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THE NATURE OF ANT ATTENDANCE AND THE SURVIVAL OF LARVAL *ICARICIA ACMON* (LYCAENIDAE)

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ABSTRACT. I examined ant attendance and its importance to larval survivorship in a facultatively myrmecophilous butterfly, *Icaricia acmon* (Westwood and Hewitson) (Lycaenidae), in a population that uses two host plant species, *Eriogonum compositum* Dougl. and *E. strictum* Benth. (Polygonaceae). Third and fourth instar larvae of *I. acmon* were tended by three ant species: *Tapinoma sessile* (Say), *Formica neogagates* Emery, and an unidentified *Formica* species. Third instar larvae were tended less frequently than fourth instar larvae on both plant species, and *T. sessile* was the attendant ant species for a higher proportion of third instar than fourth instar larvae developing on *E. compositum*. Over the duration of the study, all switches of attendant ant species on individual plants were from early *T. sessile* attendance to later *F. neogagates* attendance. An exclosure experiment revealed that ant attendance had no significant effect on larval mortality.

Additional key words: *Tapinoma, Formica,* facultative myrmecophily, Washington, *Eriogonum.*

The association of lycaenid larvae with ants (Formicidae) has provided researchers with model systems for studying the costs and benefits of mutualisms. Recent work has focused on both ecological and evolutionary aspects of these mutualisms, including host-parasitoid interactions (Pierce & Mead 1981), oviposition behavior (Atsatt 1981a, Pierce & Elgar 1985), and the evolution of host choice (Atsatt 1981b, Pierce 1985). To understand the evolution of these mutualisms, it is critical to examine the costs and benefits to both partners. Several field studies have documented the importance of ants to the survival of larval lycaenids (Pierce & Mead 1981, Pierce & Easteal 1986, Pierce et al. 1987, Fiedler & Maschwitz 1989b), but few have experimentally addressed this issue in facultative ant-lycaenid associations (but see Pierce & Mead 1981, Pierce & Easteal 1986). This is particularly surprising when one considers that most lycaenid-ant associations are facultative (see Fiedler 1989a for a recent review). Although the mutualisms studied so far provide excellent ecological and evolutionary case studies, it is important to recognize how variability in the intensity of ant-lycaenid associations might affect generalizations about these systems. To broaden our understanding of facultative ant-lycaenid mutualisms, I conducted an ant exclosure experiment to determine the importance of ant attendance and host plant choice to larval demography in a population of *Icaricia acmon* (Westwood and Hewitson) (Polyommatinae: Polyommatini) in central Washington.

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STUDY SITE AND ORGANISM

The population of *Icaricia acmon lutzi* (dos Passos) that I studied occupies a bench of the Yakima River, 11.2 miles north of Yakima, Washington at 46°47′N, 120°27′W and 375 m elevation. The habitat represents the *Artemisia/Festuca* zone described by Franklin and Dyrness (1973), but has fewer *Artemisia* and more *Eriogonum* (Polygonaceae) species than typical *Artemisia/Festuca* communities. The four commonest *Eriogonum* species were *E. compositum* Dougl., *E. strictum* Benth., *E. microthecum* Nutt., and *E. elatum* Dougl. The climate in this region is arid to semiarid with relatively warm summers and cold winters. The mean annual precipitation in nearby Yakima is 20 cm with only a small amount (2.9 cm) of this falling during June through August. Average temperatures in the Yakima area in July and January are 21.7°C and −2.5°C, respectively (Franklin & Dyrness 1973).

Although populations of *Icaricia acmon* in this area of Washington have been called hybrids with *I. lupini* (Boisduval) (Goodpasture 1973), regional systematists refer to all populations in the state as *I. acmon* (J. P. Pelham pers. comm.). *Icaricia acmon* ranges throughout much of western North America, and has been recorded feeding on *Polygonum* and at least seventeen species of *Eriogonum* (both Polygonaceae) as well as *Lotus, Astragalus, Lupinus,* and *Melilotus* (all Fabaceae) (Scott 1986). Subspecies *lutzi* ranges from British Columbia south to central Oregon and east to central Colorado (Goodpasture 1973). In Washington, *I. acmon lutzi* specializes on *Eriogonum,* having been recorded from *E. compositum, E. pyrolifolium* Hook., *E. sphaerocephalum* Dougl., and *E. strictum,* and has one or two broods, depending on the site (Peterson, unpubl. data). Larvae diapause in the third instar through winter and resume feeding when their host plant leafs out in the spring. Larvae feed on leaves or flowers by chewing holes in the surface of the structures and inserting their heads to mine out the internal tissues. Several ant species tend the third and fourth instar larvae of *I. acmon,* but earlier instars are not tended (Peterson pers. obs.). California populations of *I. acmon* have four instars and larvae have both a honey gland and eversible tentacles, structures associated with myrmecophily (Ballmer & Pratt 1988). Washington populations are similar in these regards (Peterson pers. obs.). It is not known when these structures first appear in development or if pupae of *I. acmon* are tended by ants.

METHODS

I determined host plant species of the study population of *I. acmon* by following ovipositing females and searching for eggs and young larvae. I observed 73 alightings on *Eriogonum compositum* and *E.*

strictum, two of the three commonest *Eriogonum* species at the site. These alightings resulted in 10 ovipositions, with all eggs laid singly. I saw no encounters with other *Eriogonum* species at the site. In addition, I found eggs and larvae only on these two plant species.

To test the effect of ant attendance on larval demography, I selected 24 pairs of *E. compositum* and *E. strictum* in an area approximately 70 m × 30 m. Each pair was composed of one plant of each species, with individuals in a pair matched for size and occurring within 0.25 m of, but not in contact with, each other. To exclude ants, I encircled half of the pairs with rings of aluminum flashing which I had painted with Fluon® AD 1 (Northern Products, Inc., Woonsocket, RI), a substance which forms a slippery coating on which arthropods cannot get traction. The base of the flashing was buried 1–2 cm below the soil surface and did not disturb the roots of the plants. In addition, because the soil at the study site had excellent drainage, the flashing could not have retained precipitation. Finally, the flashing was placed far enough from the plants to eliminate shading, and thus should have had no impact on plant quality. I left the remaining pairs without an arthropod exclosure as a control. Onto each of the plants, I placed either ova or early instar (first or early second) larvae of *I. acmon*. I placed two individuals on each plant, for a total of 96 individuals (13 ova and 83 larvae). It is unlikely that at such low densities, larvae would cannibalize each other, especially in light of the fact that in numerous rearings at much higher densities, I have seen cannibalism rarely in this species.

From 7 June to 18 September 1986, I conducted midday censuses at approximately weekly intervals; I resumed the censuses from 17 March to 26 April 1987 (19 censuses total: 13 in 1986 and 6 in 1987). During censuses, I noted the number of larvae on each plant and the species and number of attendant ants. Following the onset of the experiment, 35 larvae appeared in addition to those I had placed on the plants. Twenty-nine of these appeared between the onset of the experiment and 6 July, and the remaining six appeared by 6 August. Presumably, these larvae were already on the plants when I started the experiment or were from eggs that I did not see. I left these additional larvae on the plants because it was impossible to tell individual larvae apart. The distribution of these larvae was as follows: 9 larvae on *E. strictum* control plants, 11 on *E. strictum* exclosure plants, 13 on *E. compositum* control plants, and 2 on *E. compositum* exclosure plants. When larvae reached late 4th instar (the final instar), I collected them and raised them in the laboratory to obtain an estimate of the frequency of larval parasitism. On *E. compositum*, all of the larvae that reached late 4th instar did so from 18–26 April 1987. One larva matured by 6 July 1986 on *E. strictum*, but the remainder that reached late 4th instar did so from 5–26 April 1987. One of the ant-exclosure pairs was destroyed during the experiment, and larvae on these plants were excluded from the analysis of survivorship. To eliminate problems of autocorrelation, I analyzed ant attendance data with *t*-tests of mean per-plant attendance rates. Overall attendance rates were calculated using data from only the eight census dates on which at least one larva was tended. The reason for this is that on the days when no larvae were tended, it is likely that the lack of attendance had more to do with foraging conditions than larval attractiveness. Larvae were tended on 14, 21, 29 June and 6 July 1986 and 5, 12, 18, and 26 April 1987. For analyses of survivorship, I performed G-tests of independence, applying Williams' 2 × 2 correction (Sokal & Rohlf 1981). Vouchers of *I. acmon* are deposited in lot #1198 in the Cornell University Entomology Collection.

RESULTS

Ant Attendance

Three species of ants tended *I. acmon* larvae during this experiment: *Tapinoma sessile* (Say) (Dolichoderinae), *Formica neogagates* Emery, and an unidentified *Formica* species (both Formicinae). In all instances, only one ant species tended larvae on a single plant at a given time. Third and fourth instar larvae were tended by these ants, but I saw no first or second instar larvae tended during the censuses.

Tapinoma sessile is a small (2.5–3.5 mm long) dolichoderine ant which tended larvae singly or in groups of up to four ants. When disturbed during censuses, these ants ran to the base of the plant, abandoning the larva they were tending. *Formica neogagates* is larger (3.5–4.5 mm long) than *T. sessile*, tended *I. acmon* singly or in pairs, and was a much more aggressive tender than *T. sessile*. When disturbed, they assumed an alarm-defense posture (Wilson 1971) and would bite any object placed near them. The unidentified *Formica* sp. was similar in size and behavior to *F. neogagates*. I did not collect any specimens of this species. Because I saw only two of these ants and because of their similarity to *F. neogagates*, I combined these two species in the analysis of the composition of attendant ants by instar.

I saw no ant attendance from 13 July 1986 through 29 March 1987 (recall there were no censuses from 18 September 1986 to 17 March 1987); during this time larvae were quiescent and fed rarely. Midday soil temperatures were well in excess of 50°C throughout much of the summer and this may have restricted ant activity. On days when I saw ant attendance, third instar larvae were tended less than fourth instar larvae on both host species (Table 1). In addition, the species composition of attendant ants varied with instar on *E. compositum*, with the di-

TABLE 1. The incidence of ant attendance[1] of third and fourth instar *Icaricia acmon* larvae on *Eriogonum compositum* and *E. strictum* on the eight census dates when ants were observed.

Plant species	Mean % tended	SE	N
E. compositum[a]			
3rd instar	43.3	7.0	11
4th instar	88.9	6.5	7
E. strictum[b]			
3rd instar	10.9	9.1	11
4th instar	53.6	15.8	7

[1] To avoid problems with autocorrelation, I determined the percentage of larvae tended on each control plant. Values are the means of these percentages.
[a] $t = 2.66$, 16 df, $P < 0.025$.
[b] $t = 2.52$, 16 df, $P < 0.025$.

minutive *Tapinoma sessile* tending a greater proportion of third instar than fourth instar larvae (Table 2). On *E. strictum*, the composition of attendant ants varied similarly, but the differences were not statistically significant (Table 2). Most plants of both species had the same attendant species throughout the study. Interestingly, the six plants that had more than one ant species during the experiment all had *Tapinoma sessile* tending larvae early in the study and *Formica neogagates* tending larvae later.

Survivorship

Ants had no statistically significant effect on the survivorship of larvae to late fourth instar on either host species (Table 3). These data include those extra larvae that appeared after the onset of the experiment, and percentages are from data combined for all plants with similar treatments. All disappearances were interpreted as deaths for these measures of survivorship because it is unlikely that larvae leaving the plants in

TABLE 2. The percentage[1] of tended third and fourth instar *Icaricia acmon* larvae on *Eriogonum compositum* and *E. strictum* that were tended by *Tapinoma sessile*. The remainder of the larvae were tended by *Formica*.

Plant species	Mean % tended by *Tapinoma*	SE	N
E. compositum[a]			
3rd instar	92.9	7.1	11
4th instar	30.6	16.3	7
E. strictum[b]			
3rd instar	75.0	25.0	11
4th instar	40.0	24.5	7

[1] The percentage of overall attendance was determined for each control plant and values are the means of these percentages.
[a] $t = 3.69$, 11 df, $P < 0.005$.
[b] $t = 0.78$, 5 df, $P > 0.40$.

TABLE 3. Survivorship of *Icaricia acmon* larvae to late 4th instar on ant-excluded and control plants of *Eriogonum compositum* and *E. strictum*.

Plant species	Ant-excluded	Control
E. compositum[a]		
Survived	4	10
Died	22	25
% survival	15.4	28.6
E. strictum[b]		
Survived	15	11
Died	20	20
% survival	45.5	35.5

[a] $G_{corr} = 1.46$, $P > 0.2$.
[b] $G_{corr} = 0.37$, $P > 0.5$.

this harsh environment would survive. Only one parasitoid individual, an unidentified braconid, emerged from the larvae I raised in the lab.

DISCUSSION

The pronounced variability in this association over the course of larval development is notable; third instar larvae on both plant species experienced lower overall attendance rates than fourth instar larvae, and the species composition of attendant ants changed with larval development. Although these results may reflect seasonal changes in the absolute and relative abundances of ants, it seems more likely that larger larvae are more attractive to ants. Fiedler (1989b) showed in a lab study that fourth instar larvae of *Lycaena tityrus* (Lycaenidae) are tended more frequently and with greater vigor than third instar larvae and suggested that an increase in the number and size of pore cupola organs was the cause for this increase. In addition to the pore cupola organs, the honey gland has been clearly demonstrated to play an important role in recruiting ants to lycaenid larvae (Fiedler & Maschwitz 1989a), and it is likely that large larvae produce more honeydew than small larvae. Finally, lycaenid larvae produce calls that serve to recruit ants (DeVries 1991a), and it is again likely that larger larvae could produce louder calls. Any or all of these factors could be important in determining the attractiveness of larval *Icaricia acmon*: pore cupola organs are widespread in the Lycaenidae (Henning 1983, Fiedler 1988); *I. acmon* is known to possess a honey gland (Ballmer & Pratt 1988); and in his survey of lycaenids, DeVries (1991a) found larval calling in several members of the Polyommatinae. If large larvae of *Icaricia acmon* are indeed more attractive to ants, the large, aggressive *Formica neogagates* may simply usurp these larvae from the small, docile *Tapinoma sessile*.

In examining the survivorship data, it is important to recognize that in this study and all other similar studies, the effect of ants on larval survivorship may be somewhat obscured because terrestrial predators were excluded along with ants. The only way to remove ants without removing these predators is to locate all ant nests and selectively isolate or remove them from half of the study area. It was impossible to perform this experiment because the nests of both *F. neogagates* and *T. sessile* are difficult to find. Nonetheless, this is the first experiment showing that lycaenid mortality may be the same in the presence and absence of ants and terrestrial predators. Because of the small sample sizes in this experiment, analyses lacked the power to detect small differences in survivorship between the treatment and control. Had the difference in survivorship between the treatment and control been greater than 25%, the analysis would have detected it. This magnitude of difference is comparable to that found by Pierce and Easteal (1986) for tended and untended larvae of *Glaucopsyche lygdamus* (Lycaenidae). Because survivorship of *I. acmon* larvae on *E. strictum* tended to be higher in the absence of ants, I feel that insufficient statistical power cannot explain entirely the apparent absence of a beneficial effect of ant attendance.

It is quite possible that I would have seen an effect of ant attendance on larval survival had I performed this study in a different place or time. DeVries (1991b) pointed out that variation in the abundances of natural enemies could influence whether riodinid and lycaenid larvae benefit from their associations with ants. In addition, host plant quality, ant abundance, and lycaenid abundance could be important in determining overall benefits. Although temporal and spatial variation in benefits has not been examined in lycaenid-ant associations, Cushman and Whitham (1989) found that the benefits enjoyed by membracids from ant attendance varied markedly over a three year study period. It is clear from the high survivorship of larvae in this experiment that predation and parasitism pressures were low throughout the study period. Had I performed the experiment in a year or region of high larval mortality, I may have seen a difference between the treatments.

Finally, the differences in behavior of the two ant species suggest that they may differ in their effectiveness as defenders of larvae. Although the data here cannot address this issue, Bristow (1984) found that the ant species offering the best protection differed between an aphid and a membracid on New York ironweed. It would be interesting to perform a selective ant removal experiment to test whether the large, aggressive *Formica* species are more effective defenders of *I. acmon* larvae than are the smaller *T. sessile*.

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