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## THE SELECTIVE ADVANTAGE OF ATTENDANT ANTS FOR THE LARVAE OF A LYCAENID BUTTERFLY, *GLAUCOPSYCHE LYGDAMUS*

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### SUMMARY

(1) Larvae of *Glaucompsyche lygdamus* Doubleday (Lepidoptera: Lycaenidae) secrete substances that attract and appease ants. Workers of the ant *Formica altipetens* Wheeler harvest these secretions and in return protect the larvae against attacks by small larval parasitoids. We now demonstrate that attendant ants protect larvae of *G. lygdamus* against different kinds of parasitoids, including those that emerge from the pupae.

(2) Larvae whose ants have been experimentally excluded are far more likely to disappear from host plants than larvae with ants, simply because larvae drop off plants without ants.

(3) Taking into account parasitism, predation and drop-off, a cohort of ant tended larvae is four to twelve times more likely to survive to pupation than a similar group of untended larvae. Most of this difference in survivorship occurs during the final two larval instars. We argue from these results that attendant ants have had a significant effect on the distribution and structure of populations of *G. lygdamus*.

(4) In contrast with other species of myrmecophilous lycaenids, ants do not play a significant role in the oviposition behaviour of *G. lygdamus*.

### INTRODUCTION

Ants that tend honeydew- and nectar-secreting food resources such as aphids, membracids and plant extra-floral nectaries can act as effective guards in warding off parasitoids and predators (e.g. Bentley 1976, 1977; Wood 1977; McEvoy 1979; Addicott 1979; Inouye & Taylor 1979; Koptur 1979; Buckley 1983; Bristow 1984, but see Heads & Lawton 1984). Similarly, the larvae of a lycaenid butterfly, *Glaucompsyche lygdamus* Doubleday, receive protection from attendant ants against parasitoids such as braconid wasps and tachinid flies (Pierce & Mead 1981). The larvae secrete substances that attract and appease their attendant ants, including sugars and amino acids that the ants harvest from specialized exocrine glands (Maschwitz, Wust & Schurian 1975; Pierce 1983).

We now expand Pierce & Mead's (1981) experiments and investigate whether attendant ants, in addition to protecting larvae of *G. lygdamus* against small larval parasitoids, can also guard them against large parasitoids that attack the larvae but emerge from the pupae.

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We examine whether disappearance of larvae from plants where ants have been experimentally excluded is due to predation or to larvae simply falling off their food plants. Pierce & Mead (1981) found that whereas 36% of the tended larvae remained on their host plants until the final instar, only 18% of untended larvae survived until the final instar. This difference in disappearance rates suggested that attendant ants protected larvae from predators, but it was also possible that untended larvae simply dropped off plants more frequently than their tended counterparts. We assess the importance of larval drop-offs, and thus examine whether attendant ants are an effective guard against aerial predators such as sphecid wasps. We estimate the impact that attendant ants may have on the overall larval survivorship of *G. lygdamus* by comparing the fates of tended and untended groups of larvae. Using this same experimental manipulation, we also determine whether females of *G. lygdamus* use ants as cues in oviposition.

*G. lygdamus* is a univoltine butterfly with a widespread distribution, occurring across most of the cooler, temperate regions of North America and ranging from sea level to above timberline (Howe 1975). It overwinters as a pupa under stones and in the leaf litter beneath its food plants, and is one of the first butterflies to emerge in the Spring. The food plants of *G. lygdamus* include several species of legumes. At our study site at Gold Basin, 16 km southwest of Gunninson, Colorado, U.S.A. (Breedlove & Ehrlich 1968; Pierce & Mead 1981), *G. lygdamus* feeds primarily on the developing inflorescences of a herbaceous perennial, *Lupinus floribundus* Greene. Eggs are laid singly on inflorescences, and late instar larvae range in colour from bright green to brown to lavender. Larvae are cannibalistic and cannot be reared together.

At Gold Basin the main attendant ant is *Formica altipetens* Wheeler, although *G. lygdamus* has also been observed to associate with *F. obscuripes* Forel, *F. fusca* L., *F. puberula* Emery, *Myrmica brevinodis* Emery and *Tapinoma sessile* Say. (Pierce & Mead 1981). *F. altipetens* is a polygynous and polydomous species forming huge colonies and frequently establishing nest entrances at the base of lupines bearing larvae of *G. lygdamus*.

## MATERIALS AND METHODS

### *Natural history*

During daily inspections of plants containing larvae and ants, and plants where ants had been experimentally excluded from larvae (see below), we recorded the colour of each larval instar, the part of the plant it was feeding upon, its relative position or degree of prominence on the inflorescence stalk (top being most prominent to an observer) and for ant-tended larvae, the number of attendant ants.

### *Ant exclusion*

The design of this experiment was the same as that described by Pierce & Mead (1981). Shortly after females of *G. lygdamus* had begun to lay eggs on inflorescences of *L. floribundus*, we excluded ants from an experimental group of 194 plants by coating the stems with a viscous barricade of Bird Tanglefoot (Tanglefoot Co., Grand Rapids, Michigan, U.S.A.). A ring, 0.5 m in radius, was clipped around the base of each plant to eliminate grass bridges that might provide access to the larvae. A group of 183 control plants was treated in the same manner except that the Tanglefoot was applied to only one side of the stem so that ants could still reach the larvae. Only infested lupines were used and plants were randomly designated control or experimental. The experiment was set up between 24 and 30 June 1980. Plants were examined every third day and final instars removed until 14 July, whereupon they were examined every day and final instars

harvested until 22 July, when all remaining larvae were collected. The final instars were placed individually in Petri dishes and reared in a growth chamber. Within days, they either pupated or died when parasitoids emerged. The pupae were placed in separate vials, allowed to overwinter, and scored for parasitism the following spring when either butterflies or ichneumonid wasps eclosed. Since individual larvae are cannibalistic and almost always occur singly on inflorescences, we have treated them as statistically independent in our  $\chi^2$  analysis. We have also analysed the data on a plant by plant basis using the Mann–Whitney  $U$  test, which yielded the same results.

#### *Predation rates*

To analyse the possibility that untended larvae simply dropped off plants, we placed sticky drop cloths beneath plants with and without ants to catch falling larvae. Under these conditions, larvae could only disappear from plants by being carried away by aerial predators. A subset of thirty-four of the experimental and thirty-three of the control plants used in the exclusion experiment described above were fitted with clear plastic drop cloths coated with Tanglefoot. Drop cloths were secured by driving their corners into the ground with large staple tacks, and were put down on 15–16 July. At the beginning of the experiment, the mean numbers of larvae on plants without ants (4.71, S.D. = 2.52) and plants with ants (5.18, S.D. = 4.51) were not significantly different ( $t_s = 0.5354$ , d.f. = 65, N.S.). Drop cloths were checked for fallen larvae and the plants were monitored for larvae every day until 21 July, when all final instars remaining on the plants were collected and reared to determine parasitism levels, as described above.

#### *Larval survivorship and oviposition rates*

The impact of ant attendance on overall survivorship was assessed by monitoring the development and survival of individuals from eggs to pupae. From these observations we were also able to determine whether the presence of ants influenced where females of *G. lygdamus* laid their eggs.

On 24 June we conducted a census on a second subset of thirty-one experimental and thirty-one control plants from the ant exclusion experiments described above, and counted and removed all hatched eggs (newly hatched larvae do not consume the eggshell). Unhatched eggs were identified by recording their positions on individually labelled inflorescences. A week later, the original batch of eggs had either hatched, died or disappeared, and new eggs had been laid. Hatched eggs were identified, counted and removed. Dead or missing eggs and the numbers and positions on inflorescences of new eggs were recorded. Further records of hatched eggs, fresh eggs and larvae were made on 3, 7, 10 July and every day from 15 to 22 July. Final instars were collected and reared for parasitism, as before. To estimate overall larval survivorship, we compared the total number of hatched eggs with the number of larvae that survived to final instar, were collected and pupated. (This included hatched eggs counted and removed during the first census as well as eggs that were laid and hatched during the course of the experiment.) Larvae that disappeared from their food plants were assumed not to survive (but see Discussion).

## RESULTS

### *Natural history*

The characteristics of *G. lygdamus* larvae observed at Gold Basin are listed in Tables 1 and 2. Most fourth instars are green, but about a quarter are various shades of lavender.

TABLE 1. Characteristics of ant-tended and untended larvae of *G. lygdamus* on plants in Gold Basin, 1980. Observations are categorized by instar (I–IV) and expressed as percentages of the total number of observations for each instar (shown at the bottom of the table)

	With ants				Without ants			
	I	II	III	IV	I	II	III	IV
Colour of instar								
Brown	91	97	55	2	89	98	60	4
Green	9	3	45	74	11	1	39	76
Lavender	0	0	0	24	0	1	1	20
Inflorescence type where larva was found								
Bud	82	15	14	6	36	23	19	10
Some opened flowers	18	26	14	12	47	22	17	25
All opened flowers	0	53	60	58	17	55	64	65
Flowers with developing seed pods	0	6	12	24	0	0	0	0
Relative position on inflorescence								
Top	45	56	54	43	84	58	55	32
Middle	28	18	13	23	8	24	23	52
Bottom	27	26	33	34	8	18	22	16
Plant part where larva was found feeding or resting								
Flowers	91	79	65	58	100	84	84	84
Stem	0	18	24	16	0	11	13	16
Leaves	9	3	1	2	0	1	2	0
Seed pod	0	0	10	24	0	4	1	0
<i>n</i>	11	72	110	53	36	94	104	25

Colour variation is not associated with feeding position ( $G = 1.990$ , d.f. = 2, N.S.,  $n = 76$ ; Sokal & Rohlf 1969), or with parasitism [of seventy-two green fourth instars reared from a sample taken in Gold Basin in 1979, twenty-three (32%) were parasitized, and of thirty-four lavender larvae, eight (24%) were parasitized,  $\chi^2 = 0.79$ , d.f. = 1, N.S.]. It is not clear why larval colour variation arises, but selection by visually hunting predators may play a role, since lavender larvae are cryptic on flowers and green larvae are cryptic on seed pods and foliage.

Larvae of *G. lygdamus* showed preferences for different inflorescence types depending upon their age and the presence or absence of ants (Table 1). First instars were found more frequently on budding inflorescence stalks if ants were present, but on flowering stalks if ants were absent ( $\chi^2 = 5.54$ , d.f. = 1,  $P < 0.025$ ,  $n = 47$ ), whereas third and fourth instars showed no significant preference for budding or flowering stalks (excluding flowers with developing seed pods) in the presence or absence of ants (third instars,  $\chi^2 = 0.59$ , d.f. = 2, N.S.,  $n = 201$ ; fourth instars,  $\chi^2 = 1.38$ , d.f. = 2, N.S.,  $n = 65$ ). Third and fourth instars were more likely to be found on inflorescences with seed pods if ants were present (thirds,  $\chi^2 = 13.79$ , d.f. = 1,  $P < 0.005$ ,  $n = 214$ ; fourths,  $\chi^2 = 7.48$ , d.f. = 1,  $P < 0.01$ ,  $n = 78$ ). Third and fourth instars also changed preferences for different flower parts in the presence and absence of ants. Thirds were found more often on stems and less often on flowers ( $\chi^2 = 5.02$ , d.f. = 1,  $P < 0.025$ ,  $n = 198$ ) and more often on pods ( $\chi^2 = 9.56$ , d.f. = 1,  $P < 0.005$ ,  $n = 211$ ) if ants were present. Similarly, ant tended fourths were found more often on pods ( $\chi^2 = 7.66$ , d.f. = 1,  $P < 0.01$ ,  $n = 77$ ).

We were unable to make many observations of first instars because young larvae tend to burrow inside flower buds and therefore are not generally visible until the second or third instar. By the third instar, most larvae are tended by ants and the mean number of tending ants increases with larval age (Table 2). Third and fourth instars that fed on seed pods were significantly more attractive to ants than those feeding on other plant parts. Seed

TABLE 2. Mean numbers of attending ants per larva of *G. lygdamus* on various plant parts and with different colour morphs at Gold Basin (standard deviations in parentheses). The numbers of larvae observed within each category can be derived from Table 1

	Instar			
	I	II	III	IV
Mean number of ants per larva		0.43 (0.73)	1.69 (1.37)	3.13 (2.15)
Colour of larva				
Brown	0	0.43 (0.71)	1.46 (1.47)	3.00 (—)
Green	0	1.50 (0.71)	1.95 (1.20)	3.15 (2.42)
Lavender	0			3.08 (1.88)
Inflorescence type where larva was found				
Bud	0	0.36 (0.92)	1.50 (0.90)	2.33 (2.31)
Some opened flowers	0	0.21 (0.54)	2.08 (0.64)	3.17 (1.60)
All opened flowers	0	0.55 (0.72)	1.30 (1.20)	2.55 (1.40)
Flowers with developed seed pods	0	1.00 (0.82)	3.15 (2.19)	4.17 (2.86)
Plant part where larva was found feeding or resting				
Flowers	0	0.32 (0.60)	1.38 (1.13)	2.86 (1.64)
Stem	0	1.15 (0.90)	1.82 (0.80)	2.75 (2.38)
Leaves	0	0	1.00 (—)	1.00 (—)
Pod	0	0	3.40 (2.37)	4.42 (2.87)
Relative position on inflorescence				
Top	0	0.68 (0.89)	1.33 (1.13)	2.95 (1.88)
Middle	0	0.29 (0.49)	2.11 (1.96)	3.54 (2.42)
Bottom	0	0.54 (0.93)	2.15 (1.63)	3.12 (2.60)
<i>n</i>	11	72	110	53

\*  $t_s = 2.33$ , d.f. = 51,  $P < 0.05$ .

\*\*  $t_s = 4.59$ , d.f. = 108,  $P < 0.001$ .

Pods generally have a high protein content and larvae that feed on them may produce more attractive secretions for attendant ants (see Pierce 1985).

#### Ant exclusion

A significantly higher proportion of untended compared with tended larvae succumbed to attack by parasitoids (Table 3) as found in the earlier exclusion experiments of Pierce & Mead (1981). In 1980 the main parasitoid was a tachinid fly, *Aplomya theclarum* Scudder, whereas in 1979 it had been a braconid wasp, *Apanteles cyanirides* Riley (Pierce & Mead 1981). Taken together, these results show that attendant ants are effective at deterring both of these different kinds of parasitoids. There were three cases of both a fly and braconid emerging from the same larva. The pupae produced by these parasitoids were smaller than

TABLE 3. Comparison of the parasitism levels of ant-tended *v.* untended larvae of *G. lygdamus* at Gold Basin in (1980) (percentages in parentheses)

	With ants	Without ants	$\chi^2$
Total number of larvae	193	112	
Number parasitized	64 (33)	92 (82)	68.05*
Parasitism breakdown:			
Tachinid flies	27 (14)	63 (56)	
Braconid wasps	35 (18)	28 (25)	
Both, simultaneously	2 (1)	1 (1)	

\* $P < 0.001$ .TABLE 4. Comparison of the pupal parasitism of ant-tended *v.* untended larvae of *G. lygdamus* at Gold Basin and Naked Hills in 1979 and Gold Basin in 1980. Parasitoids, itemized for each group, were two species of ichneumonid wasps that attacked the larvae and emerged from the pupae

	With ants	Without ants	$\chi^2$
1979, Gold Basin			
Total number of pupae	47	19	
Number parasitized (%)	11 (23)	8 (42)	2.31
<i>A. bicolor</i> , <i>A. alpinum</i>	8, 3	6, 2	
1979, Naked Hills			
Total number of pupae	30	14	
Number parasitized (%)	3 (10)	5 (36)	2.27
<i>A. bicolor</i> , <i>A. alpinum</i>	3, 0	4, 1	
1980, Gold Basin			
Total number of pupae	129	20	
Number parasitized (%)	5 (4)	5 (25)	12.34*
<i>A. bicolor</i> , <i>A. alpinum</i>	5, 0	5, 0	

\* $P < 0.005$ .

those of confamilials obtained singly, but none of these eclosed, and we were unable to ascertain whether or not they were the same species in each case.

Two species of ichneumonid wasps, *Anisobas bicolor* Cushman and *Agrypon alpinum* Davies, emerged from the pupae of the 1979 experiments (conducted in two field sites, Naked Hills and Gold Basin; see Pierce & Mead 1981) and 1980 exclusion experiments. The level of parasitism by the wasps was higher in untended pupae in both the 1979 and the 1980 experimental comparisons and in 1980 the difference in parasitism between the tended and untended group was significant (Table 4). Thus, attendant ants can be effective in protecting the larvae against these larger parasitoids.

#### Predation rates

All differences in disappearance rates between larvae on plants with and without ants could be accounted for by larvae falling off plants (Table 5). Although disappearances due to predation were high, more than 50%, they were not significantly different between larvae on plants with and without ants. There was, however, a significant age-related difference in drop-off rates: of the larvae with ants, 5% ( $n = 21$ ) of the second instars, 8% ( $n = 74$ ) of the third instars, and 11% ( $n = 74$ ) of the fourth instars dropped off. Of the larvae without ants, none ( $n = 16$ ) of the second instars, 18% ( $n = 76$ ) of the third instars, and 35% ( $n = 68$ ) of the fourth instars dropped off (3-way  $G$  test, age  $\times$  treatment  $\times$   $\pm$ drop: age  $\times$  drop,  $G = 11.96$ , d.f. = 2,  $P < 0.005$ ; age  $\times$  treatment  $\times$   $\pm$ drop interaction,  $G = 3.45$ , d.f. = 2, N.S.).

TABLE 5. The importance of predation and drop-off in accounting for disappearance of ant-tended *v.* untended larvae of *G. lygdamus* at Gold Basin in 1980 (percentages in parentheses). Total numbers of disappearances can be calculated as the sum of the numbers found on drop cloths and the numbers taken by predators

	With ants	Without ants	$\chi^2$
Number of plants	33	34	
Starting number of larvae	169	160	
Number found on drop cloths	15 (9)	38 (24)	13.46*
Number taken by predators	90 (53)	96 (60)	2.12

\*  $P < 0.005$ .

Many larvae disappeared entirely from their food plants by being transported away by aerial predators such as mud dauber wasps, *Sphex procerus* Dahlbom, which are common in the area and which we observed preying on larvae on numerous occasions. Although we occasionally saw spiders attack young instars, there was no evidence of spider predation during the course of this experiment. Spiders were, however, more common on plants without ants than on plants with ants. Of 222 observations of plants with ants, spiders were observed on ten occasions, whereas of 226 observations of plants without ants, they were observed twenty-two times ( $\chi^2 = 4.62$ , d.f. = 1,  $P < 0.05$ ). A coccinellid beetle was once observed feeding on a second instar, but this was not during an experimental census. Finally, bird droppings were found once on a drop cloth, but birds were never observed to visit plants.

#### *Oviposition and larval survivorship*

*G. lygdamus* females laid eggs as frequently on plants from which ants had been experimentally excluded as on plants to which ants were allowed access (Table 6). This demonstrates that *G. lygdamus* lays eggs on plants in the absence of attendant ants. However, it does not necessarily show that the butterflies do not respond to ants while ovipositing. Our experimental method could not ensure that ants were always active on control plants or that there was a distinct choice available for ovipositing females between plants with and without ants. It is therefore possible that the presence of ants may somehow enhance oviposition under circumstances where females encounter ants directly, but that our experimental design was not adequate to detect this effect. Nevertheless, these results show that, unlike certain other lycaenids (e.g. Atsatt 1981; Henning 1983; Pierce & Elgar 1985), ants are not important for oviposition in *G. lygdamus*. This may be explained by the fact that the relationship between the larvae of *G. lygdamus* and its attendant ants

TABLE 6. Oviposition frequencies of *G. lygdamus* in response to the presence or absence of ants (standard deviations in parentheses)

	With ants	Without ants	
Number of plants	31	31	
Number of unhatched eggs on plants at the start of the experiment	202	236	
Mean number of unhatched eggs per plant	6.52 (7.32)	7.61 (6.44)	$t_s = 0.62$ , d.f. = 60 N.S.
Number of eggs laid on plants after six days	133	128	$\chi^2 = 1.53$ , d.f. = 1 N.S.
Mean number of new eggs laid per plant	4.35 (4.98)	4.06 (4.55)	$t_s = 0.24$ , d.f. = 60 N.S.



does not appear to be obligate, as it is for many other species (see Pierce & Elgar 1985 for discussion).

A total of 444 eggs on plants with ants and 539 eggs on plants without ants were followed from the time they were laid until the larvae either died or successfully pupated. Large numbers of eggs disappeared from both experimental and control plants before they hatched (Fig. 1; data given in Table 7). This disappearance is probably due to predation rather than parasitism. Among hundreds of eggs of *G. lygdamus* collected from Gold Basin and reared in the laboratory, we have never found an egg parasitoid. Sometimes eggs turn a dark colour and die, but this does not appear to be related to parasitism. Some of the hatched eggshells may have fallen off the plant between counts, but since most eggs are tightly glued to the substrate and are hard to remove even with forceps, this is probably not a large source of error.

There was a highly significant difference in survivorship on plants with and without ants: the probability of an ant-tended juvenile surviving from the egg to adult stage was 9.9%, whereas the probability of an untended juvenile surviving was only 0.7% (Table 7 and Fig. 1). Since the sticky Tanglefoot barrier may have also excluded crawling predators such as coccinellid larvae from plants without ants, this comparison could be slightly conservative.

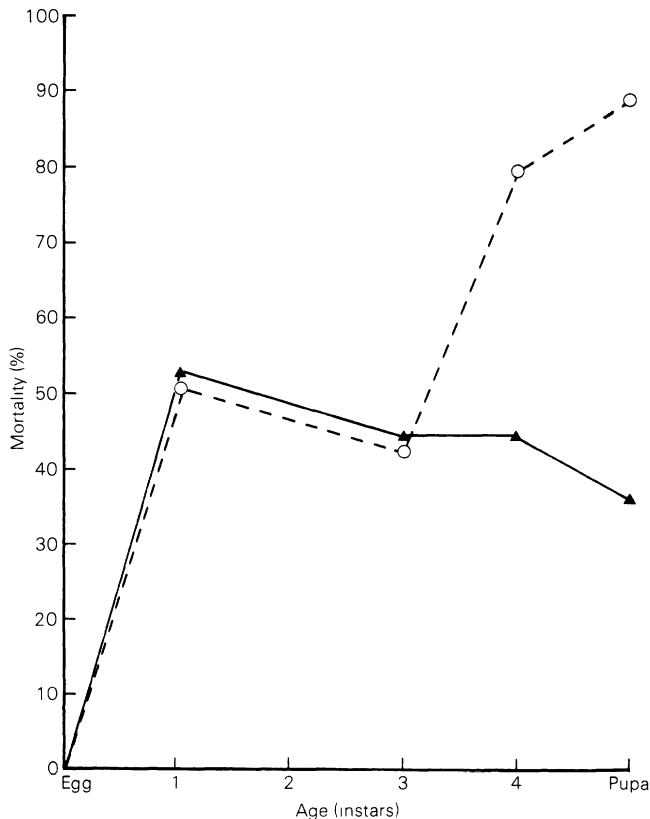


FIG. 1. Mortality percentage of each age class of *Glaucopsyche lygdamus* with and without ants at Gold Basin, Colorado in 1980 (based on data in Table 7). Note that mortality of instar III (both with and without ants) covers cumulative mortality over two instars. (▲), Larvae with ants, (○), larvae without ants.

TABLE 7. Life table for *G. lygdamus* with and without attendant workers of *F. altipetens* at Gold Basin, Colorado in 1980. Difference in survivorship between individuals with and without ants:  $\chi^2 = 37.01$ , d.f. = 1,  $P < 0.005$

Age intervals (instars)	Number surviving at beginning of age interval		Number dying during interval		Percent mortality of each age interval	
	+ ants	- ants	+ ants	- ants	+ ants	- ants
Eggs-I	444	539	236	274	0.53	0.51
I-III	208	265	93	114	0.45	0.43
III-IV	115	151	52	120	0.45	0.80
IV-pupa	63	31	23	27	0.36	0.87
Pupa-adult	40	4				

The number of third instars that survived to become fourth instars is shown in Fig. 1, but because almost all the first and many of the second instars burrowed inside the flower buds and could not be counted, a breakdown of survivorship in the first two larval instars was not possible. Recorded pupal deaths were due to parasitoids that attack the larvae but emerge from the pupae.

## DISCUSSION

We draw two main conclusions from this study. First, the presence of tending workers of *F. altipetens* significantly increases the survivorship of *G. lygdamus* in Gold Basin. The results described here clearly support the strong advantage of ant attendance reported by Pierce & Mead (1981). Second, larval parasitoids could act as a potent selective force in restricting the distribution of populations of *G. lygdamus* to only those areas where both host plants and attendant ants are concurrent.

The high drop-off rates of larvae on plants without ants indicates that in exclusion experiments such as this one, disappearance of individuals may not necessarily reflect predation. Since many of the larvae that fell off were third rather than fourth instars, it is unlikely that they were falling off to find pupation sites. Seven of the fourth instars that fell off plants without ants were recovered, and only two of these were parasitized, so it is also unlikely that higher parasitism levels of larvae on plants without ants could explain the differences in drop off. Other explanations include the following. (i) In the absence of attendant ants, predators such as wasps may select larger larvae than they normally attack. If larger larvae are better at wriggling out of the grasp of predators than smaller larvae, this could explain the age-related differences in drop-off rates on plants with and without ants. Thus, the higher incidence of fallen larvae may indeed reflect increased predation pressure, especially of larger and older instars on trees without ants. If dropping off is an avoidance reaction to predator attack, the probability of survival by falling off may be greater than that of remaining untended on plants without ants. (ii) Ants may somehow induce larvae to hold their foodplants more tightly. Larvae might spend more time feeding in order to feed their attendant ants, and might grip the plant more tightly when feeding. (iii) Larvae without ants might drop off plants to seek out new foodplants with attendant ant populations.

Whatever the reasons for untended larvae dropping off their foodplants, their chances of surviving are far less than those of their tended counterparts that remain on their host plants. Hence, although the difference in disappearance rates between larvae on plants with and without ants cannot be definitely ascribed to differential predation, the result is the

same: larvae that are tended by ants are far more likely to survive than larvae that are not tended by ants.

We determined that when larvae of *G. lygdamus* were tended by *F. altipetens* at Gold Basin 9.9% survived from egg to eclosion, whereas when ants were excluded only 0.7% survived. Thus, the net selective advantage of ant attendance is a twelve-fold increase in survivorship. This calculation of survivorship assumes that all individuals that disappear from their food plants also die. If we were to take the other extreme and assume that all unparasitized individuals that drop off their food plants survive, and that larval parasitism and drop off rates are similar to those shown in Tables 3 and 5, then the net selective advantage of ant attendance for *G. lygdamus* would be 11.9% compared with 2.7%, or four-fold. Our experiments were not designed to investigate the effects of ant attendance on either pupal or adult viability, or on fecundity. Since neither pupae nor adults normally interact with ants, these effects may be small. Overwintering pupae reared in 1979 from plants with and without ants were weighed, and there was no difference in their wet weights (without ants = 72.57 mg, S.D. = 14,  $n = 32$ ; with ants = 69.10 mg, S.D. = 1.21 S.E.,  $n = 62$ ;  $t_s = 1.342$ , d.f. = 92, N.S.). Thus, the range of four- to twelve-fold increase in juvenile survivorship is probably a fair approximation of the selective advantage of ant attendance by *F. altipetens* for *G. lygdamus* in this field site in 1980.

As first pointed out by Fisher (1930), a heritable trait that confers a selective advantage of just 1% will greatly modify the genetic constitution of a species in only a 100 generations. Clearly, the large selective advantage demonstrated here could have played a critical role in the evolution of the symbiotic ant associations of this butterfly. It would be of further interest to learn how this selective advantage might vary between field sites or in different seasons. Pierce & Mead (1981) recorded a 2.97-fold difference in survival at Gold Basin and a 2.99-fold difference at a site called Naked Hills in 1979. These estimates are conservative since the larvae in these experiments were not followed for their entire lifetimes. Taken together with the 1980 data, we can conclude that there has been a strong and consistent selective advantage of ant attendance for *G. lygdamus* in two field sites, and for one of them, over two field seasons.

The association that larvae of *G. lygdamus* have with ants may have important implications for the distribution of populations of this butterfly. *G. lygdamus* will survive most successfully in places where its food plants and effective attendant ant species are both available. When either is discontinuous, *G. lygdamus* may also be patchily distributed. At Gothic, Colorado, lupine food plants occur continuously over a wide area, but the population of *G. lygdamus* studied by Pierce & Mead (1981) is restricted to a single hilltop (see also Breedlove & Ehrlich 1968; Ehrlich *et al.* 1972) and is isolated spatially from other populations in the district. The distribution, temporal constancy and comparative protective abilities of ant species that associate with *G. lygdamus* are not known, but these variables may help to account for the surprising discontinuity observed in the distribution of *G. lygdamus*.

Population subdivision established through the overlapping requirement of suitable host plants and attendant ants would be enhanced by selection acting on any genetic component contributing to variance in dispersal rate, favouring individuals with low vagility. In populations that are small and discontinuous, individuals with low vagility would have a higher probability of remaining in areas that contain the necessary combination of habitat requirements to survive and reproduce successfully. This would not occur in large and continuous populations. Thus, even though ovipositing females of *G. lygdamus* may not show a direct behavioural response to workers of *F. altipetens*, the offspring of less vagile

females that lay eggs within a range inhabited by colonies of these ants might have a better chance of surviving and reproducing than the offspring of females that dispersed outside this range. As suggested by Pierce (1984), this effect of ant attendance on population structure may be a general feature among ant-tended lycaenid butterflies, and could have played an important role in shaping the evolution of the Lycaenidae.

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