvae in groups reacted in a similar way to increased ant attendance as solitary larvae (Figure 5). As the per capita attendance increased (Friedman test, $\chi^2 = 20.00$, $a = 3$, $p < .001$, $n = 10$) the delivery of droplets increased (Friedman test, $\chi^2 = 7.58$, $a = 3$, $p < .05$, $n = 10$). However, there was no significant variation in tentacle display (Friedman test, $\chi^2 = 0.36$, $a = 3$, $p > .5$, $n = 10$).
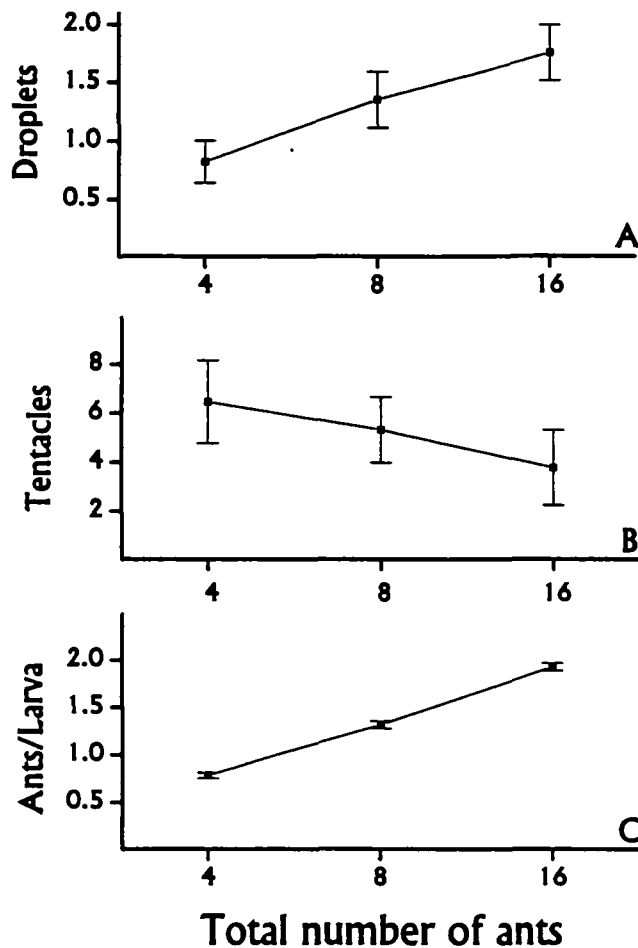
Figure 5
Larval response to level of attendance at a constant group size: number (mean±SE) of (A) secreted droplets, (B) tentacle eversions, and (C) per capita attendance during 5 min. Each group of four larvae experienced three treatments, with either 4, 8, or 16 ants in the arena (n = 10 groups).

Larval response to the size of a second larva

Methods

Larval instar affects attractiveness to ants (Pierce et al., 1987). First instar larvae do not possess a dorsal nectar organ or tentacles (Kitching, 1983), and are not frequently tended when solitary (Pierce et al., 1987). After molting to the second instar, a larva becomes more attractive to ants and progressively more attractive as it grows and molts to the fifth and final instar. Given this, it should be more beneficial to aggregate with larger larvae than with smaller ones. To test whether a larva can respond to the size of a companion larva, a fourth instar larva was placed together with either a smaller (third instar) or a larger (fifth instar) companion, and secretion rates were measured in both situations. The secretion rate of the accompanying larva was also measured.

We performed two different approaches to this experiment which controlled for either (1) total ant number (n = 10 test larvae) or (2) per capita attendance (n = 16 test larvae). In the first set of experiments, total ant density was held constant at five ants per foraging arena. In the second set of experiments, the number of ants tending the test larva was held more or less constant by taking into account per capita attendance. Because a larger larva in a pair gets more attendance than a smaller one, only three ants were allowed in the arena
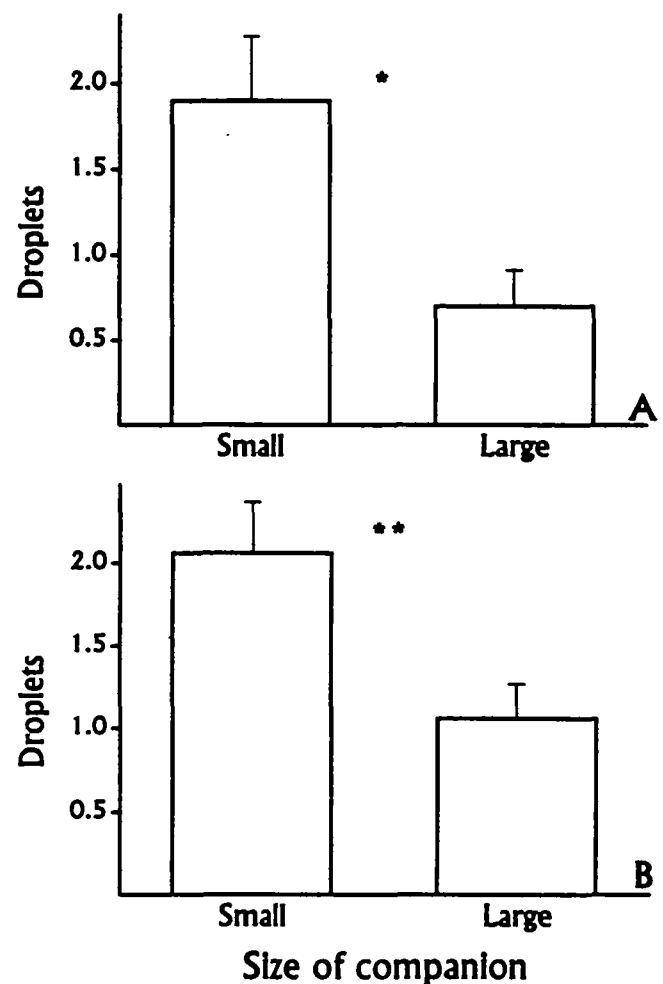

Figure 6
Larval response to the size of an accompanying larva: number (mean±SE) of droplets secreted during 5 min. Each larva experienced two treatments with a companion either smaller or larger than itself. Two sets of experiments were performed, where either (A) total number of ants (n = 10 test larvae) or (B) number of ants directly tending the test larva (n = 16 test larvae) were held constant in both treatments.

in the treatment with a small companion, whereas a total of five ants were allowed in the treatment with a larger companion. This approach equalized the mean number of ants tending the test larva.

For each trial, we placed the test larva and its companion in an arena. After 30 min with ants, the test larva and the accompanying larva were observed for 5 min each. We then changed the treatment by removing the first companion and adding the second companion. After an additional 30 min of interaction, both of these larvae were observed for 5 min each. The treatments (smaller/larger companion) were performed in a randomized order.

Results

The relative companion size affected the secretion rate, both when the total number of ants was constant (Figure 6A) and when the per capita attendance was constant (Figure 6B). In the experiment where the total number of ants was constant, the test larvae delivered more than twice as many droplets when paired with a smaller larva (mean ±SE: 1.9±0.4) than when paired with a larva bigger than themselves (0.7±0.2;

Wilcoxon test, $T = 0.0$, $n = 10$, $p < .05$; Figure 6A). In the experiment where per capita attendance was controlled, there was no significant difference in ant attendance of the test larva between the two treatments (Wilcoxon test, $T = 48.5$, $N = 16$, $p > .5$), but together with a smaller larva, the secretion rate was almost twice as high (2.1 ± 0.3) as when with a larger larva (1.1 ± 0.2; Wilcoxon test, $T = 4.5$, $n = 16$, $p < .005$; Figure 6B).

The size of the companion had no significant effect on tentacle display, either with a constant total number of ants (Wilcoxon test, $T = 10.0$, $n = 10$, $p > .5$), or with a constant per capita attendance (Wilcoxon test, $T = 39.0$, $n = 16$, $p > .2$). Large companions secreted more than twice as many droplets (1.9 ± 0.6; 2.8 ± 0.4) as small companions (0.7 ± 0.3; 0.9 ± 0.3) in both experiments. Mean weights ($\pm SE$) for large companions, test larvae, and small companions were 26.6 ± 2.3 mg ($n = 5$), 8.5 ± 0.3 mg ($n = 10$), and 3.7 ± 0.2 mg ($n = 5$) and 23.7 ± 1.4 mg ($n = 8$), 9.2 ± 0.4 mg ($n = 16$), and 3.7 ± 0.2 mg ($n = 8$), respectively, in the two experiments.

DISCUSSION

One might expect larval behavior to be aimed at regulating the number of surrounding ants to achieve an optimal balance between the benefit of ant protection and the cost of secreting rewards. Lycaenid larvae are quite flexible in their behavior toward attending ants (Axén et al., 1996; Fiedler and Hagemann, 1995; Leimar and Axén, 1993). For instance, ant-related behavior is affected by the size and continuity of the ant guard and by the perceived risk of enemy attack (Axén et al., 1996; Leimar and Axén, 1993). These factors interact in determining larval behavior so that the response to a simulated enemy attack depends on the current size of the ant guard (Axén et al., 1996). Such variation in the rate of secretion and also in behaviors like tentacle signaling can influence the ants and thus regulate the size of the ant guard.

Lycaenid species differ in how strongly the larvae and pupae depend on ants for survival, and this should be reflected in larval behavior. For *J. evagoras*, the dependence on ants for defense is essentially obligate (Pierce et al., 1987), making it crucial for a larva to have an effective ant guard. This is a likely reason for the substantial investment in secretion by *J. evagoras* and might also explain some of the patterns of behavioral response. For instance, assuming that a *J. evagoras* larva needs to be surrounded by many ants to be protected, one might expect that the larva would keep increasing the secreted reward with increasing attendance, up to a threshold. This threshold would be a function of the number of ants needed to protect a larva, as well as a larva's metabolic ability to secrete sufficient high-quality rewards. In the current study, larval secretion rates never leveled off during the time frame of the experiment, and thus this threshold is probably higher than four ants per larva (Figure 2). This result differs from a previous study on larvae of another lycaenid butterfly, *Polyommatus icarus*, were the secretion rate increased initially, leveled off at two to four ants per larva, and decreased at higher levels of attendance (Axén et al., 1996). *Polyommatus icarus* is a facultative ant mutualist that can survive without ant protection (Fiedler, 1991), so *P. icarus* larvae may have a lower per capita threshold than *J. evagoras*, and it may even be profitable to decrease the expense of secretion at high levels of attendance. The high secretion rate of *J. evagoras* may, of course, change over time and later stabilize at a lower more economic level, as has been shown for *P. icarus* (Axén et al., 1996).

When high levels of attending ants are vital for survival, it might be beneficial to join a group of conspecifics to ensure reliable access to ants. This may explain the positive correlation observed between aggregation and obligate ant association in the Lycaenidae (Kitching, 1981; Pierce and Elgar, 1985), although verification of such a relationship will require more information

regarding the phylogenetic relationships of the taxa involved. Cannibalism is widespread among the Lycaenidae (Hinton, 1951; Mattson, 1980), and thus selection for larval aggregation must have been accompanied by selection against aggression between conspecifics.

For a larva in a group, the relationship between its behavior and the protection it receives from surrounding ants will be different than for a solitary larva. It might be important for a group member to have a certain number of ants in direct attendance to notice and to ward off enemy attacks and to alert nearby ants when there is a disturbance. However, the larger the group, the smaller the influence of a single larva's behavior on total ant density. The optimal level of secretion for a group member would depend both on the information it has about the surrounding situation and on the relative importance of directly attending ants versus ants in the vicinity.

First, if a larva is only aware of the number of directly attending ants, one would not see any behavioral effect of group size per se. For *J. evagoras*, however, this alternative does not appear to be the case. Individual larvae decreased the rates of secretion and tentacle display when the size of the aggregation increased, both when ant attendance simultaneously decreased (Figure 3) and when the per capita attendance was controlled (Figure 4).

Second, assuming that ant protection is only received from the exclusive ant guard, one might expect competition among group members for access to available ants. The ants could rather easily determine which larvae are the most productive and choose to concentrate their attendance, and thus protection, on only these group members. The larvae would be selected to compete by outbidding each other in the amount of secretions they offer to the ants in a kind of biological market (Noë and Hammerstein, 1994, 1995). In such a case, the secretion rate should increase as the group size increases. However, this is not consistent with the data because delivery of droplets instead decreased with increasing group size (Figures 3, 4).

Finally, if a larva is protected not only by the ants directly attending it, but also by surrounding ants, the benefit of ant protection will be less dependent on an individual larva's contribution. Thus, the increase in benefit with increased secretion rate would be smaller in a group than when solitary, and a minimal number of ants directly tending a larva may be enough to alert other ants in case of danger. One should then expect a smaller larval investment in secretion with increasing group size. This is in fact what is observed for *J. evagoras* (Figures 3, 4)

Analogously, if the quality of group members vary, a larva's contribution might change according to the accompanying larvae's ability to attract ants. Larval attractiveness increases with larval age and instar (Pierce et al., 1987), probably due to a higher rate of secretion. Thus, older instars should be high-quality companions, and, consistent with the response to group size, one should expect a larva to have a lower secretion rate when with a large companion than when with a smaller one. This was also observed for *J. evagoras* (Figure 6). The variation in secretion seen in the experiment is not entirely determined by total ant density, as the effect was present with constant total ant number (Figure 6A), nor is it entirely determined by per capita attendance, as the effect was present for constant per capita attendance (Figure 6B). The behavioral response instead seems to be influenced by a combination of direct attendance, surrounding larvae, and/or total ant density.

The effects of surrounding larvae and total ant density on larval behavior are not fully separated in our experiments. In the field, total ant density typically varies in parallel with group size (Carper, 1989; Mathews, 1993; Pierce et al., 1987), and this was also the case in our experiments. However, regardless of the proximate cause of the reduced secretion rate of aggregated *J. evagoras* larvae, the conclusion is that larvae can decrease the cost of cooperation by joining with conspe-

cifics. Thus, gaining protection at a lower secretion cost could be one factor that promotes aggregation in lycaenid larvae. This benefit of group living is similar to the decrease in vigilance against predation with increasing group size found in many other groups of animals, such as a per capita reduction in time spent scanning for predators in larger groups, which is commonly observed in birds and mammals (Lima and Dill, 1990).

Aggregating will have consequences other than the ones examined in this study, and some of these may represent a cost for the larvae. For example, groups of larvae may experience a greater risk of detection by predators and parasitoids because aggregations are likely to be more conspicuous. In fact, when attending ants are experimentally removed, the mortality risk increases with increased group size (Pierce, 1983). Furthermore, because of the highly clumped distribution of *J. evagoras* on a host plant, with some branches crowded and others empty of larvae, the larvae often experience food shortage after consuming all available food (Common and Waterhouse, 1981; Pierce et al., 1987). Younger instars may benefit by foraging in a group by utilizing areas where larger larvae have chewed through the cuticle of the host plant to get to softer tissues beneath, but this would not apply to older instars. Overall, aggregation in *J. evagoras* appears to have mainly ant-related benefits.

Finally, it is worth noting that the quantitative effects of group size on larval secretion are quite considerable. The mean group size of *J. evagoras* in the field is about four larvae (Pierce et al., 1987), and in these experiments individual larvae secreted about three times more when solitary than when in a group of four (Figures 3, 4). Aggregation might therefore have a dramatic effect on the transfer of resources from lycaenid larvae to ants.

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