Lack of compensation by final instar larvae of the myrmecophilous lycaenid butterfly, *Jalmenus evagoras*, for the loss of nutrients to ants

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Abstract. Larvae and pupae of the Australian lycaenid butterfly, *Jalmenus evagoras* Donovan (Lepidoptera; Lycaenidae), are protected from parasites and predators by attendant ants. In return, the juveniles of *J.evagoras* secrete to the ants a solution containing substantial amounts of sugars and amino acids. Larvae of *J.evagoras* were reared from hatching until adult eclosion either with or without ants. Experiments were performed to examine whether fifth (final) instar larvae attempt to compensate for the nutrient loss to ants, by consuming more food, digesting food more efficiently, or extending development time. The presence or absence of ants had no effect on the feeding rate, efficiency of digestion or development time of fifth instar larvae. Larvae with ants converted a smaller proportion of ingested food into biomass, and consequently grew less than their counterparts without ants. Thus fifth instar larvae of *J.evagoras* do not appear to compensate for the nutrient loss to ants. Possible reasons for the failure to compensate are discussed.

Key words. Compensation, nutrient loss, myrmecophily, ant attendance, mutualism, *Jalmenus evagoras*, Lycaenidae, Lepidoptera.

Introduction

Juveniles of the Australian lycaenid butterfly, *Jalmenus evagoras* Donovan (Lepidoptera; Lycaenidae), are tended by ants. The ants protect the juveniles from predation (Pierce *et al.*, 1987; Baylis, 1989). In return the caterpillars of *J.evagoras* are known to produce for ants a secretion that is rich in sugars and amino acids (Pierce, 1983, 1989). The quantity secreted is substantial. Sixty-two larvae of *J.evagoras* on a single tree were found to provide for ants about 400 mg dry biomass over a 24 h period. This can result in the equivalent production of one hundred new workers of the attendant ant species, *Iridomyrmex anceps*, per day (Pierce *et al.*, 1987). Similarly, larvae of another lycaenid, *Polyommatus (Lysandra) hispana*, secrete a solution of sugars with a total concentration greater than 10% (Maschwitz *et al.*, 1975). A larva of the congeneric *Polyommatus (Lysandra) coridon* can secrete 3.5−7.0 mg of carbohydrate in its lifetime, and natural population densities of larvae can support 9−47%

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of the energy requirements of a tending ant colony (Fiedler & Maschwitz, 1988).

The secretions of lycaenid larvae are generally elicited by contact with ants, although exceptions to this pattern have been described. Several species of lycaenid cannot be reared in the laboratory without ants because the growth of mould on the openings of the secretory organs leads to death (Jackson, 1937; Hinton, 1951; Henning, 1987). However, in the absence of ants the larvae of many lycaenid species, including *J.evagoras*, do not secrete any visible substances.

The large amount of nutrients secreted by larvae of *J.evagoras* to ants, and the lack of secretion in the absence of ants, represents a possibly important cost of protection, and selection would be expected to favour those larvae that are able to compensate in some way for the nutrient loss to attendant ants. However, larvae of *J.evagoras* reared with ants have been previously shown to end up smaller as adults than larvae reared without ants (Pierce *et al.*, 1987). This reduced growth implies that either the caterpillars do not compensate behaviourally or physiologically for the loss of nutrients to ants, or that this compensation is insufficient. In other insects, compensation for changes in diet quality have been shown to occur by

the consumption of more food, the consumption of food of higher nutritional quality, or by the alteration of utilization efficiencies (reviewed by Simpson & Simpson, 1990). Alternatively, compensation may occur by extending development time. Over evolutionary time, this may have occurred in cicadas which have larval development times of from 2 to 17 years, and which feed on nutritionally poor root xylem fluid (Mattson, 1980).

To investigate the possible role of compensation in *J.evagoras*, experiments were performed which examined in detail the effects of ant attendance on the growth and nutrition of fifth (final) instar larvae. The effect of the presence or absence of ants on the following four features of the growth and nutrition of fifth instar caterpillars was examined: (a) development time; (b) growth rate and relative growth rate; (c) consumption rate and relative consumption rate; (d) utilization efficiencies.

Materials and Methods

Natural history of J.evagoras. 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) and are active from approximately November until April, during which time there may be up to three generations. Larvae feed on young plants of numerous species of *Acacia*, and larvae and pupae are tended by several species of ants in the genus *Iridomyrmex*.

The field site where animals were collected was Mt Nebo, Queensland (152°47'E, 27°23'S). At sub-tropical Mt Nebo, *J.evagoras* most commonly feeds on the bipinnate *Acacia irrorata* or the phyllodinous *A.melanoxylon* and is tended by ants of the *Iridomyrmex anceps* species group (sp. 25, Australian National Insect Collection, Canberra), hereafter *I.anceps* for short.

Experimental method. To examine the effect of ants on the growth and nutrition of caterpillars of *J.evagoras*, eighty caterpillars were reared from egg to adult in laboratories at Princeton University. An additional sixty caterpillars were killed as controls. Half the caterpillars were reared with ants and half were reared without. Growth rates and development times of fifth instars were calculated directly, and the consumption rates and utilization efficiencies were estimated gravimetrically (Waldbauer, 1968). The experiment required the use of laboratory cultures of *J.evagoras*, its food plant and its attendant ant.

Freshly laid eggs of *J.evagoras* were collected from a single tree of *A.melanoxylon* at Mt Nebo, Queensland, in November 1987, and transported without refrigeration to the laboratory. All larvae hatched over a 2-day period. Larvae were fed on leaves taken from approximately 100 trees of the bipinnate food plant, *A.irrorata*, which were grown from seed in a glasshouse (30–40°C; high r.h.). The seed was purchased from the Department of Forestry, Brisbane, Queensland. The trees were from 6 to 10 months old, 0.5–1 m tall and in healthy condition. Leaves of

A.irrorata consist of a central vein with five to fifteen pinnules branching from each side. Juveniles were tended by worker ants from a single, queen-right, colony of *I.anceps* collected from Mt Nebo in January 1987 and transported to a constant temperature room (LD 16:8 h; 26.5 ± 0°C; 65% r.h.) in Princeton University. The colony was maintained in a plastic container (0.4 × 0.3 × 0.3 m) lined with Fluon™ to prevent the escape of workers. Within the nest, ant larvae were housed in test-tubes containing a plug of moist cotton wool, and wrapped in aluminium foil to keep out light. The ant colony was fed daily with a standard ant diet (Bhatkar & Whitcomb, 1970) supplemented with cockroaches. At the time of the experiment the ant colony consisted of several thousand workers, many juveniles, eggs and one queen.

From hatching until pupation all caterpillars were reared in a constant temperature room (LD 16:8 h; 26.5 ± 0°C; 65% r.h.). Newly hatched first instar larvae were randomly allocated to groups of twenty. Each group was kept in a plastic test-tube (160 × 25 mm) and fed daily on leaves of the food plant. The caterpillars in half of the test-tubes were designated as 'ant tended'. Five ants were added to tubes with first instars, ten ants to tubes with second instars, and fifteen ants to tubes with third instars, and these were removed and replaced daily with new ants. The number of ants per caterpillar was similar to the number of ants tending caterpillars of each instar in the wild (Pierce *et al.*, 1987; Baylis, 1989), although the turnover rate was substantially lower. The remaining larvae were reared without ants for their entire lives, rather than being deprived of ants only for the duration of the experiment, because sudden deprivation of ants causes marked changes in larval behaviour such as a reduction in the amount of time spent feeding. Such an effect does not occur if larvae never experience tending by ants (Baylis, 1989).

Fourth and fifth instars were maintained individually in airtight 100 × 100 × 80 mm rectangular plastic containers, lined with Fluon™ to prevent the escape of ants. The tops of the containers were filled with moist agar (6 g in 1000 ml water) to maintain high humidity. The agar was replaced every 3 days. Each larva was kept in its container until pupation.

The eighty experimental larvae were subjected to the experimental regimen during their fourth and fifth stadia. Newly moulted fourth and fifth instars and pupae were weighed, and placed in their individual containers. Each day, larvae were given half of the pinnules from a leaf of the food plant. Remaining food plant and frass were collected. Fourth instars were given six ants, fifth instars were given ten ants, and ants were changed daily. Ants tended the larvae and fed on their secretions. At the end of the stadium all remaining food and frass was collected. The food plant given daily was weighed fresh. Food remains and frass, accumulated over the stadium, were weighed dry.

Each day, the remaining pinnules (the control plants) were put in identical airtight containers. They were weighed fresh, after 24 h, and then dried and weighed dry. They were used to estimate the dry/fresh weight ratio, the daily water loss and the nitrogen content of the food plant given

to the caterpillars. The dry/fresh weight ratio and nitrogen content of the larval food plant may have been affected by plant respiration and photosynthesis during the 24 h (McEvoy, 1985), although these processes will also have affected the experimental food plant between it being given to the larvae and its consumption.

The sixty control caterpillars reared with and without ants were preallocated to one of the three stages at which to be killed: as newly moulted fourth instars, fifth instars or as new pupae. Otherwise, they were treated similarly to the experimental larvae. These controls were used to estimate the dry/fresh weight ratio, and nitrogen content of the experimental juveniles.

New pupae were placed in small plastic holders which allowed ants easy access to them. The cups of ant-tended pupae were placed in a tray to which the ant colony had access via sticks. The cups of untended pupae were placed in a second tray kept adjacent to the first, but without access to ants, and adults were sexed upon eclosion.

Data recording and nitrogen analysis. All weights were measured on a Mettler AE163 balance to an accuracy of 0.1 mg. Samples to be dried were placed in an oven at 70°C until constant weight was reached. 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.irrorata*, was determined only for the pinnules, and not the mid-ribs, since the latter were not eaten by the larvae of *J.evagoras* in this experiment.

Water loss of control plants. Insect food utilization efficiencies generally decrease with decline in the water content of their food, with a consequent reduction in growth rate (Scriber, 1977). There is a possible interaction between ant attendance of *J.evagoras* and the water loss of its food plant since, under experimental conditions, workers of *I.anceps* often fragment the food plant. To investigate whether such an interaction occurs, freshly weighed leaves of food plant were placed in sixty containers identical to those used in the experiment. Ants were added to thirty of the containers and after 24 h all leaves were reweighed, and water loss (as a percentage of original leaf weight) calculated.

Calculation of indices. All nutritional indices were calculated using methods and formulae based on Waldbauer (1968). The following abbreviations will be used: DT = development time (days), measured to the nearest 8 h; GR = growth rate (mg/day); RGR = relative growth rate (mg/mg/day); CR = consumption rate (mg/day); RCR = relative consumption rate (mg/mg/day); AD = approximate digestibility (the proportion of ingested food that is digested); ECI = efficiency of conversion of ingested food (the proportion of ingested food that is converted to biomass); ECD = efficiency of conversion of digested food (the proportion of digested food that is converted to biomass); NUE = nitrogen utilization efficiency (the proportion of ingested nitrogen that is converted to biomass). All weights are dry weights. Relative rates are relative to mean body weight during a stadium.

Table 1. The effect of ants on the water loss (change in leaf weight as a percentage of original leaf weight) of pinnules of the food plant kept for 24 h under experimental conditions.

	With ants			Without ants			
	Mean	SD	*n*	Mean	SD	*n*	
Water loss (%)	7.64	3.63	29	4.95	2.71	29	$F_{1,57} = 3.91*$

* $0.06 > P > 0.05$; data log transformed for analysis.

Statistical analysis. All analyses were based on the methods of Sokal & Rohlf (1981). Analyses were by factorial ANOVA, using the Statview™ statistical program. Data were checked for normality and heteroscedasticity of variances (F_{max} test) and log transformed where appropriate. Prior to analysis of utilization efficiencies, outliers detected by Grubb's method (Sokal & Rohlf, 1981) were removed from the datasets.

Two caterpillars (one reared with ants and one without) were exceptionally small at the end of the fifth stadium and went on to have a sixth stadium. It is difficult to assess how their stadia relate physiologically to the equivalent stadia of the other caterpillars, and thus data for these larvae have been ignored in all analyses.

Results

Water loss of control plants

The per cent daily water loss of leaves of *A.irrorata* was greater in the presence of ants than in their absence (Table 1). The difference was significant at $P = 0.06$, and was almost certainly a result of the ants fragmenting the leaves.

The control leaves from the gravimetric experiment, all kept without ants, had a mean daily water loss of 7.8% (SD = 6.7%, $n = 868$). Using the observed water loss of leaves kept with and without ants (Table 1), the mean daily water loss of the food of the experimental larvae was thus estimated to be $7.8 \times 7.64/4.95 = 12.0\%$.

Fifth instar larvae (Tables 2–4)

Effect of ants. Ants significantly reduced the size of newly moulted fifth instars and new pupae. Ants had no effect on the development time of the fifth instars. The presence of ants did not change the RCR or AD of caterpillars. In other words, allowing for body size, fifth instars that were tended by ants did not alter the rate at which food was consumed, or digest that food more or less efficiently. However, the presence of attendant ants significantly reduced the growth rate, relative growth rate and consumption rate of the larvae. The ECI and NUE of the larvae were also reduced. Thus a smaller proportion of ingested food and nitrogen was converted into body mass.

Table 2. Weight of newly moulted fifth instars and pupae of *J.evagoras* reared with and without attendant ants.

	With ants			Without ants				
	Mean	SD	n	Mean	SD	n	Effect of ants	Effect of sex
Fifth instar (mg)								
Females	46.9	9.0	16	50.0	4.1	15	$F_{1.70} = 6.417$**	$F_{1.70} = 57.25$***
Males	35.0	4.5	21	39.5	6.6	22		
Pupa (mg)								
Females	208.2	27.8	16	226.7	30.6	15	$F_{1.70} = 17.51$***	$F_{1.70} = 24.81$***
Males	173.3	25.5	21	203.6	15.7	22		

** $P < 0.01$, *** $P < 0.001$.

Table 3. Development times, growth rates and consumption rates of fifth instar *J.evagoras* reared with and without attendant ants.

	With ants			Without ants				
	Mean	SD	n	Mean	SD	n	Effect of ants	Effect of sex
Development time (days)								
Females	8.9	1.1	16	8.8	1.1	15	$F_{1.70} = 0.55$ ns	$F_{1.70} = 48.66$**
Males	7.4	0.7	21	7.2	0.8	22		
GR (mg/day)								
Females	4.6	1.0	16	5.6	0.8	14	$F_{1.69} = 23.06$**	$F_{1.69} = 0.00$ ns
Males	4.5	1.1	21	5.7	0.8	22		
RGR (mg/mg/day)								
Females	0.17	0.02	16	0.18	0.02	14	$F_{1.69} = 4.29$*	$F_{1.69} = 47.74$**
Males	0.21	0.03	21	0.22	0.03	22		
CR (mg/day)								
Females	41.2	6.4	16	45.0	6.7	15	$F_{1.70} = 6.44$*	$F_{1.70} = 14.57$**
Males	35.3	7.1	21	39.2	5.6	22		
RCR (mg/mg/day)								
Females	1.53	0.18	16	1.51	0.14	15	$F_{1.69} = 1.65$ ns	$F_{1.69} = 3.91$†
Males	1.64	0.20	21	1.56	0.16	21		

GR = growth rate; RGR = relative growth rate; CR = consumption rate; RCR = relative consumption rate.

* $P < 0.05$; ** $P < 0.001$; † $P = 0.052$.

These results are summarized in Table 5. The ECD of larvae with attendant ants was considerably smaller than that of larvae without ants, although the difference was not significant.

Effect of sex. Males were significantly smaller than females, both as fifth instars and pupae. Males had significantly shorter development times, and lower consumption rates than females. Growth rates and AD (the proportion of ingested food that is digested) were equal. Males had a higher relative growth rate, relative consumption rate (at $P = 0.052$), ECI and NUE than females. In other words, allowing for differences in body size, males consumed food at a faster rate than females, converted the food and its nitrogen more efficiently into body mass, and consequently grew at a faster rate.

There was no significant interaction between sex and treatment for any of the variables.

Discussion

The results presented here demonstrate that fifth instars of *J.evagoras* in the presence of ants have a significantly lower growth and consumption rate, and convert ingested food and nitrogen into body mass significantly less efficiently, than fifth instars without ants. Since larvae that were reared with ants were substantially smaller as fifth instars than those that were reared without ants, absolute growth and consumption rates may not be appropriate variables for demonstrating the effect of ants. Allowing for body size, ants significantly reduced the relative growth rate, but had no effect on the relative consumption rate, of fifth instars. There was no effect of the presence of ants on the duration of the fifth instar period, or on the efficiency with which the larvae digested food. The efficiency of conversion of digested food (ECD) of larvae with ants was con-

Table 4. Utilization efficiencies of fifth instar *J.evagoras* reared with and without attendant ants.

Utilization efficiency (%)	With ants			Without ants			Effect of ants	Effect of sex
	Mean	SD	*n*	Mean	SD	*n*		
AD								
Females	20.9	6.8	16	21.0	2.5	15	$F_{1,69} = 0$ ns	$F_{1,69} = 0.131$ ns
Males	20.5	8.2	20	20.4	4.4	22		
ECI								
Females	11.1	1.1	16	12.0	1.2	14	$F_{1,68} = 11.14^{**}$	$F_{1,68} = 30.39^{***}$
Males	12.8	1.9	21	14.2	1.3	21		
ECD								
Females	51.7	10.1	15	55.9	9.5	15	$F_{1,65} = 11.14^{**}$	$F_{1,65} = 30.39^{***}$
Males	64.9	18.2	19	69.4	12.5	20		
NUE								
Females	28.4	2.7	16	30.5	3.9	15	$F_{1,67} = 13.30^{***}$	$F_{1,67} = 42.65^{***}$
Males	32.5	3.2	20	35.6	2.1	20		

AD = approximate digestibility; ECI = efficiency of conversion of ingested food; ECD = efficiency of conversion of digested food; NUE = nitrogen utilization efficiency.

** $P < 0.01$; *** $P < 0.001$.

Table 5. Summary of the effect of ants on the nutrition and growth of fifth instar larvae of *J.evagoras*. AD = approximate digestibility; ECI = efficiency of conversion of ingested food; ECD = efficiency of conversion of digested food; NUE = nitrogen utilization efficiency.

	With ants, relative to without ants
Size at start of fifth stadium	<
Development time	=
Growth rate (GR)	<
Relative GR	<
Consumption rate (CR)	<
Relative CR	=
AD	=
ECI	<
ECD	=
NUE	<
Size at start of pupal stadium	≪

siderably lower than that of larvae without ants, although the difference was not significant. The lack of significance is probably a result of high standard errors. It is recognized that there is a high degree of error in the measurement of ECD (Schmidt & Reese, 1986), and consequently this utilization efficiency will not be discussed further. These results are consistent with the hypothesis that larvae of *J.evagoras* do not compensate for the loss of nutrients to ants. Before discussing this in more detail, the validity of the data must be considered.

Validity of results

Water loss

The role of water in insect nutrition is well documented (Soo Hoo & Fraenkel, 1966; Scriber, 1977; Slansky & Feeny, 1977; Reese & Beck, 1978; Rausher, 1981; Bernays, 1985). In general, insect utilization efficiencies and growth rates decrease with decline in water content of diet. For example, decreasing food plant leaf water content from approximately +15% to −20% (of original leaf weight) caused changes in many aspects of the growth and nutrition of larvae of *Hyalophora cecropia* (Scriber, 1977). In the experiment described here the presence of ants increased the daily per cent water loss (measured, like Scriber (1977), by change in leaf weight as a percentage of original weight) from 7.8% to 12.0%. This increase may have significantly affected the growth and nutrition of the larvae of *J.evagoras*. Thus it is possible that the results presented are artefacts caused by the effects of ants on water loss of diet, and not the effects of ants on larvae. However, there are several reasons for believing this not to be the case. First, the values of water loss were obtained at the end of a 24 h period, while the larval feeding took place within that 24 h. Thus the values of 7.8% and 12.0% are likely to be overestimates of the actual water loss at the time of feeding. Second, the difference between 7.8% and 12.0% may be exaggerated because the fragmented leaves in containers with ants would have lost water much faster than the intact leaves in containers without ants, when the top of the air-tight container was removed and they were collected prior to weighing. Third, regarding the wide effect of diet water loss on nutritional and growth indices observed by Scriber (1977), if ants were affecting the caterpillars through diet water loss, significant effects

of ants on RCR, AD and development time might be expected. However, ants did not significantly affect these variables. Finally, as in this study, Pierce *et al.* (1987) also found that caterpillars of *J.evagoras* reared with ants grew significantly less than caterpillars reared without ants. However, Pierce *et al.* (1987) reared caterpillars upon potted food plants whose leaves were not fragmented by the attendant ants.

Effect of ants on fifth Instars

Three possible compensatory mechanisms were examined: extended development time, altered consumption rate and altered utilization efficiencies.

Development time

Attendant ants had no effect on the duration of the fifth stadium of *J.evagoras*. This is surprising. Life history theory predicts that under conditions of high mortality risk, selection should favour individuals with shorter development times (Williams, 1966; Stearns & Koella, 1986). Since the presence of ants significantly reduces the mortality risk of *J.evagoras* (Pierce *et al.*, 1987; Baylis, 1989), we might expect larvae to be able to compensate for the loss of nutrients to ants by extending development time, thereby increasing the feeding period and the final adult size, without paying the cost of higher mortality. However, extending development time could present at least one cost: adult males of *J.evagoras* which eclose earlier in the breeding season attain a higher mating success than males that eclose later (Elgar & Pierce, 1988).

A separate study of the effect of ants on the growth of *J.evagoras* revealed that ants significantly reduce the overall development time of larvae (Pierce *et al.*, 1987). This reduction appears to occur in the early stadia, and not in the fifth stadium (Baylis, 1989).

Consumption rates

Fifth instar caterpillars with ants consumed food at a slower rate than those without, but at an equal relative rate. Fifth instars therefore do not appear to be compensating for the loss of nutrients to ants by consuming more food.

This is perhaps surprising if one considers the proximate cues for feeding in insects. It has been demonstrated in *Locusta migratoria* that the amount of feeding is in part determined by the amino acid concentration and osmolality of the haemolymph (Abisgold & Simpson, 1987; Bernays & Chapman, 1974). In the former study, artificially increasing the amino acid concentration or osmolality of blood by injection resulted in an increase in the size of the interfeed period — in other words, the locusts fed less frequently. In the latter study, increasing the osmolality of blood resulted in a reduction in meal size (Bernays & Chapman,

1974). These cues may also be used by *J.evagoras*. Since a caterpillar of *J.evagoras* secretes amino acids and sugars to ants, it is possible that the concentration of the secretion may affect the resulting concentration and osmolality of the blood of the larva. If the larva secretes a solution with a higher osmolality and/or amino acid concentration than its blood, the blood may consequently have lower osmolality and/or amino acid concentration and feeding rates should increase. If the secretion has a lower osmolality and/or amino acid concentration than its blood, the blood may consequently have higher osmolality and/or amino acid concentration and feeding rates should decrease. The lack of effect of ants on the relative feeding rates of fifth instars thus suggests three possibilities. First, osmolality of the blood, or the concentration of amino acids within it, may not be proximate cues for feeding in *J.evagoras*. Second, the secretion of *J.evagoras* may be isotonic with, or have equal amino acid concentration to its haemolymph. Third, the act of secretion may not affect the osmolality and/or amino acid concentration of the blood because of the buffering action of the fat body.

Utilization efficiencies

Ants had no effect on the AD of fifth instar caterpillars. Thus fifth instars do not digest food more efficiently when ants are present.

However, ants significantly reduced the proportions of ingested food and nitrogen that were converted into biomass (ECI and NUE, respectively) by the caterpillars. In calculating conversion efficiencies, the dry mass of secretion of larvae with ants should be added to the dry mass of egesta. However, the mass of larval secretions was not measured in the present study, and thus conversion efficiencies of larvae with ants have been underestimated. Therefore, the observed lower values of ECI and NUE of larvae with ants are consistent with the suggestion that compensation by increasing the efficiency of conversion does not occur.

Growth rates

Ants significantly reduced both the growth rates and relative growth rates of larvae with ants. This reduction, like that in ECI and NUE, is a consequence of the lack of compensation.

The lack of compensation for the loss of nutrients to ants

The experiment described here found no evidence of compensation for the nutritional burden of supporting ants. Larvae with ants did not consume food at a faster rate, digest it more efficiently, or extend their feeding period by extending development time. As a consequence of the overall lack of compensation, fifth instar larvae of

J.evagoras have lower growth rates in the presence of ants. This presents a real cost to *J.evagoras*. Both the mating success of males, and the fecundity of females, are positively correlated with adult weight (Elgar & Pierce, 1988), and female weight correlates positively with egg size (Hill & Pierce, 1989).

It is thus perhaps surprising that compensation does not appear to occur. Many insects have been shown to be able to compensate for reduced nutritional intake caused by dilution of diet. The acridids *Locusta migratoria*, *Schistocerca gregaria*, *Melanoplus bivittatus* and *M.sanguinipes*, and the cockroaches *Periplaneta americana* and *Blatella germanica*, all change consumption rates in response to changes in diet quality (see reviews by Timmins *et al.*, 1988; Simpson & Simpson, 1990).

There are three main reasons why compensation may not have been detected. First, a compensatory mechanism other than those examined may occur. One possibility, which would not have been detected under the experimental conditions described here, is compensation by changes in diet selection. Several insects have been shown to be able to select the diet that is most suitable for their growth (reviewed by Simpson & Simpson, 1990). Thus larvae of *J.evagoras* in the presence of ants may select food that is richer in nitrogen and water content than larvae without ants.

Second, larvae of *J.evagoras* without ants may consume and process food at a maximal rate. This is especially likely for the final instar larvae used in the study here, because of the demands of preparing for pupation. If the larvae without ants are consuming and processing food at a maximal rate, those with ants will not be able to increase that rate to compensate for the nutrient loss. This suggests the possibility that compensation may be exhibited more clearly in younger instars.

The third possibility is that fifth instar larvae of *J.evagoras* do not have any behavioural or physiological flexibility for the presence or absence of ants. In other words, larvae have not been selected to behave differently when ants are, or are not, present. This possibility is supported by the fact that in the wild, mature larvae of *J.evagoras* are only very infrequently found without ants (Common & Waterhouse, 1981; and personal observation). Under these conditions it is perhaps not surprising that selection may not have favoured 'contingency plans'.

The effects of sex

Fifth instar males were significantly smaller than females at the start of the stadium. Interestingly, males and females had equal growth rates, and consequently males had a higher relative growth rate. This was achieved by males having a higher relative consumption rate, and higher values of ECI and NUE (but not AD) than females. Allowing for differences in body size, males in effect converted a larger amount of food more efficiently into biomass. Overall, however, males ended up even smaller than females as pupae because males had a shorter de-velopment time. This pattern is most unusual. Generally, female insects attain larger size than males by either having a higher relative consumption rate or a longer development time (Slansky & Scriber, 1985). In *J.evagoras*, females have a longer development time but males have a higher relative consumption rate. Moreover, there are usually only small differences between the utilization efficiencies of the two sexes (Slansky & Scriber, 1985).

This pattern may be the result of selection favouring males, to a greater extent than females, that attain large body size in the shortest amount of time. In other words, high relative growth rate may be at a greater premium in males than females. This may be related to the unusual mating system of *J.evagoras*. Males compete vigorously for females and male success at attaining mates is positively correlated with size, relative to that of other males (Elgar & Pierce, 1988). However, it is possible that greater size as a result of longer development time has not been favoured by selection because males that eclose earlier in the season also attain a larger number of matings (Elgar & Pierce, 1988). Thus for males, selection may have favoured a high relative growth rate. For females, on the other hand, selection may have favoured a larger size because of greater fecundity (Elgar & Pierce, 1988; Hill & Pierce, 1989), this being achieved by having a longer development time.

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