



## Mate location behaviour of the butterfly *Pararge aegeria* in woodland and fragmented landscapes

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Visually cued mate location behaviour in insects such as butterflies is typically classified by ‘wait or seek’ dichotomies. Perching males adopt a sit-and-wait strategy at a particular spot rising to intercept passing females (which is often done in an aggressive territorial way), whereas patrolling males are permanently on the wing searching for females. The potential influence of changes in landscape caused by habitat fragmentation on mate location behaviour has only rarely been addressed. We investigated this behaviour among populations of the speckled wood butterfly, *Pararge aegeria*, living in continuous woodland versus highly fragmented agricultural landscape with hedgerows and small patches of woodland. In the latter landscape males showed higher levels of aggressive fast take-offs (an indicator of territorial perching), but also higher levels of displacement (an indicator of patrolling). In an independent census, behaviour intermediate between perching and patrolling was much more frequent in the agricultural landscape than in the woodland landscape. Our results suggest that the dichotomy of perching versus patrolling as typically observed in woodland fades away in highly fragmented agricultural landscape. We discuss our results in relation to differences in densities and thermal properties of both types of landscape.

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Variation in visually cued mate location behaviour in insects has widely been classified using ‘wait or seek’ dichotomies (e.g. Odonata: Heinrich & Casey 1978; Thysanoptera: Crespi 1988; Hymenoptera: Alcock & Houston 1996). In butterflies, Scott (1974) defined the variants as perching and patrolling, respectively. Perching males adopt a sit-and-wait strategy at a particular spot rising to intercept passing females, whereas patrolling males are permanently on the wing searching for females. As male butterflies spend most of their active time locating mates (Shreeve 1992), different mate location strategies may have consequences for their local distribution and daily movements. Some butterfly species are exclusive patrollers and others predominantly perchers, whereas in some other species both behavioural strategies occur (Dennis & Williams 1987; Wickman 1988, 1992; Shreeve 1992; Van Dyck 2003). Dennis & Shreeve (1988) argued that patrolling is the ancestral behaviour; the evolution of perching depends on habitat structure, because the presence of distinct landmarks (e.g. hills, host plant clumps

and sunlit patches) is essential for a perching strategy. Male butterflies can also show aggressive, territorial behaviour. Although territoriality is most often connected to perching, they are not synonymous. Some species show perching without any aggression towards conspecific males (Shreeve 1992). Assuming that territorial behaviour is costly, the territory economics hypothesis predicts that monopolizing a perch with aggressive behaviour is viable only under low to moderate male density (Parker 1978; Thornhill & Alcock 1983; Rutowski 1991). In other words, high population density would favour nonterritorial patrolling (Scott 1974; Willmer 1991).

Although alternative mate location strategies have attracted much attention (Thornhill & Alcock 1983; Rutowski 1991; Wiklund 2003 and references therein), the potential influence of changing landscape structures on mate location behaviour has only rarely been addressed. Habitat fragmentation provides a typical framework for studies on changes in dispersal behaviour (e.g. Hill et al. 1996; Thomas et al. 1998), but other behaviours, including mate location, may also be changed (Van Dyck & Matthysen 1999). Habitat fragmentation may simply affect densities and, hence, frequencies of territorial perching and nonterritorial patrolling males in systems where both strategies occur. However, things can be more

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complicated in fragmented landscapes when conditions favouring one of the strategies change as well, but not necessarily in parallel with changes in density. Hence, habitat fragmentation may alter cost–benefit balances of alternative mate location strategies.

We tested for differences in mate location behaviour among populations of the speckled wood butterfly, *Pararge aegeria* L., living in continuous woodland versus highly fragmented agricultural landscape with some small patches of woodland and hedgerows. Males either perch in an aggressive territorial way on a sunlit patch on the forest floor, or they patrol by flying from one sunlit patch to the other through more shady conditions (Wickman & Wiklund 1983; Shreeve 1987; Van Dyck 2003 and references therein). Under relatively cool ambient conditions, as in spring or in closed shaded coniferous woodland, the value of defending a sunlit patch is high and territorial perching is then observed as the dominant strategy (Wickman & Wiklund 1983; Shreeve 1984, 1987). Furthermore, in these heliotherms patrolling flights are constrained by local climatic conditions, which are the result of both the weather and the habitat structure (Dennis & Shreeve 1988; Wickman 1988). Flight duration increases in relation to air temperature, convective body cooling being slower at high temperatures when the difference between optimal body temperature and air temperature is less (Shreeve 1984; Van Dyck & Matthysen 1998).

From a speckled wood's perspective, highly fragmented landscapes are likely to provide a different template for mate location behaviour than continuous woodland, for three reasons that we investigated in this study. First, densities per unit of habitat are likely to be higher in fragmented landscapes. Woodland represents a continuous area in terms of resources in general and for mate location sites (e.g. sunlit patches) in particular. In highly fragmented landscapes, however, resources are restricted to 'lines' (e.g. hedgerows) and 'bits' (e.g. patches of woodland) which may lead to a concentration of individuals (Chardon et al. 2003). In other words, densities per unit of habitat are expected to be higher in fragmented landscapes. Hence, in line with the territory economics hypothesis, we predicted less perching but more patrolling for fragmented landscapes. Second, thermal conditions differ considerably between woodland and hedgerows (or patches of woodland) in highly fragmented agricultural landscapes. Measurements of ambient temperature at suitable *P. aegeria* habitat during flight activity showed that average and maximal daily temperatures are higher in fragmented agricultural landscapes than in woodland (T. Merckx, S. Van Dongen, E. Matthysen & H. Van Dyck, unpublished data). So, from a thermal constraint hypothesis, we predicted a shift towards higher levels of local mobility with fragmentation. To reduce the impact of convective cooling in open fragmented landscapes, butterflies should seek shelter and fly closer to the vegetation than in woodland. Finally, the occurrence of landmarks for mate location may vary with landscape structure. Sunlit patches are landmarks where territorial perching males settle and patrolling males fly from one sunlit patch to the other. There are no oviposition or feeding sources in such a patch: it is only a spot clearly delineated by solar

radiation penetrating through holes in the canopy. In fragmented agricultural landscapes, a considerable proportion of *P. aegeria* habitat occurs as relatively small lines such as hedgerows and sunken roads. Clearly delineated sunspots are rare and a large part of the hedgerow is irradiated. Under such conditions males are predicted to make longer flights than typical territorial perchers do in woodland. In woodland, the majority of males show either a clear perching or patrolling behaviour, although a minority may have an intermediate behaviour (Van Dyck et al. 1997b). We tested these predictions using data from behavioural observations and mark–release–recapture programmes in woodland and a highly fragmented agricultural landscape in central Belgium.

## METHODS

### Study Species

The speckled wood is a temperate-zone satyrine butterfly (Lepidoptera: Nymphalidae). Throughout Europe, it is primarily a woodland species (Tolman & Lewington 1997). In the northern parts of the European distribution it is confined to woodland, whereas more to the south it also occurs in more fragmented landscapes with some woodland aspects such as agricultural landscapes with hedgerows and small patches of woodland (Dover & Sparks 2000; Merckx et al. 2003). Honeydew is the main adult feeding resource and several grasses are used as larval host plants (Shreeve 1986). In woodlands, females lay eggs singly on isolated grass plants that grow under shaded, rather wet conditions (Wiklund & Persson 1983). In Belgium, *P. aegeria* is a common and widespread species (Maes & Van Dyck 1999).

### Study Areas

We studied male mate location behaviour of *P. aegeria* in central Belgium at four different sites representing the two contrasting landscapes: woodland and a highly fragmented agricultural landscape. Meerdaalwoud (1255 ha) and Bos ter Rijst (280 ha) represent closed landscapes dominated by oak woodland. Hoegaarden (603 ha) and Rillaar (361 ha) represent open, agricultural landscapes. The latter type of landscape was composed mainly of intensively used fields and pastures (Hoegaarden: 85% of the total area; Rillaar: 67%), urban areas (4% and 20%, respectively), tiny patches of woodland (3%) and sunken roads, which are eroded agricultural tracks, bordered by steep grassy and woody banks (7% and 3%, respectively). The sunken roads are < 0.5 m to several metres deep, 5–25 m wide (Gulinck et al. 1991) and from 80 (but sometimes with gaps of some metres) to 1370 m long.

### Behavioural Observations

In spring and summer 2002, we observed the behaviour of 62 *P. aegeria* males under fine weather conditions that allowed butterfly activity: 26 in the woodland landscape

(Meerdaalwoud: 17; Bos ter Rijst: 9) and 36 in the agricultural landscape (Hoegaarden: 22; Rillaar: 14). During an observation session, an individual male was followed for 5 min. Different activities (flying, basking and resting) were recorded with a minidisk (Sony MZ-N710). When the male took flight, we also recorded take-off speed (slow versus fast) and flight altitude ( $\pm 0.5$  m). Labelled sticks were placed at positions where individuals rested or changed flight direction. After the observation session, we measured the positions of all sticks and distances between sticks, with a laser instrument (Leica Disto classic<sup>3</sup>, Leica Geosystems AG, Gallen, Switzerland). Measurements were stored on schematic drawings of the flight tracks. We calculated the following measures for each observation session: proportion of time spent flying, number of displacements, (proportional) number of fast take-offs, mean altitude of flight and mean and total distance moved. For each observation session, we also recorded ambient temperature ( $\pm 0.1^\circ\text{C}$ ) and relative wind velocity (Beaufort scale). After the observation session, individuals were captured by hand net, and killed and stored at  $-18^\circ\text{C}$  (for other studies). Individuals that did not adopt mate location behaviour (but exclusively foraged or rested) were excluded from analyses. As a result, analyses were run on 50 individuals. During behavioural observations, ambient temperature was lower in the agricultural than in the woodland landscape ( $19.6 \pm 0.3^\circ\text{C}$  versus  $23.1 \pm 0.7^\circ\text{C}$ ;  $t$  test:  $t_{25,3} = 4.74$ ,  $P < 0.0001$ ), and mean wind force was higher in the agricultural than in the woodland landscape (Fisher's exact test:  $P = 0.006$ ).

### Mark–Release–Recapture Data

We collected mark–release–recapture (MRR) data during six surveys (8–13 August 2000) at one agricultural landscape area (Rillaar) and during five surveys (23–29 August 2000) at one woodland landscape area (Meerdaalwoud). Surveys were conducted only during periods with fine weather conditions. To obtain comparative sampled areas, we did MRR experiments in a part of each study landscape: 81 ha/4.9 km and 138 ha/7.4 km (area/perimeter ratios of Rillaar and Meerdaalwoud 165.3 and 186.5, respectively). The largest recordable movements were 1550 m and 2200 m, respectively. During each survey, we checked the whole area for males and females, and altered the trajectory regularly. We captured butterflies by hand net and marked them individually at first capture with unique numbers on the ventral side of the left hindwing with fine, nontoxic, permanent markers (Staedtler Lumocolor 313, Staedtler, Nürnberg, Germany). On first capture, butterflies were released at the site of capture. For second captures, butterflies were collected by hand net, and killed and stored at  $-18^\circ\text{C}$  (for other studies). For each capture we recorded data, time, exact position and mark number. Before each capture, we observed the mate location behaviour for several minutes, to classify a male as (1) percher, (2) patroller or (3) showing a behaviour intermediate between perching and patrolling (cf. method applied by Van Dyck et al. 1997b). Distances

of movements between capture and first recapture were measured on detailed maps of the study sites. Distances were log transformed prior to analyses.

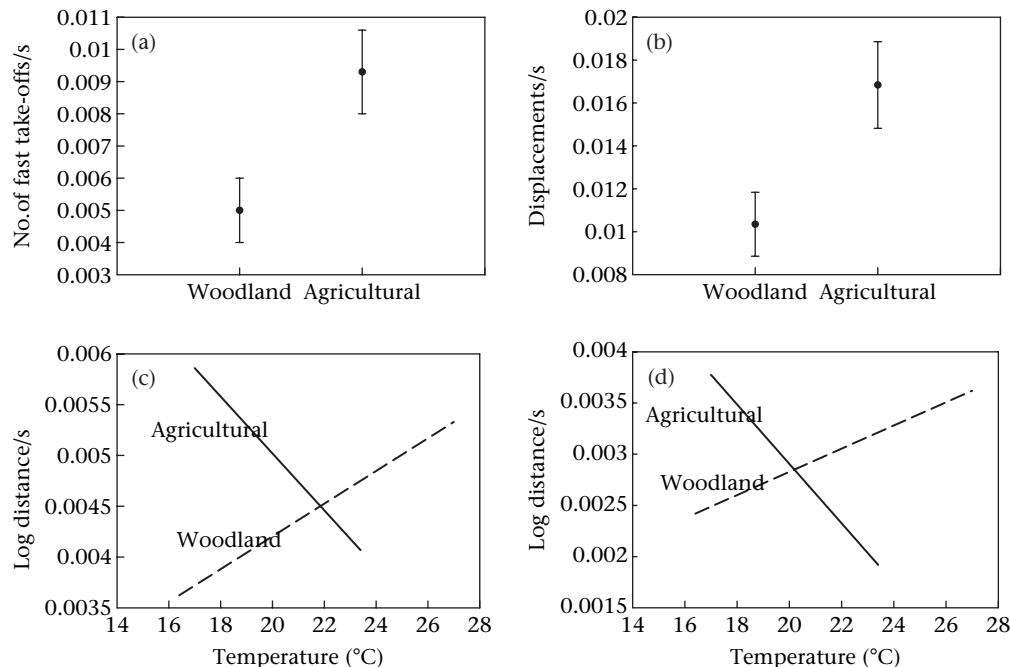
### Statistical Analyses

We used mixed regression models (Proc Mixed, SAS 2001) to analyse the behavioural data. All time, length and number variables were expressed as proportions of total observation time. Since we were mainly interested in the effects of landscape (open versus closed) and of ambient temperature, we used these variables and their interaction as fixed effects in the models. As two study sites represent each landscape structure, 'site' nested within 'landscape' was used as a random effect in each model. As data were collected during two periods (period 1: end of April–start of June; period 2: mid August), we also included period as a random effect. Backward selection of nonsignificant factors was done to obtain a final model. All final models had normally distributed residuals. Fisher's exact tests (Proc Freq, SAS 2001) were used to compare frequency distributions between woodland and agricultural landscapes for mean flying height ( $< 1.5$  versus  $> 1.5$  m).

For the analyses of the MRR data we used mixed regression models (Glimmix macro, SAS 2001). Since tracked distances did not follow a normal distribution, we reduced this information to a binomial variable: movements  $< 50$  m or  $> 50$  m. Landscape (woodland versus agricultural landscape) was used as a fixed effect. Next, mixed regression models (Proc Mixed, SAS 2001) were run on the subsample of males that covered distances of more than 50 m, with tracked distance as the dependent variable. Again, landscape (woodland versus agricultural landscape) was used as a fixed effect. Encounter rate of butterflies was used as a proxy for butterfly density among sites. We calculated this rate by dividing the number of observed individuals by the total observation time for each MRR survey day. Next, we compared mean values between the study sites or landscapes (Proc Ttest, SAS 2001). Frequencies of three types of mate location behaviour (perching, patrolling and intermediate behaviour) within the MRR-survey were compared between woodland and agricultural landscapes ( $\chi^2$ , Proc Freq, SAS 2001).

## RESULTS

Densities of both sexes, expressed as encounter rate within suitable habitat, were significantly higher in the agricultural landscape than in the woodland landscape (0.19 versus 0.13 individuals/min;  $t_{8,89} = -3.26$ ,  $P = 0.010$ ). In the agricultural landscape, males performed significantly more fast take-offs ( $\bar{X} \pm \text{SE} = 2.9 \pm 0.4$ , range 0–8 versus  $1.5 \pm 0.3$ , range 0–5 per 5 min) but also more displacements ( $5.2 \pm 0.6$ , range 1–16 versus  $3.2 \pm 0.5$ , range 1–7 per 5 min) than did males in the woodland landscape (Fig. 1a, b, Table 1). The frequency of fast take-offs also tended to increase with increasing ambient temperature. Males from the agricultural landscape covered larger total



**Figure 1.** (a) Number of fast take-offs ( $\bar{X} \pm SE$ ), (b) number of displacements ( $\bar{X} \pm SE$ ), (c) total displacement length and (d) mean displacement length of male *P. aegeria* butterflies in a woodland landscape ( $N = 20$ ) and in a fragmented agricultural landscape ( $N = 30$ ) under natural conditions, proportional to observation time.

distances during the behavioural observation session than conspecifics from the woodland landscape ( $\bar{X} \pm SE = 48.2 \pm 6.9$  m, range 3.5–173.5 m versus  $32.4 \pm 5.1$  m, range 3.3–103.4 m). However, this difference switched at relatively high ambient temperatures (Fig. 1c, Table 1). Similarly, the mean displacement or step length was larger for males in the agricultural landscape than for woodland males at low ambient temperatures, but the relation reversed at relatively high ambient temperatures (Fig. 1d, Table 1). Landscape had no effect on the proportion of time spent flying among males, but males flew more

frequently at low heights in the agricultural landscape than in the woodland landscape (Fisher's exact test:  $P = 0.008$ ).

At the agricultural landscape site, we captured 158 males and 47 females; 30.4% of the males were recaptured, but no females were. At the woodland landscape site, we captured 105 males and five females; 37.1% of the males and one female were recaptured. Females therefore had lower recapture frequencies than males, especially in the agricultural landscape site ( $\chi^2_1 = 18.64$ ,  $P < 0.0001$ ). Overall recapture percentages (i.e. for both sexes) and the proportion of mobile ( $\geq 50$  m) to sedentary ( $< 50$  m) males did not differ with landscape structure. Within the subsample of mobile males, tracked distances did also not differ between the landscape types.

The frequency of males showing pure territorial perching behaviour was significantly lower in the agricultural landscape than in the woodland landscape (based on first capture data; 42 versus 80%;  $\chi^2_1 = 37.05$ ,  $P < 0.0001$ ). Mate location behaviour intermediate between perching and patrolling was relatively rare in the woodland landscape, but much more common in the agricultural landscape (10 versus 48%;  $\chi^2_1 = 40.82$ ,  $P < 0.0001$ ).

## DISCUSSION

Our study showed significant differences in the mate location behaviour of male *P. aegeria* butterflies living in a woodland landscape versus a highly fragmented agricultural landscape. In the latter landscape, males more frequently performed fast take-offs from a resting posture than in the woodland landscape. Such take-offs are typically associated with territorial perching (cf. Rutowski 1991

**Table 1.** Results of mixed regression models (Mixed procedure, SAS 2001) for the proportional number of fast take-offs and displacements and total and mean displacement length in relation to the landscape of origin of male *P. aegeria* butterflies (woodland or fragmented agricultural landscape) and ambient temperature at the start of the observation

| Variable                  | Effect                         | df      | F     | P     |
|---------------------------|--------------------------------|---------|-------|-------|
| Number of fast take-offs  | Landscape                      | 1, 46   | 10.22 | 0.003 |
|                           | Temperature                    | 1, 46.6 | 3.72  | 0.060 |
| Number of displacements   | Landscape                      | 1, 46   | 5.76  | 0.021 |
|                           | Temperature                    | 1, 46.2 | 0.54  | 0.47  |
| Total displacement length | Landscape                      | 1, 46   | 7.75  | 0.008 |
|                           | Temperature                    | 1, 46   | 0.58  | 0.45  |
|                           | Landscape $\times$ temperature | 1, 46   | 6.97  | 0.011 |
| Mean displacement length  | Landscape                      | 1, 45.8 | 8.15  | 0.006 |
|                           | Temperature                    | 1, 45.9 | 1.51  | 0.23  |
|                           | Landscape $\times$ temperature | 1, 45.8 | 8.57  | 0.005 |

and references therein). Since densities per unit of habitat were higher in agricultural landscape, this observation is in contrast to the territory economics hypothesis and our first prediction of more patrolling rather than perching in the fragmented landscape. On the other hand, agricultural landscape males made more and wider displacements, associated with patrolling, than woodland males. This result is in line with the thermal constraint hypothesis and the second prediction of higher mobility in the fragmented landscape; during observations, however, ambient temperature was lower in the agricultural landscape, so that the assumed higher average ambient temperature is not likely to explain the difference. In the independent census, we found in the same vein a much higher frequency of behaviour intermediate between perching and patrolling in the agricultural landscape than in the woodland. This suggests that the clear dichotomy of perching versus patrolling as typically observed in woodland (Van Dyck 2003 and references therein) fades away to some extent in a highly fragmented, agricultural landscape.

In earlier studies on *P. aegeria* the vast majority of males could be classified as either percher or patroller (Davies 1978; Wickman & Wiklund 1983; Shreeve 1987; Van Dyck et al. 1997a, b). Males are consistent in adopting one of the two strategies, although switches may occur (Van Dyck et al. 1997b). In addition to males switching, we observed that some males also combine traits of both strategies into intermediate mate location behaviour. Fischer & Fiedler (2001) showed in another butterfly that aggressive, territorial males also used a flexible combination of perching and patrolling. Our study shows that the degree to which *P. aegeria* males do so depends on the type of landscape.

Although we found clear differences in mate location behaviour with landscape, the underlying mechanism requires further analysis. Mate location strategies have been described in relation to demography, but in many ectotherms (including butterflies) mate location behaviour is strongly affected by thermal conditions (Willmer 1991). Wickman (1985, 1988) concluded for two other butterflies that population density is of small, often negligible, importance for determination of mate location behaviour.

Fast take-offs from a resting posture are facilitated at higher temperatures (Berwaerts & Van Dyck 2004). We found a trend towards increased frequency of fast take-offs with increasing ambient temperature. In an open agricultural landscape, ambient temperature is typically higher than in deciduous woodland where there is a cooler, more buffered microclimate (T. Merckx, S. Van Dongen, E. Matthysen & H. Van Dyck, unpublished data). However, the influence of wind by convective cooling can be much more severe along a hedgerow in open landscape than on a sunlit patch in woodland (T. Merckx, S. Van Dongen, E. Matthysen & H. Van Dyck, unpublished data). In line with this, we observed that males more frequently flew low down, close to the vegetation, which helps to avoid convective cooling (T. Merckx, S. Van Dongen, E. Matthysen & H. Van Dyck, unpublished data). In two other butterflies, individuals compensated for higher levels of wind speed, and hence convective cooling, by flying

closer to structures that provided shelter (Merckx & Van Dyck 2002).

The higher frequency of intermediate mate location behaviour in the agricultural versus woodland landscape can be explained from an adaptive point of view. The combination of aggressive territoriality and movements could permit males in more linear, relatively narrow landscape structures to adopt a kind of 'customs strategy' towards conspecific males and females. Males would thus be able to keep an entire section of a hedgerow under surveillance. The underlying assumption is that females in an agricultural landscape fly especially along or in hedgerows and sunken roads rather than through the open space. Circumstantial evidence of this comes from censuses where we collected females in this landscape (T. Merckx, personal observation). Furthermore, we have experimentally shown that females originating from an agricultural landscape have lower propensities to cross woodland–open space boundaries than do females from a woodland landscape (Merckx et al. 2003).

On the other hand, the higher frequency of intermediate mate location behaviour in the agricultural than in the woodland landscape could be nonadaptive and related to physical, optical differences in the occurrence of sunlit patches with landscape structure. These landmarks for mate location are more clearly delineated in woodland, where solar radiation penetrates through holes in the canopy; in a fragmented agricultural landscape such clearly delineated sunspots are scarcer and a considerable proportion of the linear habitat structures are completely irradiated. Under such conditions, males cannot use the contrast of sunshine and shade as a physical border of a territory. In woodland, males follow sunlit patches when patches move during the day, indicating that only the simple light–shade contrast is used rather than particular vegetation structures per se. This nonadaptive, constraint explanation is obviously not mutually exclusive with the former explanation.

In conclusion, our study illustrates that behavioural consequences of habitat fragmentation are not limited to, for instance, dispersal, but behaviours related to reproduction such as mate location may also change. There are no reasons to believe that such changes are unique to butterflies.

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