

## ANT CONSTANCY AT *PASSIFLORA* EXTRAFLORAL NECTARIES: EFFECTS ON CATERPILLAR SURVIVAL<sup>1</sup>

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**Abstract.** I examined the role of ants in controlling the magnitude and distribution of caterpillar survival at Corcovado National Park, Costa Rica. Ants of 29 species were observed visiting the extrafloral nectary glands of *Passiflora vitifolia* and *P. quadrangularis*. Plants attended by ants had ants present 60% of the time. Approximately equal numbers of plants attended by ants and plants without ants were treated with Tanglefoot to exclude walking predators from a single branch on each plant. *Heliconius ismenius* caterpillars were placed on the treated plants and an equivalent set of unmanipulated controls, and their growth and survivorship were measured. Forty-eight percent of caterpillars died over a 2-d period on unmanipulated plants with many ants, while only 20, 22, and 23% died on unmanipulated plants with few ants, Tanglefoot-treated branches with many ants outside the Tanglefoot barrier, and Tanglefoot-treated branches with few ants outside the Tanglefoot barrier, respectively. This suggests that ants were the only significant walking predator of *Heliconius ismenius* caterpillars in this habitat, and that  $\approx 75\%$  of the deaths observed on control plants were on plants with ants. After 4 d all caterpillars were replaced by a second set of caterpillars. Measurements of these latter individuals revealed that mortality was 62, 46, and 24% on control plants on which caterpillars previously survived for 0, 2, and 4 d, respectively. No trend was observed on branches with ants excluded. This indicates that the effects of ant predation are locally stable, i.e., that ant constancy causes plants to be heterogeneous in their suitability as host plants. Caterpillars thus are much more likely to survive on some plants than on others. Analysis of caterpillar growth rates did not reveal any effects on survival; i.e., slow-growing caterpillars survived as well as fast-growing ones.

**Key words:** ant constancy; contingency analysis; extrafloral nectar glands; *Heliconius ismenius*; insect survivorship; oviposition preference; *Passiflora*; relative growth rate; tropical forest.

### INTRODUCTION

Predation, physical stress, or unsuitability of food cause high rates of mortality to most species of insects that feed on host plants in natural environments (Price 1984). Natural selection for traits that reduce herbivore mortality rates should be strong. Selection should also favor plants that reduce herbivory by attracting predators to the plants, or by producing toxic chemicals deleterious to the herbivores. Clearly, an understanding of plant and insect herbivore adaptations will require knowledge of how both taxa interact with predators on the third trophic level (Price et al. 1981). Because of their abundance, ants can be major predators on herbivorous insects in many terrestrial habitats (Jeanne 1979). Furthermore, the discontinuous distribution of many ant species suggests that survival of herbivorous insects will depend on the location of the host plant with respect to ant nests (Tilman 1978, Inouye and Taylor 1979, Laine and Niemela 1980, Messina 1981) and foraging territories (Leston 1978). Such plant-ant interactions could explain the empirical result that some plants in a population are relatively unharmed by herbivory while others are heavily defoliated (for example, see Coley 1983, Kareiva 1983).

In this paper, I report the magnitude and constancy of ant predation on *Heliconius* butterfly caterpillars

feeding on widely spaced individuals of two species of host *Passiflora* plants during an 8-d period. *Passiflora* possess extrafloral nectar glands which attract ants and other insects to the plant, and I have previously found the presence of ants on a plant to be correlated to caterpillar mortality (Smiley 1985). Here, in order to assess the effects of ant-tending on the magnitude of caterpillar mortality, I experimentally excluded walking insects (including ants) from branches on plants tended by ants and from branches on other plants not tended by ants. To investigate the constancy of ant predation, I also conducted two series of experiments on the same plants to determine whether mortality in the second series was correlated to mortality in the first. The two species of *Passiflora* differed in attractiveness to ants and butterflies, and I predicted that the butterflies would be attracted to the species with fewer ants. Log-linear contingency analysis was employed to factor out the effects of plant species, ant attendance, and ant-exclusion treatment.

### METHODS

*Heliconius* survival and growth were investigated in lowland tropical rain forest during June 1983 at the La Sirena Park Headquarters of Corcovado National Park, Puntarenas Province, Costa Rica (8°30' N, 83°35' W). Small, scattered host plants of *Passiflora vitifolia* and *P. quadrangularis* were found along  $\approx 5$  km of trails and pasture edge. For each species,  $\approx 20$  plants attended by ants and 20 plants with no visible attendant

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TABLE 1. Likely sources of mortality for *Passiflora* "treatment groups." Each treatment consisted of  $\approx 10$  widely spaced individuals, for a total of 80 plants. Each plant received two *H. ismenius* larvae, one for each experiment.

Species	<i>Passiflora</i> "treatment group"		No. plants	Source of mortality
	Ants	Tanglefoot		
<i>P. vitifolia</i>	+	0	16	Dominant ants, flying predators, walking predators, other
<i>P. quadrangularis</i>	+	0	10	
<i>P. vitifolia</i>	0	0	5	Flying predators, walking predators, other
<i>P. quadrangularis</i>	0	0	10	
<i>P. vitifolia</i>	+	+	11	Flying predators, other
<i>P. quadrangularis</i>	+	+	6	
<i>P. vitifolia</i>	0	+	5	Flying predators, other
<i>P. quadrangularis</i>	0	+	8	

ants were selected for study. Since most individuals of *P. vitifolia* were attended by ants, extensive search was required to locate ant-free plants. In contrast, most *P. quadrangularis* lacked ants, and search was required to locate individuals with ants. Of the plants chosen for study, half were selected for ant-exclusion treatment, while the other half served as unmanipulated controls; these were spaced alternately along the trails. Ants were excluded from one branch per plant, using sticky Tanglefoot applied to the stem 50 cm from the end of the *Passiflora* shoot; this excluded most walking predators such as ants, spiders, and predaceous bugs, while allowing access to flying predators such as predaceous wasps and birds (Table 1). The result was a  $2 \times 2 \times 2$  experimental design with 5–16 plants in each treatment.

Eggs of *Heliconius ismenius* were obtained from a greenhouse colony at the University of California, Irvine. The colony was founded 2 yr previously from individuals caught at the field site. Eggs were transported to the field site, and upon hatching in cups, larvae were fed on the preferred host plant, *P. quadrangularis*. Larvae were then placed singly on experimental plants in the field. Previous work has shown these experimental techniques to have little effect on survival or growth rate when compared to naturally occurring larvae (Smiley 1985).

Experimental plants were thoroughly searched every 2 d and a sample of the ants present was collected. Ants present on plants outside the Tanglefoot barrier were collected also. Since small *Heliconius* larvae do not voluntarily leave the host plant, missing larvae were assumed to be dead. Surviving larvae were photographed every 2 d and their size was estimated photometrically (Smiley and Wisdom 1982). The relative growth rate (per day) was calculated as in Smiley (1985). To investigate the constancy of ant predation, all surviving caterpillars were removed from the experimental plants after 4 d (first experiment), and a second set of caterpillars was placed on all plants (second experiment). The survivors among these caterpillars were also collected after 4 d.

Mortality was recorded over each 2-d interval. The

effects of (1) *Passiflora* species, (2) presence of attending ants (including those outside the Tanglefoot barrier, if present), (3) Tanglefoot treatment, and (4) first vs. second experiment, were analyzed using BMDP log-linear contingency analysis (Dixon 1983). For this analysis, plants were scored as "ant-tended" if they had ants present three, four, or five times, and "untended" otherwise. The effects of larval growth rate on survival were analyzed by linear regression in two ways. The number of days survived was plotted against growth rate to see if faster growing larvae lived longer. Here, larvae had to live at least 2 d for growth rate to be measured. To estimate growth rate for larvae that died immediately, i.e., in  $< 2$  d, a second analysis was conducted. The number of days survived in one experiment was plotted against the growth rate of the caterpillar on the same plant in the other experiment. Eighteen plants, including five Tanglefoot treatments, had no caterpillars survive 2 or more d, and growth rate could not be calculated.

To compare the constancy with which different ant species attended plants I calculated a "% occupancy" index. I divided the number of times ( $n_o$ ) an ant species was observed by the maximum number of times ( $n_{max}$ ) it could have been observed if the ant were consistently present on plants in its foraging range. Since each plant was checked for ants five times,  $n_{max} \approx 5N$ , where  $N$  is the number of plants on which the ant species was found at least once. The resulting quotient ( $100 n_o/n_{max}$ ) is given for each ant species in Table 2.

I also tested the hypothesis that some plants would be consistently attended by ants while others would be infrequently attended. I reasoned that if all plants were equally likely to be attended by ants, the number of plants on which ants were observed 0, 1, 2, . . . 5 times would fit a binomial distribution, with probability  $P = .546$  (194 samples with ants/355 total samples) and  $n = 0, 1, \dots 5$ . I then compared the observed number of plants with ants present 0, 1, 2, . . . 5 times against the expected number generated by the binomial distribution. A goodness-of-fit test, using Williams' correction, was employed (Sokal and Rohlf 1981). I also used analysis of variance (Stegner and Bostrom 1983)

TABLE 2. Ants attending nectaries of *Passiflora vitifolia* (*vit*) and *P. quadrangularis* (*qua*) at Corcovado National Park, Costa Rica. Ants identified by J. T. Longino. Each of the 71 plants was examined for ants five times.

Ant subfamily, species	No. times observed	No. plants recorded on		% occupancy*	Ants present	
		<i>vit</i>	<i>qua</i>		During 2-d trial	≥ 1 time during study
<b>Ponerinae</b>						
<i>Ectatomma tuberculatum</i> (Olivier)	58	16	0	65	13/18	18/27
<i>Pachycondyla striatinodes</i> (Emery) or <i>lineaticeps</i> (Mayr)	2	1	0	40	...	1/3
Unidentified ponerinae	2	1	0	40	...	...
<b>Pseudomyrmecinae</b>						
<i>Pseudomyrmex delicatulus</i> or <i>pallidus</i>	3	0	2	30	1/1	2/2
<i>P. c.f. brunneus</i> (F. Smith)	2	0	2	20	...	3/6
<i>P. boopis</i> (Roger)	6	2	1	40	1/2	4/8
<i>P. gracilis</i>	1	0	1	...	2/2	...
<i>P. unidentified</i>	6	3	1	30	2/4	...
<b>Myrmecinae</b>						
<i>Pheidole radoszkowski pugnax</i> Della Torre	6	1	1	6	0/2	2/5
<i>Crematogaster erecta</i>	47	5	10	63	12/19	17/26
<i>C. limata parabiatica</i> Forel	8	2	0	80	...	0/4
<i>C. limata</i> "B"	1	1	0	1	...	...
<i>C. limata</i> "C"	4	2	0	40	1/4	2/6
<i>C. nigropilosa</i> Mayr	3	1	0	60	1/2	1/4
<i>C. sumichrasti</i> Mayr	1	1	0	...	0/1	1/2
<i>C.</i> "yellow"	1	1	1	0	0/1	1/3
<i>C. unidentified</i>	5	0	2	25	...	...
<i>Solenopsis geminata</i> (Fab.)	10	0	2	100	2/2	2/2
<i>S. (Diplorhoptrum)</i> "B"	1	0	1	...	...	...
<i>Leptothorax echinatinodis</i> Forel	2	1	0	20	0/1	2/2
<i>Wasmannia auropunctata</i> (Roger)	3	2	0	30	2/2	4/8
<b>Formicinae</b>						
<i>Camponotus c.f. brevis</i>	16	6	5	29	5/7	11/25
<i>C. novogranadensis</i>	1	1	0	...	...	...
<i>C. sanctafidai</i>	1	1	0	...	...	...
<i>C. unidentified</i>	1	0	1	...	0/1	...
<i>Paratrechina</i> sp.	1	1	0	...	0/3	0/4
<b>Dolichoderinae</b>						
<i>Dolichoderus validus</i> (Kempf)	1	0	1	...	0/1	0/4
<i>Conomyrma</i> sp.		0	1	1	...	...
<i>Azteca</i> sp.	8	3	0	53	2/2	2/2
Ants observed (of any species)	194	...	...	59	...	...
No ants observed ("ants absent")	161	...	...	59	...	...

\* Percent of sampling occasions that ant species was present on plants attended by that ant species at least once.

to test for different rates of ant visitation to individual plants, and chi-square tests to determine the statistical significance of frequency of caterpillar mortality (Sokal and Rohlf 1981).

## RESULTS

Certain plants were more likely to be attended by ants than others. For example, 25 plants had ants present 4–5 times, 22 plants had ants present 0–1 times, and only 24 plants had ants present 2–3 times. The corresponding binomial expectations if all plants were equally likely to be attended would be 18, 10, and 43, respectively, and the goodness-of-fit test between observed and expected was highly significant ( $G = 47.7$ ,  $df = 2$ ,  $P < .0001$ ). For convenience in the analysis of ant effects on survival, I designated plants with ants

present 50–100% of time as "ant plants" and plants with ants present 0–49% of the time as "plants with few ants," as defined above. The overall percentage occupancy of ants was calculated by dividing the number of times ants of any species were present on plants by  $5N$ , where  $N$  is the number of plants that had "ants present" at least once. The quotient indicated that if ants were present at all on a plant, they were likely to be there 59% of the time. Using the same formula for "ants absent" revealed that plants that lacked ants at least once, also lacked them 59% of the time.

Approximately 30 species of ants were collected while they were visiting *Passiflora* extrafloral nectar glands (Table 2). Three ant species, *Ectatomma tuberculatum*, *Crematogaster erecta*, and *Camponotus c.f. brevis*, were collected on 16, 15, and 11 plants respectively. *E. tu-*

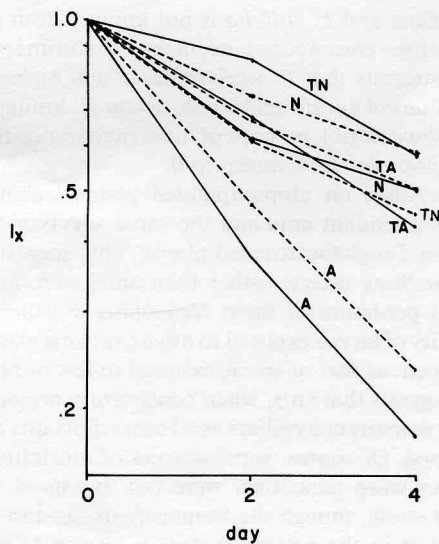


FIG. 1. Survivorship ( $l_x$ ) of *Heliconius ismenius* caterpillars to day  $x$  on wild plants of *Passiflora vitifolia* (—) and *P. quadrangularis* (---). Treatment groups consisted of unmanipulated plants with few ants (N), Tanglefoot-treated branches on plants with many ants (TA), Tanglefoot-treated branches on plants with many ants (TA), and unmanipulated plants with many ants (A).

*berculatum* and *C. erecta* had occupancy rates of 65 and 63%, respectively, but *Ca. c.f. brevis* had an occupancy rate of only 29% (20% is the minimum possible). This ant and ants in the genus *Pseudomyrmex*, with occupancy rates of 20–40%, were much less constant or frequent in their visitation to *Passiflora* nectaries than *E. tuberculatum* and *C. erecta* ( $F = 12.2$ ,  $P < .0001$ ) and tended to be found on plants with few ants, as defined above. The overall percentage occupancy by ants (species not distinguished) was 59%, indicating that if ants were present at all on a plant they were likely to be there 59% of the time. Similarly, the “percentage occupancy” for “ants absent” was 59%, indicating that a plant that lacked ants at least once, lacked them 59% of the time.

*Crematogaster erecta* and *Camponotus c.f. brevis* were found on both *P. vitifolia* and *P. quadrangularis*, while *E. tuberculatum* was found only on *P. vitifolia* (Table 2). This is probably because the colonies of *E. tuberculatum* were concentrated in one area where only *P. vitifolia* was growing. *E. tuberculatum* has been observed to visit *P. quadrangularis* nectaries. Other, less frequently sampled ant species were not significantly associated with one or the other *Passiflora* species. Mortality rates were not significantly different among caterpillars exposed to *E. tuberculatum*, *C. erecta*, and *Ca. c.f. brevis* ( $\chi^2 = 3.4$ ,  $P > .1$ ).

Survivorship of larvae was significantly reduced on unmanipulated plants which were ant-tended as compared to the other treatments (Fig. 1). Larvae on unmanipulated plants that were not tended by ants had the same survivorship as larvae protected by Tanglefoot, indicating that (1) the occasional ant visitors to these plants were not significant sources of mortality, (2) ants were the only significant walking predator, and (3) disappearance was not caused by caterpillars walking off the plant, since this would have been prevented by the Tanglefoot barrier.

Contingency analysis revealed that, on unmanipulated plants, the presence of attending ants affected survival ( $P < .005$ ; Table 3). Plant species had no effect, nor did the two experimental series differ in survival rates. There were significantly more ants attending *P. vitifolia* than *P. quadrangularis*, on unmanipulated plants and on plants with a Tanglefoot treatment ( $P < .001$  and  $.003$ , respectively). There were also fewer ants present in the second experiment on unmanipulated plants ( $P < .01$ ).

On unmanipulated plants, 41 out of 54 disappearances occurred on the 25 plants with attending ants present, while 36 of the 69 survivals occurred on the 15 plants with few ants. Thus, over half of the surviving caterpillars were found on a relatively small proportion of *Passiflora* distinguished by the relative absence of attendant ants.

Caterpillars in the second experiment died more fre-

TABLE 3. Contingency analysis of larval survival data on unmanipulated plants (U) and on plants where larvae were “protected” by a Tanglefoot barrier (T).

Interaction effects	df	Treatment	G statistic of partial association	Trend
Ant attendance × survival	1	U	8.3 ( $P = .004$ )	higher mortality with ants; Tanglefoot prevents this
	1	T	0.0	
Plant species × survival	1	U	1.0	none
	1	T	0.1	none
Experimental series × survival	1	U	0.7	none
	1	T	0.3	none
Plant species × ant attendance	1	U	9.9 ( $P = .002$ )	fewer ants on <i>P. quadrangularis</i>
	1	T	10.6 ( $P = .001$ )	fewer ants on <i>P. quadrangularis</i>
Experimental series × ant attendance*	1	U	7.0 ( $P = .008$ )	fewer ants in second series
	1	T	0.5	none

\* The interaction between experimental series and ant presence on plant was only seen on unmanipulated plants. It probably represents random variation in sampling.

TABLE 4. Mortality of caterpillars in second experiment (4 d long). Among unmanipulated plants (U), mortality was significantly higher on plants with high mortality during the first experiment ( $\chi^2 = 6.9$ ,  $P < .05$ ). This effect was not seen on ant-exclusion plants (T) ( $\chi^2 = 2.5$ ,  $P > .10$ ).

Treatment	Survival time in first experiment (d)	Survival in second experiment	
		No. died	No. lived
U	0	16	10
U	2	6	7
U	4	5	16
T	0	6	9
T	2	1	8
T	4	7	17

quently if they were on plants upon which caterpillars had died in the first 2 d of the first experiment (Fig. 2). Survivorship increased on plants upon which caterpillars had lived 2 d, and was maximal on plants upon which caterpillars had lived 4 d. Thus, plants that yielded high or low survivorship in the first experiment tended to yield similar survivorship in the second experiment. This trend was statistically significant on control plants but not on plants bearing caterpillars protected by the Tanglefoot barrier (Table 4). This suggests that the effect was caused by ants attending plants, rather than by flying predators such as wasps or birds.

Relative growth rates (per day) of caterpillars were similar on *P. vitifolia* and *P. quadrangularis* ( $\bar{x} = 0.53$  and  $0.51$ , respectively). Growth rate on a plant was not correlated with survival, or with survival of other caterpillars on the plant ( $r = -0.06$ , and  $0.04$ , respectively). The variance in growth rate was significantly higher on *P. vitifolia* than on the preferred host, *P. quadrangularis* ( $s^2 = 0.28$ , and  $0.10$ , respectively,  $F = 2.8$ ,  $P < .025$ ).

#### DISCUSSION

When consistently present on a plant, ants caused high rate of mortality to caterpillars of *Heliconius ismenius* feeding on *Passiflora vitifolia* and *P. quadrangularis*. Female butterflies should therefore avoid plants with ants when laying eggs. However, female *Heliconius* apparently do not recognize the presence of ants when laying eggs (Smiley 1978, Longino 1984). While locating the experimental plants for this study, it was very apparent that *P. vitifolia* individuals were frequently attended by ants, while *P. quadrangularis* were seldom attended. Selection to avoid ants could therefore cause evolution of a preference for *P. quadrangularis* over *P. vitifolia*. This prediction is supported by available data on *H. ismenius* oviposition behavior in the field: most eggs are laid on *P. quadrangularis*, although some are laid on *P. vitifolia* (J. Mallet, *personal communication*).

The basis for differential ant attendance to *P. qua-*

*drangularis* and *P. vitifolia* is not known. Both plants have large, conspicuous nectaries. Preliminary evidence suggests that *P. vitifolia* has much higher concentrations of amino acids in its nectar (J. Smiley, *personal observation*), perhaps of different composition (J. Horn, *personal communication*).

Caterpillars on unmanipulated plants lacking numerous attendant ants had the same survivorship as those on Tanglefoot-treated plants. This suggests that small walking insects (other than ants) were not significant predators of these *Heliconius*. Furthermore, mortality of larvae exposed to attendant ants was twice as frequent as that of larvae exposed to few or no ants. This suggests that ants, when consistently present, kill at least as many caterpillars as all other mortality agents combined. Of course, some sources of mortality such as fly or wasp parasitism were not measured in the present study, though the frequency of egg and larval parasitism in the present system is known to be low (J. Smiley, *personal observation*).

Although sample sizes were small, the data suggested that ants with high percentage occupancy (such as *Eciton tuberculatum* and *Crematogaster erecta*) had similar effect on *H. ismenius* survival (67 and 65%, respectively, Table 2). *Camponotus c.f. brevis*, with low percentage occupancy, may cause less mortality (44%), although the difference was not statistically significant ( $\chi^2 = 3.38$ ,  $P < .10$ ). Other ants reported to be aggressive to herbivores, such as *Wasmannia auropunctata*, *Azteca* sp., and *Solenopsis geminata* (Schemske 1980,

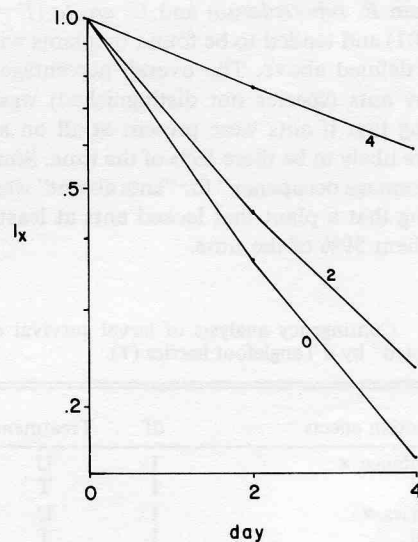


FIG. 2. Survivorship ( $I_x$ ) of *H. ismenius* caterpillars on unmanipulated control plants which had previously supported 0, 2, or 4 d survivorship for another caterpillar. Survivorship was higher on plants with surviving larvae in the previous experiment, indicating that high mortality was specifically associated with certain individual plants. This effect was not seen on Tanglefoot-treated plants (Table 4), indicating that ants were the causative agents.

Longino 1984) were rare and their effects could not be quantified.

Comparison of the first and second experiment demonstrated that unmanipulated plants were consistent in having either high or low probability of caterpillar mortality. This consistency was not seen in Tanglefoot-treated plants, indicating that the effect was caused by ants rather than other predators. These data suggest that some individual plants were relatively ant-protected while others were not. Furthermore, the observed differences were quite large. For example, if mortality rates in Table 4 are extrapolated from 4 d to the full 10-d larval lifespan, only 7% of the larvae on the "0 d" plants would survive, while 60% would survive on the "4 d" plants. This suggests that a plant's location with respect to ant distribution is of crucial importance to the probability of success for a caterpillar, and to the amount of defoliation for the plant.

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