5 Mating Success and Fecundity in an Ant-Tended Lycaenid Butterfly

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THE AUSTRALIAN LYCAENID BUTTERFLY *Jalmenus evagoras* Donovan exhibits an unusual mating system that derives in part from its close association with ants. Both larvae and pupae of *J. evagoras* secrete food rewards for workers of several species of *Iridomyrmex*. In return the ants protect the larvae and pupae against predators and parasitoids. Populations of *J. evagoras* deprived of their attendant ants cannot survive (Pierce 1983; Pierce et al. 1987), and females of the species even use ants as cues in ovipositions (Pierce and Elgar 1985).

The larvae of *J. evagoras* aggregate and pupate in clusters on the upper branches of their *Acacia* host plants. Adult males search for mates by regularly investigating trees containing juveniles of the species. They hover around the trees, sometimes tapping a pupa with their antennae, perhaps thereby "tasting" its age and sex. When a pupa is about to eclose (emerge as an adult) as many as twenty males may gather around it, forming a "mating ball." The males engage in a frenzied scramble as the pupa ecloses and copulation takes place before a teneral female has even had time to expand her wings (see fig. 5.1). Pairs remain mating on a tree for several hours. Females mate only once, and mated females vigorously reject further advances by males. Although mating in *J. evagoras* does not always involve the formation of a visually dramatic mating ball (eclosing pupae are often found by single males), females are almost always mated before their wings have hardened, and virtually every mating is readily and unmistakably observable because of the conspicuous location of pupae and the lengthy copulation time. It is therefore possible to obtain a comprehensive record of matings in a field population of this butterfly.

In this chapter we describe several of the cues that males use to search for females. These include males' response to the presence or absence of ants, their interest in male and female pupae of different sizes and ages, and their attraction to clusters of conspecific adults. We then

Figure 5.1: Male *Jalmenus* surround an eclosing pupa.

analyze the lifetime mating success of males, which is an important component of their lifetime reproductive success. We assess whether particular morphological and behavioral traits are correlated with the components of a male's lifetime mating success. Using a combination of field and laboratory observations, we examine the importance of size and longevity for female fecundity. Finally, we discuss how associations with ants may have shaped the evolution of the mating system of *J. evagoras*.

5.1 Natural History and Study Site

J. evagoras is a multivoltine butterfly found along the east coast of Australia from Melbourne in the south to Gladstone in the north. Although widespread in its distribution, where it occurs *J. evagoras* forms discrete, highly localized populations. Males and females show almost no sexual dimorphism in wing color or pattern (Common and Waterhouse 1981, Pierce 1984). Although there are no differences in adult wing length, female pupae are larger than male pupae, and adult females are 60% heavier than adult males (see table 5.1). Males of *J. evagoras* eclose several days before females. According to our field estimates, males also live longer than females (although this may simply reflect lower emigration rates).

Our study site was around the village of Mount Nebo in Queensland, approximately 10 km west of Brisbane (152° 47' E, 27° 23' S). Here *J. evagoras* feeds predominantly on the foliage of young plants of *Acacia irrorata* and *A. melanoxylon*, which come up as second growth after land has been cleared. The larvae and pupae are tended by ants in the

Iridomyrmex anceps group (sp. 25, Australian National Insect Collection) that form large polygynous and polydomous colonies. Populations of *J. evagoras* overwinter as eggs that hatch in early spring, usually by mid-November. There are a minimum of three broods per season. The general biology of *J. evagoras* has been described in Kitching (1983), Pierce (1983, 1984, 1985, 1987), Pierce and Elgar (1985), Pierce and Young (1986), and Pierce et al. (1987). Our observations were made in a garden approximately 20 m by 20 m, from January through March 1984. All correlations described below are Spearman rank coefficients unless otherwise specified.

5.2 Methods and Results

Male Mate-Searching Behavior

Response to Ants

Methods. The methods used in this field experiment are a modification of those described by Pierce and Elgar (1985). Four fifth-instar larvae were placed on each of twelve potted plants of *A. irrorata* that had been

Table 5.1 Comparison of Mean Body Size, Longevity, and Eclosion Date for Males and Females of *J. evagoras*

	Females	Males	t_s
Juvenile body size			
Pupal length (mm)	13.9	12.8	4.35**
	(1.2)	(1.2)	
	n = 46	n = 46	
Pupal width (mm)	5.4	4.8	4.39**
	(0.7)	(0.7)	
	n = 46	n = 46	
Median day of eclosion[a]	14	8	
Adult body size			
Forewing length (mm)	21.5	21.0	1.79
	(2.3)	(2.0)	
	n = 116	n = 126	
Body length (mm)	16.2	16.1	0.56
	(1.7)	(1.6)	
	n = 116	n = 126	
Body weight (mg)	72.2	45.7	5.30**
	(30.4)	(17.3)	
	n = 42	n = 52	
Estimated longevity (days)	3.1	6.9	3.59*
	(3.5)	(5.9)	
	n = 45	n = 35	
Proportion of observed life span[b]	0.63	0.73	
	(0.26)	(0.21)	
	n = 45	n = 29	

Note: With the exception of body weight, all data were collected from individuals caught in the field. Numbers in parentheses are standard deviations.
[a] First pupa eclosed on day 1.
[b] Number of days observed per life span.
* $p < .05$; ** $p < .01$.

Table 5.2   First Approaches of Males of *J. evagoras* to Plants Containing Larvae
with and without Ants

	Approaches		
	Previous Days	*Swap Day*	*Subsequent Days*
Plants with ants	98	80	90
Plants without ants	52	79	60
x^2	13.50**	0.00	5.61*

*$p < .05$; **$p < .01$.

arranged in a circular arena about 4 m in diameter. This spacing of plants
was within the range of distances found between plants in natural
populations. Ants from nests in the garden were allowed to tend the larvae
on six adjacent plants in the arena but were excluded from the other six
plants. This arrangement was left for four days, and on the latter two days,
for about three hours each, we recorded the first plant visited by individual
males as they entered the arena (Pierce and Elgar 1985). There were at
least nine males active in the study site during the experiment, and
individual butterflies were observed more than once during the five days of
observation. Our data reflect the behavior of most of these males rather
than the behavior of just one or two individuals. After two days we
removed all the plants in the arena and replaced them with new plants that
had not been previously infested with larvae and ants. The positions of
plants with and without ants were swapped so that those positions where
ants had been excluded now had ants and vice versa. Larval density was
kept constant on each day during the entire seven-day experimental
period.

Results. The presence of ants influenced the mate-searching behavior
of the males (table 5.2). Males preferentially approached and landed on
plants with larvae and ants. However, they became confused when the
positions of these plants were changed (on the swap day) and were equally
likely to approach and land on plants with and without ants on that day.
Thus males of *J. evagoras* can learn the positions of plants containing
larvae and ants.

Response to Pupae

Methods. We arranged twelve potted food plants (*A. melanoxylon*) in
a circular arena with a diameter of 4 m. A single pupa was measured
(length and width) and then hung onto each plant. All pupae were tended
by ants. We observed individual males that entered the arena and recorded
their approaches and landings on the plants (see above). We also noted the
eclosion date and sex of each pupa and made several recordings each day
of the number of ants tending it. When a pupa eclosed it was replaced with
another one. The experiment was conducted over a period of three weeks,

during which time thirty-one pupae eclosed (seventeen males and fourteen females). The time each pupa was on a plant before eclosing averaged three days (s.d. = 1.7 days).

Results. There was no correlation between the proportion of times a pupa was visited by males and the number of days before it eclosed (see fig. 5.2a), indicating that males apparently have to approach a pupa before they can assess its state. However, there was a significant negative correlation between the proportion of times a pupa was landed on and the number of days before it eclosed (fig. 5.2b). Thus, males visit pupae randomly with respect to age but land on them more frequently when they are about to eclose.

We examined whether males prefer certain types of pupae by analyzing the residuals about the regression curve (see fig. 5.2b). For example, if males spend more time with female pupae, the positive residuals should represent mostly female pupae. There was no relationship between the sex of the pupa and whether it was preferentially landed upon (χ^2 = 0.039, d.f. = 1, n = 31). Males could use size as an indicator of sex, since female pupae are larger than male pupae (table 5.1), but there was no evidence that males preferentially landed on larger pupae (χ^2 = 0.017, d.f. = 1, n = 31). There was a tendency for males to spend more time with pupae that were tended by more ants on the day before it eclosed (Fisher's exact probability = 0.06, n = 31), although there was no association between the sex of the pupa and the number of ants tending it on that day
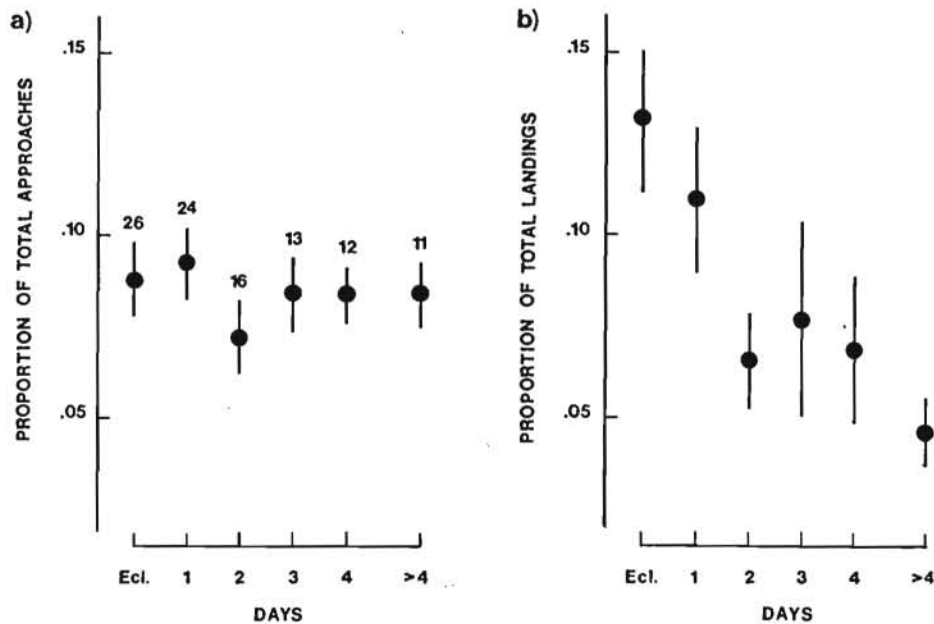

Figure 5.2: Proportion of total visits (a) was not correlated with the number of days before eclosion, but the proportion of total landings (b) was negatively correlated with the number of days before eclosion (r_s = −.305, p < .001, n = 105). Bars represent standard errors, with sample sizes above.

Table 5.3 Frequency of Visits and Landings by Males of *J. evagoras* to Plants with Varying Numbers of Pinned Adults

	Number of Trees	Total Visits	Total Landings
No pupae, no adults	3	54	0
One pupa only	3	65	2
One pupa and one pinned adult	3	71	5
One pupa and three pinned adults	3	108	22
x^2		22.08*	41.76*

*$p < .001$, d.f. = 3.

(Fisher's exact probability = 0.32, $n = 31$). In summary, males are sexually indiscriminate in their mate-searching behavior, and this often results in attempted copulations with eclosing males.

Response to Adults

Methods. In this experiment we used the same twelve-plant arena described above, but instead of placing single pupae on each plant, we employed four treatments. The plants contained either one pupa and three dead conspecific adults pinned next to the pupa; one pupa and one pinned adult; one pupa only; or nothing. Each treatment had three replicates, randomly assigned to different plants. Again, we observed the approaches and landings of males for about six hours over a two day period. The treatments on different plants were changed on the second day to control for possible pupal maturity or tree-position effects. None of the experimental pupae eclosed during the course of the experiment or for two days afterwards.

Results. Males visited and landed on trees with pinned adults significantly more frequently than on trees without pinned adults (table 5.3). Males did not interact with the pinned adults but simply landed beside them. Therefore males use conspecific adults as cues in their mate-searching behavior.

Male Reproductive Success

Methods

Each pupa on trees bearing juveniles of *J. evagoras* in the study site was marked and followed. To the best of our knowledge the individuals in this garden were isolated by a distance of at least 1 km from other colonies of *J. evagoras*. Five emigrant males from our marked sample were retrieved from a second study site slightly over 1 km away, suggesting that the actual population of *J. evagoras* we were studying was larger than simply those individuals contained in the garden. However, the extremely high recapture rate of our marked individuals and the comparatively low rate of immigration into our study site indicated that we were sampling

most of the breeding individuals in a colony that was isolated by distance from other individuals.

After a male had eclosed and his wings had expanded and hardened (about 30 min), we captured him by either encouraging him to walk off the plant onto our hands or simply picking him up by the thorax and wing between thumb and forefinger. It was never necessary to use a butterfly net. We measured his forewing, hind wing, antenna, and body length, then wrote an identifying number on his right forewing using an enamel-based marker pen. The age of two males that were not caught immediately after eclosion was estimated by wing wear. Females were captured, measured, and marked in a similar manner approximately one hour after they had eclosed, while they were still in copula.

Continuous observations were made each day from about 0630 h until midafternoon for the entire twenty-nine-day breeding period. Individuals that were present at the field site and the outcome of all mating tournaments were recorded for each day. Pairs remained in copula for at least two hours ($\bar{x} = 4.32$ h, s.d. $= 1.80$, $n = 41$); hence we were able to observe every mating in our study site.

Male Survival

Forty males that eclosed were marked and observed over a period of four weeks. Male survivorship is shown in fig. 5.3. A quarter of the "eclosed" male population disappeared within the first day, but there was
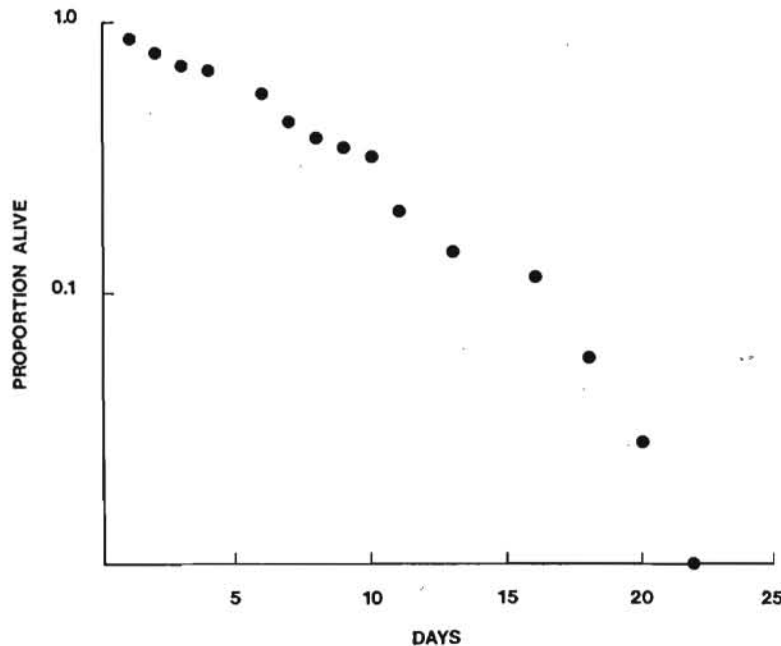

Figure 5.3: Survivorship curve of thirty-five males of *J. evagoras* observed at Mount Nebo, Queensland, during February and March 1983. The proportion alive is given on a $\log_{10}$ scale.
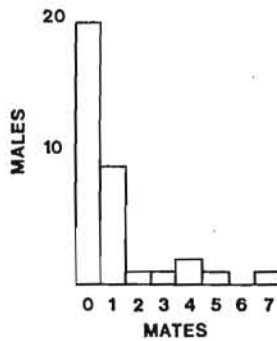
Figure 5.4: Frequency distribution of male lifetime mating success in *J. evagoras*.

a steady rate of disappearance over subsequent days. Since recapture rates were extremely high (table 5.1), we assumed that disappearance within the first day was due to both emigration and mortality, whereas later disappearances primarily reflect mortality. The basis for this assumption rests on our observations of five known emigrants that were observed at another field site, about 1 km away. All these emigrants left their original site within twenty-four hours of eclosing. These five emigrants were excluded from the analysis of male mating success (see below). Furthermore, on the basis of wing wear, there were no "old" male immigrants into our study site during the observation period. We saw numerous birds attempt to eat adults of *J. evagoras*, including willie wagtails (*Rhipidura leucophrys*), pied butcherbirds (*Cracticus nigrogularis*), Lewin honeyeaters (*Meliphaga lewinii*), and kookaburras (*Dacelo gigas*). Most of these attempts were made while the butterflies were on the wing or sitting in the grass, and we never saw a male taken while it was in a "mating ball" or sitting beside a pupa on a plant.

Male Mating Success

Our analysis of male lifetime mating success refers only to those males that reached adulthood and excludes larval and pupal mortality. Therefore our measures of the variance in male lifetime mating success are overestimated. There was considerable variability in the lifetime mating success of males of *J. evagoras*: the most successful male mated with seven females, whereas 57% of the males failed to mate at all (fig. 5.4). The overall variance in lifetime mating success among the thirty-five males was 2.65, and the mean number of female mates per male for these males was 0.97, reflecting an unbiased overall sex ratio (although the operational sex ratio was almost purely male biased). The distribution of male lifetime mating success was almost significantly different from that derived from a Poisson probability function (Kolmogorov-Smirnov test: $D = 0.203$, $.1 > p > .05$), suggesting that lifetime mating success may not be a random process.

Components of Lifetime Mating Success

We have identified three components of male lifetime mating success for *J. evagoras*: longevity, encounter rate, and mating efficiency. Thus, male lifetime mating success in *J. evagoras* is expressed as LMS = LS × ER × ME, where for each male LS = male lifetime (estimated from the number of days from first to last sighting); ER = encounter rate (total number of females that eclosed during the male's lifetime per male lifetime); ME = mating efficiency (number of mates per total number of females that eclosed during the male's lifetime).

Out of thirty-five males, twenty-nine were alive on days when females eclosed and therefore had an opportunity to mate. These males will be referred to as "breeding" males. The mean, variance, and standardized variance of the components and products of the components of lifetime mating success among breeding males are shown in table 5.4. The percent contributions of the components, derived using the method of Brown (this volume, chap. 27) are shown in table 5.5. The 94% of the variance in male lifetime mating success due to breeding males can be broken down into 12.3% attributable to variation in life span, 9.6% attributable to variation in encounter rate, and 40.4% attributable to variation in mating efficiency.

Most of the variance in male lifetime mating success lies in longevity and mating efficiency and their covariances. The considerable simultaneous independent variation and covariation between longevity and mating efficiency is due to the highly significant correlation between these two variables (see below). This high degree of covariance makes the analysis

Table 5.4   Mean and Variance of the Components of Lifetime Mating Success of Breeding Males of *J. evagoras*

Component	Original		Standardized Variance
	Mean	*Variance*	
LS	7.45	36.76	0.66
ER	1.61	1.34	0.52
ME	0.06	0.01	2.78
LS ER	10.69	63.36	0.55
LS ME	0.81	2.50	3.81
ER ME	0.09	0.02	2.47
LS ER ME	1.05	3.02	2.74

Note: LS = lifetime; ER = encounter rate; ME = mating efficiency (see text for details). Standardized variance is the variance divided by the square of the mean.

Table 5.5   Percentage Contribution of the Components of Lifetime Mating Success to Variation in LMS in Breeding Males of *J. evagoras*

Component	Longevity	Encounter Rate	Mating Efficiency
Longevity	13.08		
Encounter rate	−14.61	10.24	
Mating efficiency	157.69	−21.91	43.03
3+	−87.51		

difficult to interpret biologically, because it is impossible to determine which is the most important component of a male's making success. The analysis of male lifetime mating success excludes nonbreeding males, many of which survived less than one day (see fig. 5.2). The importance of longevity might increase if this mortality were included.

Determinants of Male Lifetime Mating Success

Male forewing length was significantly correlated with both longevity ($r_s = .370$, $p = .014$, $n = 35$) and mating efficiency (table 5.6) but not with the encounter rate of males with eclosing females ($r_s = .227$, $p = .100$, $n = 35$), and encounter rate was not correlated with longevity ($r_s = .153$, $p = .200$, $n = 35$). However, there was a significant correlation between eclosion date and encounter rate; males that eclosed earlier had a higher encounter rate than males that eclosed later in the breeding period ($r_s = .421$, $p = .006$, $n = 35$).

Since body size (measured by forewing length) was correlated with longevity, it was necessary to derive partial correlation coefficients in order to establish whether body size or longevity had a greater influence on mating efficiency. This analysis revealed that mating efficiency was

Table 5.6 Relationship between the Absolute Forewing Length, Longevity, and Mating Efficiency of Thirty-five Males of *J. evagoras*

| | Mating Efficiency | |
	r_s	Partial Correlation Coefficient
Forewing length	0.385*	0.292
Longevity	0.497**	0.395*

*$p < .01$; **$p < .001$.

Table 5.7 Mean Forewing Length, Longevity, Age, and Number of Mates of Males of *J. evagoras* Present for Each One-Week Period during the Twenty-eight-Day Season

| | Week | | | | |
	1	2	3	4	$F_{3,60}$
Number of males present during the week	18	24	12	11	
Forewing length	22.6	21.1	20.6	21.1	2.607
	(1.8)	(2.6)	(2.3)	(1.9)	$p = .06$
Days present	3.4	3.8	5.5	3.5	2.946
	(2.1)	(2.3)	(2.3)	(1.6)	$p = .04$
Age	2.6	4.8	8.3	10.6	7.171
	(1.2)	(3.2)	(5.1)	(7.2)	$p < .001$
Number of mates	0.3	0.7	0.5	0.4	0.928
	(0.6)	(0.1)	(0.8)	(0.5)	$p = .43$

Note: Several males were observed for more than one week. The *F*-statistic is derived from one-way ANOVA, and the age data were transformed before analysis. Standard deviations are given in parentheses.

directly correlated with longevity, whereas it was correlated with body size only through the effects of longevity (table 5.6).

The Effects of Relative Body Size and Age

Although absolute body size was not directly correlated with mating efficiency (table 5.5), it was still possible that an individual's relative size affected his mating ability. This is because the average size of males varied during the course of the breeding period (table 5.7), and thus each individual's relative size also varied. We analyzed the importance of a male's relative size to his mating efficiency in two ways.

The first approach was to examine the relationship between male relative size and mating efficiency. For every male that contested for a female, we calculated the proportion of other males during each contest that were smaller than he was. We calculated relative size per contest rather than relative size per day because a male's relative size alters when males in copula are effectively removed from the population. The median relative size per contest for each male during his lifetime was significantly correlated with mating efficiency (fig. 5.5). However, relative size was also correlated with male longevity ($r_s = .381$, $p = .02$, $n = 35$), and male longevity was correlated with mating efficiency (see table 5.6). Partial correlation analysis reveal that mating efficiency was still correlated with both relative body size ($r = .356$, $p < .05$) and longevity ($r = .388$, $p < .05$).

The second approach was to look at a male's mating success over a week. The mating season was divided into four weeks. Each male was assigned to one of the four weeks, depending upon which week was most representative of his life. Where a male overlapped two whole weeks, he was assigned to the week that adjoined the maximum number of additional
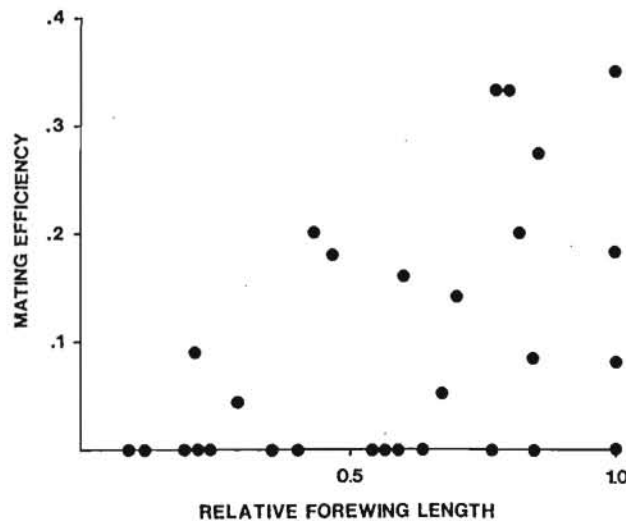

Figure 5.5: Relationship between mating efficiency and relative forewing size of breeding males ($r_s = .475$, $p < .005$, $n = 29$).

days he was alive. The average male size, number of mates, days present, and age were calculated for each of the four weeks (table 5.7), and we then derived the deviation from the average for each male by simply subtracting the average score from his score for each variable.

Deviations in size, mates, and days were significantly correlated with each other (deviation in size with deviation in mates, $r_s = .485, p < .005$, $n = 35$; deviation in size with deviation in days, $r_s = .369, p < .02, n = 35$; deviation in days with deviation in mates, $r_s = .604, p < .001, n = 35$). Partial correlation analysis revealed that deviation in number of mates was still correlated with deviation in size ($r_s = .354, p < .05$) and deviation in days present ($r_s = .523$, p $< .05$). Age at time of mating was not an important variable determining mating efficiency. Deviation in age at time of mating was correlated with deviation in mates ($r_s = .389, p < .01$), but this was primarily due to the effects of longevity. Deviation in days present and deviation in age were also correlated ($r_s = .625, p < .001$), and the partial correlation of deviation in age on deviation in number of mates, controlling for deviation in days present, was not significant ($r = .122, p > .2$). Thus there was no evidence for age-specific mating success among males.

Determinants of Female Fecundity

Methods

Females were reared in the laboratory on *A. irrorata* and tended by colonies of *Iridomyrmex* sp. 25 ants (see Pierce 1983). After eclosion, females were weighed, measured, and allowed to mate with males of known age and size. They were then placed in individual oviposition cages containing a small cutting of *A. irrorata* and lengths of scored wooden dowling upon which they could lay eggs. Females were fed three times daily with a 3:1 mixture of water and honey. We recorded the total number of eggs each female laid during her lifetime.

Results

Females were observed in the field site for a much shorter period than males (see table 5.1). We do not know whether this is because females have a shorter life span than males or because they emigrate more frequently and at all ages. Unlike males, there was no correlation between female body size and longevity in the field (forewing length: $r_s = .187, p > .10$; body length: $r_s = .158, p > .15, n = 45$). In the laboratory, females survived between ten and twenty-two days (mean = 14 days, s.d. = 1.8, $n = 16$) and laid between 55 and 455 eggs with a mean of 237 (s.d. = 131, $n = 16$). There was a highly significant correlation between female weight and the number of eggs she laid per day (fig. 5.6). The total number of eggs a female laid was not correlated with either the number of days she lived in the laboratory ($r_s = .090, p > .35, n = 16$) or the weight of her male mate ($r_s = .075, p > .35, n = 16$).
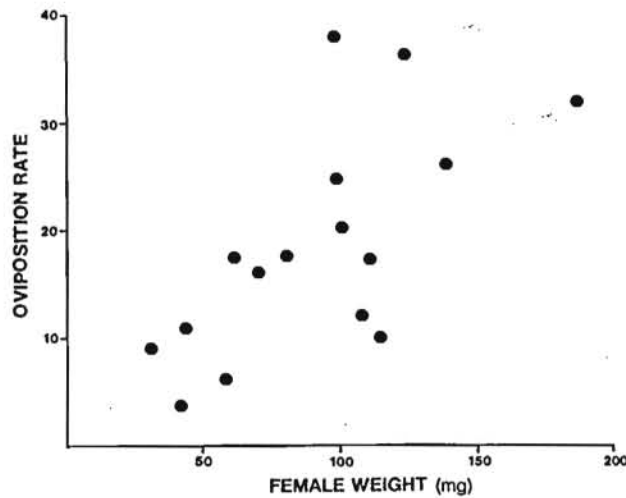
Figure 5.6: Relationship between female body weight and oviposition rate in *J. evagoras* under laboratory conditions ($r_s = .641$, $p = .004$, $n = 16$). Oviposition·rate is the total number of eggs laid per total number of days alive.

Size-Selective Mating

Since larger females have a higher fecundity than smaller females and larger males have a competitive advantage, we might expect to find size-selective mating in *J. evagoras*. We found no evidence of this; relatively larger males did not mate with larger females ($r = .046$, $p > .4$, $n = 31$). The lack of linear size-selective mating may be related to a male's expectations about potential future matings. In our study site, the probability that at least two females of *J. evagoras* would eclose on any day during the breeding period was .34. It seems unlikely that a male could increase his reproductive success by rejecting a smaller female and waiting for a larger one.

5.3 Discussion

Two types of mate-locating behavior are commonly described for butterflies: perching (or territorial ·behavior), in which a male alights in a characteristic location and investigates passing butterflies that might be potential mates; and patrolling, in which males fly almost continuously in search of females (see Scott 1972, 1974, 1975; Rutowski 1982, 1984; Silberglied 1984). In both cases, a male's searching behavior is dependent upon the unpredictable arrival of adult females. In *J. evagoras*, the location of female pupae *is* predictable. Males locate plants with conspecifics and ants, learn their positions, and trapline from one plant to the next in search of eclosing females. Although they may remain on one plant for several hours, they will readily leave that position for another (for example, to join a mating ball); they are not territorial as are other lycaenids (e.g., Powell 1968; Scott 1972; Douwes 1975; Suzuki 1976; Alcock 1983).

It is not surprising that males have incorporated ants into the set of cues they use in locating conspecifics, because of the obligate association between *J. evagoras* and its attendant ants. Healthy larvae and pupae are never found in the field without attendant ants, and females use workers of *Iridomyrmex* sp. 25 as cues in oviposition (Pierce and Elgar 1985). Males are capable of learning the positions of plants with and without ants, and this may decrease energetic costs and the risks of predation by reducing the time spent searching for females.

Males also used pupal age as a cue in their mate-searching behavior. The cue the pupa emits is probably a volatile pheromone that the males detect through olfaction, because if an observer crushes a late-stage pupa, his fingers also become attractive to males. Males of birdwing butterflies *Ornithoptera priamus caelestis* (Borch and Schmid 1973) and *O. p. poseiden* (A. Hiller, pers. comm.) as well as several species of *Heliconius* (Bellinger 1954; references in Brown 1981; Boppré 1984) gather around pupa that are about to eclose. In certain Heliconiinae, males can apparently detect the difference between male and female pupae (Gilbert and Longino, cited in Boppré 1984). This is not the case for *J. evagoras*, which is surprising, since there is considerable competition for mates and selection for sex discrimination might be expected. One possible explanation for the lack of sex discrimination by males of *J. evagoras* is that if the probability of two or more pupae eclosing simultaneously is very low, then there simply may not be a cost to waiting for a male pupa to eclose.

The presence of males sitting in a group around a pupa is a good indicator that a pupa is about to eclose, and males of *J. evagoras* use each other as cues in mate searching. Attraction to conspecific adults is quite common among butterflies, including lycaenids (Douwes 1975), although the context in which attraction occurs is not always distinguished (see discussion in Silberglied 1984).

Body size in *J. evagoras* is clearly an important feature of male reproductive success. This is because male body size is correlated with both longevity and mating efficiency, two components of male lifetime mating success. It is interesting to note that although variation in male lifetime mating success does not greatly exceed a random model, it does not necessarily indicate that mating is in any sense random (cf. Sutherland 1985a). Our data show that larger males are generally more successful, and hence the assumptions of a Poisson distribution are not met.

One important result from our observations of *J. evagoras* concerns the relationship between absolute and relative body size. We found that mating efficiency was more strongly correlated with relative size than with absolute body size. Relative size was a more appropriate measure than absolute size once longevity was controlled for in these mating contests, because the average size of individuals changed over the course of the season. This may be a common feature of insect mating systems, and future analyses of male mating success in insects should consider relative as well as absolute size. Interestingly, there was no evidence for age-

specific mating success; relative mating success was not correlated with male age at time of mating except through the effects of longevity.

Little evidence exists for a relationship between body size and mating success in other butterflies. Territorial defense in the black swallowtail butterfly *Papilio polyxenes* depends largely on the length of tenure (Lederhouse 1982), and the outcome of disputes over territories in the speckled wood butterfly *Parage aegeria* is usually resolved by an ownership convention (Davies 1978). Both these studies implied that mating success was positively correlated with territory ownership. Wickman's (1985) study of the small heath butterfly *Coenonympha pamphilus* is the first to confirm this assumption.

Female fecundity was strongly correlated with body size, suggesting that body size is an important component of female lifetime reproductive success in *J. evagoras*. The relationship between body size and fecundity has been commonly found in the Lepidoptera (e.g., David and Gardiner 1961; Baker 1968; Labine 1968; Marks 1976; Suzuki 1978; Lederhouse 1981; Hayes 1981; but see Boggs 1986) and in other insects (see Thornhill and Alcock 1983 for review). Although we do not have direct field measurements of female lifetime fecundity, our field results indicate that female longevity is probably quite short. It seems likely that selection would favor females that lay most of their eggs within the first few days after mating (see also Boggs 1986).

Our results also provide evidence for a possible selective advantage of early male emergence in this species. The eclosion of males before females (often referred to as "protandry"; see Thornhill and Alcock 1983 for review) is a widespread characteristic of butterflies and other insects. Although protandry is commonly regarded as a mechanism that increases a male's encounter rate with females and thereby increases his reproductive success (Wiklund and Fagerström 1977; Singer 1982; Wiklund and Solbreck 1982), there have been no quantitative studies of the effects of protandry on mating success. Males of *J. evagoras* that eclosed earlier in the season encountered more females than males that eclosed later. This result was not confounded by male longevity or size, since neither variable was correlated with encounter rate. The analysis of the components of male lifetime mating success indicated that some of the variation can be explained by encounter rate, suggesting a selective advantage for protandry. This benefit may impose an upper limit on male body size; if there is a positive correlation between developmental time and body size, larger males may encounter fewer females and hence experience a lower mating success (Darwin 1871; Lederhouse, Finke, and Scriber 1981; Singer 1982; Partridge and Farquhar 1983).

The close association that larvae and pupae of *J. evagoras* have with ants may have influenced the mating system of this butterfly in several important ways. The propensity of myrmecophilous lycaenids to aggregate and to occur in highly localized populations is likely to be the result of relying upon attendant ants for defense (Pierce 1983; Pierce and Elgar

1985). Because of their effective ant guard, the larvae of species such as *J. evagoras* are able to pupate openly in clusters on their host plants. The dense, localized populations of *J. evagoras* and its conspicuous pupation sites would have the effect of promoting intense competition among males for females. Males are able to investigate regularly every plant in an area bearing conspecific pupae and engage in active tournaments for eclosing females. This would not be possible for a butterfly species that was widely dispersed or whose pupae were concealed and difficult to find.

Since attendant ants also play a role in male mate-searching behavior, selection may have favored those females that are able to maintain a retinue of attendant ants. Males are attracted to plants with workers of *Iridomyrmex* sp. 25 and investigate pupae with more ants more frequently than pupae with fewer ants. By generating competition among males, a female may end up mating with a male of higher quality or better competitive ability. Therefore, rather than excluding the possibility of female choice, the intense competition among males of *J. evagoras* may in fact allow females to make a passive mate choice (see Halliday 1983; Partridge and Halliday 1984). One observation that conflicts with this idea is the absence of sex discrimination by males of *J. evagoras*. If it were advantageous for females to maximize competition among males, then selection would favor any mechanism that allowed males to recognize female pupae.

Finally, attendant ants may exert a direct effect on the reproductive success of both males and females of *J. evagoras*. Our study has shown that body size is an important correlate of both male mating success and female fecundity. However, the presence of attendant ants places a considerable limitation on body size. In laboratory experiments examining the effect of ants on development of *J. evagoras*, Pierce et al. (1987) found that the pupae and adults of tended larvae were significantly smaller than the pupae and adults of their untended counterparts, presumably because of energy lost in feeding attendant ants, and this effect was especially true for females. Of course, in the field, the larvae and pupae of *J. evagoras* cannot survive without ants (Pierce 1983; Pierce et al. 1987). However, for *J. evagoras*, one of the costs of associating with ants is levied in the final adult size, and this cost is surely reflected in the reproductive success of these butterflies.

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