



## Mate acquisition by females in a butterfly: the effects of mating status and age on female mate-locating behaviour

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### ARTICLE INFO

#### Article history:

Received 26 May 2010  
 Initial acceptance 20 July 2010  
 Final acceptance 8 October 2010  
 Available online 13 November 2010  
 MS. number: 10-00361

#### Keywords:

courtship solicitation  
 Lepidoptera  
 life history  
*Pararge aegeria*  
 sexual selection  
 speckled wood butterfly  
 territoriality

In most species, female reproductive success is determined by realized fecundity, which depends on the amount of female reproductive reserves and the availability of time for oviposition. Consequently, selection is likely to favour behaviour in virgin females that increases the likelihood of encountering males and thereby minimizing time without sperm. We used the speckled wood butterfly, *Pararge aegeria*, to test the hypothesis that virgin females increase the probability of encountering males by behaving more conspicuously. We also tested for an effect of age on behaviour, with the prediction that females behave more conspicuously if they remain unmated for a longer period. To do this we conducted controlled behavioural studies in large outdoor cages, comparing the behaviour of young and old, virgin and mated, females. We also assessed the time it took for a male to discover virgin versus mated females. Our results show an effect of age and mating status: old virgin females behaved more conspicuously than young virgin females and mated females, and spent more time in flight and performed more individual flights. Males also discovered virgin females faster than mated females. Furthermore, virgin females did not specifically locate the large sunspot, where perching males are found. Hence, females of *P. aegeria* adjust their behaviour in accordance with mating status and age, making them more likely to encounter a male and thereby maximize their reproductive success. This study underlines the importance of taking the distribution and behaviour of receptive females into account when studying mate-locating behaviour.

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In sexually reproducing species, the acquisition of mates is under strong selection in both sexes. In most species, however, selection to acquire additional matings once mated is expected to be stronger in males than in females. In most insects, male lifetime reproductive success is strongly dependent on the number of matings, resulting in sexually selected male–male competition over mating opportunities. Female reproductive success, on the other hand, is likely to be determined by realized fecundity, which depends on the amount of female reproductive reserves and the availability of time and hosts for oviposition. A female that stays unmated for an extended time will lose valuable time for oviposition, and potentially also reproductive reserves, if mature but unfertilized eggs have to be dumped to keep the physiology of the ovaries undamaged. Consequently, selection is likely to favour female behaviours that increase the likelihood of encountering males and thereby minimizing time without sperm (Rutowski 1984; Wickman & Rutowski 1999). Virgin females can increase the probability of encountering males either by behaving in a more

conspicuous way or by actively locating and approaching males or male territories (Wickman 1986). In contrast, already mated females are expected to behave in a way that reduces the risk of further courtship and lengthy matings in order not to lose valuable time for oviposition (Odendaal et al. 1989; Baguette et al. 1996; McLain & Pratt 1999; Sirot & Brockmann 2001; Gibbs et al. 2005). This has resulted in adaptations to avoid further matings and curtailing male courtship duration, such as mate refusal postures (Obara 1964; Andersson et al. 2000, 2004) and rapid ascending flights by females (Rutowski 1978).

In butterflies, mate-locating behaviour of males can be divided into two main types: ‘perching’ and ‘patrolling’ (Scott 1974; Wiklund 2003). In perching butterfly species, the male sits at some vantage point on the lookout for females that pass by, whereas males of patrolling species fly around in the landscape in the search for mates (Wiklund 2003). As the mating system of species is a result of the interactions between both male and female behaviour, several researchers have pointed out the importance of taking female behaviour into account when studying the evolution of mate-locating behaviour (e.g. Rutowski 1991; Rutowski et al. 1996; Wickman & Rutowski 1999; Kemp 2001; Wiklund 2003). Nevertheless, studies on the behaviour and distribution of receptive females are relatively few. Most studies on courtship

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solicitation behaviour in females, where receptive females actively pursue males or behave in a highly conspicuous way, have been done on patrolling or lekking species (e.g. Rutowski 1980; Rutowski et al. 1981; Wiklund 1982; Wickman 1986, 1992; Wickman & Jansson 1997; Hiroki & Obara 1998; Daniels 2007); however, little is known about the behaviour of receptive females in perching species. Here, the behaviour of females is of utmost importance for the mate location system, since it is basically the females that fly around and search for mates (Wiklund 2003). If females of perching butterfly species try to minimize time spent unmated then two predictions follow: (1) they should display behaviours that increase the likelihood of being detected by perching males, and (2) they should actively locate areas used as male perching sites (Rutowski 1991).

Most female butterflies mate soon after eclosion (Wiklund 2003). The benefit of mating with particular males with specific traits, however, can influence time from eclosion to mating. Mate choice is highly context dependent and theory suggests that when the cost of mate choice increases, choosiness should decrease (Real 1990). Studies have shown that female choosiness is affected by male density (Gotthard et al. 1999) and time stress (Johnstone 1997; Friberg & Wiklund 2007; Larsdotter Mellström et al. 2010). Because the adult life of butterflies is time limited, the cost of mate choice should increase with age: older females should be less choosy than younger females. A third prediction is that the longer a female remains unmated, the more likely selection is to favour an active search for mates (Scott 1973). Even though an active search for mates with increased age has been recorded occasionally (e.g. Crane 1955), there are only a few empirical studies on the influence of age on behaviour in receptive females in butterflies. Females of the pierid butterflies *Eurema daira* (Daniels 2007) and *Eurema hecabe* (Hiroki & Obara 1998) have been shown to solicit matings when they remain unmated for several days.

We used the territorial speckled wood butterfly, *Pararge aegeria*, as a model to study the influence of female behaviour on the mating system. We investigated whether females adapt their behaviour to minimize time without sperm, to maximize time for egg laying and feeding. To test the hypothesis that females behave in a more conspicuous way before first mating than after, we performed controlled experiments in large outdoor cages. Additionally, we measured the influence of age on behaviour, to test the prediction that the longer virgin females remain unmated, the more conspicuously they will behave, which will increase the probability of encountering a mate.

## METHODS

### Study Species

*Pararge aegeria* is a perching butterfly species (Bergman & Wiklund 2009b). The males establish territories in large sunspots on the forest floor, from where they sit on the lookout for females passing by (Davies 1978; Wickman & Wiklund 1983; Bergman & Wiklund 2009b). Territory residency is advantageous because it generates higher mating success (Bergman et al. 2007). Female oviposition sites (the underside of leaves of various species of grass) are not associated with male perching areas (Wickman & Wiklund 1983) and the mechanism of mating success asymmetry between residents and nonresidents has therefore been obscure (Bergman et al. 2007). However, recent studies have indicated an advantage for visual performance when perching in large sunspots (Bergman & Wiklund 2009a). The females are fundamentally monandrous: less than 5% of the females mate more than once in their lifetime (Wickman & Wiklund 1983).

### Experimental Cages

The experiments were done at Kronängen, ca. 100 km south of Stockholm in central Sweden, in a large, semicylindrical, tunnel-shaped cage with a base 16 m long and 8 m wide and a radius to the roof of 4 m. The cage roof had an area of 201 m<sup>2</sup> and was covered with a green tarpaulin. We removed one section of 2 × 2 m and several smaller (0.2 × 0.2 m) sections in the tarpaulin, which created one large sunspot and a mosaic of smaller sun flecks on the cage floor, to create an artificial, open forest habitat.

### Butterfly Rearing

We used a population of *P. aegeria* originating from Madeira, Portugal, reared as a laboratory stock at the Department of Zoology, Stockholm University. The male butterflies were kept at ca. 10 °C until the day of the experiment as were the virgin females used in the experiment; mated females used in trials were mated 1 day before the experiment. The butterflies were brought to Kronängen in coolers and were taken out and released in the cage at the start of each experimental trial.

### Behavioural Observations

These trials were performed during June and July 2009. We performed 51 trials with 20 mated and 31 virgin females. The age of the females ranged from 3 to 49 days, and females were categorized as 'young' when they were less than 10 days of age, and as 'old' if they were older than 10 days. The relatively wide range of female age within categories was necessitated because the experiments could only be performed during sunny weather, which meant that females often had to spend some days (between 3 and 49) in the 10 °C room before the weather made experimental trials possible. In total, the sample sizes for the four categories of females were 10 young virgin females, seven young mated females, 21 old virgin females and 13 old mated females. We introduced a female into the cage and recorded, by taking notes, the time spent flying and the time spent resting during 20 min. When the female alighted, we recorded whether she landed in the large sunspot, in a small sunspot, in the shade or on the cage net. If the female oviposited, we recorded where this occurred: in the large sunspot, in a small sunspot or in the shade.

### Detection by Males

These trials were performed during August 2009. We conducted 31 trials with 16 mated and 15 virgin females. In this experiment we used only 'old' females, as the previous behavioural experiment had shown that the behavioural differences between virgin and mated females were only accentuated among the category of 'old' females (see Results), and the age of the females ranged from 10 to 56 days. First, we introduced a male into the cage and allowed him to establish himself as a resident of the large sunspot territory. We then introduced a female in a small sunspot, approximately 3–4 m from the large sunspot. When the female had warmed up, we measured the time elapsed between female take-off and the time when she was detected and pursued by the male. Additionally, we recorded where in the cage the male detected the female. If the female remained undetected after 30 min the trial was ended.

### Statistical Analysis

To test for differences in time spent flying and number of flights we carried out two-factorial ANOVAs with mating status (mated/virgin) and age category (young/old) as factors. Females less than

10 days old were categorized as young and females more than 10 days were categorized as old. We also carried out a general linear model, GLM, with mating status (mated/virgin) as a categorical factor and age as a continuous predictor.

The data on the proportion of landings in the shade were not normally distributed, owing to several zero counts. To test this variable for differences between mated and virgin females the nonparametric Mann–Whitney  $U$  test was applied. In the analysis of the probability of landing in a large sunspot, we calculated the proportion of the landings that were made in the large sunspot. Since this variable did not meet the assumption of normality it was square-root transformed prior to the application of a two-way ANOVA.

To test whether female mating status influenced time to detection by males we used Cox proportional hazards regression (Cox 1972), which is appropriate for time to event data such as detection times (Fox 2001).

## RESULTS

### Time Spent Flying

The effect of mating status on time spent flying was dependent on age. There was a difference in time spent flying between mated and virgin females, but only among old females (ANOVA: mating status\*age group:  $F_{1,47} = 12.21$ ,  $P = 0.001$ ; GLM: mating status\*age:  $F_{1,47} = 23.87$ ,  $P < 0.0001$ ; Fig. 1a). In virgin females, individuals older than 10 days spent approximately 60% of their time in flight, while individuals younger than 10 days spent significantly less (approximately 20%) of their time in flight (Fig. 1a). In mated females, individuals both older and younger than 10 days spent ca. 20% of their time in flight (Fig. 1a).

### Flights and Landings

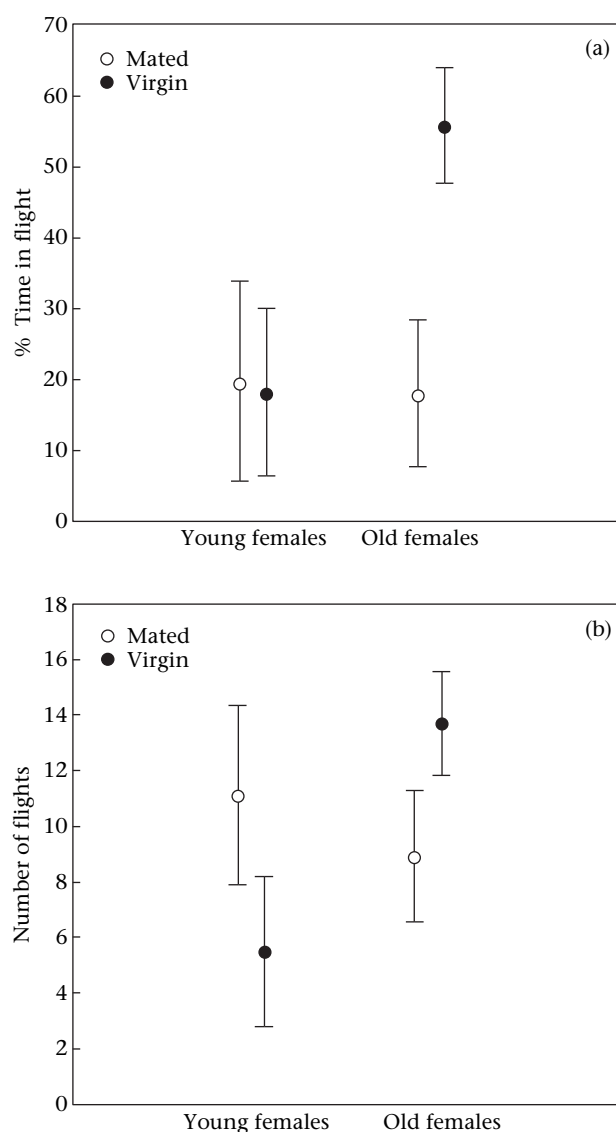
There was also an age-dependent effect of mating status on the total number of flights (ANOVA: mating status\*age group:  $F_{1,47} = 16.41$ ,  $P < 0.001$ ; Fig. 1b). Virgin females older than 10 days made on average 13.7 flights during the 20 min trials while virgin females younger than 10 days made only 5.5 flights (Fig. 1b).

Mated females landed in the shade more often than virgin females (two-tailed Mann–Whitney  $U$  test:  $Z = 3.42$ ,  $N_{\text{mated}} = 19$ ,  $N_{\text{virgin}} = 31$ ,  $P = 0.0006$ ), and 74% of the mated females landed once or several times in the shade while only 26% of the virgin females landed in the shade.

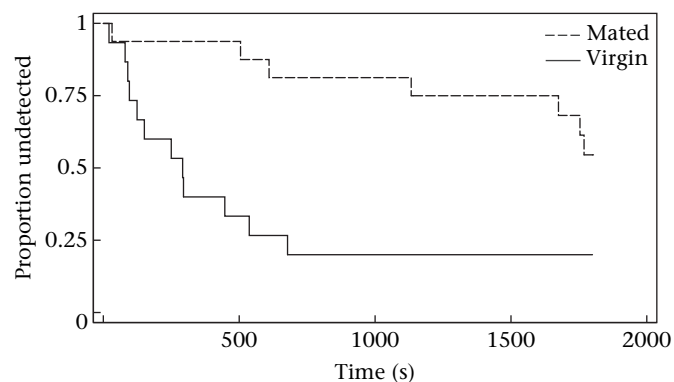
There were no differences between mated and virgin females in the probability of alighting in the large sunspot (ANOVA:  $F_{1,47} = 0.06$ ,  $P = 0.81$ ). Furthermore, there was no interaction between age and the probability of landing in the large sunspot (ANOVA: mating status\*age:  $F_{1,47} = 1.11$ ,  $P = 0.30$ ).

### Detection by Males

Virgin females were detected more quickly than mated females (Cox regression: effect of mating status:  $Z = 2.66$ ,  $N_{\text{mated}} = 16$ ,  $N_{\text{virgin}} = 15$ ,  $P = 0.008$ ; Fig. 2). The mean detection time for mated females was 23 min and 59 s, while the mean detection time for virgin females was 9 min and 24 s. Eight of the 16 mated females and three of the 15 virgin females remained undetected after 30 min. For 18 of the 20 females that were detected and pursued by a male during the experiment, we could also note the location in the cage where the female was detected. In 16 of these 18 trials the female was detected when she entered the large sunspot, resulting in the perching male flying up and initiating a pursuit of the female. In the other two cases the females were detected when the male



**Figure 1.** (a) The percentage of time spent flying and (b) the number of flights by females of the speckled wood butterfly, *Pararge aegeria*, during a 20 min trial.  $N_{\text{young mated}} = 7$ ;  $N_{\text{young virgin}} = 10$ ;  $N_{\text{old mated}} = 13$ ;  $N_{\text{old virgin}} = 21$ . Old females: females over 10 days; young females: females less than 10 days. Values are given as mean  $\pm$  95% confidence intervals.



**Figure 2.** The difference between mated ( $N = 16$ ) and virgin ( $N = 15$ ) females in the probability of being detected by a male. If the female remained undetected for 1800 s (30 min) the trial was ended.

was making a scouting flight in the cage, and were consequently detected outside the large sunspot area.

### Egg Laying

Fourteen of the 20 mated females laid between one and six eggs (mean = 2.4) during the 20 min trials, in total 34 eggs. Of these 34 eggs, 30 were laid in the shade, three were laid in the large sunspot and one was laid in a small sunspot. There was no effect of age on the probability of ovipositing: younger females were as likely to lay eggs as older ones (simple linear regression:  $F = 2.77$ ,  $P = 0.11$ ).

## DISCUSSION

We have shown that females of *P. aegeria* behave in a way that is consistent with the idea that females are selected to minimize time spent unmated: older virgin females were more active and spent more time in flight, and made more individual flights than mated and young virgin females, and so behaved more conspicuously. We have also shown that this conspicuous behaviour made the older virgin females easier to detect by a male. Hence, females minimize the time spent unmated and maximize the postmating time available to allocate to egg laying and feeding.

There was a difference between mated and virgin females in flight activity that was contingent on female age. As *P. aegeria* females start maturing eggs prior to being mated (Berger et al. 2008), not only time costs but also potential resource costs of staying unmated are likely to increase with female age. Old virgin females spent approximately 55% of their time in flight, while young virgin and mated females spent only 20% of their time in flight (Fig. 1a). This study also confirms that matings in *P. aegeria* are initiated by a female being detected in flight by a perched male (cf. Bergman et al. 2007). In this study 90% (16 of 18) male–female interactions were initiated by a flying female being detected by a perching male. Hence, an increase in flight activity strongly affects the probability that a female will be detected by a male. Accordingly, the higher flight activity shown by old virgin females meant that they were detected sooner by the territorial male, and this can be regarded as a behavioural mechanism by females to minimize the time spent unmated.

In a perching butterfly species, such as *P. aegeria*, the males sit at a vantage point on the lookout for passing females. When a female comes within the visual range of the male he immediately takes off and intercepts her; upon perceiving that she is being pursued, the female rapidly alights, whereupon the male alights close by and proceeds to perform the species-specific courtship behaviour, followed by mating if the female is receptive (Wiklund 2003). Our results confirm earlier studies (Bergman et al. 2007) that a majority of the matings are preceded by the female entering the large sunspot used as a perching site by the male. This also reflects the mating success asymmetry between resident and nonresident males, where resident males achieve approximately twice as many matings (Bergman et al. 2007). If females in perching species adjust their behaviour to minimize the time spent unmated they would be expected to search for and enter areas used as perching sites by males (cf. Wickman 1986). However, our results do not support the idea that virgin females have a preference for flying into larger sunspots where males are found. Virgin females did not alight more often than mated females in the large sunspot in this study, consistent with findings by Bergman et al. (2007). A possible explanation for why females do not appear to seek out male perching sites may be that sunspot territories and perching males are rather well spread out in natural forest habitats, which means that females behaving conspicuously will be rapidly detected by males and so do not 'need

to' seek out male perching sites in a manner that has been observed in lekking species (Wickman 1986; Wickman & Jansson 1997).

These results, which show a strong effect of age on the behaviour of virgin females, are novel. Sexual selection theory suggests that mate choice should be relaxed when the cost of mate choice increases (Real 1990). An increased age means an increased cost of being virgin, since the time left for laying eggs and feeding is diminishing. Friberg & Wiklund (2007) showed that receptive females of the pierid butterfly *Leptidia reali* become more prone to accept a courting male when they get older. In nocturnal and crepuscular lepidopterans, virgin females are known to change their calling (use of pheromonal signals) with increasing age, and start calling earlier (Webster & Carde 1982; Delisle 1992; Gemeno & Haynes 2000), a pattern that has been described as an adaptation to increase the probability of attracting mates (Swier et al. 1977; Delisle 1992). An age-related change in mating behaviour can also be an effect of a general pre-reproductive period, where females delay mating until their ovaries mature (e.g. Kemp 2001). However, previous studies have shown that females of *P. aegeria* are able to mate on the same day as they eclose from the pupa (Gotthard et al. 1999). Hence, the age-related behavioural change in virgin females is not an effect of a prereproductive maturation period, but more likely an adaptation to minimize the cost of remaining unmated for a long time.

In our experiments, 70% of the mated females oviposited during the 20 min trial, and 88% of the eggs were laid in the shade, which is very much in line with earlier studies of female egg-laying behaviour. Wickman & Wiklund (1983) followed mated *P. aegeria* females in the field and found that 90% of the eggs were laid in shady places. Like Wickman & Wiklund (1983), we can conclude that the distribution of eggs does not correlate with the location of male territories and resident males do not have an advantage of being close to female eclosion sites.

This study underlines the importance of female behaviour for mate locating in territorial species. Females of *P. aegeria* adjust their behaviour in accordance with mating status and age, to maximize their reproductive success. However, they do not specifically locate areas used as perching sites, which would be predicted in a species where the males are territorial. Instead, they increase their flight activity and thereby also increase the probability of being detected by a male. Hence, we conclude that the fitness benefit for males of defending larger than average sunspots is not caused by a behavioural preference by females to enter these sunspots. Females utilize sunspots for thermoregulation when flying in open forest habitats, but with no preference for sunspot size and males utilize the larger sunspots because they are beneficial for visual performance.

We believe that adaptations similar to those found here, where females adapt their behaviour according to their own mating status and age, might be common in other species and that further studies are needed to understand fully the evolution of mate-locating behaviours in insects.

### Acknowledgments

We thank Bertil Borg and two anonymous referees for helpful comments on the manuscript. This study was supported by grants from the Swedish Research Council to C.W. and to K.G.

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