The effect of adult diet on the biology of butterflies

1. The common imperial blue, *Jalmenus evagoras*

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Summary. This study examines the effect that sugars and amino acids in the adult diet of *Jalmenus evagoras* can have on female feeding behaviour, somatic maintenance, longevity, fecundity and egg weight. The presence of sugars in their adult food stimulated butterflies of this species to feed, and they appeared to compensate for low (1% wt/wt) sugar diets by feeding for longer periods. Butterflies were also more likely to feed on diets containing amino acids than on water controls. The availability of sugar allowed females to maintain or even increase their body weight and fat body size, but amino acids had no effect on these variables. Individuals on the medium (25% wt/wt) sugar diet attained the greatest longevity. Female fecundity was increased as much as threefold by the availability of sugar. However, amino acids in the diet had no effect on either longevity or fecundity. Egg weight was not affected by the concentration of sugars or amino acids in the adult diet, but was correlated with the weight of the female butterfly. These results demonstrate that the availability of carbohydrates in the adult diet could play an important role in the population dynamics of this species. However, the presence of amino acids had little effect on most of the variables measured, nor was there any interaction effect between sugars and amino acids.

Key words: Adult diet – *Jalmenus evagoras* – Butterfly biology – Longevity – Fecundity

Most field studies of butterfly population biology have concentrated on mortality in the pre-adult life history stages of the butterfly (see Dempster 1984; Ehrlich 1984 for review). However studies by Courtney and Duggan (1983) and Hayes (1981) have found that egg shortfall due to insufficient oviposition time can be a key mortality factor (sensu Varley et al.1973) for some species. Climatic conditions that are adverse for flight activity have been suggested as a primary cause of egg shortfall, but other factors may also affect both the length of time which a butterfly has to lay its eggs and the number of eggs which it has available to lay. One such factor, the availability of adult food re-

sources, has long been known to influence both the longevity and fecundity of certain butterfly species (Norris 1935; Stern and Smith 1960; David and Gardiner 1962; Murphy et al. 1983). However, most of these studies have examined only the effect of sugars in the diet, and all of them used only a limited range of concentrations. Gilbert (1972) first described pollen feeding by *Heliconius* butterflies, and subsequently Dunlap-Pianka et al. (1977) showed that the availability of pollen (as a source of amino acids) in the adult diet greatly increased egg production in these butterflies. Baker and Baker's (1973a) discovery of relatively high concentrations of amino acids in the nectar of butterfly pollinated flowers has led to an interest in the importance of amino acids in the adult diet of Lepidoptera. Few studies so far have attempted to determine the importance of amino acids in floral nectar. Murphy et al. (1983) found that amino acids had a beneficial effect on egg weight of *Euphydryas editha*, although Moore and Singer (1987) were unable to replicate this result. The aim of this study is to determine whether the composition and concentration of the sugars and amino acids in the adult diet of the Australian lycaenid butterfly, *Jalmenus evagoras* affect the longevity, fecundity, somatic maintenance and egg weight of females of this species.

Materials and methods

The species

Jalmenus evagoras (Donvan) is a locally common lycaenid of the eastern coast of Australia. The source of the individuals used in this study was a population at Mount Nebo near Brisbane which has been studied extensively over a number of years (Kitching and Taylor 1981; Kitching 1983; Pierce and Elgar 1985; Pierce et al. 1987).

On hatching, the first instar larvae were transferred to potted *Acacia spectabilis*, one of several species of *Acacia* that have been recorded as food plants of *J. evagoras* (Common and Waterhouse 1981), and reared in a greenhouse at 28° C. Although in the field the larvae of this species are always tended by ants in the genus *Iridomyrmex*, they can be reared successfully without ants in the laboratory as was the case in this study. The larvae were allowed to pupate on the host plants and were then transferred to a 60 cm³ mating cage. Mating pairs were removed from the cage and remained isolated until mating was completed.

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Table 1. The experimental design for examining the effects of adult diet in *Jalmenus evagoras* (*N*: treatment number; (*n*): sample size; a: experiment 1; b: experiment 2)

	Sugar conc.			
	Zero (0%)	Low (1%)	Medium (25%)	High (50%)
Amino acid conc.				
Zero (0.0 mM)	1a (18)			2a (14)
Low (0.1 mM)		3a (19)	9b (15)	4a (13)
Medium (1.0 mM)		10b (15)	5(i)a (15) 5(ii)b (15)	11b (15)
High (10 mM)	6a (17)	7a (15)	12b (15)	8a (15)

Each individual was then weighed, numbered and females were assigned to an experimental treatment.

The female butterflies were placed in a clear perspex cylinder (diameter = 17.5 cm, height = 13 cm) with a gauze top. Attached to the sides of the container were two wooden rods, each with three horizontal grooves, and a glass tube containing cuttings of *Acacia irrorata*, a host plant of *J. evagoras* at Mt. Nebo (Pierce and Elgar 1985). The cuttings were renewed every two days. In the field, the butterfly usually lays its eggs in crevices on the trunk and branches of its host plant (Kitching 1976; Common and Waterhouse 1981). In the laboratory, the presence of *A. irrorata* stimulated the females to oviposit both on the cuttings and on the grooves in the wooden rods. The containers were arranged at random on a bench in a greenhouse at 28° C and under natural lighting conditions.

The adult diet. Table 1 shows the design used for this experiment. In each treatment, butterflies were fed a solution containing different combinations and concentrations of sugars and amino acids. The bases for these combinations are discussed below:

Water

Treatment 1 consisted solely of distilled water, which was also used to make up the solutions for all the other treatments.

Sugars

In this study the sugars used were fructose, glucose and sucrose in a ratio of 2:2:1 respectively. This ratio of sugars was found in the flowers visited by *Colias alexandra* (Watt et al.1974) and was used by Murphy et al. (1983) in a similar experiment. A number of studies have demonstrated that the average nectar concentration of butterfly pollinated flowers lies between 20–30% (Pyke and Waser 1981; Baker 1976). Heyneman (1983, Table 1) found a mean value of 25% when data from several sources were combined. Thus a concentration of 25% (wt/wt) was chosen as the medium level for this experiment. The low (1%) and high (50%) concentrations were selected with respect to the medium value.

Amino acids

In this study the six amino acids used were alanine, arginine, glycine, lysine, proline and serine. These amino acids are among those which commonly occur in the nectar of flowers which are visited by butterflies (Watt et al. 1974; Baker 1976). It should be noted that, given the number of naturally occurring amino acids, the amino acids selected for this study may not fulfil the nutritional requirments of *J. evagoras*. The concentration of amino acids in butterfly-visited flowers ranged from 1.0 to 5.0 mM (Baker and Baker 1973b; Watt et al. 1974; Heyneman 1983). In this study three levels of amino acid concentration were used. The medium concentration was set at 1.0 mM, the high and low concentrations were 10 mM and 0.1 mM respectively.

In summary, the composition of the sugars and amino acids in the artificial diets were selected to fall within the range of those found in the floral nectars of butterfly pollinated flowers. The medium concentration levels of sugars and amino acids approximates those found in the floral nectar of butterfly pollinated flowers. Therefore treatment 5 most closely resembles floral nectar. The high and the low concentration levels were selected with respect to the values chosen for the medium concentration level.

The variables measured

Feeding behaviour. Female *J. evagoras* would not feed normally under laboratory conditions, therefore each butterfly was fed twice daily on 0.5 cm^3 of the appropriate food solution from a plastic test tube cap. No attempt was made to force feed the butterfly, each individual was simply placed on the food solution up to three times. The number of times a female fed each day was recorded. This variable was called the 'feed status' and had values of either 0, 1 or 2. In addition, the time spent feeding was recorded for some individuals during the course of the experiment.

Longevity

The eclosion date and date of death were recorded for each butterfly, to provide a measure of longevity.

Fecundity

At the end of each day (1700hrs) all eggs laid by an individual were removed from the oviposition chamber, counted and weighed. The eggs were weighed as daily batches, to give a mean daily egg weight for each individual. In addition each female was dissected after death and the number of mature (i.e. chorionated) eggs present in its ovaries were counted. This procedure has been used in other studies of this type (Stern and Smith 1960; Leather 1984). The sum of the eggs laid and the mature eggs present on death was used as the total number of eggs for each female. The presence of mature eggs on the death of the female, particularly in long-lived individuals, suggested that not all individuals were stimulated to oviposit in the experimental containers. There was considerable variation in this respect, some individuals did not oviposit at all whereas others laid all their eggs.

Somatic maintenance

As soon as possible after death, each female butterfly was weighed and this value, together with its weight at eclosion,

was used to calculate the percentage change in weight. In addition, when the butterfly was dissected to count the remaining eggs, a subjective estimate was made of the size of its fat body using three categories: small, medium and large.

Experiments 1 and 2. The initial experimental design involved only treatments 1 to 8 (Table 1) and these were carried out from 10/9/84 to 13/2/85. The eggs from which the adult butterflies were obtained for this first experiment came from a laboratory population of *J. evagoras* which had been established prior to the experiment. Having completed the first experiment, it was considered desirable to carry out additional treatments, enabling a 2-way analysis of variance to be performed (Table 1). In addition to these, treatment 5 was repeated thereby providing a reference point with which to compare the results of the two experiments. The second experiment was carried out from 10/7/85 to 10/10/85, and the eggs used in this experiment were collected in the field. In all other respects the experiments were identical.

Analysis

The initial analyses were conducted using 2-way ANOVAs employing only the treatments with low to high concentration levels (Table 1). For each variable two analyses were performed, the first with treatment 5(i) and the second with treatment 5(ii). Subsequently a 1-way ANOVA was carried out incorporating all the treatments and Scheffé's multiple comparison test was used to determine significant differences between them. Both the 2-way and 1-way ANOVAs were conducted using the SPSS statistical package (Nie et al. 1975).

Results

Feeding behaviour

The sugar concentration of the diet had a highly significant effect on the feed status of the butterflies, whereas amino acid concentration had no effect (Table 2). In addition there was no interaction between sugar and amino acid and no difference in the results when the analysis was conducted using either treatment 5(i) or 5(ii).

A 1-way ANOVA using all the treatments showed a significant treatment effect, $F_{(12,188)} = 38.65$, $P < 0.0001$. The mean values of each treatment are shown in Fig. 1. As the sugar concentration of the diet increased so did the feed status of the butterfly, the maximum value being reached at the medium and high sugar concentration levels. There were no differences between treatments within each sugar concentration with the notable exception of treatments 1 and 6 which were significantly different (Scheffé's multiple comparison test, $P < 0.05$).

Individuals on a low sugar concentration diet spent, on average, 32 min feeding compared with 1–2 min spent by those on other sugar concentration diets, these times are significantly different (Table 3).

Somatic maintenance. Two measures of somatic maintenance were used in this experiment: percentage change in body weight and the size of the fat body. Sugar concentration had a highly significant effect on the percentage change

Table 2. The variables exhibiting significant differences between treatments according to two way analyses of variance using treatment 5(i) or 5(ii)

| Variable	Treatment	Main effects and interactions exhibiting significant effects	F (df)	Probability
Feed Status	5(i)	Sugar	33.09 (2,128)	$P < 0.001$
	5(ii)	Sugar	33.86 (2,128)	$P < 0.001$
Percentage weight change	5(i)	Sugar	62.55 (2,128)	$P < 0.001$
	5(ii)	Sugar	66.87 (2,128)	$P < 0.001$
Longevity	5(i)	Sugar	49.11 (2,127)	$P < 0.001$
	5(ii)	Sugar	81.33 (2,127)	$P < 0.001$
Total egg number	5(i)	Sugar	35.49 (2,127)	$P < 0.001$
	5(ii)	Sugar	37.58 (2,127)	$P < 0.001$
Total egg weight	5(i)	No significant effects		
	5(ii)	No significant effects		
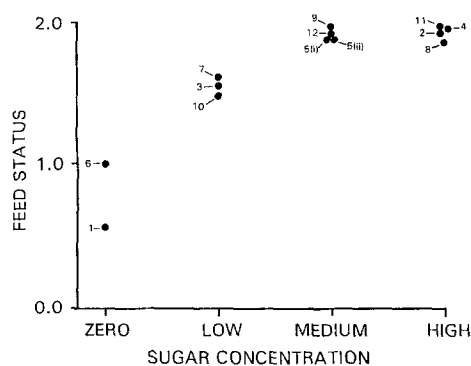
Fig. 1. The mean likelihood that a butterfly would feed (recorded as 'feed status' on a scale of 0–2) for each treatment (n = treatment code number)

Table 3. The time spent feeding by individuals on zero, low, medium and high sugar concentration diets (concentrations with different superscripts are significantly different ($P < 0.05$) Student's t-test)

Sugar conc.	Feeding time (min)	SE	N
Zero	1.32	0.82	6[a]
Low	32.60	5.73	15[b]
Medium	1.55	0.14	30[a]
High	2.07	0.31	23[a]

in body weight (Table 2), but amino acid concentration had no effect. Results were similar for both treatments 5(i) and 5(ii), and there was no interaction between sugar and amino acid concentration.

When all treatments were included in the analysis, treatment had a significant effect on percentage change in body weight, $F_{(12,188)} = 18.24$, $P < 0.0001$. Individuals on the zero and low sugar diets did not differ with respect to percent weight change, whereas females on a medium sugar diet lost significantly less weight than those on a zero or
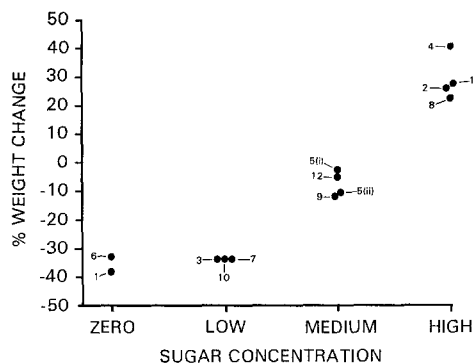
Fig. 2. The mean 'percentage weight change' of females for each treatment (n = treatment code number)
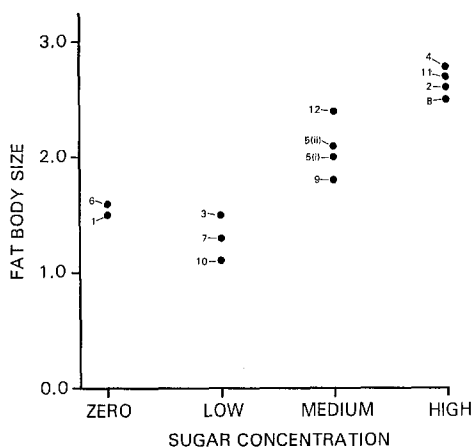

Fig. 3. The mean 'fat body size' values for females on each treatment (n = treatment code number)

low sugar diet, and females on the high sugar diet actually gained weight during the course of the experiment (Fig. 2).

The results for the size of the fat body could not be analysed using the methods previously described because the data were ordinal. Nevertheless the results were in close accordance with those found for the percentage change in body weight (Fig. 3). There was little difference in the size of the fat body of females fed zero and low sugar treatments, but there was an increase in the fat body size of females fed on medium and high sugar diets.

Longevity

Butterflies used in the first and second experiments differed with respect to their longevity. Accordingly, experiment number was included in the analysis as a covariate. In addition a preliminary analysis showed that, for some treatments, female weight on emergence was positively correlated with longevity (Table 4) and therefore female weight on emergence was also included as a covariate, although this relationship was only significant for those females in treatments with a zero or low sugar concentration diet.

A 2-way ANCOVA showed that sugar concentration had a highly significant effect on the longevity of the butterflies but that amino acid concentration had no effect, nor was there any interaction between these variables (Table 2). In addition, there were no differences in the results obtained using treatments 5(i) and 5(ii).

Since female weight did not show a significant effect

Table 4. Results of tests for correlations (Pearsons correlation coefficient) between female weight on emergence and longevity within each treatment (**: $P<0.01$; *: $P<0.05$; NS: not significant)

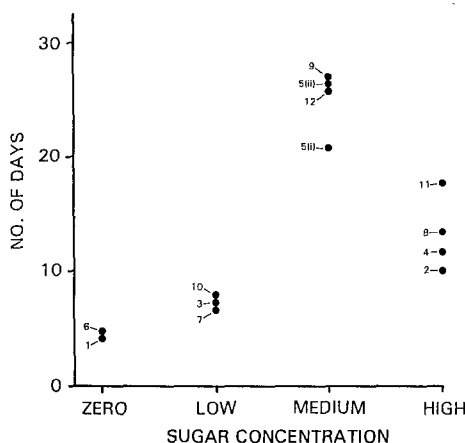|	Sugar concentration			
Amino acid conc.	Zero (0%)	Low (1%)	Medium (25%)	High (50%)
Zero (0.0 mM)	0.4357 $n=18$			-.3005 $n=14$ NS
Low (0.1 mM)		0.5589 $n=19$ **	0.3498 $n=15$ NS	-0.3659 $n=13$ NS
Medium (1.0 mM)	0.4634 $n=15$ *	-0.1173 $n=15$ NS	-0.2818 $n=15$ NS	-0.4157 $n=15$ NS
High (10 mM)	0.5031 $n=17$ *	0.5593 $n=15$ *	-0.0561 $n=15$ NS	0.1657 $n=15$ NS

Fig. 4. The mean 'longevity' of females for each treatment (n = treatment code number)

in the 2-way ANCOVA, it was not included in the 1-way ANOVA. The results of the 1-way ANOVA show that there is a significant treatment effect $F_{(12,188)} = 40.94$, $P < 0.0001$. In Fig. 4 the mean longevities for each treatment are shown. At the medium and high sugar levels, individuals in the second experiment lived longer than those in the first experiment, but the relative differences between treatments within each experiment was the same for both experiments. Butterflies on a diet without sugars had the lowest longevity, whereas those on a low sugar level diet lived slightly longer, and those on medium sugar level treatments had the greatest longevity. Individuals on the high sugar concentration diet did not live as long as those on the medium level diet, but lived longer than the individuals on the low sugar level diet.

Fecundity

The weight of the female butterfly on emergence was positively correlated with the total number of eggs it laid in most of the treatments (Table 5), and thus weight on emergence was used as a covariate in the analyses. Sugar concen-

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Table 5. Results of tests for correlations (Pearsons Correlation Coefficient) between female weight on emergence and its total number of eggs within each treatment (**: $P<0.01$; *: $P<0.05$; NS: not significant)

	Sugar conc.			
	Zero (0%)	Low (1%)	Medium (25%)	High (50%)
Amino acid conc.				
Zero (0.0 mM)	0.9121 $n=18$ **			0.4477 $n=14$ NS
Low (0.1 mM)		0.8797 $n=19$ **	0.7325 $n=15$ **	0.7803 $n=13$ **
Medium (1.0 mM)		0.8523 $n=15$ **	0.1173 $n=15$ NS	0.4043 $n=15$ NS
				0.8826 $n=15$ **
High (10 mM)	0.9489 $n=17$ **	0.9074 $n=15$ **	0.3914 $n=15$ NS	0.4144 $n=15$ NS

Table 6. Results of tests for correlations (Pearsons correlation coefficient) between female weight on emergence and the mean egg weight over lifetime within each treatment (**: $P<0.01$; *: $P<0.05$; NS: not significant)

	Sugar conc.			
	Zero (0%)	Low (1%)	Medium (25%)	High (50%)
Amino acid conc.				
Zero (0.0 mM)	0.2091 $n=14$ NS			0.7151 $n=10$ *
Low (0.1 mM)		0.0859 $n=14$ NS	0.6226 $n=12$ *	0.6583 $n=11$ *
Medium (1.0 mM)		−0.1806 $n=8$ NS	0.4801 $n=15$ *	0.6888 $n=13$ **
				0.7443 $n=13$ **
High (10 mM)	0.3312 $n=14$ NS	0.7430 $n=13$ **	0.1814 $n=14$ NS	0.4859 $n=13$ *

tration had a highly significant effect on the total number of eggs produced by this species, but amino acids had no effect (Table 2). There was no interaction, and no difference in the results between treatments 5(i) and 5(ii).

A 1-way ANCOVA using all the treatments showed a significant treatment effect for fecundity $F_{(12,187)}=12.12$, $P<0.001$. There was no difference in the total number of eggs produced by the females on the zero and low sugar level diets, but medium and high sugar level diets led to a two fold increase in egg production (Fig. 5).

Egg weight

Table 6 shows that for most treatments, there was a positive correlation between female weight on emergence and the
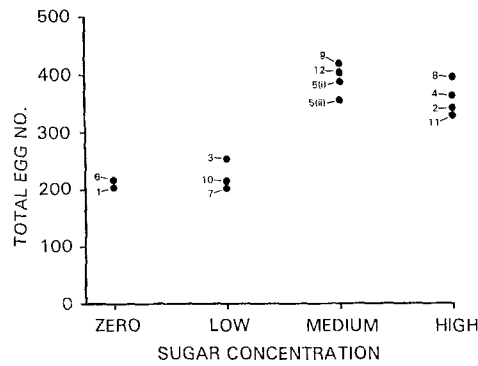

Fig. 5. The mean 'total egg number' (adjusted for female weight on emergence) for each treatment ($n=$ treatment code number)

Table 7. The mean weight of eggs produced over the lifetime of the butterfly for each treatment

Treatment number	Expt No.	Mean egg weight	SD	N
1	1	0.0686	0.0037	14
2	1	0.0661	0.0058	10
3	1	0.0684	0.0058	14
4	1	0.0640	0.0068	11
5(i)	1	0.0694	0.0061	15
6	1	0.0701	0.0041	14
7	1	0.0656	0.0069	13
8	1	0.0673	0.0057	13
5(ii)	2	0.0582	0.0069	13
9	2	0.0576	0.0100	12
10	2	0.0648	0.0033	8
11	2	0.0578	0.0075	13
12	2	0.0598	0.0055	14

mean egg weight over the lifetime of the individual. Therefore, it was necessary to include female weight as a covariate in the analysis. In addition a comparison of mean egg weights between treatments (Table 7) suggested that they were lower in the second experiment and so experiment number was also included as a covariate. The results of the 2-way ANCOVAs (Table 2) showed that neither sugar nor amino acid concentration had an effect on mean egg weight, nor was there an interaction. Treatments 5(i) and 5(ii) yielded similar results.

The above analysis was carried out on mean egg weight over the lifetime of the female, but two additional factors were also taken into account in this analysis. Firstly, females of *J. evagoras* emerge with a number of mature eggs already present, and the number of these eggs is positively related to the weight of the butterfly on emergence. Figure 6 shows this relationship for females which were killed and dissected after they had emerged. Also shown in Figure 6 is the same relationship for the total egg number of females in treatment 1 of this experiment. A test for the comparison of regression lines (Snedecor and Cochran 1967) showed that there was no difference between these two regression lines ($F_{2,45}=4.12$, $P<0.05$). Therefore, for the purposes of this analysis, the treatment 1 regression line was used. Mature eggs which a female butterfly carries upon eclosion are unlikely to be affected by its subsequent adult diet. Thus for each individual, the number of mature eggs on emergence (first batch) was estimated using the regression equation obtained from treatment 1. From this value, the
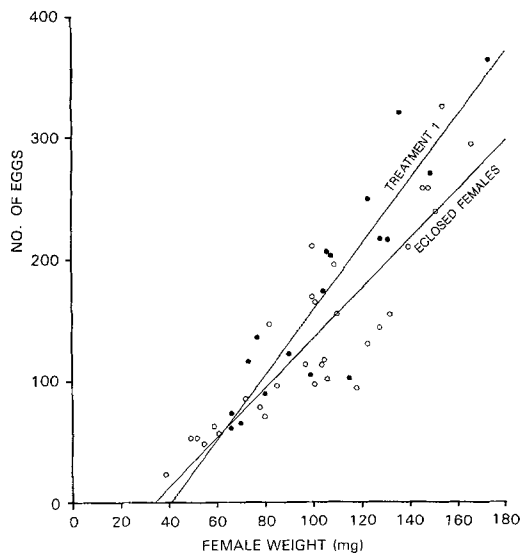
Fig. 6. The relationship between the weight of female *J. evagoras* on emergence and its total number of eggs: data for treatment 1 (solid circles) and for females dissected upon eclosion (*open circles*). *Treatment 1* $r=0.9121$; $n=18$; $p<0.001$; $y=-110.16+2.68\times$; *Eclosed Females* $r=0.8842$; $n=31$; $p<0.001$; $y=-67.63+2.03\times$
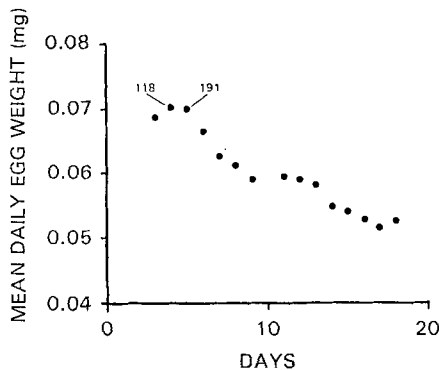

Fig. 7. An example of how the percentage change in egg weight with respect to the mean first batch egg weight was calculated for each female. Female number $=36$. Female weight on emergence $=94$ mg. $n=$ Cumulative number of eggs laid. Using regression equation from treatment 1: $y=-110.16+(2.68\times94)=142$. Predicted number of eggs in the first batch (i.e. eggs already mature on emergence) $=142$. Therefore the first batch of eggs was laid by the second egg-laying day (see below)

	Mean egg weight	N
First batch	0.0696	2
Rest	0.0585	13
% Change in egg weight	−15.95	

day was identified on which all the eggs in the first batch were laid and the mean first batch egg weight was calculated.

The second factor to be taken into account in this analysis is that the mean egg weight of an individual butterfly tends to decrease during its lifetime. This phenomenon has been observed for several other lepidopteran species (Jones et al. 1982; Murphy et al. 1983; Wiklund and Persson 1983; Karlsson and Wiklund 1984; Wiklund and Karlsson (1984). The butterflies may be incorporating adult food into the

Table 8. The mean percentage change in egg weight with respect to the first batch egg weight for all treatments (figures in brackets are one standard deviation)

	Sugar conc.			
	Zero (0%)	Low (1%)	Medium (25%)	High (50%)
Amino acid conc.				
Zero (0.0 mM)	$n=0$			−2.88 (3.16) $n=4$
Low (0.1 mM)		−1.55 (0.61) $n=3$	−4.81 (6.02) $n=6$	−8.16 (4.93) $n=2$
Medium (1.0 mM)		−3.28 (___) $n=1$	−7.61 −0.38 (9.24) (___) $n=7$ $n=1$	+2.57 (___) $n=1$
High (10 mM)	$n=0$	$n=0$	−4.12 (3.20) $n=5$	−7.55 (6.22) $n=6$

eggs which develop after the 'first batch' eggs have been laid. If this is so, then the relative change in mean egg weight with respect to the mean egg weight of the first batch should measure this effect. Figure 7 gives an example of how this value (the percentage change in mean egg weight with respect to the mean egg weight of the first batch) was calculated for a particular female. By using this relative measure, the effect of different absolute values in the mean egg weight between the two experiments was removed. Table 8 shows the results of this analysis for the treatments for which results were obtained. The small sample sizes reflect the few individuals which actually laid a greater number of eggs than their predicted first batch egg number. The small sample sizes which were available for this analysis precluded any statistical tests but neither sugar nor amino acid concentration appeared to influence this variable in any obvious way.

Discussion

Feeding behavior

Butterflies in this experiment were not force fed, because individuals of this species are small and fragile and it was felt that repeated force feeding would damage them. Also force feeding is an attempt to override the variation in feeding response due to the phagostimulatory nature of the food but simply uncoiling the proboscis and placing it in the food solution does not necessarily achieve this effect. The results of this experiment thus reflect not only the physiological effects of adult diet on the parameters measured but also, to a certain extent, the behavioural effects.

Sugar concentration had a strong effect on a butterflies' willingness to feed. As the sugar concentration of the diet increased, so did the stimulation to feed, with the maximum level of two feeds per day being reached at the medium concentration level.

Of equal interest is the significant difference in feed status between treatments 1 (water) and 6 (amino acid only). This showed that the presence of amino acids in the food

solution stimulated the butterflies to feed, although any amino acid effect appeared to be overridden by the sugar concentration effect at higher sugar concentration levels. Since amino acids did not affect on either longevity or fecundity, it is perhaps surprising that the presence of amino acids exerted such a strong response. An ovipositing female of *J. evagoras* will occasionally unfurl its proboscis and appear to "taste" the host plant. Females are more likely to oviposit on fertilised than unfertilised host plants (Baylis and Pierce, unpubl. data), so this phagostimulatory response to amino acids may be related to oviposition behaviour rather than adult nutrition.

Individuals on a low sugar level diet fed for longer periods than those on other diets, suggesting that they were attempting to compensate for a carbohydrate – poor diet by increasing intake volume. This behaviour has also been found for *Pieris brassicae* by David and Gardiner (1961).

The capacity of females of *J. evagoras* to sense the presence of both sugars and amino acids in their adult diet and the ability to compensate (behaviourally) for low sugar concentrations suggests that they can regulate, in a relatively sophisticated manner, the food which they obtain as adults.

Somatic maintenance

Percentage weight change and fat body size showed similar responses to the experimental treatments. At the zero and low sugar levels the butterflies lost weight and their fat body was relatively small. On the medium sugar diet their fat body was larger and they maintained their weight at approximately the same level as their weight at eclosion. On the high sugar concentration diet, individuals gained weight and their fat bodies were large. These individuals were, in some cases, extremely obese, presumably because their flight activity was restricted. Similar effects of sugar concentration have been found for several other lepidopteran species (Stern and Smith 1960; Leather 1984; Murphy et al. 1983). Amino acid concentrations had no effect on body weight maintenance in this species (cf. Murphy et al. 1983).

Longevity

Dietary factors affecting longevity were the same in experiments 1 and 2 even though the absolute longevity values differed between experiments. On sugar-poor diets, heavier individuals lived longer than lighter ones but with sufficient sugar in their adult food small (i.e. light) individuals lived as long as heavier ones. The maximum longevity was attained by individuals on a medium sugar concentration diet. This concentration (25% wt/wt) corresponds most closely to that of the floral nectar of butterfly pollinated flowers. A value of 20–25% has also been predicted as the optimum sugar concentration, in terms of uptake of a solution by a butterfly, by several uptake rate models (Kingsolver and Daniel 1979; Heyneman 1983) although others have predicted an optimal concentration of 35–40% (May 1985; Pivnick and McNeil 1985). Individuals on the high sugar concentration diet did not live as long as those on the medium sugar level diet. This result may indicate the inability of this species' physiology to cope with highly concentrated sugar solutions, or reflect the cost associated with assimilating them. Alternatively, it has already been noted that some individuals on the high sugar concentration diet became

obese. This might have led to restricted movement, greater stress, and shorter lifespan.

The influence of sugar concentration on longevity in the Lepidoptera has long been recognised (Norris 1935), and sugar concentration has been shown to have important effect on most species which have been studied (Stern and Smith 1960; David and Gardiner 1962; Murphy et al. 1983 and Leather 1984). However reduced longevity at high sugar concentrations has not been documented before.

Fecundity

As in many other lepidoptera (e.g. Haukoija and Neuvonen 1985), larger *J. evagoras* were more fecund. However, sugar concentration of the adult food also affected fecundity. *J. evagoras* resembles several other lepidopteran species in this respect (Norris 1935; Stern and Smith 1960; David and Gardiner 1962; Murphy et al. 1983 and Leather 1984). Individuals on a zero and low sugar concentration diet had similar fecundities, which were essentially determined by the number of mature eggs present on emergence. A medium or high sugar concentration diet approximately doubled fecundity. There was considerable variation in the degree to which females of *J. evagoras* responded to the adult diet. One individual laid 950 eggs, which represented approximately a three fold increase in fecundity over the initial number of eggs present at eclosion.

Dunlap-Pianka et al. (1977) found that amino acids (in pollen) could greatly prolong the egg production of *Heliconius charitonius*. In this study amino acids (in nectar) had no effect on the fecundity of *J. evagoras* and in this respect our results are comparable to those found for *E. editha* by Murphy et al. (1983).

Egg weight. Adult diet had no effect on the egg weight of *J. evagoras*. This result conflicts with that of Murphy et al. (1983), who found that high amino acid concentrations led to relatively heavier egg weights in the later egg masses of *E. editha*. However more recent work on *E. editha* found no effect of adult diet on egg weight (Moore and Singer 1987).

In most treatments there was a direct correlation between female weight on emergence and egg weight. *J. evagoras* appears to be the first lepidopteran species for which such a relationship has clearly been shown, although Boggs (1986) did find a correlation between these two variables in one of her data sets which contained unusually large and small animals. In contrast, Jones et al. (1982) found an inverse correlation between female size and egg size.

Implications for population biology

Sugar. The availability of sugar in the adult food of *J. evagoras* can greatly increase longevity and fecundity. By following marked individuals in the field, Elgar and Pierce (1988) estimated the lifetime of females of *J. evagoras* to be only 3–4 days, whereas males of this species survived to approximately 7 days. If this estimate of longevity is correct, then adult food resources may not be an important factor in the biology of this species. However, on their optimal diet, females of *J. evagoras* lived considerably longer in the laboratory (treatment 5(i): 20.7 days, s.d. = 7.8, n = 15; treatment 5(ii): 26.9 days, s.d. = 7.1, n = 15; treatment 9: 26.9 days, s.d. = 9.1, n = 15; treatment 12: 26.5 days, s.d. = 7.4, n = 15). The very short estimated lifespan found
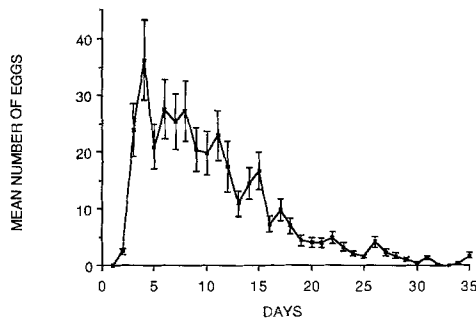
Fig. 8. The lifetime-fecundity curve for *J. evagoras* using data from treatments 5(i), 5(ii), 9 and 12 (bars represent one standard error)
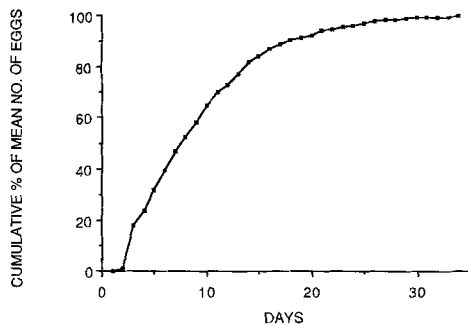

Fig. 9. The mean number of eggs (expressed as cumulative percentage of the total) produced during the lifetime of *J. evagoras* using data from treatments 5(i), 5(ii), 9 and 12

for females of *J. evagoras* in the field may in fact be an estimate of residency time rather than longevity, as it is in *Anthocharis cardamines* (Courtney 1983). If female *J. evagoras* live for a week or more in the field (as do male *J. evagoras*) the availability of adult food resources may well increase their fecundity. Females produce most of their eggs between the second and twentieth days of their life (Fig. 8). If only water is available to a female in the field, then the laboratory results suggest she will live for approximately four days (Fig. 4) and lay between 15 to 20% of her total number of eggs (Fig. 9). But if nectar is available and a female lives for even half of her laboratory lifetime, she may produce more than 70% of her total number of eggs. Therefore the availability of carbohydrates in the adult diet could have a profound impact on the realised fecundity.

Amino acids. The larvae of *J. evagoras* associate mutualistically with ants in the genus *Iridomyrmex*: larvae provide attendant ants with nutritious secretions that contain sugars and amino acids, and in return, the ants protect the larvae against predators and parasitiods. Since larvae of *J. evagoras* secrete proteins for their attendant ants and pupate at a smaller size than they would if they did not have to feed ants (Pierce et al. 1987), we were particularly interested in determining what role, if any, amino acids might play in the adult diet. If female larvae are substantially protein limited because of their association with ants, then we might expect amino acids to be important in the adult diet. Assuming that our choice of dietary amino acids was correct, the results of this experiment provide at least two lines of evidence that this is not the case. First, females of *J. evagoras* carry a large complement of mature eggs upon eclosion, suggesting that they are not severely protein lim-

ited as larvae. Second, amino acids in the adult diet appear to have no effect on longevity and fecundity in this species. Thus we conclude that larval reserves of protein are sufficient for egg production in *J. evagoras*. However, it should be noted that since the butterflies used in these experiments were reared without attendant ants and on young, fresh host plants, nitrogen may never have been a limiting resource to them in the way that it might be under natural field conditions. Subsequent experiments might investigate whether low levels of nitrogen in the larval diet result in an increased importance of amino acids in the adult diet.

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