Cost and evolution of a facultative mutualism between ants and lycaenid larvae (Lepidoptera)

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Larvae of *Arawacus lincoides* (Lycaenidae) reared in the lab with ants took 0.68 d longer to complete development than larvae without ants. Pupal weight was independent of whether a larva had been ant-tended. A 0.68 d delay in reaching age of first reproduction represents an estimated 1.0%–2.2% lowered intrinsic rate of increase for this continuously brooded species. I show that mutualism will be favored when the ratio of larval survival with ants to that without ants is greater than $\exp(dr)$, where d is the additional larval development time caused by feeding ants and r is the intrinsic rate of increase. Other things being equal, species with higher intrinsic rates of increase will be less likely to be mutualistic than their relatives with lower rates of increase.

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Butterfly larvae in the families Lycaenidae and Riodinidae may interact mutualistically with ants (Pierce and Young 1986, Friedler and Maschwitz 1989a, Thomas et al. 1989, DeVries 1990a). The benefit for ants is that they may obtain a significant portion of their energy budget by eating larval secretions (Fiedler and Maschwitz 1988, 1989b, DeVries and Baker 1989). The benefit for larvae is that they are not attacked by these ants. Also, the ants protect larvae from parasitoids and predators (Pierce and Mead 1981, Pierce and Easteal 1986, Pierce et al. 1987, DeVries 1990b).

Although demonstrating mutual benefits is necessary to document a mutualism, understanding its evolution requires a comparison of cost as well as benefits in mutualistic and non-mutualistic individuals (Keeler 1981, 1985 and included references). In obligate larva-ant mutualisms, larvae do not survive in nature without ants (Pierce et al. 1987, Fiedler and Maschwitz 1989b), which makes it difficult to estimate costs and benefits for non-mutualistic individuals. Further, subsequent adaptations that reinforce an obligate mutualism may alter the original costs and benefits of the interaction. These difficulties are partially overcome by examining facultative mutualisms in which larvae in nature are sometimes tended and sometimes not tended by ants.

Facultative larva-ant mutualisms vary among eumaeine hairstreak butterflies (Lycaenidae: Theclinae: Eumaeini) (DeVries 1990a). Larvae of some species have dorsal nectary organs (terminology of larval organs follows Cottrell 1984). Secretions from these organs are eaten by ants and are involved in a larva's ability to recruit ants (Fiedler and Maschwitz 1989a). Other eumaeine species lack dorsal nectary organs or have them reduced (Malicky 1969). These larvae do not recruit ants, but apparently appease ant aggressiveness with secretions from pore cupola organs (Malicky 1969, Fiedler and Maschwitz 1989a). Larvae of eumaeines with dorsal nectary organs may or may not be tended by ants in nature (Robbins and Aiello 1982).

The purposes of this paper are to estimate cost to a eumaeine larva of feeding an ant in a laboratory setting and to determine when the benefit of feeding ants from dorsal nectary organs will be greater than its cost. Most measurements of cost in ecological interactions have
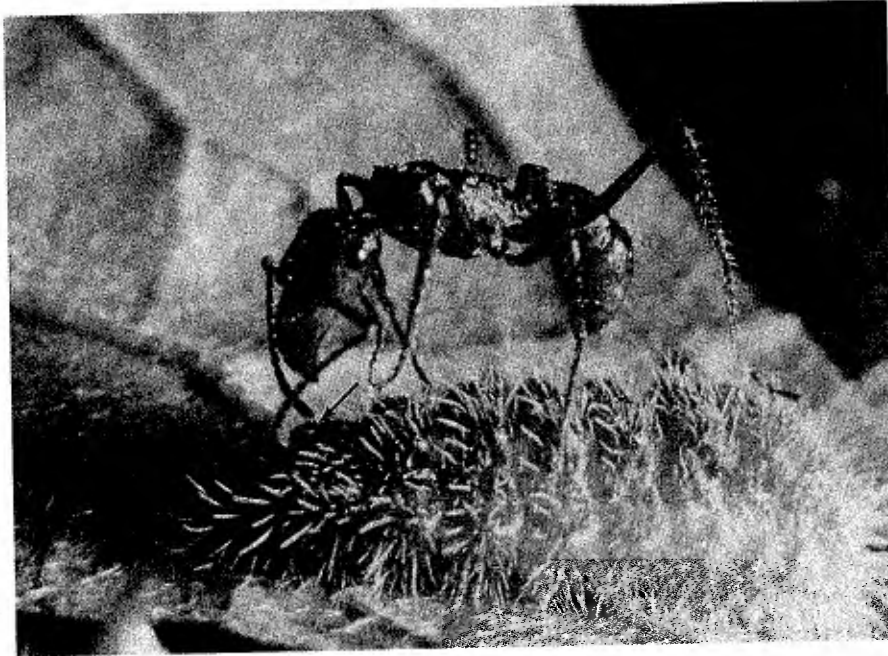
Fig. 1. *Ectatomma* ant and larva of *Arawacus lincoides*. Rear of larva to left. Arrow points to secretion from larval dorsal nectary organ on abdominal segment 7.

estimated the energetic cost of the interaction (Chew and Rodman 1979, O'Dowd 1979, Keeler 1981, Fagerström 1989 and included references, but see Morse 1985), which assumes that energetic cost will be reflected in a lowered rate of increase. In the lycaenid *Jalmenus evagoras* Donovan, however, costs and benefits of an obligate mutualism were measured in terms of life-history traits (Pierce et al. 1987, Elgar and Pierce 1988). Ant-tended larvae pupated earlier than non-ant-tended larvae, but at a smaller weight, which was a reproductive cost to the adult. In this paper, I (1) estimate cost in terms of life-history traits, but for a facultative mutualism, (2) calculate this cost in terms of a lowered rate of increase, and (3) mathematically derive the conditions under which this cost will be less than the benefit of the mutualism.

Natural history

Arawacus lincoides (Draudt) occurs from the Pacific drainage of southern Costa Rica to western Ecuador and northern Venezuela and Trinidad (Robbins, unpubl.). In Panama, its larvae eat leaves of various *Solanum* species (Solanaceae), are tended by *Ectatomma* or *Pheidole* ants, and are parasitized by a chalcidid wasp (Robbins and Aiello 1982). Although *A. lincoides* has been treated as a subspecies of *A. aetolus* Sulzer, it is a distinct parapatric species with different genitalia, androconial patches, and ventral wing pattern (Robbins, unpubl.). It is continuously brooded throughout the year in Panama.

Arawacus lincoides has four larval instars (Robbins and Aiello 1982). Ants ignore the first two instars, but stroke third and fourth instars. Tended larvae secrete fluid, which the ants remove from their dorsal nectary organ, (Fig. 1). The ants do not otherwise appear to alter larval behavior. Larvae tended by *Ectatomma* ants in Panama are tended by one individual at a time, in contrast to many simultaneously tending ants of the smaller *Pheidole*. Ants ignore pupae. After each molt except for pupation, larvae eat their cast skin, but not the head capsule.

Ectatomma ants tend extra-floral nectaries, homopterans, and myrmecophilous lycaenid and riodinid butterfly larvae in the Gamboa area, including larvae of *A. lincoides* (Robbins and Aiello 1982, DeVries 1988, 1990b). By placing larvae of different butterfly families near *Ectatomma* ants in the field (Robbins, unpubl.), I found that these ants attack and kill most non-myrmecophilous larvae except for those that are too large and setose. When first approaching a lycaenid or riodinid larva, ants open their mandibles, as if they are going to attack, but then begin stroking the larva. They may then tend the same larva for days (DeVries 1987, 1988). *Ectatomma* ants attacked and killed one unidentified myrmecophilous riodinid larva in the field and one late second instar *A. lincoides* larva in the laboratory (Robbins, unpubl.). They have also been recorded as predators of riodinid larvae in Mexico (Ross 1966, cf. discussion in DeVries 1988, 1990b). These ants catch and kill adult flies (Houston 1987) and presumably can do the same to insect parasitoids and predators that attack lycaenid and riodinid larvae.

Table 1. Larval development time (instars 3 and 4) for offspring of females A, B, and C, reared with and without an ant. Sex was determined after eclosion; a question mark (?) designates sex unknown. Statistics were calculated from data accurate to four decimal places.

Female	A		B		C	
Number of ants	0	1	0	1	0	1
Development time (d)	8.5 ?	9.0 ♂	10.0 ♂	10.0 ♀	9.7 ♀	10.7 ♀
	8.5 ?	9.5 ♂	10.7 ♂	11.7 ♂	10.0 ♂	11.0 ♂
	9.0 ♀	9.5 ♀	10.7 ♂	11.7 ♂	10.0 ?	11.0 ♀
	9.0 ♀	9.5 ♀	10.7 ♂	12.0 ♂	11.0 ♂	11.3 ♂
	9.0 ♀	10.0 ♂	10.7 ♀	12.0 ♂	11.0 ♀	11.7 ♀
	9.5 ♂	10.0 ?	10.7 ?	12.0 ♂	11.0 ♀	12.7 ?
	10.0 ♀	10.5 ♂	11.0 ♂	12.3 ♀	12.0 ♂	
			11.7 ♀	12.3 ♀		
			12.7 ♀	12.7 ♀		
			12.7 ♀	13.0 ♂		
			13.0 ♂			
Mean	9.07	9.71	11.30	11.97	10.67	11.39
Variance	0.286	0.238	1.055	0.653	0.667	0.507
N	7	7	11	10	7	6
X_2-X_1	0.64		0.67		0.72	
t_s	2.350		1.634		1.684	
p	0.0367		0.1188		0.1203	

Combined test of significance: $\chi^2_{\,df\,=\,6} = 15.11, 0.01 < p < 0.02$

Materials and methods

Wild collected females of *Arawacus lincoides* were brought to the lab and fed daily on a dilute solution of honey and water. To elicit oviposition, females were placed in net bags with cuttings of *Solanum lancaeifolium*. Eggs were collected daily and placed singly in 9.0 × 1.5 cm plastic petri dishes. The petri dishes had been prepared by putting gypsum (plaster of paris) in the bottom of the dish, covering it with Whatman No. 1 filter paper and with aluminum foil (Chew 1980). The gypsum was moistened every other day to maintain a moisture reservoir and the aluminum foil kept eggs, larvae, and pupae from contact with the wet surface of the filter paper.

Larvae were derived from three females. Female A was collected in Gamboa, Canal Area, Panama on 1 November 1979. Gamboa is a tropical lowland forest with about 225 cm annual precipitation (Rand and Rand 1982). Female B was caught on the Cerro Campana Road (this locality is detailed in Robbins and Small 1981), Panama Province, Panama on 18 January 1980. Female C was collected in Gamboa on 19 January 1980.

Larvae were reared singly in the petri dishes described above and were fed fresh leaves of *S. lancaeifolium* from the Gamboa area ad libitum. Larvae from female A were checked at 12 h intervals while those from females B and C were examined every 8 h. I noted whether larvae were feeding or had entered a premolt stationary phase (which lasts approximately 1–1.5 d) and recorded molts when a cast head capsule was found.

An *Ectatomma* ant (Formicidae: Ponerinae) - collected in Gamboa - was added to approximately half the petri dishes when a second instar larva stopped feeding preparatory to molting. Although isolating an ant from its nestmates altered its behavior, I had found that ants continued to tend larvae in this situation (discussed further below). If the ant died during the experiment, another was added. I recorded whether the ant was feeding on secretions of the larva's dorsal nectary organ when I checked larvae with ants. Development time was recorded for instars 3 and 4. Pupae were weighed 6–30 h after pupation. I also determined sex of eclosed individuals. The null hypothesis that there is no prolonged larval development time or decreased pupal weight for ant-tended larvae was tested for significance by one-tailed t-tests. Significance of results for offspring of all females was tested using a combined test of significance (Sokal and Rohlf 1969).

Results

Of 67 larvae that were about to enter the third instar, 48 (72%) survived to pupation. Causes of mortality were handling by me (2 larvae), being bitten and stung by a tending ant (1 larva), and "disease" (16 larvae that stopped feeding, turned black, and died). All ants actively tended larvae in the petri dishes and fed on secretions from the dorsal nectary organ (Fig. 1). Larval feeding was not interrupted by ants.

Larvae with attending ants took 0.64, 0.67, and 0.72 d longer ($0.01 < p < 0.02$) to develop than their sibs without ants (Table 1). Sex ratios of larvae reared with and without ants were similar for the offspring of female B

Table 2. Pupal weight for offspring of females A, B, and C, reared with and without ants. One pupa (Female C, with an ant) was deformed and omitted.

Female	A		B		C	
Number of ants	0	1	0	1	0	1
Pupal weight (mg)	82.1	83.1	87.9	80.5	81.0	92.3
	88.4	94.7	93.8	81.6	85.0	95.5
	90.7	94.7	95.5	82.8	92.7	104.3
	92.6	95.1	96.1	91.2	98.7	105.1
	97.2	97.3	98.6	96.4	100.2	115.3
	97.9	101.2	101.8	103.8	113.2	
	107.8	101.8	103.0	105.9	116.0	
			108.5	119.3		
			109.2	124.0		
			110.1	127.2		
			130.5			
Mean	93.81	95.41	103.18	101.27	98.11	102.50
Variance	66.911	38.428	131.230	314.056	174.395	81.720
N	7	7	11	10	7	5
t_s	0.4124		0.2965		0.6391	
p	0.6870		0.7732		0.5371	

Combined test of significance: $\chi^2_{df = 6} = 2.51$, not significant

(6♂, 4♀, 1? without ants; 6♂, 4♀ with ants) and female C (3♂, 3♀, 1? without ants; 2♂, 2♀, 2? with ants). Although sex ratios differed for the offspring of female A (1♂, 4♀, 2? without ants; 4♂, 2♀, 1? with ants), male and female larvae had the same prolonged development time when reared with ants. Pupal weights did not differ significantly between larvae reared with and without ants (Table 2).

When should larvae feed ants?

The purpose of this section is to determine mathematically the cost and benefit of feeding ants from a dorsal nectary organ for those continuously brooded species, such as *A. lincoides,* in which a tending ant prolongs larval development. Intrinsic rate of increase is highly sensitive to onset of first age of reproduction (Lewontin 1965), and the longer development time for an ant-tended larva lowers its rate of increase relative to that of a non-ant-tended individual. The presumed benefit for a larva of feeding ants is higher larval survival.

In the following discussion and in the Appendix, demographic parameters with a prime (') after them refer to ant-tended specimens while those without a prime refer to non-ant tended specimens. I follow standard notation (May 1976) for demographic parameters "r" (intrinsic rate of increase), "l_x" (age specific survivorship), "m_x" (age specific birth rate), "R_o")number of offspring per individual), and "T_c" (mean cohort generation time). I designate prolonged larval development by "d", probability of survival to adulthood by "l_a" and of adult survival given succesful eclosion by "$l_{x/a}$", where

x is greater than the age at eclosion. Thus, ($l_x = [l_a]$ $[l_{x/a}]$).

The mathematical relationships between l_x and m_x for ant-tended and non-ant-tended individuals are straightforward. Because weight at pupation is independent of whether or not a larva was ant-tended, age specific survivorship for adults and birth rates after eclosion are also independent of whether a larve was ant-tended (see discussion below). Mathematically, ($l_{x/a} = l'_{y/a}$) and ($m_x = m'_y$) where x and y are greater than ages at eclosion and ($y = x + d$).

In the Appendix, I show that the benefit of feeding ants with dorsal nectary organ secretions will outweigh its cost ($r'>r$) if, and only if, (l'_a/l_a) > exp (dr)). The ratio (l'_a/l_a) is survivorship to eclosion for ant-tended larvae divided by that for non-ant-tended larvae. Thus, larval survivorship with and without ants, duration of larval development with and without ants, and the intrinsic rate of increase determine whether the benefit of feeding ants outweights its cost.

Cost in fitness

The purpose of this section is to estimate the cost of feeding ants in *A. lincoides,* measured as the percentage lowered rate of increase ((($r-r'$)/r) × 100%) caused by a prolonged larval development period. Thus, the idea is to compare r for a non-ant-tended larva that successfully ecloses with r' for a similarly successful individual that was ant-tended; the only difference is prolonged larval development of the ant-tended individual. Specifically, I calculate upper and lower bounds in *A. lincoides* for (($r-r'$)/r).

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It is possible to estimate $((r-r')/r)$ as a function of T_c and d. Survivorship curves are the same as in the previous section, except that $l_a = l'_a$ since cost is being measured without including benefits. Substituting in equations for R_0 and T_c (May 1976), $(R_0 = R'_0)$ and $(T_c = T'_c-d)$. Using the approximation $(r = \ln(R_0)/T_c)$ (May 1976), $r' = (\ln(R'_0)/T'_c) = (\ln(R_0)/(T_c + d))$. Substituting and simplifying, $((r-r')/r) = (d/(T_c + d))$.

The needed demographic information for *A. lincoides* is minimal. An individual that is ant-tended during its last two larval instars takes 0.68 d longer, averaged over all three trials, to reach reproductive age than an individual that is not ant-tended. Development time of immatures among the offspring of female A was about 30 d (4–5 d as egg, 14.5–17.5 d as larva, 8.5–9.5 d as pupa) and of adults was approximately 40 d. (Of 18 adult males marked on the morning of eclosion and released in the field in Gamboa, I sighted two of them, worn and weak flying, 37 d later.) Thus, T_c cannot be less than 30 d (age at first reproduction) or more than 70 d (maximum life span). Substituting $d = 0.68$ d and the extreme values for T_c in the equation above, I calculated 1.0% as an extreme lower and 2.2% as an extreme upper estimate of $((r-r')/r)$. The cost to plants of feeding ants from extra-floral nectaries (O'Dowd 1979, Keeler 1981) is very similar.

Discussion

Larval behavior in petri dishes with and without ants was similar except that larvae with ants secreted fluid from their dorsal nectary organ. Larvae fed continuously in both treatments except just prior to and during molts.

Ant behavior in petri dishes was altered. A possible bias of the experiment was that larvae with ants were always tended whereas in the field there might be periods without tending ants. However, DeVries (1987, 1988) found that marked individuals of *Ectatomma* stayed with individual larvae of the riodinid, *Thisbe irenea*, for up to 10 d. Another possible bias is that ants could not pass secretions collected from larvae to nestmates (DeVries 1988). However, ants stroked larvae and removed dorsal nectary secretions throughout the development of third and fourth instar larvae, just as they did in the field. Although one ant attacked and killed a late second instar larva in the experiment, I observed the same behavior in the field with a myrmecophilous riodinid larva (Robbins, unpubl.).

The main assumption of the theoretical section is that adult survivorship and birth rates are correlated with pupal size (or with eclosed adult weight), which has been demonstrated in another lycaenid (Pierce et al. 1987, Elgar and Pierce 1988) and other butterflies (Rahman 1968, Lederhouse 1981, Jones et al. 1982). In *A. lincoides*, pupal size is independent of whether a larva

was ant-tended (Table 2). I cannot rule out the possibility, however, that fat or protein content of equal-sized pupae differed as a result of having been ant-tended and affected subsequent survivorship or fecundity.

The experimental results in this paper differ from those of other larva-ant mutualisms. Some myrmecophilous larvae take months longer to develop than related larvae of non-ant-tended species, but the longer development time in these cases appears to be an adaptation for living in ant nests (Henning 1983). Ant-tended larvae of *Jalmenus evagoras* (Theclinae: Zesiini) develop faster than those from which ants are experimentally barred, but pupate at a smaller size (Pierce at al. 1987, Elgar and Pierce 1988). Larvae of *J. evagoras*, unlike those of *A. lincoides*, do not survive in nature without ants (Pierce at al. 1987), which may account, at least in part, for their more rapid development time with ants than without

For continuously brooded species in which the cost of feeding ants is prolonged larval development, as appears to be the case with *A. lincoides*, Eq. 1 (Appendix) gives exact conditions under which the benefit of feeding ants is greater than its cost. The benefit to larvae is increased larval survival, meaured by the dimensionless ratio (l'_a/l_a), while the cost is decreased reproductive potential, measured by the dimensionless exponential $(\exp(dr))$. However, the cost and benefit are interdependent and comparisons require delicate interpretation. For example, a change in larval survival directly affects calculation of the benefit and indirectly alters the cost via the effect of larval survival on the intrinsic rate of increase (r).

An example shows the significance of Eq. 1. If ants increase larval survival by 50% and increase larval development time by one day, then the benefit of feeding ants will outweigh the cost only if the intrinsic rate of increase is less than 0.41. All other things being equal, this model predicts that discrete brooded species, such as *Glaucopsyche lygdamus* Doubleday (Pierce and Easteal 1986), and continuously brooded species with low intrinsic rates of increase are more likely to be myrmecophilous than their continuously brooded relatives with high intrinsic rates of increase.

Appendix

Notation for demographic parameters is from May (1976). Parameters with a prime (') are for ant-tended

individuals. "l_a" is survivorship to eclosion and "$l_{x/a}$" is adult survivorship given survival to eclosion. "x" and "y" represent age greater than that at eclosion. The additional duration of larval development resulting from feeding ants is designated "d". The purpose of the appendix is to show that

$$((l'_a/l_a) > e^{rd}) \text{ if and only if } (r' > r) \qquad (1)$$

From May (1976)

$$1 = \int (e^{-rx} l_a l_{x/a} m_x dx) \text{ for non-ant tended individuals} \qquad (2)$$

$$1 = \int (e^{-r'y} l'_a l'_{y/a} m'_y dy) \text{ for ant-tended individuals} \qquad (3)$$

As discussed in text, on biological grounds, we have

$(m'_y = m_x)$, $(l'_{y/a} = l_{x/a})$, and $(y = x + d)$

so that Eq. (3) can be rewritten

$$1 = \int (e^{-r'(x+d)} l'_a l_{x/a} m_x dx) \qquad (4)$$

Dividing Eq. (4) by Eq. (2) yields

$$1 = [(l'_a)/(l_a e^{rd})] \left[\frac{\int (e^{-r'(x+d)} l_{x/a} m_x dx)}{\int (e^{-r(x+d)} l_{x/a} m_x dx)} \right] \qquad (5)$$

The term in square brackets is less than 1 if, and only if, $r' > r$. It therefore follows that $l'_a > l_a e^{rd}$ if, and only if, $r' > r$.

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