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The effect of host-plant quality on the survival of larvae and oviposition by adults of an ant-tended lycaenid butterfly, *Jalmenus evagoras*

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Abstract. 1. Juveniles of the Australian lycaenid butterfly, *Jalmenus evagoras* (Donovan), secrete to ants a solution of sugars and amino acids, primarily serine. The attendant ants protect the larvae and pupae from parasites and predators.

2. The effect of caterpillar nutrition on the defence provided by ants was investigated. Potted food plants of *Acacia decurrens* were either given water containing nitrogenous fertilizer or were given water alone. Fertilized plants had a higher nitrogen content than unfertilized plants.

3. Fifth instar larvae of *J.evagoras* feeding on fertilized plants attracted a larger ant guard than those feeding on unfertilized plants. In the absence of caterpillars, ants were not differentially attracted to fertilized and unfertilized plants.

4. In the presence of ants, over a 10-day period, larvae on fertilized plants survived better than larvae on unfertilized plants. In the absence of ants larvae survived equally on fertilized and unfertilized plants. It is concluded that larvae on fertilized plants attracted a larger ant guard, and thereby survived better, than larvae on unfertilized plants.

5. Adult females of *J.evagoras* preferred to lay egg batches on fertiized, rather than unfertilized plants, but they did not lay larger egg batches.

Key words. Host-plant quality, nitrogenous fertilizer, oviposition, ant attendance, *Jalmenus evagoras*, Lycaenidae, Lepidoptera.

Introduction

There have been many investigations of the effect of nitrogen levels of food plant on the survival of phytophages. The nitrogen level of food plants has generally been varied by the application of fertilizer or by sampling from a range of food plant species or populations and usually higher nitrogen levels have been found to increase survival (Myers & Post, 1981; Myers, 1985; Ohmart *et al.*, 1985; Taylor, 1988), although in some studies increases in nitrogen have been found to have no effect (Lincoln, 1985; Ohmart *et al.*, 1985) or even a negative effect (Stark, 1965; Myers, 1985). Since nitrogen and water levels are often correlated in plants (Scriber & Slansky, 1981), it is difficult to separate their effects (and, indeed, those of any

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other factors which change concentration with the application of fertilizer or between plant species or populations) on phytophage survival. This has been overcome in some studies by the use of artificial diets. Increasing the protein content of artificial diets while holding water content constant has been shown to increase survival (Lincoln *et al.*, 1982; Cates *et al.*, 1987) although the effect may depend on the type of protein used (Johnson & Bentley, 1988).

Phytophages have developed numerous mechanisms that enable them to take advantage of nitrogen and water-rich (more 'nutritious') food (Simpson & Simpson, 1990). For example, the feeding stage of some insects may exhibit facultative carnivory, feed on the most nitrogen-rich plant part, change position or plant with season and may alter host plant chemistry (McNeill & Southwood, 1978; Mattson, 1980). Furthermore, insects on nutritionally poor diets may maximize their nutrient uptake by increasing feeding rates or development time (Simpson & Simpson, 1990; Taylor, 1989). Female insects may also selectively oviposit on plants most nutritionally suitable for their offspring (Williams, 1983; Myers, 1985; Ng, 1988).

The reason for the increased survival shown by many insects when feeding on more nutritious food plants is generally unstated, but is probably related to the ability to increase growth rates and hence reduce development time (thereby reducing mortality risk), to decrease feeding rates (thereby reducing mortality risk) and/or to the ability to invest more in defence mechanisms such as distasteful substances, trichomes, etc., or immunological responses to pathogens. The association of larvae of *Jalmenus evagoras* (Donovan) with ants suggests a novel mechanism by which diet quality may affect survival.

Caterpillars and pupae of *J.evagoras* secrete to ants an aqueous solution that has been shown to contain high concentrations of amino acids (primarily serine) and sugars (Pierce, 1983, 1989). The tending ants have been shown to be highly attracted to artificial solutions of those amino acids found in the secretions, and the attractiveness of pupae to ants has been correlated with the concentration of serine in washings (Pierce, 1983). Ants provide protection in return for the secretions (Pierce *et al.*, 1987; Baylis, 1989). This suggests that caterpillars feeding on more nutritious food plants, apart from possibly gaining a direct nutrition-related increase in survival for the reasons described above, might additionally gain an increase in survival via an enhanced ability to attract ants. In other words, by producing a larger volume of secretion, or providing secretion with a higher concentration of nutrients, caterpillars of *J.evagoras* might be able to attract more ants for defence and thereby survive better.

Here we describe experiments which investigate the effect of host plant quality, varied by the application of nitrogenous fertilizer, on the attractiveness of larvae of *J.evagoras* to ants, the survival of the larvae in the wild, and finally the ovipositional responses of adult females of *J.evagoras* to higher and lower quality larval food plants.

Materials and Methods

Natural history and study sites. J. evagoras is a multivoltine, Australian lycaenid butterfly that ranges from Melbourne, Victoria, in the south to Gladstone, Queensland, in the north and occurs both inland and near the coast. Populations are common but local (Common & Waterhouse, 1981). The field season is approximately November–April, in which time there may be up to three generations. Larvae feed on young plants of *Acacia* spp., and larvae and pupae are tended by *Iridomyrmex* spp. ants. Adult females use ants as cues in oviposition (Pierce & Elgar, 1985), and usually lay eggs in crevices on the stems and branches of the larval food plants. Several egg batches may be laid during one bout of oviposition.

The field site where this research was performed was Mt Nebo, Queensland (152° 47′E, 27° 23′S). At sub-tropical Mt Nebo, *J.evagoras* most commonly feeds on the bipinnate *A.irrorata* (Sieb. ex. Spreng.) and is tended by ants of the *I.anceps* species group (sp. 25, Australian National Insect Collection, Canberra), hereafter *I.anceps* for short.

The effect of fertilizer application to food plant on the attractiveness of larvae to ants. One hundred potted food plants of *A.decurrens* (Wendl.), grown from seed by the Department of Forestry, Forbes, N.S.W., were reported in a mixture of 60% (by volume) vermiculite and 40% clay soil from Mt Nebo. The plants were 66±10 cm (mean ±SD, n = 100) tall.

Plants were randomly assigned to one of two treatments: (a) From early February to April 1988 fertilized plants were watered every 2 days with 200 ml water containing Aquasol™ fertilizer (N:P:K ratio = 23:4:18) and chelated iron (both Hortico (Aust) Pty Ltd, Victoria), at concentrations of 0.8 g/l and 0.2 g/l respectively. Iron was added because this is often a limiting element in Australian soils, and thus might prevent the uptake of additional nitrogen. (b) For the same time period, unfertilized plants were watered every 2 days with 200 ml water.

During especially hot periods, when there was a risk of dehydration, all plants were given an additional 200 ml water on the intervening days.

In early April 1988 all plants were examined for the presence of root nodules. All of the unfertilized plants, and none of the fertilized plants, were found to have root nodules. This is expected: nitrogen fixation is energetically costly and when an alternative source of nitrogen is available (in this case, fertilizer) nodules are not maintained (Lie, 1974).

Experimental method. Twenty-four food plants from the pool of one hundred were randomly assigned to two experimental groups of twelve, with equal numbers of fertilized and unfertilized plants in each group. At each of two sites in paddocks around Mt Nebo the groups of twelve plants were arranged in random order in a semicircle around a natural tree on which ants were tending larvae of *J.evagoras*. The trees at the two sites were tended by different colonies of *I.anceps*. The stems of the potted plants were banded with tape and the bands half-coated with tanglefoot (Tanglefoot Co., Grand Rapids, Michigan). Ants were still able to climb the plants. Metal wire fences around the experimental sites prevented interference from horses.

At the start of the experiment (day 0) fifth instar caterpillars of *J.evagoras* were collected from natural trees of *A.irrorata* around Mt Nebo. Four individuals were placed on each of three fertilized and three unfertilized plants at both sites (hence twelve plants in total). On day 4, two more caterpillars were placed on each of the twelve plants. At each site, six plants were not given any caterpillars.

The number of ants tending each larva was recorded daily for 10 days. Ants were defined as 'tending' if they were in physical contact with a larva. To obtain an estimate of the inherent attractiveness of fertilized and unfertilized plants to ants, the number of ants on the plants without larvae was also recorded.

The effect of fertilizer application to food plant on the survival of larvae. In the arrangement described above, larval survival was measured by scoring the number of larvae present on each plant (out of the original four or six) on each of the 10 days.

To examine the direct effect of fertilizer application to the food plant on caterpillar survival, a control group of twelve plants was randomly selected from the pool. These plants were set up without ant protection by banding their stems with tape, and completely coating the bands with tanglefoot. Since caterpillars of *J.evagoras* cannot survive in the wild without ants (Pierce *et al.*, 1987; Baylis, 1989), the plants were randomly arranged in a bush house (a wooden construction lined with plastic mesh) which excluded predators and parasites. The bush house was immediately adjacent to a natural tree bearing ant-tended *J.evagoras* and was within 10 m of one of the experimental sites.

Final instar larvae were placed on the plants as described above, and the number of surviving larvae was scored daily for 10 days.

The effect of fertilizer application to larval food plant on the ovipositional behaviour of J.evagoras. In late March 1988, four hundred pupae of *J.evagoras* were collected from trees of *A.binervata* at Ebor, N.S.W. (150° 00′ E, 30° 34′ S). Upon eclosion, adults were randomly allocated to five 1 m^3 butterfly cages. The cages were wooden, with wire-mesh sides, and the wood was covered in aluminium foil to prevent oviposition on the cage itself. The number of butterflies in each cage ranged from thirty to sixty during the experiment. Each day the butterflies were provided with a 10% honey solution for food.

Four fertilized and four unfertilized plants were placed in each cage. The plants used were selected randomly from the pool described earlier. The butterflies were allowed to mate and oviposit freely within each cage. After 5 days all plants were removed and the number and size of egg batches laid on each plant was scored.

Water and nitrogen content of leaf samples. Sample leaves (in each case the fourth leaf from the tip of the plant) were collected from the fertilized and unfertilized plants used in the experiments described above. Water content (per cent fresh weight) was determined by weighing fresh samples, drying to constant weight at 60°C and reweighing. Dried samples were digested with the micro-Kjeldahl method (Allen *et al.*, 1986) and analysed for total nitrogen content with a Technicon AA2 autoanalyser at the Department of Zoology, Oxford. Nitrogen content of the bipinnate food plant, *A.decurrens*, was determined for the pinnules, and not the mid-ribs, since these are the leaf part eaten by larvae of *J.evagoras*.

Statistical analysis. All analyses were based on the methods of Sokal & Rohlf (1981).

Results

Effect of fertilizer application on ant attendance

The leaves of plants treated with fertilizer had a higher nitrogen content than the leaves of unfertilized plants, but there was no difference in water content of the leaves or height of the plants (Table 1A).

Fifth instar caterpillars of *J.evagoras* feeding on fertilized plants were tended by a significantly larger number of ants than caterpillars feeding on unfertilized plants (Fig. 1; two-way ANOVA of site and treatment on mean number of ants per larva per plant, $F_{1,8}$ = 5.29, P = 0.05). Larvae on unfertilized plants were tended on average by five to six ants each, whereas those on fertilized plants were tended by seven to eight ants each.

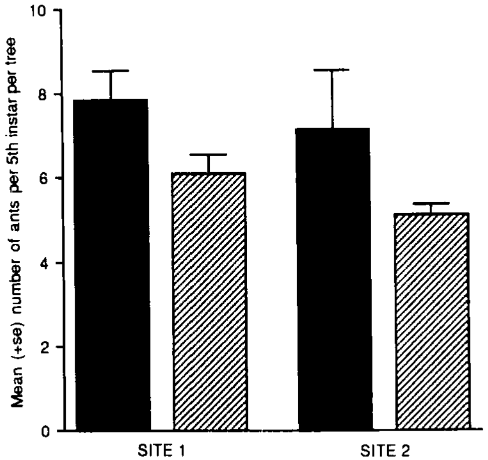

Fig. 1. Mean (+ SE) number of ants tending fifth instar caterpillars of *J.evagoras* on host plants which did (solid columns), or did not (hatched columns), receive nitrogenous fertilizer.

In the absence of caterpillars, fertilized plants were not more attractive to ants than unfertilized plants. There were six plants without caterpillars at each site: a single ant was observed on an unfertilized plant at site 1 on one occasion; many ants were observed on an unfertilized plant at site 2, but these were tending an homopteran.

Table 1. Height of plant, nitrogen content (% dry weight) and water content (% fresh weight) of fertilized and unfertilized host plants used for: (A) the ant attendance and caterpillar survivorship experiments; and (B) the oviposition experiment. Data were log transformed prior to analysis by unpaired *t*-test.

	Fertilized plants			Unfertilized plants			*t*-value
	Mean	SD	*N*	Mean	SD	*N*	
A. Height (cm)	68.44	10.25	24	67.86	7.29	24	− 0.209
% nitrogen	3.89	0.74	23	2.38	0.40	24	8.703**
% water	65.23	2.92	23	64.91	3.44	24	0.358
B. Height (cm)	73.86	9.11	20	69.15	11.00	20	1.51
% nitrogen	4.76	0.63	20	2.96	0.50	20	10.08**
% water	69.31	3.42	20	62.99	2.42	20	6.72**

** $P<0.0001$.

Effect of fertilizer application on caterpillar survival

In the absence of ants, fertilizer application had no effect on the survival of caterpillars over the 10-day period (Fig. 2, control). On no occasion did the proportion surviving differ significantly between fertilized and unfertilized plants.

When ants were present, caterpillars on fertilized plants survived better than caterpillars on unfertilized plants (Fig. 2, sites 1 and 2). The difference in proportion surviving was most marked after 6 or 7 days (two-way ANOVA of treatment and site on proportion surviving per plant, data arc-sine square root transformed; day 6, $F_{1,8} = 4.40$, $P<0.07$; day 7, $F_{1,8} = 4.00$, $P = 0.08$). The proportion surviving did not differ between sites. It thus appears that the enhanced ant attendance of larvae caused by the application of fertilizer to the host plant led to increased survival of the larvae, although the increase was not significant at $P = 0.05$.

At both the experimental and control sites the overall survival was low. This may in part be attributed to emigration. Transferring caterpillars from *A.irrorata* to the closely related *A.decurrens* caused some to leave or fall off the plant soon after being placed on it.

Effect of fertilizer application on adult oviposition

The leaves of plants treated with fertilizer had a higher nitrogen and water content than the leaves of unfertilized plants, but there was no difference in height of the plants (Table 1B).

Females of *J.evagoras* oviposited a total of 1659 eggs on fertilized plants and 274 eggs on unfertilized plants. This difference could be achieved in three ways: ovipositing on a larger number of fertilized plants; laying more egg batches on fertilized plants; or laying larger egg batches on fertilized plants.

Females oviposited on a larger number of fertilized than unfertilized plants although the difference was not significant (Fig. 3; Fisher's method of combining probabilities, found for each trial from the binomial expansion, $\chi^2 = 9.96$, d.f. = 10, $P < 0.1$). Considering only those trials in which eggs were found on plants of both treatments (trials 2, 4 and 5), significantly more egg masses were laid on fertilized plants than unfertilized plants (Fig. 3; Fisher's method of combining probabilities, found for each trial by Mann-Whitney *U*-test, $\chi^2 = 15.13$, d.f. = 6, $P < 0.05$). However, the mean number of eggs within each of these egg batches did not differ significantly (Table 2). The larger number

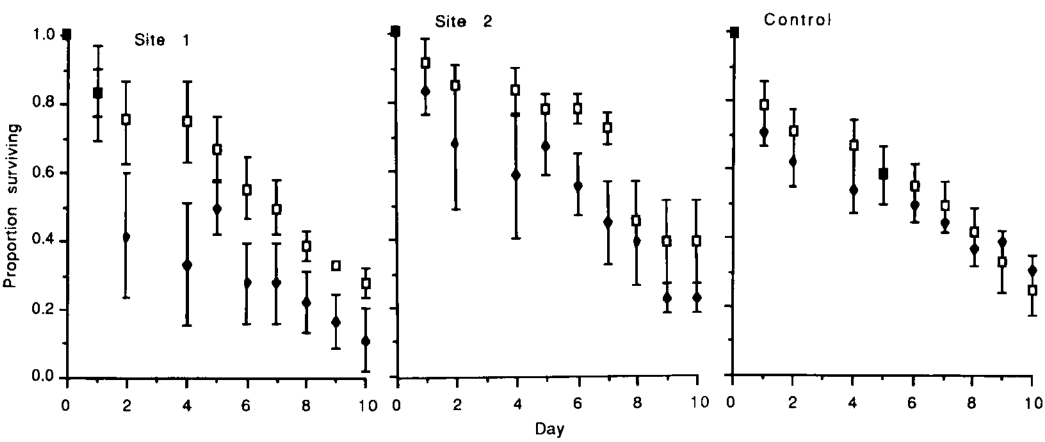

Fig. 2. The effect of fertilizer application on the survival of larvae of *J.evagoras* at two sites where ants were allowed to tend, and one control site where ants were excluded. Points are means (±SE) of the proportion of larvae surviving on three plants (sites 1 and 2) and six plants (control). On day 0, four larvae were placed on each plant, and two more added on day 4. Open squares = fertilized plants; closed diamonds = unfertilized plants.

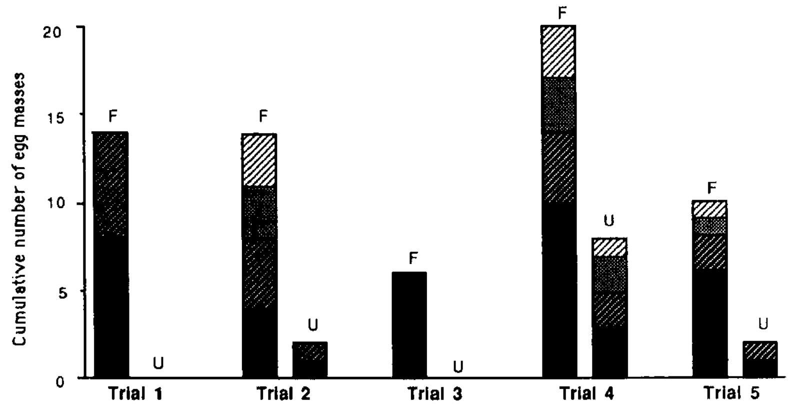

Fig. 3. The oviposition preferences of *J.evagoras* presented with fertilized (F) and unfertilized (U) host plants. The number of blocks per column is the number of plants (out of four) on which the butterflies oviposited. The size of each block represents the number of egg masses laid.

of eggs laid on fertilized plants is thus due to females choosing these plants more frequently for oviposition, rather than females laying significantly larger egg batches on these plants.

A possible cue used by females of *J.evagoras* to discriminate between the fertilized and unfertilized plants was colour. The intensity of green colour of leaves from the plants was ranked on a scale from 1 to 7 by an independent observer without knowledge of their fertilized or unfertilized status. The leaves of fertilized plants were darker than those of unfertilized plants (Mann-Whitney *U*-test, $P < 0.01$).

Discussion

The experiments described in this paper demonstrate that larvae of *J.evagoras* feeding on fertilized food plants are able to attract a larger ant guard which thereby enables them to survive better. Female adults of *J.evagoras* prefer to oviposit upon fertilized food plants.

The attractiveness of larvae to ants

Larvae on fertilized plants were more attractive to ants than larvae on unfertilized plants. The reason for this increased attractiveness is unclear, but is probably related to two factors: (a) The rate of secretion of larvae may have been higher on fertilized plants. To increase the rate of secretion would require the increased loss of both water and nutrients. Since the fertilized plants had higher nitrogen, but not higher water contents than the unfertilized plants, such increased water loss would probably have resulted in lower fresh growth rates, unless there

Table 2. Mean size of egg batches laid on host plants which either were, or were not, given nitrogenous fertilizer. Data were log transformed prior to analysis by two-way ANOVA. The effects of trial were removed from the analysis.

	Fertilized plants			Unfertilized plants			
	Mean	SD	*N*	Mean	SD	*N*	
No. of eggs	27.2	34.1	44	22.8	15.4	12	$F_{1,14}=0.80$ ns

was dietary compensation. Growth rates were not examined in this experiment. (b) The concentration of nutrients in the secretion may have been higher for larvae feeding on fertilized plants. Secretions were not analysed chemically, and therefore it is not possible to specify which nutrients (if any) were of increased concentration in the secretions of larvae feeding on fertilized plants. However, the fertilized plants had significantly higher nitrogen contents than the unfertilized plants, and the secretions of larvae of *J.evagoras* have been shown to contain amino acids to which ants are highly attracted (Pierce, 1983, 1989). An important role for the amino acid serine is possible. There is a positive correlation between the concentration of aqueous solutions of serine and their attractiveness to foraging ants, and a positive correlation between the concentration of serine in washings of pupae of *J.evagoras* and their attractiveness to ants (Pierce, 1983). Unfortunately, in the latter experiment possible covariances of serine concentration with that of other nutrients (such as sugars, which are also highly attractive to ants) were not investigated.

The two hypotheses discussed above can be readily distinguished by collecting secretions from larvae feeding on fertilized/protein-coated plants and on unfertilized/untreated plants, and finding the protein concentration, or by observing the rate of secretion of larvae feeding on the different diets.

The survival of caterpillars on fertilized plants

Many studies have demonstrated that increase in the nitrogen content of host plant or diet increases larval survival (Myers & Post, 1981; Lincoln *et al.*, 1985; Myers, 1985; Ohmart *et al.*, 1985; Cates *et al.*, 1987; Johnson & Bentley, 1988; Taylor, 1988), although this is not always the case (Stark, 1965; Lincoln, 1985). In the absence of ants, larvae of *J.evagoras* did not survive better on fertilized plants. There are several possible explanations. Firstly, the leguminous food plants of *J.evagoras* may be sufficiently rich in nitrogen that it is not a limiting element in physiological processes: further increases in nitrogen content may not stimulate greater health and/or allow greater investment in defence mechanisms. For example, the effect of changes in nitrogen content (induced by fertilizer application) on the growth of *Paropsis atomaria* was dependent on the nitrogen level of the host plant (Ohmart *et al.*, 1985). At nitrogen contents below 1%, increases in nitrogen led to increased size. At nitrogen contents between 1% and 3%, increases in nitrogen content had no effect on size. The unfertilized food plants of *J.evagoras* used here had nitrogen contents of between 2% and 3%.

A second explanation is that the application of fertilizer may not have altered the level of those chemical compounds related to survival. The application of ammonium sulphate to plants of the ragwort, *Senecio jacobaea*, reduced the levels of three amino acids but had no effect on the levels of the other thirteen examined (Wilcox & Crawley, 1988). We used a P:K:N fertilizer: caterpillars of *Pieris rapae* survived better on plants fertilized with ammonium sulphate and ammonium nitrate, but application of urea did not affect survival, and application of a P:K:N fertilizer actually decreased survival (Myers, 1985).

In contrast, in the presence of ants, caterpillars of *J.evagoras* survived better on fertilized plants, although the difference was not quite significant. This suggests a novel mechanism by which diet quality may effect survival. On fertilized plants, larvae of *J.evagoras* are able to attract a larger ant guard which provides a greater defence against predators and parasites (Pierce *et al.*, 1987; Baylis, 1989). If such a process is common to myrmecophilous lycaenids, one would expect an intimate link between diet and myrmecophily in the family. This is, in fact, the case. At the levels of species and genus, myrmecophilous lycaenids tend to feed on leguminous (nitrogen-fixing) plants, other nitrogen-fixing plants and on mistletoes (Pierce, 1985). Nitrogen-fixing plants are likely to have either higher nitrogen levels in their leaves (Akeson & Stahman, 1966, cited in Pierce, 1985) or to exhibit less temporal variation in nitrogen content because they are less dependent upon fluctuations in the nitrogen availability in the soil. Similarly, as a result of their parasitic lifestyle, mistletoes may exhibit little temporal variation in nitrogen content (Urness, 1969, cited in Pierce, 1985). The link between myrmecophily and diet in lycaenids is demonstrated further by their predilection for nitrogen-rich plant parts such as flowers, seeds and terminal foliage (Mattson, 1980; Robbins & Aiello, 1982).

Ovipositional responses of butterflies of J.evagoras

Ovipositing females laid eggs on a greater number of fertilized than unfertilized plants, and on fertilized plants laid a larger number of egg batches. Similarly, females laid a larger number of egg batches on plants containing the attendant ant, *I.anceps*, than on plants without ants (Pierce & Elgar, 1985). In neither case did the butterflies lay more eggs per egg mass. This adjustment of number of egg masses laid, rather than the number of eggs within each mass, in response to environmental cues may not be common to all lycaenids. Atsatt (1981) found that caged females of *Ogyris amaryllis*, when presented with branches of food plant, oviposited on branches both with and without ants, but laid larger egg masses on branches with ants.

The ability of ovipositing butterflies to select food plants most suitable for their offspring has been demonstrated by various other studies (Ives, 1978; Jones & Ives, 1979; Rausher, 1981; Rausher & Papaj, 1983; Williams, 1983; Ng, 1988; and see discussions by Singer, 1984; Chew & Robbins, 1984). Our study adds to those that have demonstrated ovipositional preferences for nitrogen rich plants (Wolfson, 1980; Myers, 1985; Taylor & Forno, 1987). Such preferences may not always occur. Cinnabar moths, *Tyria jacobaeae*, presented with ragwort host plants, *Senecio jacobaea*, did not oviposit upon more fertilized than unfertilized plants or lay larger egg batches on fertilized plants (Wilcox & Crawley, 1988). No mention is made of the number of egg batches per plant. Interestingly, the application of fertilizer did not increase the total nitrogen content of the plants, and larvae of *T.jacobaeae* on fertilized plants actually grew less than those on unfertilized plants.

The exact cues by which female *J.evagoras* detect physiological differences in larval food plants were not investigated. The fertilized plants had a higher nitrogen and water content (Table 1B) and darker colour than unfertilized plants, but the application of fertilizer is likely to have caused a large number of physiological changes which were not measured, but which may be used as cues by the butterflies. *Pieris rapae* probably use colour as a long-distance cue and water/nutrient cues upon contact (Myers, 1985). *J.evagoras* may be similar. Females use long-distance visual cues in the detection of trees with ants (Pierce, 1983) and seem to use chemical cues at short distance: adults flying around a tree appear to tap it with their antennae (Pierce & Elgar, 1985).

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