

# The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies

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As landscapes change, mobility patterns of species may alter. Different mechanistic scenarios may, however, lead to particular patterns. Here, we tested conflicting predictions from two hypotheses on butterfly movements in relation to habitat fragmentation. According to the resource distribution hypothesis, butterflies in more fragmented landscapes would have higher levels of mobility as resources are more scattered. However, these butterflies could have lower levels of mobility as they experience 'hard' habitat boundaries more frequently (i.e. higher crossing costs) compared with butterflies in landscapes with continuous habitat; i.e. the behaviour-at-boundaries hypothesis. We studied movements, habitat boundary crossing and habitat preference of laboratory-reared individuals of *Pararge aegeria* that originated from woodland and agricultural landscapes, by using an experimental landscape as a common environment (outdoor cages) to test the predictions, taking into account sexual differences and weather. Woodland butterflies covered longer distances, were more prone to cross open–shade boundaries, travelled more frequently between woodland parts of the cages and were more at flight than agricultural butterflies. Our results support the behaviour-at-boundaries hypothesis, with 'softer' boundaries for woodland landscapes. Because the butterflies were reared in a common environment, the observed behavioural differences rely on heritable variation between populations from woodland and agricultural landscapes.

**Keywords:** dispersal; movements; habitat exploration; fragmentation; butterflies

## 1. INTRODUCTION

As habitats become more fragmented, changes in habitat patch geometry and quality may affect the costs and benefits of dispersal, resulting in changed dispersal rates among differently fragmented landscapes (Thomas 2000). If a continuous distribution of resources has broken up to a scattered distribution, responses towards higher or lower mobility can be expected depending on the spatial scale of fragmentation, or the spread of resources, relative to the maximum range of exploration and dispersal of a species (Van Dyck & Matthysen 1999). Theoretical models (e.g. Leimar & Norberg 1997; Olivieri & Gouyon 1997) and indirect empirical evidence from changes in flight morphology (e.g. Dempster 1991; Thomas *et al.* 1998) have suggested evolutionary responses as a result of selection on mobility in relation to landscape structure.

More recently, behavioural aspects of dispersal have received more attention (e.g. Jonsen & Taylor 2000; Conradt *et al.* 2001; Bowman *et al.* 2002; Hanski *et al.* 2002) and several studies suggest a direct relation between variation in behavioural responses at habitat boundaries and variation in dispersal (e.g. Haddad 1999; Schultz & Crone 2001; Berggren *et al.* 2002). Ries & Debinski (2001) showed that a less mobile habitat specialist butterfly returned more frequently at habitat boundaries than did a more mobile habitat generalist. Moreover, the specialist responded strongly to different types of boundary,

whereas the generalist responded only to boundaries of high contrast. At the intraspecific level, returning behaviour at boundaries occurred more frequently in a highly fragmented habitat network compared with a more aggregated network in the localized butterfly *Proclissiana eunomia* (Schtickzelle & Baguette 2003).

In this paper, we compare movements and behaviour of speckled wood butterflies (*Pararge aegeria* L.) from differently fragmented landscapes—woodland versus agricultural landscape—in an experimental common environment consisting of large outdoor cages. Our main purpose is to test predictions on adult butterfly mobility that follow from a resource distribution hypothesis versus a behaviour-at-boundaries hypothesis. For butterflies, the presence of suitable egg-laying sites is an important habitat characteristic. For *P. aegeria* in agricultural landscapes, habitat occurs in the form of hedgerows and tiny woodlots, and will be much more fragmented than the corresponding habitat in woodlands. One might then predict higher mobility in agricultural landscapes, for instance a higher incidence of long flights, as an adaptation to the scattered resource distribution (Taylor & Merriam 1995). However, one can make the opposite prediction when considering differential behavioural responses at habitat boundaries with type of landscape. For butterflies from a woodland landscape, most boundaries are soft boundaries in the sense that crossing them will bring a butterfly to another piece of woodland habitat after a few to tens of metres of open, but mostly sheltered, areas such as rides or clearings. By contrast, butterflies from agricultural landscapes would rather use boundaries, like hedgerows, as their

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habitat *per se*, and leaving them can be interpreted as crossing hard boundaries in the sense of encountering open, unsheltered areas for tens to hundreds of metres (e.g. fields and pastures). Hence, as boundaries mean on average different things in the two landscapes, one may predict higher incidence of boundary crossing, or higher mobility at this local scale, in woodland butterflies compared with agricultural landscape butterflies.

Comparative field studies between landscapes may point at relevant behavioural differences, but are less powerful to test for selection on mobility as they cannot rule out behavioural flexibility. We are particularly interested in selection on behavioural responses and movements relative to landscape structure, which has often been assumed—for instance to interpret morphological variation among landscapes (e.g. Hill *et al.* 1999)—but has been directly tested far less. Therefore, we adopted an experimental approach by releasing butterflies from woodland and agricultural landscapes simultaneously in a common environment. We used naive butterflies that were reared under controlled conditions in the laboratory from females collected in both types of landscape. Hence, any behavioural differences would be a consequence of heritable variation.

Besides the effect of landscape of origin, we also examined sexual differences in mobility and how movements and behaviour were affected by weather conditions. In several butterflies (including *P. aegeria*), females have been considered the more dispersive sex (Baker 1984). However, males are likely to be more frequently observed flying, as they spend most of their time locating females. Two strategies of mate-location behaviour co-occur in *P. aegeria*: territorial perching (i.e. aggressive sit-and-wait behaviour on a sunlit patch) and patrolling (i.e. searching behaviour in more or less permanent flight in a wider area) (Davies 1978; Wickman & Wiklund 1983). Being flying heliotherms, weather conditions may have a severe impact on several aspects of butterfly biology, in particular on activity and movements (Dennis 1993). As ambient temperature increases, both males and females of *P. aegeria* fly for longer and they change microhabitat selection within woodland habitats (Shreeve 1984). So, in this paper we test the conflicting predictions in relation to landscape structure, as well as sexual and weather-related differences and their interaction effects.

## 2. METHODS

### (a) *Study species*

Throughout Europe, the speckled wood butterfly (*P. aegeria* L.) is primarily a woodland butterfly (Tolman & Lewington 1997), but may also occur in other habitat types with some kind of woodland aspect, including parks, gardens and along hedgerows. Adults are rarely seen on flowers, and mainly feed on other resources like honeydew. Several grasses can be used as a larval host plant (Shreeve 1986). Eggs are deposited on isolated grass plants, surrounded by some bare ground, that grow under shaded, rather wet conditions (Wiklund & Persson 1983).

### (b) *Sampled landscapes and breeding procedure*

In August 2002, females of *P. aegeria* were captured at several sites in two different types of landscape in Belgium. The first

was a closed landscape dominated by deciduous woodland with differently sized clearings, pastures and rides (Meerdaalwoud). The other was an open, agricultural landscape composed of intensively used fields and pastures (ca. 80% of the area), houses and farms (ca. 10%), commercial orchards (ca. 5%), tiny woodlots (ca. 2.5%) and several sunken roads with hedgerows (ca. 2.5%) (Rillaar). Hence, from a speckled wood butterfly's perspective, Meerdaalwoud is a rather continuous landscape as far as egg-laying sites and sheltered sunlit patches for mate location are concerned, whereas in Rillaar such sites can only be found along or in hedgerows and tiny woodlots that are scattered in the landscape. Collected females were allowed to oviposit on tufts of grass (*Poa annua*) in small cages in the laboratory. Next, eggs were transported to Stockholm where the individuals were reared on *Poa annua* in climate rooms under controlled conditions (22 °C, 22 L : 2 D cycle). After emergence, adults—from 6 woodland and 12 agricultural landscape families—were sexed and individually marked by writing a unique number on the ventral side of both hindwings with a fine permanent, non-toxic and waterproof pen with silver ink. Until release in the outdoor cages, adults were stored in climate chambers (8 °C, 21 L : 3 D cycle).

### (c) *Observations in outdoor cages*

Behavioural observations were done by one person between 11–18 September 2002 in a manipulated environment in two identical, rectangular outdoor cages with half-circle shaped cross-sections (Serres de France S.A.), 8 m wide × 30 m long × 4 m high (Norberg *et al.* 2002). Both cages were located side by side with their longitudinal axes positioned in an east-west orientation in a sheltered pasture near Tovetorp field station (ca. 100 km southwest of Stockholm, Sweden). The first cage was somewhat more exposed than the second cage that was positioned between the first cage and a third cage that was not used. The cage roof and walls consisted of fine-meshed netting. The experimental cage set-up was similar to Leimar *et al.* (2003): both ends (8 m each) had a closed, rather shady habitat condition (i.e. mimic for woodland structure) and the central zone (14 m) was an open meadow. The closed habitat, providing shade with scattered sunlit patches, was created by the use of camouflage netting and non-transparent tarpaulin in which holes of varying size were cut. In addition, several sheets of camouflage netting were hanging down from the roof and two artificial Christmas trees were placed in each end part. In each cage we provided six adult feeding stations (i.e. sugar solution on a sponge).

In each of the two cages five individuals of each sex and origin (woodland or agricultural landscape)—hence 20 individuals per cage in total—were placed at random positions. Densities were kept constant over time; if an individual was not observed during an entire day, it was replaced by another one of corresponding sex and origin. After 5 days of observations, all individuals were collected and replaced by a new sample of individuals according to the same experimental design. In total, 92 individuals were released.

A first group of individuals was observed during a 3 day period that was significantly warmer than the period of the second group of individuals (mean ambient temperature at noon: 20 ± 1 °C versus 14 ± 1 °C,  $U = 0$ ,  $n = 3$  and 5,  $p = 0.036$ ). Hence, weather condition was taken into account for the analyses as a categorical variable (warm versus cold weather).

During 1 h long observation sessions, the observer walked slowly through the cage and binoculars were used to read indi-

vidual marks on the wings from a distance without disturbing the butterflies. The location of each butterfly (using a 2 m × 2 m grid system) and its behaviour (three categories: flying, resting and basking) were recorded. A subsample of flying individuals ( $n = 75$ ) was also followed until they alighted; individual tracks and behaviours were recorded. From the observations (i.e. locations and behaviours) we inferred the following variables: (i) traversal rate (i.e. the number of movements from one shady end of the cage to the other divided by the time between the first and last observation, including only those parts of the day when weather conditions would allow butterfly activity; available time for active flight was assessed for each day separately); (ii) moved distance rate within an observation session (i.e. the summed moved distance divided by the summed time between the first and last observation within the session); (iii) tracked distance (i.e. the summed moved distance during the times the individual was followed divided by the number of these tracking events); (iv) crossing tendency (i.e. the number of open–shade boundary crossings per tracking event); (v) proportion of observations in the open (the middle third, not including the 2 m wide boundary sections of the cage); and (vi) proportions of observations an individual was flying, basking or resting.

#### (d) *Statistical analyses*

Preliminary tests (including variable transformation choice, tests for variance homogeneity and detecting outliers) were carried out using R software v. 1.6 (Ihaka & Gentleman 1996). The individual butterfly was used as statistical unit. Data were analysed in relation to landscape of origin (woodland or agricultural landscape), weather condition (warm or cold) and sex. We also included cage as a factor, as well as interaction terms, but we dropped such terms from the final models if they neither improved the fit of a model nor gave rise to  $p$ -values smaller than 0.1.

To analyse the data on traversals, we used SAS v. 8.2 (SAS 2001, GENMOD procedure). Assuming that an individual has a given probability per time unit to traverse the open middle part of a cage, the number of traversals over a period of time will follow a Poisson distribution. For this reason, we used generalized linear models with Poisson response (and log link function). Effects of variation in the time available for traversal were taken into account by using the logarithm of this time as the so-called offset variable in the models (this is analogous to a covariate). We judged the fit of a model by noting how close the scaled deviance per degree of freedom (d.f.) was to one.

For the other analyses we applied general linear models by using the same SAS software (GLM procedure). We used the so-called Akaike information criterion to judge the fit of a model. In the analysis of moved distance rate within an observation session, we excluded individuals with less than 15 min summed within-session time, as the random variation in the rate becomes very high for short times. For the measures based on proportions of observations (measures (v) and (vi) above) we excluded individuals with five or less observations in total, to reduce random variation in the proportions. By suitable choice of transformations for the dependent variables, and in some analyses removal of outliers, we achieved homogeneous variances in the different tests (we also checked that any statistical significances did not depend on the removal of outliers). Means are given  $\pm$  s.e.m.

### 3. RESULTS

#### (a) *Movements between shaded parts*

Males seemed to be somewhat more variable in their traversal rate between the shaded ends of the cage than females. This could reflect variation in mate-location strategies, in which case the model assumption of Poisson distribution of the number of traversals might be violated. The best-fitting model that included both sexes showed a higher traversal rate in woodland butterflies compared with agricultural butterflies, and some non-significant tendencies for the other factors and interaction terms (table 1a). If sexes were analysed separately, we found a very good fit for the females (scaled deviance per d.f. of 1.006). Woodland females moved more frequently from one shaded part to the other than did agricultural females and traversal rate was higher under warmer weather conditions (table 1b; figure 1). However, the analysis for males showed a less good fit (scaled deviance per d.f. of 1.124) and no significant effect of either landscape of origin or weather conditions (table 1c; figure 1).

#### (b) *Movements and boundary crossing within observation sessions*

Flight distances per time unit within observation sessions were longer in woodland butterflies than in agricultural butterflies and were longer under cooler weather conditions (table 2a; figure 2a). There was a non-significant tendency for a difference in those distances between the two cages as distance moved tended to be longer in the second cage. Within the subsample of followed individuals, there was no significant effect on distance covered per tracking event (table 2b). However, woodland butterflies were found to cross open–shade boundaries more often than did agricultural butterflies (table 2c; figure 2b).

#### (c) *Habitat preference*

Only 20% of all butterfly observations were in the open middle part of the cages. The open part was, however, more used under cooler conditions than under warm conditions, with no significant differences between sexes or landscape of origin (table 2d; figure 2c). Considering only the boundary stripes, butterflies were observed predominantly along the open irradiated site of the boundary rather than in the shaded site ( $t = 6.73$ , d.f. = 74,  $p < 0.0001$ ).

#### (d) *Flight activity*

Woodland butterflies were more often observed flying than agricultural butterflies, but this effect of landscape was larger for females than for males. None the less, males were more observed at flight compared with females. The proportion of observations of flying butterflies differed between the cages as butterflies were more often at flight in the second cage. There was no significant effect of weather condition (table 2e; figure 2d). As there were no significant differences for basking, the results for resting largely represent the inverse of those for flying: woodland butterflies rested less than agricultural butterflies, and females more than males. There was an interaction effect of landscape of origin with weather: under relative cooler conditions butterflies were observed less frequently resting, and this effect was larger for woodland than for agricultural butterflies (table 2f).

Table 1. Results of a generalized linear model for the traversal rate between shaded ‘woodland’ parts in the outdoor cages in relation to the landscape of origin of the speckled wood butterflies (woodland or agricultural landscape) and weather condition (see § 2) when taking into account (a) both sexes, (b) females and (c) males only. The GENMOD procedure was applied (SAS) using type III sums of squares.

variable	effect	$\chi^2$	<i>p</i>
(a) traversal rate (movements h <sup>-1</sup> ) both sexes	landscape	9.19	0.0024
	sex	0.10	0.75
	weather	2.99	0.084
	landscape × sex	2.02	0.16
	landscape × weather	3.27	0.070
	sex × weather	2.97	0.085
(b) traversal rate (movements h <sup>-1</sup> ) females	landscape	17.33	< 0.0001
	weather	10.60	0.0011
(c) traversal rate (movements h <sup>-1</sup> ) males	landscape	1.77	0.18
	weather	0.06	0.81

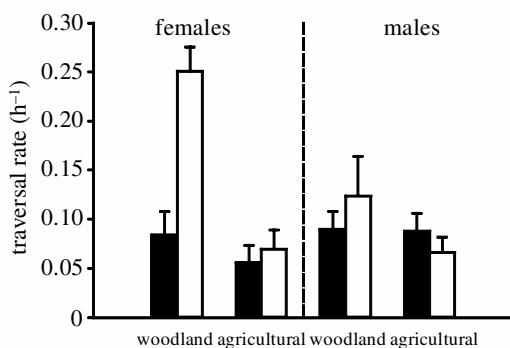


Figure 1. Traversal rate of female ( $n = 43$ ) and male ( $n = 45$ ) speckled wood butterflies from woodland landscape origin and agricultural landscape origin under warm (open bars) and cooler weather conditions (filled bars) in large outdoor cages. Traversal rate is expressed as the number of movements from one shady end of the cage to the other plotted against time between the first and last observation, including only those parts of the day when weather conditions allow butterfly activity. We used weighted means (with corresponding time present as weight)  $\pm$  s.e.m. (by bootstrapping).

#### 4. DISCUSSION

Our experimental approach to compare behavioural responses and movements among speckled wood butterflies in a large cage set-up revealed differences with landscape of origin. Woodland butterflies covered longer distances, were more prone to cross the open–shade boundaries, travelled more frequently between the shaded cage ends and were more frequently at flight than agricultural butterflies. Hence, the results support the prediction of the behaviour-at-boundaries hypothesis rather than the contrasting prediction of the resource distribution hypothesis. Particularly for the traversal rate between the shaded ends, the differences between landscapes were clearly present in females. In a similar cage set-up, Leimar *et al.* (2003) found higher traversal rates in speckled wood butterflies compared with another woodland satyrine, *Lopinga achine* (both from Sweden), which agrees with their differences in habitat exploration and dispersive nature. Within *P. aegeria*, a Swedish woodland population (north European subspecies *tircis*) was found to be more mobile than a Madeiran population (south European subspecies *aegeria*)

living in more open habitat (Leimar *et al.* 2003). Our results suggest similar behavioural differences at a much smaller geographical scale within Belgian populations occurring in woodland versus agricultural landscapes.

The naive butterflies used in our experiment were the F<sub>1</sub> generation (reared under common garden conditions in the laboratory) of wild-caught females from both landscape types. Hence, this study provides evidence for heritable behavioural differences—a prerequisite for selection—and suggests that differences among landscapes do not follow from behavioural flexibility alone. So, in addition to environmental differences among the landscape types that may directly mediate differences in behaviour, there are also intrinsic differences in responses.

Although there are, to our knowledge, no empirical studies yet available on long-distance dispersal movements and capacity in speckled wood butterflies (see Hill *et al.* 1999), one may argue whether the observed differences have any relevance for dispersal. Observed movements in the outdoor cage mainly reflect explorative or ‘daily’ movements (Norberg *et al.* 2002; Leimar *et al.* 2003). In a study by Van Dyck *et al.* (1997) recapture distance of males within a complex of woodland fragments was on average less than 40 m within woodland vegetation, but some males moved between fragments covering up to 450 m. The spatial dimensions of the used cages do not allow a direct comparison of dispersal capacity *per se*. However, several recent studies have pointed out the significance of behaviour at boundaries to emigration decisions (Haddad 1999; Ries & Debinski 2001; Schultz & Crone 2001; Morales 2002; Schtickzelle & Baguette 2003). It is important to realize that behaviour at boundaries relates to dispersal propensity and not necessarily to dispersal capacity (in terms of covered distance), although both could be interrelated as well. Variation in the behaviour at boundaries can be studied at relatively small scales, like in our cages. Therefore, our results are at least relevant in terms of habitat exploration and dispersal propensity. Lower traversal rates and boundary crossing for speckled wood butterflies in agricultural landscapes do make sense as resources are much scarcer and travelling in open unsheltered land is likely to be more costly for this primarily woodland butterfly. So, our study suggests that behavioural responses that affect dispersal in speckled wood butterflies have been changed by selection

Table 2. Summary of the analyses of different movement and habitat preference variables in relation to the landscape of origin of the speckled wood butterflies (woodland or agricultural landscape), sex, weather condition and cage (see § 2) using GLM procedure (SAS). Type III sums of squares were used.

variable	effect	F-value	p
(a) moved distance rate within session (m h <sup>-1</sup> )	landscape	<i>F</i> <sub>1,63</sub> 4.62	0.036
	sex	0.56	0.46
	weather	6.14	0.016
	cage	3.36	0.071
(b) tracked distance (m)	landscape	<i>F</i> <sub>1,71</sub> 2.34	0.13
	sex	1.00	0.32
	weather	2.70	0.10
(c) crossing tendency (crossings per tracking event)	landscape	<i>F</i> <sub>1,71</sub> 6.65	0.012
	sex	3.13	0.081
	weather	0.06	0.80
(d) proportion of observations in open part	landscape	<i>F</i> <sub>1,70</sub> 2.10	0.15
	sex	0.24	0.63
	weather	17.33	< 0.0001
	sex × weather	2.85	0.096
(e) proportion of observations flying	landscape	<i>F</i> <sub>1,67</sub> 14.21	0.0003
	sex	11.40	0.0012
	weather	1.07	0.30
	cage	11.13	0.0014
	landscape × sex	4.68	0.034
(f) proportion of observations resting	landscape	<i>F</i> <sub>1,66</sub> 9.40	0.0031
	sex	11.40	0.0012
	weather	5.98	0.017
	cage	3.80	0.055
	landscape × weather	4.44	0.039
	sex × weather	3.33	0.072

as woodland landscapes change to agricultural landscapes (i.e. increasing degree of habitat fragmentation).

Only a little is known on landscape perception distances in butterflies (Conradt *et al.* 2000). However, the two separated 'woodland parts' in the experiment are within the perceptible—most likely visual—detection range of speckled wood butterflies (T. Merckx and H. Van Dyck, unpublished data). Therefore, it would be highly relevant to test their movements in a much longer cage (e.g. length of *ca.* 100 m). The potential role of visual stimuli (like another piece of woodland within a few metres of an open area) relative to boundary crossing decisions requires further research. We hypothesize that this may contribute significantly to traversal rates (particularly in woodland species), and that its role varies among populations from woodland or agricultural landscapes. Hence, we predict that, in a much longer cage, woodland butterflies would move less between the woodland parts compared with agricultural butterflies, and that the overall mobility will be lower than in the current experiment, assuming all other factors (e.g. weather conditions, densities) are equal.

Speckled wood butterfly males were more frequently

observed flying than females. This is in agreement with basic behavioural differences between the sexes in butterflies as males spend most of their active time budget to mate location, while females rest and bask during considerable time periods between oviposition, foraging and dispersal flights (Shreeve 1992). This sexual difference in time budget use probably caused the fact that effect of landscape on flight activity—woodland butterflies were more often observed flying than agricultural butterflies—was larger in females than in males (i.e. significant landscape × sex interaction). Higher flight incidence is not always related to higher levels of net displacement (Merckx & Van Dyck 2002). The two distinct types of mate-location behaviour that co-occur in speckled wood butterflies and also in our cages—territorial perching versus patrolling—provide an explanation for the less good fit to a Poisson distribution of traversals among males compared with females. Territorial perchers are more likely to stay in one part compared with patrollers who will move on.

In contrast to movement rates and crossing tendency, we did not find differences in habitat preference among

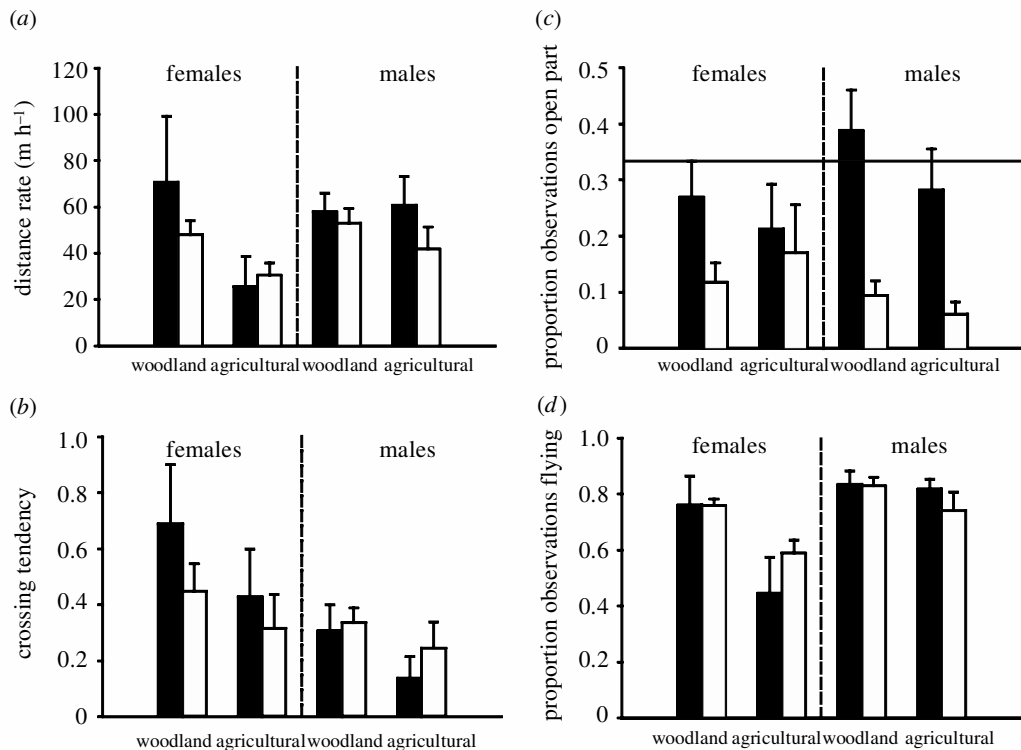


Figure 2. Movement, habitat preference and behavioural variables of speckled wood butterflies in relation to landscape of origin (woodland versus agricultural landscape), sex and weather (open bars, warm; filled bars, cold; see § 2) as derived from observations in large outdoor cages: (a) distance within session per time unit, using weighted means (with corresponding time present as weight)  $\pm$  s.e.m. (by bootstrapping); (b) boundary crossing tendency; (c) proportion of observations in the middle third of the cages for individuals with six or more observations (line represents random expectation); and (d) proportion of observations of flying butterflies.

the woodland and agricultural butterflies; all preferred the shady, 'woodland' parts. However, there was a significant effect of weather condition. Under cooler weather, more butterflies were observed in the open, more irradiated part of the cage. This is in agreement with thermal microhabitat selection under natural conditions; in a British woodland population, Shreeve (1984) observed that speckled wood butterflies were more frequently present on rides and clearings (i.e. higher levels of irradiance and ambient temperature) than on small sunlit patches in the woodland when ambient temperature was low, but the use of the latter type of microhabitat increased with temperature. Weather condition also affected female traversal rate in the predicted way; flight duration increased with ambient temperature (Shreeve 1984), which resulted in higher traversal rates under warmer weather conditions. There was no effect of weather on flight incidence, but as habitat preference changed towards warmer, irradiated sites under cooler conditions (see above), the butterflies were able to compensate and keep the time budget for flight unchanged (at least within the weather conditions of the experiment). Proportions of butterflies seen at flight or at rest are obviously not entirely independent (see § 3), but apart from the effect of sex, there were highly significant differences with landscape of origin for both variables. Moreover, in the analysis of proportion of resting, it is intriguing to notice that the effect of weather was larger in woodland than in agricultural butterflies (i.e. significant weather  $\times$  landscape interaction). Being flying heliotherms, both landscape types have quite different thermal properties for butterflies and the degree of variation is

likely to interact with weather conditions. In our common arena approach, both populations were faced with the same environmental set-up, and so the differences point at intrinsic differences in how woodland and agricultural speckled wood butterflies deal with the environment. Such behavioural differences are likely to be underpinned by thermal physiological differences.

So far, most research on dispersal has in particular focused on movement patterns (e.g. frequency distributions of distances, maximum distance, etc.). However, mechanistic research on movements is, as a complementary field, also required for a better understanding of dispersal and how this is affected in fragmented landscapes. Hill *et al.* (2001) observed a 40% slower expansion rate in speckled wood butterflies in a landscape that had 24% less woodland. However, different mechanistic scenarios could lead to such a pattern, and remedying conservation strategies in fragmented landscapes would benefit considerably from a better understanding of the mechanisms. Hedgerows have often been assumed to be corridors for woodland species, but for butterflies (among several other taxa) there is hardly empirical evidence for this (Dover & Sparks 2000). From our experiments and preliminary work on woodland perception from varying distances (T. Merckx and H. Van Dyck, unpublished data), we hypothesize that woodland butterflies may be encouraged to cross a woodland boundary if there is a landscape feature that is perceived as woodland (e.g. a hedgerow). Hence, networks of hedgerows would rather function according to a stepping stone principle than to corridors *sensu stricto*. This requires careful testing, and we believe, more generally,

that further experiments on behaviour at habitat boundaries and on landscape perception will contribute significantly to conservation strategies at the landscape level.

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