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Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models

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The dispersal patterns of animals are important in metapopulation ecology because they affect the dynamics and survival of populations. Theoretical models assume random dispersal but little is known in practice about the dispersal behaviour of individual animals or the strategy by which dispersers locate distant habitat patches. In the present study, we released individual meadow brown butterflies (*Maniola jurtina*) in a non-habitat and investigated their ability to return to a suitable habitat. The results provided three reasons for supposing that meadow brown butterflies do not seek habitat by means of random flight. First, when released within the range of their normal dispersal distances, the butterflies orientated towards suitable habitat at a higher rate than expected at random. Second, when released at larger distances from their habitat, they used a non-random, systematic, search strategy in which they flew in loops around the release point and returned periodically to it. Third, butterflies returned to a familiar habitat patch rather than a non-familiar one when given a choice. If dispersers actively orientate towards or search systematically for distant habitat, this may be problematic for existing metapopulation models, including models of the evolution of dispersal rates in metapopulations.

Keywords: correlated random walk; incidence function model; metapopulation viability; non-random dispersal; systematic search

1. INTRODUCTION

Dispersal patterns have important effects on the dynamics and survival of animal populations, particularly when habitat fragmentation causes small 'local populations' to become spatially isolated (e.g. Dempster 1991; Harrison *et al*. 1993; Ims & Yoccoz 1997). In such circumstances, regular recolonization of extinct local populations through dispersal from other local populations plays an important role in the survival of the metapopulation (i.e. the network of local populations) as a whole (e.g. Levins 1969; see also Hanski (1998) for a review).

Several authors have recently pointed out that it is important to integrate individual behaviour into the study of ecological processes in order to be sure that interpretations of observed patterns are truly process based (e.g. Sutherland & Dolman 1994). However, although the pattern of dispersal is a crucial part of all metapopulation models, detailed information about how individual animals disperse is limited because of the difficulty in keeping track of dispersing individuals in the field (see Zollner & Lima 1999*a*). Most studies rely on resightings of marked animals (e.g. Brakefield 1982; Harrison 1989) but these do not provide information about a dispersing individual's actual trajectory or about the mechanism by which it finds a suitable destination. Consequently, for most of the species of interest to metapopulation biology it is not known whether dispersing individuals navigate or follow systematic search strategies, as opposed to moving randomly. Most metapopulation models simply assume random movement (see Hanski (1998) for a review) and, based on this assumption, generate colonization patterns for patches depending on variables such as patch size and isolation.

Our aim was to investigate the dispersal movements of individuals in a non-migratory species which has a metapopulation structure. We chose the meadow brown butterfly (*Maniola jurtina*) because it lives in fragmented habitats with networks of local populations and shows dispersal rates that are typical of butterfly metapopulations. Brakefield (1982) reported average dispersal distances for meadow browns of 40–70 m within a habitat and stated that their between-habitat dispersal distances were similar. In order to simulate dispersal (see Harrison 1989; Zollner & Lima 1997, 1999*a*), we released individual adult meadow browns in an unsuitable habitat at various distances from a suitable habitat and mapped their subsequent flight trajectories. The objectives were (i) to determine whether individuals sought a suitable habitat by flying randomly from the release point or by some non-random strategy, and (ii) to investigate whether butterflies preferentially sought the closest, the most obvious or their 'home' habitat patch. We discuss the implications for metapopulation models that assume random dispersal.

2. METHODS

(a) *Study area*

The study was conducted in July and August 1999 in the Cambridgeshire fens along the 'Devil's Dyke', an elongated man-made earthwork *ca.* 8.5 km long, 20 m broad and 5 m high, which is surrounded by flat agricultural landscape. It is mainly covered by tall, calcareous grassland where *M. jurtina* breeds prolifically. We released butterflies in two fields on opposite sites of the dyke (see figure 1): there was a short-cropped pasture field on one side and a harvested wheat field on the other. These

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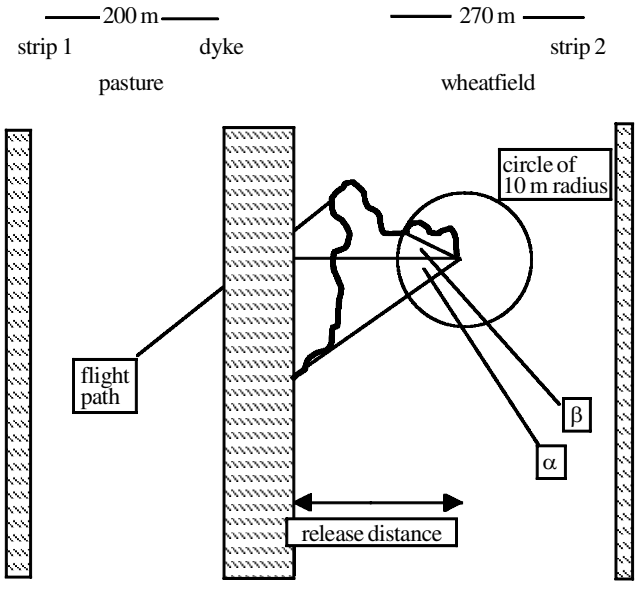

Figure 1. Schematic drawing of the study site (not to scale). α, final angular divergence, and β, starting angular divergence at 10 m from the release site.

fields contained no suitable oviposition sites and very few nectaring plants, so they constituted unsuitable habitat for the species. It can be assumed that butterflies, when released in these fields, were motivated to return to suitable habitat as quickly as possible for the following reasons. First, adult *M. jurtina* live only a few days (on average, approximately seven days) (L. Conradt, unpublished data) and are active only during warm, dry hours. Therefore, even a few hours of lost opportunity for ovipositing or mating are likely to represent a considerable proportion of their potential total reproduction. Second, *M. jurtina* usually feed regularly during active hours (L. Conradt, personal observation) and, therefore, require the proximity of nectaring plants: many butterflies on return to their habitat immediately began feeding. Third, the wheat field and the pasture were both very open, so the butterflies were more exposed to avian predation in these fields than they were within a suitable habitat.

Both fields were bordered by an additional strip of suitable habitat (long grassland) along the side furthest from the dyke and parallel to it (strips 1 and 2) at distances of 220 and 270 m, respectively. There was no other suitable habitat within 400 m on either side of the dyke.

(b) *Procedure*

(i) *Experiment 1*

Experiment 1 was aimed at seeing how butterflies that were released in an unsuitable habitat would find their way to a suitable habitat. Individual butterflies ($n = 209$) were caught on the dyke, sexed, marked and immediately transported in the capture net, in such a manner that they could not see out, to a release site located in unsuitable habitat (pasture or wheat field) on either side of the dyke. The release sites were at distances of 15, 30, 50, 75, 100, 125 and 150 m from the dyke (see figure 1). Because the results from the pasture and wheat field were not different, we report the combined results below. Butterflies were transferred to a release box (12 cm × 12 cm × 12 cm) covered in fine nylon mesh at the release site, were given 3 min to settle and were then released by opening the box by means of a string pulled by an observer standing 5 m away. The observer position did not influence any aspect of the subsequent flight pattern. The observer followed each butterfly (from a distance of > 30 m) until it either (i) returned to a suitable habitat (strip 1, the dyke or strip 2), (ii) had reached a distance of > 300 m from the release point without finding a suitable habitat, or (iii) was lost from view prematurely. The 300 m termination threshold was chosen in order to reduce the problem of non-navigating butterflies eventually flying into habitat by chance (see Goodwin *et al.* 1999). Multiple linear regression models were used to investigate the influence of the release distance and environmental factors on various aspects of the butterflies' flight pattern subsequent to release; we report only significant results below.

(ii) *Experiment 2*

Since the butterflies in experiment 1 returned to the dyke at an unexpectedly high frequency (see § 3), we examined whether this was because the dyke was the largest and most obvious habitat patch or whether it was because it was their home patch. Butterflies ($n = 69$) were caught alternately from the dyke and strip 1 and released in the pasture field between the dyke and strip 1 at distances of 110 and 150 m from the dyke and 110 and 70 m from strip 1. We predicted that, if butterflies fly to the largest or most conspicuous habitat patch, they should return to the dyke regardless of where they were captured. However, if they preferentially return to their home habitat patch, strip 1 butterflies should return more often to strip 1 and dyke butterflies should return more often to the dyke. When the results did not differ between the release distances, we combined samples (this was conservative from the point of view of our question since, on average, strip 1 butterflies had been released closer to the dyke than dyke butterflies). We also compared the behaviour of strip 1 butterflies to the results of regression models from experiment 1.

(c) *Data*

We measured the starting angle and flight time at 10 m from the release point, total flight time, flight height (scale 1–6), flight speed (scale 1–3), final position, angle of the final position relative to the release point, arrival habitat, approximate flight path and approximate flight length. We also measured the following environmental factors: wind speed and direction, sun direction, temperature, humidity, light intensity, cloud cover and the proportion of time for which the sun was behind clouds during a flight. The last three factors were closely correlated so we combined them into two visibility classes: 'good' or 'bad'. We defined 'angular divergence' from a habitat patch as the difference in the angular direction between the position of a butterfly and the nearest point of the habitat patch, as seen from the release point (see figure 1). Thus, the angular divergence was a maximum of 180°. Since we did not observe significant differences between sexes or wing-wear classes, the data for all butterflies were lumped.

(d) *Distinguishing between non-random and random flight*

The 'performance' (i.e. the rate of successful arrivals in a habitat and starting and final angular divergence) of butterflies in a non-random flight should be better than expected from a random flight and should decrease with increasing distance between the release site and habitat patch (e.g. Zollner & Lima 1997). In order to examine whether the observed flights were

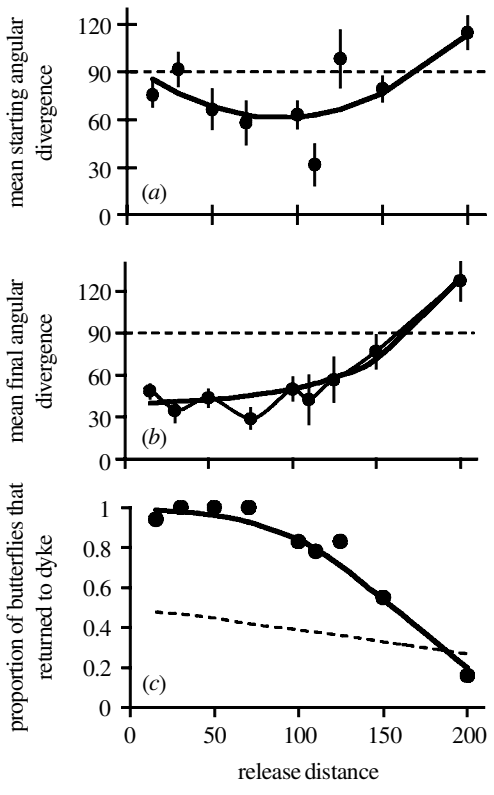

Figure 2. Mean (± s.e.) starting and final angular divergence and proportion of butterflies that returned to the dyke in experiment 1 when released from various distances from the dyke. The regression curves are given as solid lines and the expected values for a linear, random flight as dotted lines.

random or non-random, we distinguished between two types of random flights: linear, random flights (i.e. straight, random flights) and nonlinear, random flights (i.e. 'random walks' with a degree of correlation of < 1) (e.g. Turchin *et al.* 1991; Kindvall 1999). The expected mean starting and final angular divergence is 90° for linear, random flights (with an s.e. of $\pm 52°/\sqrt{n}$), while the expected proportion of butterflies arriving in a patch depends on the release distance and threshold at which observations are terminated (300 m in this study) and is arccos (release distance/threshold)/p_i. In order to distinguish between non-random and linear, random flights, we compared these predicted values to our observed data. It is difficult to make similar quantitative predictions for the final angular divergence and rate of successful arrival for nonlinear, random movements because the termination of observations when an animal arrives in a habitat biases the resulting data: animals which do not move directly into a habitat will be watched for a longer time and over a longer distance and will therefore be more likely to drift into a habitat eventually by chance (Goodwin *et al.* 1999). Therefore, we made testable qualitative predictions for nonlinear, random flights as follows: (i) with increasing nonlinearity of flights the regression slope of the arrival success on the distance to a habitat should increase (as shown in the simulations by Goodwin *et al.* (1999)), and (ii) because less linear flights cover more area and, therefore, have more opportunity of drifting into a habitat by chance, they should have a lower final angular divergence and a higher success rate than more linear flights. If these predictions were not supported, we would conclude that the dispersal movements were non-random.

3. RESULTS

(a) *Random versus non-random dispersal movement*

(i) *Starting angle*

The starting angular divergence in experiment 1 decreased up to a release distance of 75 m from the dyke and increased thereafter ($F_{1,207} = 17.7$ and $p < 0.001$) (see figure 2). Thus, the maximal orientation towards the dyke was found at intermediate release distances, and between 50 and 110 m the proportion of butterflies that started in a direction of ± 45° towards the dyke was significantly higher than random (Fisher's exact tests, $p < 0.05$ in each case and $n = 11–34$). At 15 and 30 m, the butterflies may have shown a low motivation for 'aiming' at a habitat accurately (since from short release distances divergences in the starting angle lead to only small detours and might therefore not have mattered to the butterflies), while for release distances over 110 m they were probably no longer able to orientate towards the dyke at the start. The starting angle of the butterflies was still significantly orientated towards the dyke when we controlled for the wind direction (*t*-test, $t = 3.16$, d.f. = 207 and $p < 0.002$), which was the only environmental factor that influenced the starting angle ($F_{1,207} = 52.5$ and $p < 0.0001$).

(ii) *Final angle*

The final angular divergence relative to the dyke in experiment 1 was significantly lower than the starting angular divergence (*t*-test, difference = − 17.4°, $t = -4.13$, d.f. = 181 and $p < 0.001$). In addition, the final angular divergence increased with distance from the release site to the dyke ($F_{2,179} = 29.3$ and $p < 0.0001$) (see figure 2) and, up to 125 m, the butterflies orientated significantly more towards the dyke than expected from a linear, random flight (*t*-test, $t = 5.59$, d.f. = 178 and $p < 0.001$). Only at a release distance of 200 m from the dyke (i.e. 70 m from an alternative habitat) was the final angle more orientated towards an alternative habitat than towards the dyke and this orientation was significant (*t*-test, $t = 2.10$, d.f. = 18, $p < 0.05$ and $n = 19$).

We observed two distinct types of flight: flight type 1 was relatively linear, while flight type 2 was clearly nonlinear (see figure 3 and § 3 (b)). Contrary to predictions for nonlinear, random flights, we found that (i) the slope of the correlation between the final angular divergence and release distance did not differ between the less and more linear flight types ($F_{1,178} = 1.12$ and $p > 0.4$, n.s.), and (ii) the less linear flight type did not lead to a lower final angular divergence than the more linear flight type ($F_{1,178} = 0.6$ and $p > 0.5$, n.s.). We concluded that the final angular orientation of the butterflies could not be explained by random flight behaviour.

(iii) *Rate of successful return to habitat*

The proportion of successful returns to the dyke in experiment 1 decreased significantly with release distance from the dyke ($F_{1,181} = 64.9$ and $p < 0.00001$) (see figure 2) and, for release distances of up to 150 m, the return rate to the dyke was significantly higher than expected from a linear, random flight (Fisher's exact test, $p < 0.0001$ and $n = 164$). In contrast, the proportion of butterflies arriving in alternative habitat was only

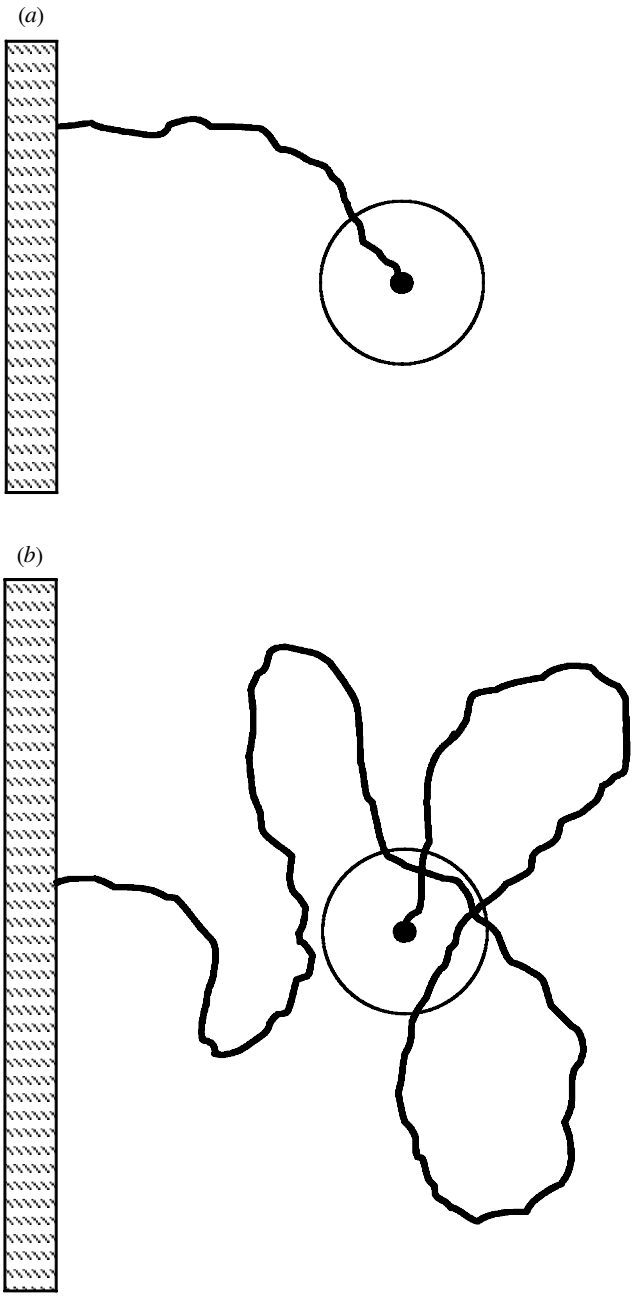

Figure 3. Examples of flight paths of (*a*) type 1 and (*b*) type 2.

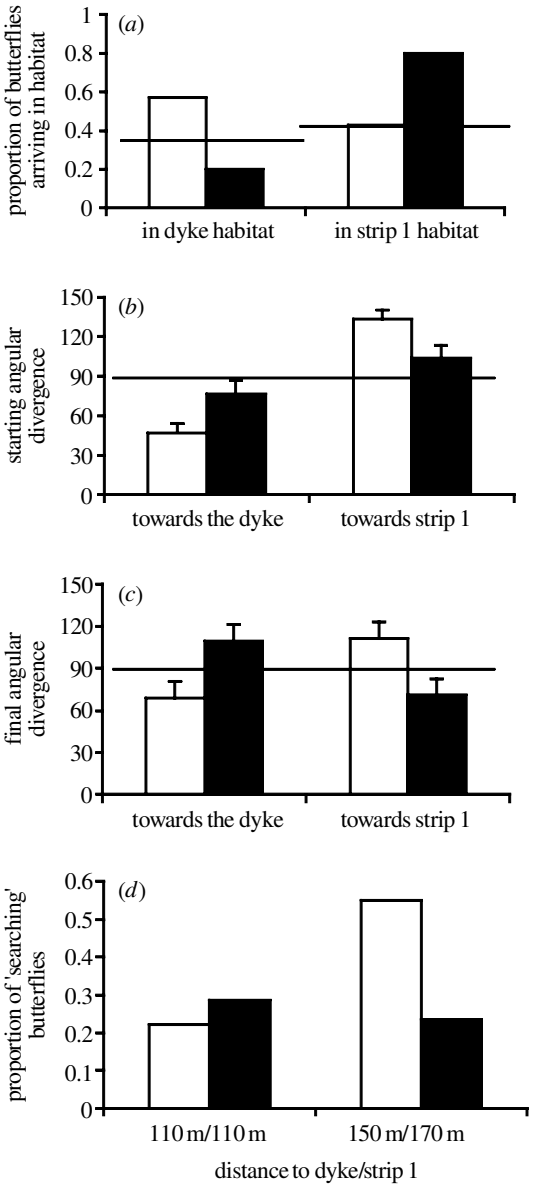

Figure 4. Differences between the dyke (open bars) and strip 1 (filled bars) butterflies in experiment 2 with respect to the proportion of butterflies returning to the dyke and to strip 1. The mean (s.e.) starting and final angular divergences towards the dyke and strip 1 and the proportion of butterflies searching when released halfway (110/110 m) between the dyke and strip 1, or closer to strip 1 than to the dyke (150/170 m). The horizontal lines give the expected values for linear, random flights.

significantly higher than expected (observed = 0.74, expected = 0.43, $n = 19$ and Fisher's exact test, $p < 0.002$) at a release distance of 200 m from the dyke (70 m from alternative habitat).

Contrary to predictions for random flights, we found that (i) the proportion of successful returns decreased more steeply with release distance to the dyke than was expected by a linear, random flight ($F_{1,181} = 40.5$ and $p < 0.00001$), (ii) the slope of the regression of the return rate on distance did not differ between the less and more linear flight types ($F_{1,171} = 0.44$ and $p > 0.5$, n.s.), and (iii) the less linear flight type did not have higher return rates than the more linear flight type ($F_{1,161} = 2.84$ and $p > 0.05$). This constitutes further evidence that the high return rate to the dyke could not be explained by random flight behaviour.

(b) *Searching behaviour*

The flight patterns fell clearly into two categories (see figure 3). After their initial start, butterflies of flight type 1 flew relatively linearly with few large-scale changes of direction (mean ± s.e. number of changes = 0.83 ± 0.07 and $n = 200$, and mean ± s.e. turning angle = 69.0° ± 3.7° and $n = 99$). They moved steadily further away from the release site and never flew in loops or returned to the release site. In contrast, butterflies of flight type 2 flew relatively low, slowly and in large circles or ellipses in a succession of petal-like loops around the release site (mean ± s.e. number of loops = 1.8 ± 0.1 and $n = 46$, and mean ± s.e. radius = 29.2 ± 2.8 m, range = 5–140 m and $n = 77$). They returned one or more times to within 10 m

of the release point (mean ± s.e. number of returns = 1.1 ± 0.1 and $n = 52$). Flight type 2 was thus distinctly non-random (cf. Mueller & Wehner 1994). Only two out of 308 observed flight patterns could not be clearly assigned to one of these two types.

Since flight type 2 was suggestive of searching behaviour, we examined it in more detail. First, we asked whether butterflies returned to the release point by following a simple rule such as 'always turn right'. However, no more butterflies orientated all their circles either only right or only left than expected by chance (observed number, 10 out of 26 and expected number, 11 out of 26) suggesting that return to the release point was achieved by genuine navigation. Second, we investigated whether the butterflies increased the radius of consecutive circles so as to search increasingly large areas. We found no difference in radius between first and second circles (*t*-test, $t = 0.78$, d.f. = 25 and $p = 0.4$, n.s.), but an average increase in radius of 13.1 m between second and third circles (*t*-test, $t = 2.66$, d.f. = 8 and $p = 0.03$). Finally, we examined the relationship between the release distance or environmental conditions and flight pattern. The proportion of butterflies showing flight type 2 increased significantly with release distance to the dyke (logistic regression, proportion $= 1/(1 + 7.6 \times 0.99^{\text{distance}})$, $F_{1,158} = 5.2$ and $p < 0.01$) and in conditions of poor visibility ($F_{1,157} = 6.3$ and $p < 0.01$) suggesting that, from further distances or when visibility was poor, a higher proportion of butterflies needed to search for a suitable habitat. Once distance to the dyke had been controlled for, the two flight types did not result in significantly different return rates ($F_{1,174} = 0.31$ and $p > 0.9$, n.s.).

(c) *Homing behaviour*

Strip 1 butterflies returned to strip 1 in experiment 2 with a significantly higher rate than expected at random (Fisher's exact test, $p < 0.0001$ and $n = 25$) (see figure 4), and dyke butterflies returned to the dyke with a significantly higher rate than expected at random (Fisher exact test, $p = 0.013$ and $n = 28$). The two groups of butterflies also behaved differently to one another with respect to their starting angular orientation (*t*-test, $t = 2.23$, d.f. = 67 and $p < 0.02$) (see figure 4), final angular orientation (trend only, $t = -1.67$, d.f. = 49 and $p > 0.05$, n.s.) and arrival rate in the dyke habitat (χ^2-test, $\chi^2 = 7.6$, d.f. = 1, $p < 0.01$ and $n = 53$), orientating and returning preferentially to their own home patches. In addition, the proportion showing searching behaviour (i.e. flight type 2) increased in both groups of butterflies with the release distance to their own patch so that, when released further from the dyke than from strip 1, dyke butterflies searched at a higher rate than strip 1 butterflies (at 150 m from the dyke and at 70 m from strip 1) ($\chi^2 = 3.8$, d.f. = 1, $p = 0.05$ and $n = 33$) (see figure 4).

In addition, we compared the behaviour of the strip 1 butterflies to that of the dyke butterflies in experiment 1. The final angular divergence of the dyke butterflies towards their home patch (i.e. the dyke) increased monotonously in experiment 1 and their return rate decreased monotonously with release distance from their home patch (see figure 2). We found that the strip 1 butterflies in experiment 2 moved towards strip 1 (but not towards the dyke) in the manner in which the dyke butterflies had moved towards the dyke in experiment 1, that is the final angular divergence of the strip 1 butterflies towards their home patch (i.e. strip 1) and their return rate to their home patch did not differ from the regression predictions for the relevant release distances (the release distances to strip 1 in this study) in experiment 1 (final angular divergence, $F_{1,204} = 0.8$ and $p > 0.3$, n.s., and return rate, $F_{1,203} = 0.95$ and $p > 0.5$, n.s.) (compare figures 2 and 4). Correspondingly, strip 1 butterflies showed a significantly higher final angular divergence towards the dyke ($F_{1,204} = 9.4$ and $p < 0.003$) and a significantly lower return rate to the dyke ($F_{1,203} = 20.3$ and $p < 0.00001$) than predicted for the relevant release distances (to the dyke in this study) by the regressions in experiment 1. These results strongly imply that *M. jurtina* was able to distinguish between a familiar and a non-familiar habitat patch and preferred the former when given a choice.

4. DISCUSSION

Our results provide three reasons for supposing that meadow brown butterflies disperse non-randomly. First, when released in an unsuitable habitat, meadow browns did not move randomly away from the release site but directed their movements towards a familiar habitat patch from distances of at least 125 m and towards an unfamiliar patch from distances of at least 70 m. This suggests that the normal dispersal distance of meadow browns (40–70 m) (Brakefield 1982) lies in the range within which they can actively orientate towards a suitable habitat patch ('perceptual range') (Harrison 1989; Zollner & Lima 1997, 1999*a*).

Second, with increasing release distance from a suitable habitat, butterflies increasingly chose a flight pattern suggestive of systematic search: specifically, they flew in large loops in a petal-like manner around the release point. Similar behaviour has been described in various species of central-place foragers including ants and bees when searching for their nest sites or for foraging opportunities in the vicinity of the nest (e.g. Hoffmann 1983; Mueller & Wehner 1994; Durier & Rivault 1999). However, as far as we know, it has not yet been described in a non-territorial or non-central-place forager, nor has it been suggested that dispersing individuals could use this kind of systematic search in detecting suitable habitat patches. An obvious advantage of this particular search pattern is that it enables the disperser to return to the starting point. This could be highly advantageous in a fragmented landscape where the probability of finding another habitat patch may be low, so that a disperser may be forced to either abandon the search for a new patch altogether or return to the original patch in order to replenish its resources before embarking on a further search.

Third, we found that meadow browns preferentially returned to their familiar habitat patch when given a choice between this and an unfamiliar patch. Such 'homing' behaviour cannot be explained by random movements of individuals outside of habitat patches. This result was surprising in that homing has not yet been described in non-migratory butterflies and rarely in other species that are non-territorial and non-central-place foraging, but it is in good agreement with anecdotal

reports that individual butterflies return repeatedly to favourite perching and feeding sites (A. Kelber, personal communication) and that meadow browns restrict their activity to familiar areas (Brakefield 1982).

All of these results undermine the assumption that meadow browns disperse randomly, yet the random dispersal of animals, including butterflies, is assumed by the majority of metapopulation models (see Hanski & Gilpin (1997) and Hanski (1998) for reviews). The relationship between the dispersal rate and dispersal distance is crucial for the predictions of metapopulation viability models and it is usually described by a negative exponential function that fits the distribution of the dispersal distances expected if individuals disperse in straight, random walks with a fixed per-distance probability of stopping. This function is parameterized by fitting regression curves to mark–release–recapture or patch-incidence data (e.g. Hanski & Gilpin 1997). However, the assumed shape of the regression curve can be crucial for estimates of dispersal rates at particular distances and, in particular, at long distances because these are often particularly badly documented by empirical data. Thus, the assumed theoretical relationship between the dispersal rate and distance needs to be justified by the dispersal behaviour of individuals.

The simulations by Zollner & Lima (1999*b*) showed that the patch-finding success of dispersers depends to a large degree on their search strategy and that random and systematic search strategies differ in their success rates and also therefore in the dispersal and colonization patterns to which they give rise. Therefore, in the event of non-random, systematic searches, the shape of the relationship between the dispersal rate and distance might not follow a negative exponential curve. Only simulation models can determine the expected shape of this relationship for such complex searching behaviours as are described in the present study. However, since the described searching behaviour concentrates the search effort close to the starting patch, we would expect fewer long-distance dispersals in a single dispersal event (from one patch to another) than expected by a negative exponential curve. On the other hand, if butterflies dispersed repeatedly during their lifetime, a systematic searching pattern could lead to a relatively large number of long-distance dispersers because the resulting 'stepping-stone dispersal' and the likely higher search efficiency should reduce the losses of individuals during dispersal over longer net dispersal distances. More empirical information on butterfly behaviour will be needed before specific predictions can be made.

Simulation models are needed in order to examine the specific consequences of violation of the assumption of random dispersal for metapopulation models. However, the results from related models that have examined the expansion rates of newly establishing populations suggested that misestimation of long-distance dispersal rates can have significant effects on the outcome (R. O'Hara, personal communication). In addition, non-randomness in dispersal is relevant to evolutionary studies since, in existing models, the mortality of migrant individuals is estimated on the assumption of random dispersal and predictions concerning the evolution of dispersal rates in fragmented landscapes depend greatly on the mortality rates of migrants (e.g. Travis & Dytham 1998).

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