



## Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L.

THOMAS MERCKX\* & HANS VAN DYCK†

\*Laboratory of Animal Ecology, Department of Biology, University of Antwerp, Belgium

†Biodiversity Research Centre, Ecology and Biogeography Unit, University of Louvain (UCL)

(Received 27 September 2006; initial acceptance 15 November 2006;  
final acceptance 19 December 2006; published online 4 September 2007; MS. number: 9121)

The ability of an organism to find new habitat is likely to contribute to dispersal success in different landscapes. We compared the ability of male speckled wood butterflies from two types of landscape to orientate towards forested habitat as a behavioural assay of the ability to perceive forested habitat at a distance (25–200 m). This field release-experiment showed that butterflies of fragmented agricultural landscape origin were better able to orient towards habitat at a greater distance than butterflies of continuous woodland landscape origin. They followed more linear tracks, displayed flight angles that deviated less from orientation towards habitat, and showed orientations that were significantly directed towards habitat at greater distances than butterflies of continuous landscape origin. Attraction was facilitated when target habitat had a high profile. Our behavioural experiment provides novel insights into landscape connectivity and points to interpopulation differences in the ability to find habitat associated with landscape type.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** dispersal; flight angle; flight track linearity; landscape connectivity; landscape matrix traversal; landscape perception; Lepidoptera; orientation; *Pararge aegeria*; release-experiment; speckled wood butterfly

Although dispersal is widely recognized to be a process with important ecological and evolutionary implications, there is yet much to learn about behavioural mechanisms, like search strategies, that dispersing animals use to detect new habitat (Clobert et al. 2004; Bowler & Benton 2005; Kokko & López-Sepulcre 2006). There is increased interest in dissecting the behavioural variation behind dispersal patterns, but so far, most studies have focused on dispersal propensity when comparing the tendencies with cross-habitat boundaries between species or populations (e.g. Ries & Debinski 2001; Schultz & Crone 2001; Berggren et al. 2002; Schtickzelle & Baguette 2003; Schtickzelle et al. 2006). Dispersal propensity is only one part of the process of dispersal, which has three stages, including emigration (crossing of habitat boundary), traversing a landscape matrix and settlement (immigration or colonization) (Ims & Yoccoz 1997). The ability of animals to

perceive habitat at a distance as they move through the landscape may contribute to dispersal success in fragmented landscapes (Lima & Zollner 1996; Zollner 2000). However, empirical information on the perceptual abilities of animals in real landscapes is still limited (but see Desrochers & Hannon 1997; Gillis & Nams 1998; Zollner & Lima 1999; Zollner 2000; Schooley & Wiens 2003; Bonte et al. 2004).

In this article, we report on orientation behaviour in a woodland butterfly, the speckled wood, in particular, the ability to find woodland habitat. We test the hypothesis of difference in orientation ability between individuals originating from a highly fragmented agricultural landscape versus individuals from a continuous woodland landscape. In the former landscape the habitat of speckled wood butterflies is confined to scattered fragments such as hedgerows, copses and woods. From an adaptive point of view, the time spent searching for forested habitat in a hostile agricultural matrix could be reduced by an increased ability to find habitat (e.g. increased perceptual range) compared to populations living in a woodland landscape with continuous habitat. Hence, we predict that butterflies from a fragmented landscape have better orientation abilities than butterflies from a continuous

*Correspondence:* T. Merckx, Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, U.K. (email: [thomas.merckx@zoology.oxford.ac.uk](mailto:thomas.merckx@zoology.oxford.ac.uk)). H. Van Dyck is at the Biodiversity Research Centre, Ecology and Biogeography Unit, University of Louvain (UCL), Place Croix du Sud 4, B-1348 Louvain-la-Neuve, Belgium.

landscape. To the best of our knowledge, intraspecific differences in perceptual range with landscape of origin have not been tested before. Additionally, we test the responses of the butterflies at two sites to evaluate the role of the vertical dimension of the target habitat using a pasture with a high woodland fringe and one with a hedgerow. Given a similar horizontal dimension, a high woodland fringe is expected to facilitate stronger habitat attraction than a hedgerow.

We used, in a manner similar to Zollner & Lima (1997), the ability of speckled wood butterflies from both types of landscape to orient towards forested habitat from a distance as a behavioural assay of the ability to perceive forested habitat at a distance. We captured speckled wood butterflies in both continuous and fragmented landscapes and released them in distant and unfamiliar pasture at different distances from forested habitat, to follow and quantify their flight trajectories. Critical to this approach is the assumption that movement orientated towards the forested habitat is equivalent to the perception of habitat. In an earlier experiment in outdoor cages, Merckx et al. (2003) provided evidence that speckled wood butterflies originating from both types of landscape preferred sheltered woodland conditions to open conditions like pasture. Based on detailed oviposition studies (Wiklund & Persson 1983; Shreeve 1986), females prefer to use host plants that grow under sheltered, rather humid conditions. Open arable fields and pastures do not fit this environmental profile. Males on the other hand make use of the interference of sunlight and canopy structure as they perch territorially on sunlit patches or patrol between such sunlit patches (Wickman & Wiklund 1983; Shreeve 1984). Although some behavioural aspects differ in males locating mates in and along hedgerows in agricultural landscapes compared to conspecifics in woodland, the connection with forested habitat clearly remains (Merckx & Van Dyck 2005). So, for both sexes there are functional reasons to believe that open fields and pastures (agricultural land per se) are relatively hostile. Therefore, it is reasonable to assume that the butterflies released in pasture are motivated to search immediately for wooded habitat. Open, relatively short-turf pasture has also been considered to be a hostile environment for speckled wood butterflies in other studies (e.g. Chardon et al. 2003).

## METHODS

### Study Species, Landscapes and Release Sites

The speckled wood butterfly is a satyrine butterfly (Lepidoptera: Nymphalidae). Throughout North and Northwest Europe the prime habitat is woodland (e.g. Shreeve 1984; Karlsson & Wiklund 2005), but the species also occurs in fragmented landscapes with some kind of woodland aspect such as hedgerows, scrub, lanes, copses and woods in agricultural landscapes (Merckx et al. 2003). Adults mainly feed on honeydew and to a lesser extent on nectar.

We captured equal numbers of speckled wood butterflies males at two different types of landscape in central Belgium ( $N_{\text{combined}} = 98$ ). The first was closed landscape

dominated by deciduous woodland with clearings and rides of varying size (Meerdaalwoud). The second was open, agricultural landscape composed of intensively farmed fields and pastures (85% of the area), houses and farms (4%), copses (3%) and hedgerows or woody sunken rural roads (Hoegaarden). Hence, the landscapes represent a contrast between rather continuous habitats for speckled wood butterflies versus highly fragmented landscape (habitat <5% of the area, and scattered across the landscape). We captured butterflies at several sites in each landscape (cf. Merckx et al. 2003). Captures within each landscape most probably represent members of different lineages as the distance between individual captures was 0.5–5.0 km. Hill et al. (2003) estimated maximum dispersal rate of speckled wood butterflies to be 1.03–2.7 km/year, but the dispersal range of the average individual is likely to be considerably less than such values at an invasion front (Hill et al. 1999). We captured butterflies by hand net, stored them temporarily in individual plastic jars (<1 h for all individuals; no difference in storing time between landscape types) and transported the butterflies in a cool box (ca. 15°C) to the release sites.

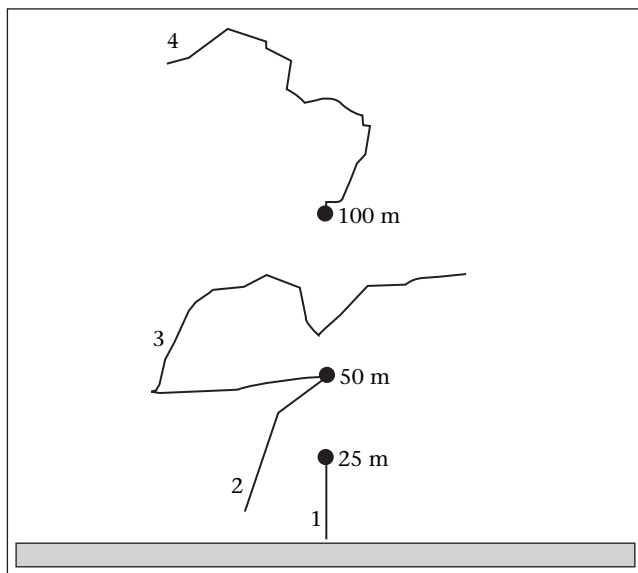
The release-experiment was done during 9 days between the end of July and the beginning of September 2002 when weather conditions were highly conducive for butterfly flight activity (i.e. sunshine, temperatures > 20°C, and wind levels ≤ BF1). These very low levels of wind prevent wind speed and wind direction to act as possible confounding factors with regards to the interpretation of results. We released butterflies, one at the time, at two sites, both representing open agricultural landscapes with forested habitat at one side only. It is very unlikely that one of the butterflies was familiar with the site of release since distances between sites of capture and release sites were far more (ca. 5–17 km) than the typical or average range of daily movements of speckled wood butterflies (see above). At one of the release sites, the forested habitat was a 40-m-high broadleaved woodland fringe. At the other site, it was a 5-m-high hedgerow. At each site, the forested habitat, a mixture of deciduous tree and shrub species, extended for more than 300 m along the western side of the site, which otherwise consisted of short-grazed pasture. Release distances from this habitat edge were 25, 50, 100 and 200 m. We randomized releases between distances, and butterflies from both landscapes were tested on the same day. Every individual was tested only once (i.e. at only one particular release distance and release site). Before release, the observer transferred an individual from the cool jar into a butterfly net without any direct handling. The butterfly typically crawled out of the net, started to bask by spreading the wings and took off spontaneously after a short time. The behaviour was recorded immediately the butterfly was airborne. Two observers tracked the butterfly: one placed tagged sticks to register the flight track (minimal spatial resolution: 0.5 m), the other timed, using a stopwatch, and recorded the observed behaviours. The observers remained at a distance more than 10 m from the butterfly to avoid interference with the butterfly's behaviour. An observation session lasted until the butterfly either: (1) reached the forested habitat; (2) did not reach habitat but flew more than 250 m away

from the point of release and continued to fly into the open, agricultural landscape away from the forested habitat; or (3) interrupted its flight and rested more than 1 min. The latter category ( $N = 7$ ) was not used in the analysis as these butterflies were not involved in any habitat-finding behaviour. After each release, we determined the XY-coordinates of the placed sticks by triangulation, using a laser instrument (Leica Disto classic<sup>3</sup>, Heerbrugg, St Gallen, Switzerland). On average ( $\pm$ SE), butterflies were followed for  $85.6 \pm 8.5$  m ( $N = 91$ ), while an average observation lasted for  $68 \pm 11$  s ( $N = 91$ ).

### Reaching Target Habitat, Trajectories and Velocity

From the flight trajectories (including positions and timing) and behavioural observations, we derived several parameters that typified the movement pattern. For each individual, total distance covered, total flight time, mean flight velocity, and whether or not it reached the forested habitat were recorded. Flight trajectories were classified as: (1) straight; (2) mainly straight, but with one curve; (3) with several curves, without returning to the point of release; and (4) petal-like loop pattern (i.e. an at least almost complete ellipse or more ellipses from and back to the point of release; Fig. 1). For each release event, we also measured average wind speed and ambient temperature.

We tested whether frequencies of flight trajectory classes differed between the landscapes of origin, release distances and release sites (Proc Freq, SAS 2001, SAS Institute Inc., Cary, NC, U.S.A.). Mean flight velocity was analysed as a function of landscape of origin, release distance, release site, and all mutual interactions as fixed effects and



**Figure 1.** Examples of the four flight trajectory classes: (1) straight; (2) mainly straight, but with one curve; (3) petal-like loop pattern (i.e. an at least almost complete ellipse or more ellipses from and back to the point of release); and (4) several curves, without returning to the point of release. Positioning of forested habitat (grey rectangle) and release points (25, 50 and 100 m) is indicated.

residual ambient temperature as a covariate (Proc mixed, SAS 2001). The response variable 'reaching habitat or not' was analysed using a model with a binomial error structure using landscape of origin, release site and distance to habitat as fixed effects (Glimmix macro, SAS 2001). Wind speed was included as a random effect in the models although we only worked on days with low to very low levels of wind. We carried out backward selection of nonsignificant factors (highest  $P$  values) to obtain the final statistical model. We used differences of least squares means as a posteriori test among groups. We always checked for normality of model residuals.

### Linearity of Flight Trajectories and Flight Angle

We established a series of lines parallel to the forested habitat edge at 25-m intervals. Each time a flight track crossed such a 25-m line, we determined the angle between the flight track and the perpendicular line to the habitat from that spot. The linearity of flights between two successive 25-m-section lines was expressed as Euclidean distance/real covered distance. We transformed measures of linearity before analysis to reach normality (arcsine square-root transformation).

We used mixed regression models to analyse the movement parameters (movement angle:  $0^\circ$ – $180^\circ$ , and linearity) in relation to landscape of origin, distance to habitat and their interaction as fixed effects. We only used four classes (25, 50–75, 100–150 and 175–225 m) for the parameter 'distance to habitat' because a larger number of classes reduced goodness-of-fit of the models. Since the flight track of an individual may cross several 25-m line sections, we included 'individual' in the model as a random effect. Because of significant three-way interaction effects (landscape of origin\*distance to habitat\*release site), we analysed the two release sites separately since landscape of origin and its interaction with distance to habitat are the factors of highest interest. Wind speed was always included as a random effect. We carried out backward selection of nonsignificant factors (highest  $P$  values) to obtain the final statistical model. We used differences of least squares means as a posteriori test among groups. We always checked for normality of model residuals.

### Flight Directedness

We analysed directedness towards the forested habitat using circular statistics (Oriana version 1.01, Kovach Computing Services, Anglesey, Wales). As this could not be done in a multivariate way, we carried out three separate tests: (1) distance to habitat for both release sites together; (2) distance to habitat for both landscapes of origin separately; and (3) distance to habitat for both release sites separately. Here, five classes could be used for the distance to habitat (25, 50, 75, 100 and 125–225 m). We used Rayleigh tests to assess whether flight angle distribution ( $0^\circ$ – $360^\circ$ ) differed significantly from randomness. We calculated mean vector length ( $r$ ) and 95% confidence

intervals (CIs) as measures of the variation around mean direction (Batschelet 1981).

## RESULTS

### Reaching Target Habitat, Trajectories and Velocity

The probability that a released speckled wood butterfly reached the target habitat decreased with distance from habitat ( $F_{3,256} = 16.25$ ,  $P < 0.0001$ ; at 25 m: 100%; at 50 and 100 m: 76%; at 200 m: 20%). Incidence of success in reaching habitat was higher at the site with a high woodland fringe as target (90%) than at the site with a hedgerow as target (75%;  $F_{1,29.9} = 7.10$ ,  $P = 0.012$ ).

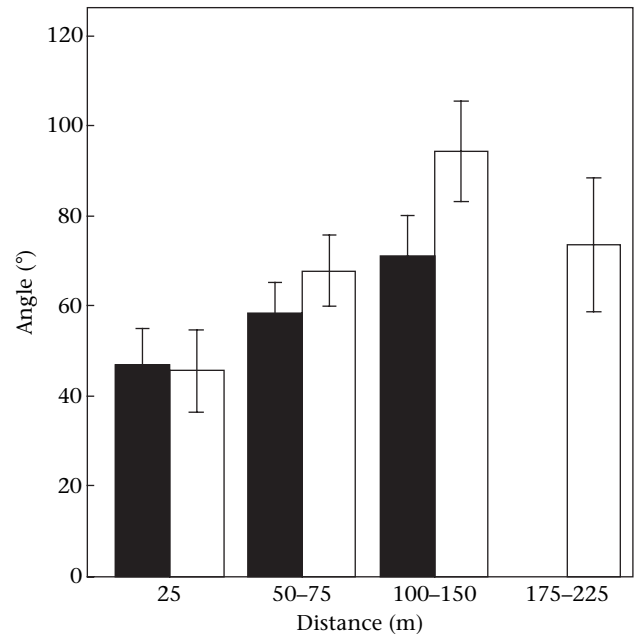
A flight track with several curves, without returns to the release point, was performed by 45.1% of the butterflies. One-quarter of the observed flight tracks were straight (25.3%). A straight flight track with only one curve was followed by 13.2% of the individuals, and a petal-like loop pattern by 16.5%. Frequencies of flight track classes did not differ between landscapes of origin ( $\chi^2_3 = 1.40$ ,  $P = 0.71$ ), release distances ( $\chi^2_9 = 8.47$ ,  $P = 0.49$ ) and release sites ( $\chi^2_3 = 1.96$ ,  $P = 0.58$ ). Mean velocity increased with release distance from habitat ( $\bar{X} \pm \text{SE}$ : at 25 m:  $2.0 \pm 0.2$  m/s; at 50 m:  $2.3 \pm 0.3$  m/s; at 100 m:  $2.5 \pm 0.2$  m/s), but was considerably lower in the butterflies released at 200 m:  $0.9 \pm 0.1$  m/s ( $F_{3,85} = 4.24$ ,  $P = 0.0077$ ). Velocity did not differ with landscape of origin, release site or ambient temperature ( $P > 0.08$ ).

### Linearity of Flight Trajectories

At the woodland fringe site, flight tracks of butterflies of fragmented landscape origin had a significantly higher level of linearity than flight tracks of butterflies of continuous landscape origin ( $\bar{X} \pm \text{SE}$ :  $0.91 \pm 0.02$  versus  $0.84 \pm 0.03$ ;  $F_{1,48.8} = 6.16$ ,  $P = 0.017$ ). This effect could not be detected at the hedgerow site ( $P > 0.15$ ). There was no effect of distance on linearity at the woodland fringe site, but we observed a trend for higher linearity at 25 m from habitat than at distances greater than or equal to 100 m at the hedgerow site ( $t_{114} = 1.95$ ,  $P = 0.054$ ).

### Flight Angle Relative to the Target Habitat

At the woodland fringe site, flight angles of butterflies of fragmented landscape origin deviated significantly less from perpendicularity to the habitat than flight angles of butterflies of continuous landscape origin ( $\bar{X} \pm \text{SE}$ :  $51.9^\circ \pm 6.3$  versus  $75.9^\circ \pm 7.1$ ;  $F_{1,46.8} = 4.53$ ,  $P = 0.039$ ). For both groups combined, there was an additive effect of distance from habitat, with flight angles deviating more from perpendicularity to the habitat with distance from habitat ( $F_{3,117} = 2.81$ ,  $P = 0.043$ ; Fig. 2). At the hedgerow site, there was no significant effect of landscape of origin, nor of release distance ( $P > 0.12$ ). However,



**Figure 2.** Mean  $\pm$  SE of flight angle ( $0^\circ$ – $180^\circ$ ) relative to the target habitat for individuals from both landscapes of origin (black: fragmented landscape; white: continuous landscape) as a function of distance to forested habitat (four classes: 25, 50–75, 100–150 and 175–225 m).

angles deviated more from perpendicularity to the habitat at distances greater than or equal to 100 m than they did at 25 m from habitat (both groups combined:  $t_{118} = -2.04$ ,  $P = 0.044$ ).

### Flight Directedness

In the overall test, the distribution of the orientation of the butterflies differed significantly from nonrandom at less than 100 m from the habitat. Nonrandom flight patterns were always orientated towards the habitat (i.e. mean vector directions close to  $0^\circ$ ). Vector directions became more scattered around the mean vector with increasing distance from the habitat (Table 1, Fig. 3a).

When testing for the effect of the landscape of origin, different thresholds for the distance at which flights were orientated towards the habitat were found. Butterflies of fragmented landscape origin showed significant differences from randomness up to 100 m, whereas butterflies of continuous landscape origin did so up to 50 m only. So, mean vector lengths at 75 and 100 m were larger in butterflies of fragmented landscape than of continuous landscape (Table 1, Fig. 3b). Comparing the effect of release site, butterflies at 75 m from habitat possessed orientations that differed significantly from randomness at the woodland fringe site, whereas orientations were only marginally significantly directed at the hedgerow site. For the same distance, mean vector direction was close to habitat direction at the woodland fringe site only (woodland fringe  $357^\circ$  versus hedgerow  $37^\circ$ ). The mean vector length was also larger at the woodland fringe site (woodland fringe 0.57 versus hedgerow 0.33; Table 1, Fig. 3c).

**Table 1.** Analyses of flight directedness towards forested habitat as a function of distance (m) to habitat using circular statistics

	$\mu$	$r$	95% CI	$P$
Data of both release sites and landscapes of origin combined				
25	8°	0.59	352°–24°	<0.01
50	10°	0.34	343°–37°	<0.01
75	13°	0.42	347°–39°	<0.01
100	9°	0.24	326°–51°	0.03
125–225	39°	0.04	241°–196°	0.95
Sorted by landscape of origin				
25 F	11°	0.61	349°–32°	<0.01
25 C	6°	0.56	342°–30°	<0.01
50 F	353°	0.37	317°–28°	0.01
50 C	29°	0.35	351°–67°	0.02
75 F	12°	0.57	345°–39°	<0.01
75 C	14°	0.29	321°–67°	0.12
100 F	5°	0.35	328°–43°	0.01
100 C	26°	0.09	207°–205°	0.82
125–225 F	195°	0.28		0.65
125–225 C	302°	0.05	25°–220°	0.92
Sorted by release site				
25 H	19°	0.64	359°–39°	<0.01
25 W	357°	0.56	333°–20°	<0.01
50 H	8°	0.31	326°–51°	0.04
50 W	12°	0.37	336°–47°	0.01
75 H	37°	0.33	351°–83°	0.06
75 W	357°	0.57	331°–24°	<0.01
100 H	354°	0.26	300°–48°	0.12
100 W	26°	0.23	323°–89°	0.21
125–225 H	191°	0.53	120°–262°	0.25
125–225 W	326°	0.07	125°–166°	0.86

Mean vector length ( $r$ ) and 95% CIs are calculated as measures of around mean vector direction ( $\mu$ ) variation (F, fragmented landscape; C, continuous landscape; H, hedgerow site; W, woodland fringe site). Rayleigh tests are used to assess whether flight angles differ significantly from randomness ( $P$ ; Batschelet 1981).

## DISCUSSION

Our release-experiment showed that speckled wood butterflies were less likely to orientate towards forested habitat at a greater distance in open agricultural land within a range of release distances of 25–200 m. Attraction towards the forested habitat was greater if the target habitat was more apparent (high woodland fringe versus lower hedgerow but with equal horizontal dimension). In line with our key prediction, butterflies from fragmented landscape populations differed in their orientation behaviour compared to butterflies from continuous landscape populations. They followed tracks with a higher degree of linearity, displayed flight angles that deviated less from direct orientation towards the habitat, and showed orientations that were significantly directed towards the habitat at greater distances than butterflies from a continuous landscape. From an adaptive viewpoint, this suggests that individuals from fragmented agricultural landscapes are better able to detect and respond to habitat than individuals from landscapes with continuous woodland habitat. Although the differences between the experimental groups were clear, the interpretation in adaptive and mechanistic terms requires further careful evaluation. Several points need to be made here about: (1) the issue of replication at the landscape level; (2)

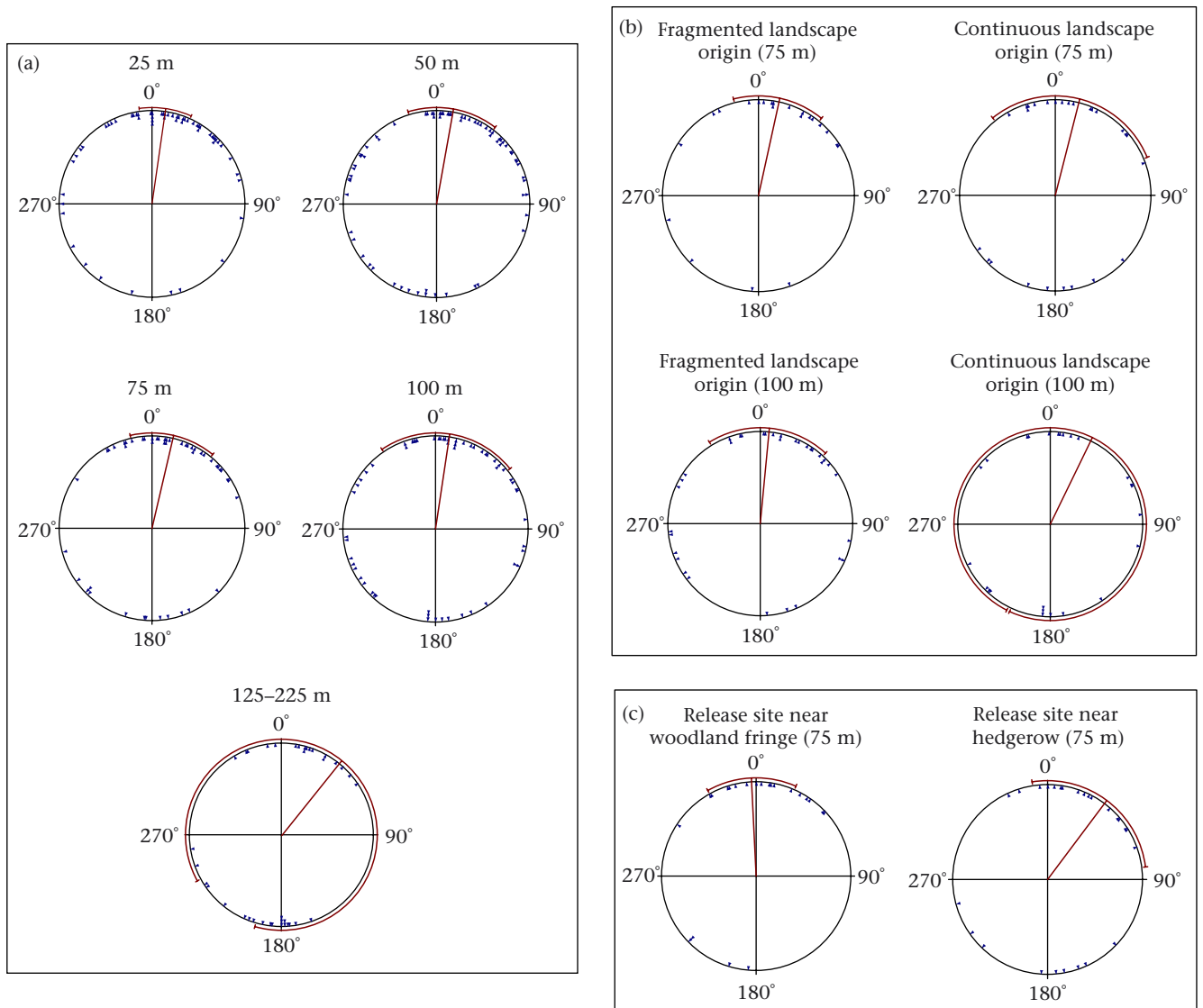
intrinsic differences between butterflies from different landscapes versus potential difference in pre-experimental experience; and (3) the expected differences relative to sex.

In both landscapes we sampled several sites that were at distances well beyond the average dispersal range of the average individual butterfly (cf. Methods). This makes it likely that the tested individuals were genetically variable (i.e. replication at the individual level). Nevertheless, we used butterflies from only one agricultural landscape area and one woodland landscape area. Hence, there was no replication of the landscape of origin effect per se. This seems to be a general, practical limitation of evolutionary ecological studies making comparisons among types of landscape (e.g. Partecke et al. 2004; Karlsson & Van Dyck 2005).

The release sites were unfamiliar to the individuals of both landscape origins (see Methods). However, the physiological state (e.g. age, nutritional status, mating history) may in principle have been different between the two experimental groups, although there is no obvious evidence for such effects. Hence, with the purpose of testing the adaptive hypothesis, the butterflies used in the experiment would have ideally been the naïve offspring (reared under standard conditions) of females collected in different landscapes. Such an approach was followed for testing other behavioural and life history traits in the same speckled wood butterfly–landscape system (Merckx et al. 2003; Karlsson & Van Dyck 2005). In this paper, we directly compare captured adults from both types of landscape as was done in a similar study with small mammals (Zollner 2000). So, from a causal point of view, we cannot yet discriminate safely at this stage between nongenetic differences in experience and intrinsic, genetic differences. But, in line with our earlier results on landscape-related differences in behaviour and life history, we tend to conclude that there is an intrinsic, heritable component behind the observation that the landscape of origin affects habitat-finding. Given our results, a more complete experimental set-up to test the adaptive hypothesis for differences in perceptual range with landscape structure would now be worthwhile.

We also observed that height of target habitat plays a significant role in attracting butterflies of this species. The data are consistent with a positive effect of tree height, which presumably increases perception, although some other effect of the target habitat, or other difference between the release sites, cannot be ruled out. This is another issue that needs to be controlled for in future experiments (i.e. including release site replication). Since we tested males only, the role of sexual differences in habitat-finding ability and orientation behaviour also requires investigation, particularly if one sex is known to be more dispersive (Van Dyck 2003).

The observation of insect dispersers needing to approach potential habitat relatively closely to be attracted to it has been made a few times before. Coyne et al. (1987), for instance, showed that *Drosophila* flies moved distances of several kilometres between oases, but were only able to detect an oasis from less than 10 m. *Euphydryas* butterflies also moved up to 5 km between habitat patches, but they



**Figure 3.** Angular orientation of released butterflies, defined relative to the point of release and the place at which tracking was stopped. The dots on each unit circle represent the angular orientations of individual butterflies. The part of the habitat closest to the point of release is defined as  $0^\circ$  for each release. Vectors indicate average angle (mean vectors ( $\mu$ ); Batschelet 1981) and are surrounded by 95% CIs. Data are given for (a) butterflies from both release sites together at five distance classes from forested habitat (25, 50, 75, 100 and 125–225 m); (b) butterflies from both landscapes separately at distances from forested habitat of 75 and 100 m; and (c) butterflies from both release sites separately at a distance from forested habitat of 75 m.

only orientated towards a serpentine grassland habitat at a distance of less than 50 m (Harrison 1989). But the differences between speckled wood butterfly populations of different landscapes suggest that detection ability may vary considerably at the intraspecific level. Butterflies from a fragmented landscape orientated towards forested habitat from twice as far as butterflies from a continuous landscape (100 versus 50 m). Besides the clear average differences with landscape of origin, there was considerable interindividual variation. For example, two individuals released at 200 m from habitat successfully reached habitat adopting a flight track with a high degree of linearity (values of 0.98 and 0.93).

Although our study does not provide insight into the sensory mechanism of habitat perception, butterfly

movements are, at least partly, visually cued. However, considering the relatively poor acuity of the butterfly eye, Rutowski (2003) predicts that even large objects such as trees several metres high may not be resolvable at distances of more than 20–30 m. However, empirical data on landmark detection at the landscape level are to our knowledge lacking in butterflies. The size of the compound eyes relative to body size did at least not differ between specimens from both types of landscape (T. Merckx, unpublished data), but there are several other traits that may relate to visual detection capacity (Rutowski 2003 and references therein). We cannot exclude an additional, or even to some extent alternative, role of olfactory cues (Fownes & Roland 2002; Schooley & Wiens 2003). Hansson (1995) suggested plant-produced odours to be

potentially important cues for locating and evaluating foraging sites in Lepidoptera, but direct evidence has yet to be experimentally shown in butterflies. If olfactory cues do play a role in orientation behaviour of speckled wood butterflies, wind velocity and direction would be important factors to be considered. In our experiment, we avoided any potential bias caused by differential wind conditions by only working when winds were light, and by testing individuals from both landscapes in a random order (cf. *Methods*).

The relative amount of habitat across the landscape has been shown to affect expansion rates in speckled wood butterflies in different areas in the U.K. (Hill et al. 2001). At a smaller spatial scale, the incorporation of habitat elements into a landscape connectivity measure significantly improved modelling patterns of presence/absence for speckled wood butterflies in woodland fragments compared to the use of Euclidean distance in two Belgian landscapes (Chardon et al. 2003). Merckx et al. (2003) showed that in a common arena test, speckled wood butterflies from a continuous landscape had a higher propensity to cross-habitat boundaries than conspecifics from a fragmented landscape. In combination with our current results on differential perceptual ability, we hypothesize that speckled wood butterflies living in fragmented landscapes are better able to deal with a coarse-grained ecological infrastructure (e.g. loose network of hedgerows or copse 'stepping stones') than butterflies of continuous landscape populations. Relatively high boundary crossing propensity and low perceptual ability are likely to be associated with more time spent searching in the hostile matrix (Schtickzelle et al. 2006). This in turn may increase mortality risks that are considered important costs associated with dispersal (Waser et al. 1994; Mennechez et al. 2004). It would be valuable to test whether this idea of differentially required 'corridor' and 'stepping stone' configurations corresponding to distinct types of landscape also applies to other species, particularly those of high conservation interest. Our observation that a strong contrast was necessary to facilitate orientation to forested habitat is significant in this respect. The woodland fringe was eight times higher than the hedgerow at our release sites. So, hedgerows and copses with much taller dimensions, particularly higher trees, are predicted to be landmarks with a wider attraction across the landscape for this type of organism. Such insights can be taken into account in modelling connectivity using cost distance approaches (Chardon et al. 2003). They further contribute to an improved understanding of how structural landscape connectivity is translated into functional connectivity (Bowman & Fahrig 2002; Schooley & Wiens 2003; Stevens et al. 2004). More generally, this shows that a better understanding of perceptual ranges and the effects on movements will contribute to analyses of population dynamics in fragmented landscapes and hence to conservation strategies (Lima & Zollner 1996).

Before a butterfly reaches the threshold of habitat detection and attraction, it would be expected to show different movement behaviours. Our experiment focused on the spatial range in which this switch occurs. Some of the movements before the butterfly switches to a more

directed movement towards detected habitat may represent information on the second stage of dispersal, that is, traversing through the landscape matrix. However, there are different views on the behavioural nature of such movements outside habitat. Conradt et al. (2000, 2001) and Conradt & Roper (2006) concluded from their release-experiments with two other butterfly species that dispersers search systematically for habitat by flying in a succession of progressively larger ellipsoidal loops away from and back to their starting point. In contrast, other authors consider fast, directed, so largely linear, movements to be typical for dispersal (Baker 1969; Johnson et al. 2002). Selection for directed flight in fragmented, agricultural landscape populations is in line with an adaptive response in such an environment as it reduces the time budget spent within the hostile matrix; it is likely to lower associated costs in terms of energy, predation risk and loss of active time for reproduction (Zollner & Lima 1999; Yulikovich 2005; Baguette & Schtickzelle 2006). One particular butterfly that was released at 100 m from the habitat edge clearly showed such a fast and directed movement: it took off with a strong vertical component and flew at high level (30 versus typically 1–2 m) and very fast (6.2 versus average of  $2.1 \pm 0.13$  m/s) in a straight line to the woodland fringe. Both slow explorative movements with lots of curves and petal-like patterns in the trajectories and fast, directed movements may contribute to net displacement (Van Dyck & Baguette 2005). Yet, we are only at the beginning of understanding the behavioural mechanisms of dispersal and in particular of how organisms perceive and respond to landscape elements and target habitat once they are in a landscape matrix.

### Acknowledgments

We thank E. Matthysen, F. Adriaensen, and M. Townsend for discussion and valuable comments on the manuscript, and E. Janssens, K. Borghgraef and T.M.'s mother for field assistance. T.M. was research aspirant with the Fund of Scientific Research Flanders-Belgium (FWO). Funding was provided by grants from the University of Antwerp (GOA 15R/3942) and from the Belgian Federal Office of Scientific, Technical and Cultural Affairs (OSTC-PADD II).

### References

- Baguette, M. & Schtickzelle, N. 2006. Negative relationship between dispersal distance and demography in butterfly metapopulations. *Ecology*, **87**, 648–654.
- Baker, R. R. 1969. The evolution of the migratory habit in butterflies. *Journal of Animal Ecology*, **38**, 703–746.
- Batschelet, E. 1981. *Circular Statistics in Biology*. London: Academic Press.
- Berggren, A., Birath, B. & Kindvall, O. 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metriopectera roeselii*). *Conservation Biology*, **16**, 1562–1569.
- Bonte, D., Lens, L. & Maelfait, J.-P. 2004. Lack of homeward orientation and increased mobility result in high emigration rates from

- low-quality fragments in a dune wolf spider. *Journal of Animal Ecology*, **73**, 643–650.
- Bowler, D. E. & Benton, T. G.** 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, **80**, 205–225.
- Bowman, J. & Fahrig, L.** 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. *Canadian Journal of Zoology*, **80**, 1556–1561.
- Chardon, J. P., Adriaensen, F. & Matthysen, E.** 2003. Incorporating landscape elements into a connectivity measure: a case study for the speckled wood butterfly (*Pararge aegeria* L.). *Landscape Ecology*, **18**, 561–573.
- Clobert, J., Ims, R. A. & Rousset, F.** 2004. Causes, mechanisms and consequences of dispersal. In: *Ecology, Genetics, and Evolution of Metapopulations* (Ed. by I. A. Hanski & O. E. Gaggiotti), pp. 307–355. London: Academic Press.
- Conradt, L. & Roper, T. J.** 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: implications for dispersal. *Ecology*, **87**, 125–132.
- Conradt, L., Bodsworth, E. J., Roper, T. J. & Thomas, C. D.** 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society of London, Series B*, **267**, 1505–1510.
- Conradt, L., Roper, T. J. & Thomas, C. D.** 2001. Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos*, **95**, 416–424.
- Coyne, J. A., Bryant, S. H. & Turelli, M.** 1987. Long-distance migration of *Drosophila*. 2. Presence in desolate sites and dispersal near a desert oasis. *American Naturalist*, **129**, 847–861.
- Desrochers, A. & Hannon, S. J.** 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology*, **11**, 1204–1210.
- Fownes, S. & Roland, J.** 2002. Effects of meadow suitability on female behaviour in the alpine butterfly *Parnassius smintheus*. *Ecological Entomology*, **27**, 457–466.
- Gillis, E. A. & Nams, V. O.** 1998. How red backed voles find habitat patches. *Canadian Journal of Zoology*, **76**, 791–794.
- Hansson, B. S.** 1995. Olfaction in Lepidoptera. *Experientia*, **51**, 1003–1027.
- Harrison, S.** 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology*, **70**, 1236–1243.
- Hill, J. K., Thomas, C. D. & Blakeley, D. S.** 1999. Evolution of flight morphology in a butterfly that has recently expanded its geographic range. *Oecologia*, **121**, 165–170.
- Hill, J. K., Collingham, Y. C., Thomas, C. D., Blakeley, D. S., Fox, R., Moss, D. & Huntley, B.** 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters*, **4**, 313–321.
- Hill, J. K., Thomas, C. D. & Huntley, B.** 2003. Modeling present and potential future ranges of European butterflies using climate response surfaces. In: *Butterflies: Ecology and Evolution Taking Flight* (Ed. by C. L. Boggs, W. B. Watt & P. R. Ehrlich), pp. 149–167. Chicago, Illinois: University of Chicago Press.
- Ims, R. A. & Yoccoz, N. G.** 1997. Studying transfer processes in metapopulations: emigration, migration and colonization. In: *Metapopulation Biology: Ecology, Genetics, and Evolution* (Ed. by I. A. Hanski & M. E. Gilpin), pp. 247–265. London: Academic Press.
- Johnson, C. J., Parker, K. L., Heard, D. C. & Gillingham, M. P.** 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, **71**, 225–235.
- Karlsson, B. & Van Dyck, H.** 2005. Does habitat fragmentation affect temperature-related life-history traits? A laboratory test with a woodland butterfly. *Proceedings of the Royal Society of London, Series B*, **272**, 1257–1263.
- Karlsson, B. & Wiklund, C.** 2005. Butterfly life-history and temperature adaptations: dry open habitats select for increased fecundity and longevity. *Journal of Animal Ecology*, **74**, 99–104.
- Kokko, H. & López-Sepulcre, A.** 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science*, **313**, 789–791.
- Lima, S. L. & Zollner, P. A.** 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, **11**, 131–135.
- Mennechez, G., Petit, S., Schtickzelle, N. & Baguette, M.** 2004. Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. *Oikos*, **106**, 243–252.
- Merckx, T. & Van Dyck, H.** 2005. Mate location behaviour of the butterfly *Pararge aegeria* in woodland and fragmented landscapes. *Animal Behaviour*, **70**, 411–416.
- Merckx, T., Van Dyck, H., Karlsson, B. & Leimar, O.** 2003. The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies. *Proceedings of the Royal Society of London, Series B*, **270**, 1815–1821.
- Partecke, J., Van't Hof, T. & Gwinner, E.** 2004. Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proceedings of the Royal Society of London, Series B*, **271**, 1995–2001.
- Ries, L. & Debinski, D. M.** 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *Journal of Animal Ecology*, **70**, 840–852.
- Rutowski, R. L.** 2003. Visual ecology of adult butterflies. In: *Butterflies: Ecology and Evolution Taking Flight* (Ed. by C. L. Boggs, W. B. Watt & P. R. Ehrlich), pp. 9–25. Chicago, Illinois: University of Chicago Press.
- Schooley, R. L. & Wiens, J. A.** 2003. Finding habitat patches and directional connectivity. *Oikos*, **102**, 559–570.
- Schtickzelle, N. & Baguette, M.** 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration–patch area relationships in fragmented landscapes. *Journal of Animal Ecology*, **72**, 533–545.
- Schtickzelle, N., Mennechez, G. & Baguette, M.** 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology*, **87**, 1057–1065.
- Schultz, C. B. & Crone, E. E.** 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology*, **82**, 1879–1892.
- Shreeve, T. G.** 1984. Habitat selection, mate-location, and micro-climatic constraints on the activity of the speckled wood butterfly *Pararge aegeria*. *Oikos*, **42**, 371–377.
- Shreeve, T. G.** 1986. Egg-laying by the speckled wood (*Pararge aegeria*): the role of female behaviour, host plant abundance and temperature. *Ecological Entomology*, **11**, 229–236.
- Stevens, V. M., Polus, E., Wesselingh, R. A., Schtickzelle, N. & Baguette, M.** 2004. Quantifying functional connectivity: experimental evidence for patch-specific resistance in the natterjack toad (*Bufo calamita*). *Landscape Ecology*, **19**, 829–842.
- Van Dyck, H.** 2003. Mate location: a matter of design? Adaptive morphological variation in the speckled wood butterfly. In: *Butterflies: Ecology and Evolution Taking Flight* (Ed. by C. L. Boggs, W. B. Watt & P. R. Ehrlich), pp. 353–366. Chicago, Illinois: University of Chicago Press.
- Van Dyck, H. & Baguette, M.** 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*, **6**, 534–545.
- Waser, P. M., Creel, S. R. & Lucas, J. R.** 1994. Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behavioral Ecology*, **5**, 135–141.

- Wickman, P. O. & Wiklund, C. 1983. Territorial defence and its seasonal decline in the speckled wood butterfly (*Pararge aegeria*). *Animal Behaviour*, **31**, 1206–1216.
- Wiklund, C. & Persson, A. 1983. Fecundity, and the relation of egg weight variation to offspring fitness in the speckled wood butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? *Oikos*, **40**, 53–63.
- Yukilevich, R. 2005. Dispersal evolution in fragmented habitats: the interplay between the tendency and the ability to disperse. *Evolutionary Ecology Research*, **7**, 973–992.
- Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology*, **15**, 523–533.
- Zollner, P. A. & Lima, S. L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos*, **80**, 51–60.
- Zollner, P. A. & Lima, S. L. 1999. Search strategies for landscape-level interpatch movements. *Ecology*, **80**, 1019–1030.