

ORIGINAL ARTICLE

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Mating system evolution in response to search costs in the speckled wood butterfly, *Pararge aegeria*

Received: 14 May 1998 / Accepted after revision: 13 December 1998

Abstract A general and intuitive prediction from models of mate preference is that when the cost of searching for mates increases, individuals should become less choosy. Here, we test this prediction by comparing the mating propensity of females in two populations of the butterfly *Pararge aegeria*. The populations originated from southern Sweden and Madeira and due to different adult emergence patterns throughout the year, the average density of males per female is likely to be lower on Madeira. Therefore, we expected that the cost of searching should be greater on Madeira and, consequently, that the Madeiran females should be less choosy. In line with predictions, the Madeiran females mated significantly sooner after the first interaction with males than did females from southern Sweden. This difference may reflect a weaker preference for territorial males over non-territorial patrollers in the Madeiran population, because of the greater costs of searching. The Madeiran females also showed a shorter time lag between mating and the start of oviposition. We discuss this unexpected result and propose that the same mechanism could also explain this population difference, i.e. different costs of searching for suitable host plants. Both search processes are fundamental for female reproductive success and we find it plausible that they can be generalised into the same theory of optimal search behaviour.

Key words Mate choice · Search theory · Costs and benefits · Satyrinae · Lepidoptera

Introduction

The evolution of female mating preferences is an intensively debated issue in evolutionary biology (Borgia 1979; Bateson 1983; Thornhill and Alcock 1983; Andersson 1994; Gibson and Langen 1996). The benefits to females of mating with particular males may be direct, by enhancing female survival and fecundity, or indirect through heritable differences between males that influence offspring fitness (Thornhill and Alcock 1983; Reynolds and Gross 1990). However, it is necessary to take into account not only the benefits but also the costs of the particular feature investigated. Including costs of searching into models of mate choice has been shown to alter fundamental predictions (Real 1990; Reynolds and Gross 1990). This is quite intuitive, since if there were no costs of searching, the optimal strategy would be to assess all potential mates in the population before making a decision (Real 1990). Finding this type of strategy in nature should be very unlikely. Possible costs of mate choice include energy expenditure, time lost and enhanced predation risk facing searching individuals (Alatalo et al. 1988; Slagsvold et al. 1988; Milinski and Bakker 1992; Hedrick and Dill 1993; Wickman and Jansson 1997). A general prediction from models of mate choice is that as the costs of searching increase, choosiness should decrease (Real 1990; Reynolds and Gross 1990). We test this prediction by comparing the mating propensity of females in two populations of the speckled wood butterfly, *Pararge aegeria* (Satyrinae), where the cost of searching for males is likely to be different. This measurement is relevant, since the propensity of a female to accept a courting male is likely to have a strong effect on her choosiness.

In most insect species without parental care, female reproduction has two more or less distinct phases: mate location and mating followed by host searching and oviposition. Because the length of the adult life is limited, selection will favour an efficient usage of time and females are expected to allocate time to these different

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activities in a manner that maximises fitness. The reproductive success of insect females, typically, shows a strong correlation with the number of eggs laid during the lifetime and, therefore, selection should act to maximise the amount of time allocated to host search and oviposition. However, if there are benefits of female mate choice, there may also be selection on females to postpone mating long enough to assess the quality of different males. For a short-lived insect female, then, the optimal amount of time allocated to the pre-mating period of adult life will be a balance between the benefits of mate choice and the costs of searching, mainly due to time lost for oviposition. The populations investigated here were expected to face different costs of searching due to differences in the seasonal emergence pattern of adults.

The populations originate from southern Sweden and the Atlantic island Madeira. Due to climatic differences, the two populations are adapted to very different degrees of seasonality. In southern Sweden, butterfly growth and development is restricted to approximately 7 months of the year (April to October) and the winter is survived in diapause. As a result, the adult flight is highly synchronised. The population has two to three generations a year and reproduction occurs during each flight period lasting some 2–3 weeks (C. Wiklund, unpublished data). On Madeira, temperatures allow development and growth during the whole year and seasonality is primarily evident by the lack of rain during July and August on some parts of the island. There is no evidence from the field that the Madeiran butterflies enter diapause and it could not be experimentally induced in the laboratory (Nylin et al. 1995). Further evidence comes from the fact that all developmental stages of *P. aegeria* can be found simultaneously on Madeira (Shreeve and Smith 1992; Nylin et al. 1993), and adults fly more or less all year round at lower elevations (Higgins and Hargreaves 1983; Jones and Lace 1992; Shreeve and Smith 1992; personal observations). Hence, in southern Sweden, generations are discrete and non-overlapping while the Madeiran population reproduces continuously throughout the year and well-defined generations do not occur. In line with theory (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982), the Swedish population is protandrous (males emerge before females), and males have shorter development times than females. In the Madeiran population, there is no protandry or sexual difference in development time (Nylin et al. 1993; Gotthard et al. 1994).

Two studies have measured adult life span of *P. aegeria* males in the field, one in England (Davies 1978) and one in Sweden (Wickman and Wiklund 1983). In both studies, the mean adult life span expectancy of males was estimated to be approximately 6 days, although individual males could survive up to 28 days. There are no field estimates of female life span in *P. aegeria*, but in laboratory conditions, females have longer life spans than males in both of the populations

investigated here (K. Gotthard, S. Nylin, C. Wiklund, unpublished data). Together with observations on other butterfly species (Scott 1973), this suggests that on average females also have a somewhat longer life span expectancy in the field. Females of *P. aegeria*, typically, only mate once (Wiklund and Forsberg 1991), and spend the rest of their lives searching for suitable host plants (grasses) on which they deposit eggs singly. In the laboratory, *P. aegeria* females lay eggs during their entire adult life (personal observations). All this implies that newly emerged females should be under strong selection to mate quickly after adult emergence to maximise the time available for oviposition. There is, however, evidence that females of many butterfly species are not willing to mate until some time after eclosion, and field observations of virgin females of *P. aegeria* in Sweden indicate that they show a preference for territorial males over non-territorial patrolling males (Wickman and Wiklund 1983).

We hypothesised that the difference in adult emergence pattern of *P. aegeria* on Madeira and in southern Sweden would differentially influence the selection pressure on females to reduce the time between adult eclosion and mating in the two populations. The lack of synchronised adult emergence on Madeira should lead to a relatively lower average abundance of possible mates for a newly emerged female, compared to the typical situation in southern Sweden, where a majority of the population is on the wing simultaneously. This argument is supported by the observation that the density of flying adults is approximately twice as high in southern Sweden during the flight period compared to the highest recorded densities on Madeira (Jones and Lace 1992; C. Wiklund, unpublished data). Moreover, the protandry of the Swedish population is likely to enhance the density of adult males per adult female (Nylin et al. 1993). Typically, a large proportion of the Swedish males is already on the wing when the females start to emerge, resulting in a male-biased operational sex ratio during most of the emergence period. Hence, we expected that the cost for an unmated female to reject a male would be higher on Madeira since she will on average have to wait longer before she finds another mating partner.

Given that the benefits of female choice are similar in the populations, females on Madeira should be under stronger selection to mate soon after adult emergence and therefore be more likely to accept the first male they meet. Alternatively, the time lag between adult emergence and mating is due to some unavoidable refractory period that is minimised by equally strong selection in both populations. If so, there should be no difference between populations and female age at first male encounter may instead influence the propensity to engage in mating. We tested these hypotheses by investigating how soon after first male encounter females of different ages, from both populations, were willing to mate.

Methods

Study organism

The speckled wood butterfly, *P. aegeria* is widely distributed throughout Europe, Asia and northern Africa. The larvae feed on various grasses from several genera. In Europe two subspecies are recognised; north of the Alps *P. aegeria tircis* and south of the Alps *P. aegeria aegeria*. The two subspecies hybridise and intermediate forms are found where they meet in the field (Higgins and Hargreaves 1983). In the 1970s, the southern subspecies, *P. a. aegeria*, colonised the Atlantic island Madeira from an unknown source (Higgins 1977), and has now expanded all over the island (Jones and Lacey 1992; Shreeve and Smith 1992).

Laboratory stocks

The Madeiran butterflies originated from eight mated females caught in the surroundings of Funchal, Madeira (33°N). Prior to the experiment, the population had been in the laboratory for six generations. During this period we actively tried to avoid selection in general, and selection for fast larval development in particular, by collecting eggs in equal amounts from the whole period of female oviposition. The butterflies from southern Sweden were the F2 generation of approximately ten mated females caught in Ransvik (56°N). Their offspring were kept in conditions leading to direct development (20 h light:4 h dark, 20 °C). All larvae from both populations were reared individually in plastic jars where a tuft of the grass *Dactylis glomerata* was cultured. Individuals were sexed as pupae and sexing was confirmed in the adults.

Experimental procedure

Females from both populations were allowed to encounter a male from their own population individually in flying cages (0.5 × 0.5 × 0.5 m). One Swedish male died after 2 days without mating and was replaced by a reserve male. Females encountered males either at the day of adult eclosion (age 0), or 1 day after adult eclosion (age 1). Sugar-water and grass for oviposition were constantly available. The photoperiod was 6 h light:18 h dark and temperatures were 25 °C during the day and 20 °C during the night. A period of 6 h with temperatures allowing activity is approximately what the Swedish butterflies experience on a warm day in natural conditions. On Madeira, the activity period may be slightly longer during hot summer days. Each cage was lit with a 75-W incandescent lamp. Females were always put in the mating cages in the morning, before the lights were turned on. During the light part of the day, we constantly walked along all the cages and noted the time of day that individual females started to mate and

what day they started to lay eggs. We also noted the duration of matings. Since a mating pair stays in copula for a minimum of 15 min, and the butterflies do not mate during the night, this procedure allowed us to detect practically all matings.

Statistical analysis

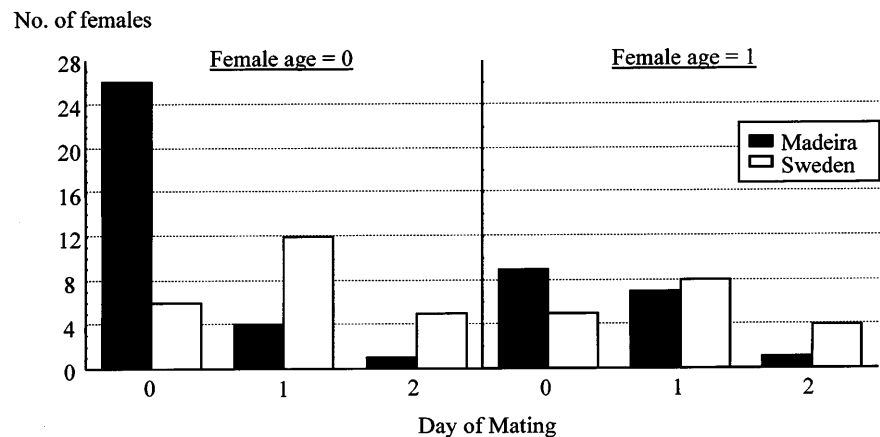
The measurements of time to mating and time to oviposition both violated the assumptions of parametric methods. Therefore, we used non-parametric methods and tested the main factors in separate tests. We adjusted the significance levels with the sequential Bonferroni method (Rice 1989) when we performed several tests of a single measured variable.

Results

Most females of both populations mated within 2 days after being given access to males in flying cages. In total, 104 females were used in the experiment and 16 were never observed to mate (13 Swedish and 3 Madeiran). Only 1 female was observed to mate after more than 2 days (1 Swedish female mated after 5 days). In none of the populations did female age significantly affect how long they waited before mating (Fig. 1; Mann-Whitney, difference between ages, Sweden: $U = 193$, $n_0 = 23$, $n_1 = 17$, $P = 0.95$; Madeira: $U = 183$, $n_0 = 31$, $n_1 = 17$, $P = 0.085$). Since female age did not influence the time to mating, the age categories were pooled in the analysis of population differences. Females from Madeira mated significantly more quickly than Swedish females (Fig. 1; Mann-Whitney, difference between populations at the level of days: $U = 494.5$, $n_m = 48$, $n_s = 40$, $P < 0.0001$). A majority of the females from Madeira mated on the day of adult emergence, while a majority of the Swedish females waited for 1 or 2 days. This is true for both age categories although the proportion of Madeiran females mating on the first day of male presence (day 0) was larger in females of age 0 (Fig. 1). This explains the relatively low P -value in the test for an age effect in the Madeiran population.

There was no difference between populations in the age of the males that were used in the experiment (mean \pm 1 SE for Sweden = 0.9 ± 0.1 days, and for

Fig. 1 Number of females from both populations that mated on the same day, 1 day or 2 days after being given access to males (females of age 0 encountered males on the same day they eclosed as adults while females of age 1 were 1 day old on first encountering males)



Madeira = 0.9 ± 0.3 days; ANOVA: $F_{1,86} = 0.01$, $P = 0.91$). Males from both populations were ready to mate on the day of eclosion (5 of 12 Madeiran and 5 of 17 Swedish males mated on the same day they emerged), and no differences in male activity could be observed.

We also investigated how fast females engaged in mating activities within days, by using the more fine-scaled data on how soon matings were initiated after the onset of light. Since female age did not influence the propensity to mate, the two age categories were pooled. In the group of females that mated on the same day they had access to males (day 0), those from Madeira started mating significantly earlier in the day than Swedish females (Fig. 2; Mann-Whitney: $U_{\text{day0}} = 86$, $n_m = 35$, $n_s = 11$, $P_{\text{day0}} = 0.006$). The same type of analysis of the females that mated on day 1 indicated that the population difference was smaller and non-significant (Fig. 2; Mann-Whitney: $U_{\text{day1}} = 70.5$, $n_m = 11$, $n_s = 20$, $P_{\text{day1}} = 0.10$). Since only two Madeiran females mated on day 2, a similar comparison for this day seemed less meaningful. The intensity of mating activities of both populations varied in a similar way during the day and 49% of all matings were started within 90 min after the lights in the laboratory were turned on (Fig. 2). The other period with high levels of mating activity started around 240 min after daybreak and 40% of all matings took place from this time on (time classes 240–360 min in Fig. 2). Nevertheless, no Swedish females mated during the early activity period (<90 min) on the first day of male encounter (day 0). On day 1 and 2, however, the Swedish females also mated frequently during the first 2 h of the day (Fig. 2). There was no difference between the populations in the duration of matings (ANOVA: $F_{1,80} = 0.48$, $P = 0.49$) and the average mating duration (± 1 SE) was 22.0 ± 0.7 min.

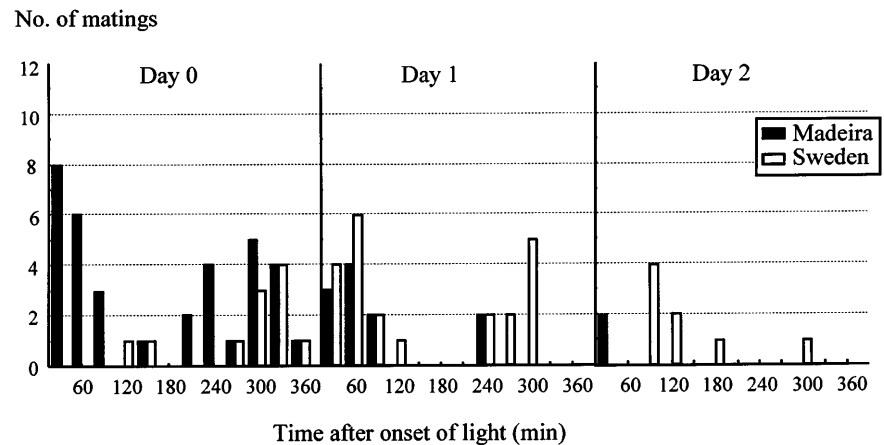
The females from Madeira also had a significantly shorter period between mating and the start of egg laying compared to the Swedish females (Fig. 3; Mann-Whitney: $U = 441$, $n_m = 45$, $n_s = 39$, $P < 0.0001$). However, these measurements are made at the level of days and since the Madeiran butterflies on average mated earlier in the day, they are more likely to start

oviposition on the day they mated for that reason alone. Dividing the females into early maters (mating within the first 180 min of the day) and late maters (mating within the last 180 min of the day) and testing them separately for differences in the start of oviposition did not, however, produce a different result (Mann-Whitney, difference between populations, early matings: $U = 136$, $n_m = 26$, $n_s = 21$, $P = 0.0005$; late matings: $U = 78$, $n_m = 18$, $n_s = 17$, $P = 0.0018$, with Madeiran females starting oviposition earlier in both cases). Consequently, the total time between encountering males and the start of oviposition was significantly shorter for the Madeiran females (Mann-Whitney: $U = 184.5$, $n_m = 45$, $n_s = 39$, $P < 0.0001$). The median female from Madeira started oviposition 1 day after meeting males (range between 0 and 2 days, $n = 45$) while the median Swedish females started 2 days after encountering males (range between 1 and 3 days, $n = 39$, not counting the extreme female that mated after 5 days).

Discussion

Females of *P. aegeria* from Madeira are more likely to accept and mate on the first day of male presence (Fig. 1). In none of the populations did female age significantly influence how fast females were willing to engage in matings. Males in both populations were ready to mate on the day of emergence and we observed no differences in male behaviour between populations. The temporal dynamics of mating activities within days suggest a mechanism producing this population difference (Fig. 2). In both populations, there appears to be one peak of mating activity just after daybreak and a second within 2 h before the lights were turned off. However, on the first day of male presence (day 0), no Swedish females mated during the first 90 min of daylight, while in the Madeiran population this was the period of highest mating activity. One day after the first encounter with males (day 1) females from both

Fig. 2 Temporal dynamics of mating activity within the 3 days of mating. Each bar represents a time interval of 30 min and shows the number of females from each population that started mating within each period. The two different age categories are pooled



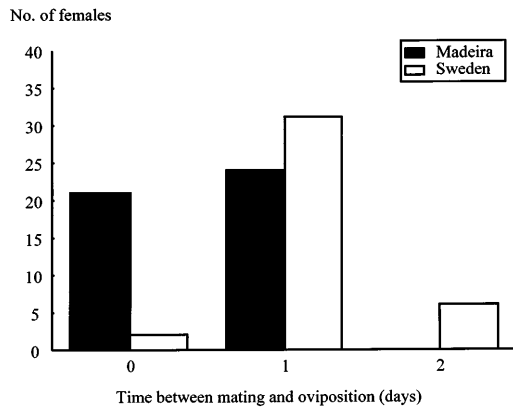


Fig. 3 Time between mating and oviposition in the two populations (*day 0* day of mating)

populations mated in the morning. Hence, for some reason, the Swedish butterflies did not use the early activity period on the first day of interactions between males and females. This pattern was the same in both female age categories (6 females of age 0 and 5 of age 1 mated on day 0, and none during the first 90 min of the day). Since the Swedish females of age 1 did not mate in the first morning, it appears that the lack of motivation to mate is not just a physiologically determined refractory period between adult eclosion and mating. The females from Madeira also started to oviposit significantly faster after mating (Fig. 3). Consequently, the median time between the first mating opportunity and the start of oviposition was 1 day shorter in the Madeiran population.

Based on these results it appears that females from Madeira can use the first period of adult life more efficiently. This is especially striking in view of the fact that the Madeiran females also have significantly longer adult life spans compared to the Swedish females, at least in laboratory conditions (K. Gotthard, S. Nylin., C. Wiklund, unpublished data). The higher motivation to mate quickly in the Madeiran population is in line with the hypothesis that the time cost for a female of rejecting a male should be higher on Madeira. That this cost may be non-trivial was shown in a study of another satyrine butterfly, *Coenonympha pamphilus* (Wickman and Jansson 1997). In the field, virgin females of this species lost an average 201 min by not approaching males on their way to leks, and this translated into an average fecundity reduction of 2.8% using field estimates of fecundity and mortality. However, the same logic can only apply in *P. aegeria* if there is some benefit to be gained for a Swedish female by not mating with the first male encountered. Alternatively, the unwillingness to mate on the first day represents an unavoidable refractory period due to some developmental constraint present in the Swedish population but not in the Madeiran population. If none of these alternatives are true, it is difficult to understand why the Swedish females behave as they do, no matter how small the cost of waiting.

Given the results from the Madeiran population, and the behaviour of 1-day-old Swedish females, the con-

straint explanation seems less likely. The mating system of the species, however, indirectly suggests that females may benefit from refraining from mating with the first possible male. Males of *P. aegeria* display two mate location strategies, territorial perching in sunspots or patrolling, and they engage furthermore in aggressive fights over ownership of these sunspots (Davies 1978; Wickman and Wiklund 1983). The available evidence from another Swedish population suggests that virgin females actively search for territorial males in sunspots and avoid patrolling males during this search (Wickman and Wiklund 1983). Hence, females seem to prefer either the territorial males or their sunspots, indicating that they receive direct or indirect benefits from choosing to mate with these males. It is possible that the difference between populations in the motivation to mate early in life reflects a difference in the strength of this preference. If so, females on Madeira would be more likely to accept patrolling males since the time cost of rejecting a mating opportunity is higher than in the dense population in southern Sweden.

The difference between populations in the time lag between mating and oviposition was unexpected. Apparently females in both populations need some time to handle the spermatophore they have obtained, mature eggs, and perhaps go through some physiological adjustment before they can start oviposition. We see, however, no obvious reason why this should be more time consuming for the Swedish females. In fact, the theoretical framework and empirical patterns presented here would predict that natural selection to minimise this time lag should be equally severe in both populations. The results are, however, robust, and we can only speculate about the causes. One possibility is that the oviposition behaviour is different in the populations due to some difference in the density of host plants. Suitable host plants appear to be a scarce resource during the very dry summer on Madeira while they are very abundant in southern Sweden during the period of oviposition. Hence, the distribution of host plants differs between the two locations in a manner that is similar to the difference in distribution of potential mates. If so, the population difference in the time lag between mating and oviposition may be due to exactly the same mechanism, i.e. a difference in the cost of searching. In such a scenario, females on Madeira would be under strong selection to use suitable host plants whenever they find them, since the cost of searching for a new one is very high. In southern Sweden, however, the cost for a female of rejecting a bad host plant is very low since she will very soon find another, and therefore females in southern Sweden could afford to be more discriminative. Field evidence supports our impression that suitable grasses are a scarcer resource on Madeira; when searching for *P. aegeria* larvae, it is not unusual to find suitable grass tufts with up to six larvae in different stages. In southern Sweden, larvae are widely spread and during approximately 50 h of searching in the field, two or more larvae have never been found on the same grass tufts, although

about 100 wild larvae were located during this time (C. Wiklund, unpublished data).

Another possibility is that the Swedish population has been somehow constrained to evolving a shorter time lag between mating and oviposition. Such constraints may be lack of genetic variation or some trade-off related to the difference in developmental rates between the populations. The Swedish butterflies have significantly shorter developmental periods (Nylín et al. 1993; Gottthard et al. 1994) which may result in females eclosing as adults with less matured gonads compared to the more slowly developing Madeiran females. This would imply that aspects of juvenile development are involved in a trade-off with the usage of time in the adult stage.

It may be beneficial for females to mate with particular males in any given population but searching for mates is also likely to incur costs. Theoretical models indicate that the cost of searching is a crucial parameter for understanding patterns of mate choice among organisms, and they furthermore predict that when the cost is high, individuals should be less choosy (Real 1990; Reynolds and Gross 1990). Several studies have indeed shown that individual females may become less discriminating when they experience higher costs of searching (Alatalo et al. 1988; Milinski and Bakker 1992; Hedrick and Dill 1993). The results presented here also support this prediction, and the difference between populations in the propensity of females to mate indicates that it has a genetic basis. We suggest that differences in the cost of mate searching are a likely reason why females of the two populations investigated here have evolved different criteria for when to accept a male.

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Communicated by M.A. Elgar