Response to topography in a hilltopping butterfly and implications for modelling nonrandom dispersal

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Animal movement between habitat patches is often considered a random process. However, responses to landscape heterogeneity can direct the movement of animals and affect connectivity patterns. Topographical heterogeneity is a major source of habitat heterogeneity, which often directs animal movements and yet is scarcely studied in the context of dispersal. We investigated the mechanisms of response to topography and movement rules, using hilltopping as a behavioural case study. Hilltopping is a mate-searching strategy where males and virgin or multiple-mating females seek a topographical summit on which to mate. Mated females descend from the summits thereafter to search for host plants. We investigated the behavioural rules of hilltopping in males and virgin females of the butterfly *Melitaea trivia*, and female postmating movements. We released butterflies in different topographical formations, in a landscape that contained no larval host plants. We followed them individually, mapped the flight routes, and analysed them with respect to the surrounding landscape, using a Digital Elevation Model. Males and virgin females initiated hilltopping behaviour only in the absence of other individuals. After an initial orientation phase, butterflies flew towards the maximal inclination available. However, some downward movements interrupted the upward flight. When arriving at or released on a summit, males strongly adhered to it. After copulating, females showed little response to topography. Males and virgin females responded to topographical cues within about 50 m of their location. Our results show that nonrandom movements, such as hilltopping, are based on simple and predictable decision rules. We discuss the relation between hilltopping and dispersal, and the implications for modelling dispersal.

The dynamics of spatially structured populations are governed by dispersal (Opdam 1990; Hanski et al. 1994; Frank & Wissel 1998; Thomas 2000; Wilson & Thomas 2002). Consequently, the forces that direct dispersal and the resulting pattern of connectivity between patches are of great importance to the existence of such populations. The response of animals to landscape heterogeneity can direct their movement between patches, thereby altering the pattern of connectivity between patches (Wiens et al. 1993; Gustafson & Gardner 1996; Ricketts 2001; Ries & Debinski 2001). The interactions between animals and their surroundings can present barriers and corridors to dispersal, and channel their movements into specific routes (corridors). This, in turn, affects the pattern of connectivity between patches of suitable habitat, and in the long term determines the dynamics of population networks and shapes their spatial structure. Consequently, responses to landscape heterogeneity, at the individual level, are key to understanding and predicting the large-scale and long-term dynamics of spatially structured populations.

However, models of dispersal and connectivity commonly consider the landscape between patches to be uniform and assume that movement across the landscape is random (Adler & Nuernberger 1994; Hanski et al. 1994;

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Bascompte & Sole 1996; Kuussaari et al. 1996; Frank & Wissel 1998; Moilanen & Hanski 1998). A major reason for this assumption is that the incorporation of non-random movements into such models requires knowledge of the rules that govern the decisions of animals during dispersal, which is rarely available (South et al. 2002).

The process of dispersal through nonhabitat matrices involves constant decision making in response to landscape heterogeneity. However, the mechanisms that direct the decisions of animals within such landscapes remain generally unknown. To date, field studies that address the forces that direct dispersal have concentrated mainly on the behaviour of animals while leaving their habitat patches (Hanski et al. 1996; Moilanen & Hanski 1998; Schultz 1998; Schultz & Crone 2001), and their response to barriers during dispersal (Haddad 1999a, b; Bélisle & St. Clair 2001). Another approach taken in studying dispersal is to recognize the landscape types that are preferred by animals while moving between patches of suitable habitat (Beier 1995; Pither & Taylor 1998; Palomares et al. 2000; Shkedy & Saltz 2000; Palomares 2001). However, the mechanisms that direct animals during their movement remain poorly understood. This is reflected, for instance, by the occurrence of directional movements even within landscapes that appear uniform (e.g. Conradt et al. 2000, 2001). Thus, understanding the mechanisms that direct dispersal is crucial for predicting the actual route taken by a dispersing animal (Bakker & Van Vuren 2004). This is especially true with respect to gradual changes in the landscape, as opposed to the more intensively studied situation of abrupt changes between habitats.

Topographical heterogeneity is a major source of landscape heterogeneity. It exists in many terrestrial landscapes and on many spatial scales, from the microscale to the continental one. Various authors have recognized the impact of topographical elements, such as rivers, mountain ranges and cliffs, on dispersal patterns (Harrison 1989; Fritts & Carbyn 1995; Kuussaari et al. 1996; Nève et al. 1996; Akçakaya & Atwood 1997; Roland et al. 2000; Shkedy & Saltz 2000; Gillespie 2001), migration routes (e.g. Beebe 1949, 1950a, b; Schmidt-Koenig 1993; Srygley & Oliveira 2001; Williams et al. 2001; Shamoun et al. 2003) and foraging movements (e.g. Bustamante et al. 1997; Mysterud et al. 2001; Hastie et al. 2003). Several mechanisms have been suggested for the response of animals to topography, such as moving along cliffs to avoid predation (Shkedy & Saltz 2000), moving upstream to compensate for downstream drift in rivers (Lowe 2003), or through mountain passes to avoid wind-draft risks (Srygley & Oliveira 2001). Others have suggested indirect responses, through vegetation patterns and climatic gradients that are related to topography (e.g. Peterson 1997; Roland et al. 2000; Mysterud et al. 2001).

Since topography affects animal movements, it potentially directs or impedes the movement of dispersing animals, with broad implications for connectivity and population dynamics of spatially structured populations. However, because of the difficulties associated with studying dispersing animals in general (Zollner & Lima 1999; Nathan 2001; Williamson 2002), and animal movements in topographically complex landscapes in particular,

mechanisms of response are rarely addressed experimentally. Thus, little is known about the decision making involved in responses to topography, and the subsequent movement and connectivity patterns in topographically complex landscapes. Therefore, identifying the mechanisms of response to topography is a crucial first step in studying the role of topography in determining dispersal patterns (Pe'er 2003).

We investigated the response to topography of a hilltopping butterfly *Melitaea trivia*. Hilltopping is a common mate-searching strategy in many insects and other organisms, where males and virgin or multiple-mating females seek a topographical summit for the purpose of mating (Shields 1967; Lederhouse 1982; Ehrlich & Wheye 1988; Singer & Thomas 1992; Tennent 1995). Males tend to stay on the summit and form 'leks' (Alexander 1975; Lederhouse 1982; Thornhill & Alcock 1983; Queller 1987), whereas females leave the summit immediately after mating to search for host plants. Hilltops can be considered unsuitable habitats, as they usually do not provide host plants on which the larvae can develop. Therefore, this behaviour enables us to understand the mechanisms that direct dispersal, because it drives animals out of habitat patches and directs their movement thereafter. As we knew the aim of the hilltopping process (to find mates), the object of our study was to investigate its mechanisms. Specifically, we were interested in the behavioural rules that direct males and virgin females while moving towards the summits, and the postmating movement patterns of the females. We tried to recognize the topographical cues to which butterflies respond, the perceptual range of this response, and the consistency of this behaviour through time and distance. We attempted to describe the initiation of the hilltopping behaviour, its en route process and the performance upon reaching a summit. We also re-examined the perception that females actively descend from the summits after copulation (Shields 1967), hypothesizing that the postcopulation movement away from summits may occur as passive diffusion (Wickman 1988).

METHODS

Field Observations

Melitaea trivia syriaca (Nymphalidae) is a small butterfly (wing span 15–23 mm) that exhibits strong hilltopping behaviour (Benyamini 1990). It is distributed throughout southern Europe, the Levant, and eastward to Pakistan. In Israel it is found throughout the Mediterranean region and in desert areas of the Negev highlands. Since its distribution is often patchy, its hilltopping behaviour may serve as part of the dispersal mechanism between habitat patches.

We conducted field observations in southern Israel for the duration of the activity period of adult butterflies, from the end of March to the beginning of June 2000. The landscape, 'Lahav hills', is located 20 km north of Be'er Sheva, Israel (31°25′N, 34°50′E, annual precipitation ca. 300 mm). It is characterized by high topographical complexity and a relatively uniform vegetation of semiarid
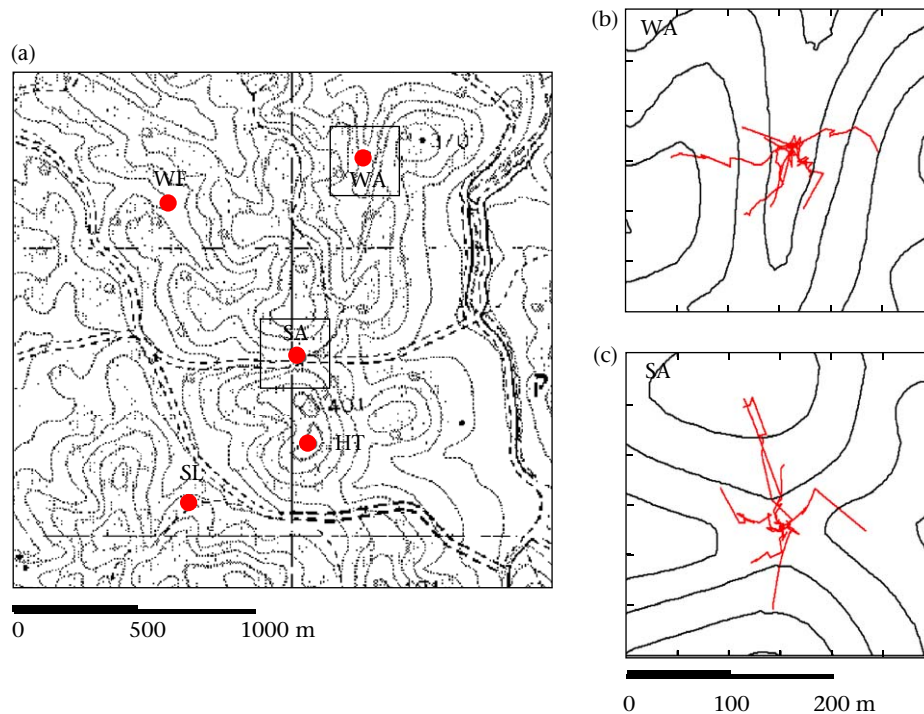
Figure 1. (a) Map of study area, indicating the five release points: HT = hilltop, SA = saddle, WF = wadi fork, WA = wadi bottom and SL = slope. Elevations range from 330 to 401 m within the study area. Contour lines represent 10-m changes in elevation. Rectangles represent two sections of the map, depicting the movement trajectories of males and virgin females when released in (b) the Wadi and (c) the Saddle. Short trajectories are obscured because of the scale.

scrubland (with plants up to 50 cm in height; Fig. 1a). Thus, we have assumed that vegetation structure has no impact on butterfly behaviour.

Most of the butterflies in our study were collected as larvae and reared in captivity. We fed the larvae on *Verbascum fruticulosum* plants, which were placed in net-cages inside a greenhouse. Adults were collected into cooling boxes immediately after hatching, to avoid mating events. Some of the males and all mated females were collected as adults in the field, with a sweep net. Mated females were recognized as such by oviposition events, refusing males or typical searching flight around host plants. All butterflies were placed in cooling boxes during the day until release, and in no case were they held for more than 4 days. They were then released in areas that contained no larval host plants for the subject species, to induce the hilltopping behaviour (following Turchin et al. 1991; Schultz 1998; Turchin 1998; Conradt et al. 2000, 2001; Haddad 2000; Nathan 2001; Gobeil & Villard 2002; Goheen et al. 2003). After the experiments we released captive butterflies near suitable habitat patches.

Nearly 100 butterflies were released individually at one of five release points located in five topographical formations: hilltop (HT), saddle (SA), wadi bottom (a dry stream bed; WA), wadi fork (WF) and slope (SL). An additional 'treatment', referred to as 'cleared hilltop' (CHT), was added because of the strong influence of interactions with other individuals on butterfly behaviour,

observed on hilltops. In this treatment, we carried out releases on the summit after all butterflies from all species had been removed from the hilltop and placed in cooling boxes, where they were kept until the trial ended. The use of several release points ensured that the butterflies met various topographical configurations and a large range of steepness levels.

During each observation, butterflies were placed on the ground to warm up and allowed to feed on a sugar solution until voluntary take-off. They were then tracked by a single observer, who kept at least 1 m from the butterflies, positioning himself so that his shadow would fall away from the butterflies and changing his relative direction during observation to ensure that no disturbances, such as herding, occurred (Turchin et al. 1991). During observations, movement trails were flagged with numbered flags, which were placed at each turning point and landing location. At the end of each observation, the spatial coordinates of each flag were determined by triangulating back to a 'baseline' using a compass (following Turchin et al. 1991). In addition, if a fast-flying butterfly disappeared from sight during an observation, we estimated the bearing of its last flight and the distance from the last turning point to the location where it was last seen. In the case of slow individuals that did not disappear by the end of the observation (see below), we followed them for up to four more turning events, and their movements were mapped using turning angles and distances from point to point (without triangulating to

the baseline). In a preliminary analysis based on five categories of flight speed, we found no difference in flight pattern between the different mapping methods and between short and long observations. Therefore, we used all data in our analysis.

All observations were made between 1000 and 1500 hours on clear or hot days (up to 60% cloud cover; up to 100% cloud cover if the temperature was above 25 °C), and only when the sun was not hidden by clouds. For each observation we noted butterfly sex and state (males, mated females and virgin females), time held in captivity and wing wear. The wind direction during each of the observations was measured with a compass, and a sweep net was used as a 'wind-sock' at 2 m above ground. In choosing the measuring height, we considered that at lower heights the wind became turbulent and less consistent through time because of boundary layer effects. This decision was conservative since *M. trivia* fly most of the time at less than 1 m above the ground. We also recorded wind intensity (six categories, from 0 = no wind to 5 = very strong wind, parallel to about 0–6 in the Beaufort scale), cloud cover (%), and observed inter- and intraspecific interactions which may have influenced flight directionality. Observations lasted up to 15 flags or up to 15 min (whichever came last). If inactive, butterflies were recollected and the observation was not used. If we lost the butterfly within four movements, its route was not recorded. Under the conservative limitations for conducting observations and accepting their data for analysis, we typically collected three to five movement routes on each observation day. We recorded and analysed the movement paths of 59 butterflies using 5–21 flags for each individual (12.4 flags/butterfly; Table 1). In these observations, butterflies moved a total distance of 11–374 m (median 84.7 m), and displacing from the point of release by 3–211 m (median 51.8 m). Figure 1 shows the movement trajectories of males and virgin females in two sample locations. Since we were interested in understanding the general mechanisms that direct flight movement, and not evaluating dispersal rates, we analysed movement decisions made during flight, and left out analyses relating to flight speed.

Table 1. Locations of butterfly releases

Topographical formation	Number of successful observations		
	Males	Virgin females	Mated females
Hilltop (HT)	2	3	6
Saddle (SA)	4	5	4
Wadi fork (WF)	1	6	0
Wadi bottom (WA)	5	6	3
Slope (SL)	4	2	0
Cleared hilltop (CHT)	4	4	0
Total	20	26	13

Owing to the small number of mated females, they were not released in the wadi fork or on the slope and hilltop releases were conducted without the cleared hilltop treatment.

Flight Analysis

We depicted the 59 routes on a map using the location of the five release points as reference points. The exact location of these five points was determined using Differential GPS (DGPS) with an accuracy of 35 cm. Movement patterns and movement decisions were analysed in two steps. In the first, we explored the general factors that influence flight patterns apart from topography: wind conditions, animal characteristics and the presence of conspecifics. In the second step, we explored the impact of topography on the process of decision making itself.

Analysis of flight patterns excluding topography

We estimated the impact of wind direction on flight direction by comparing the net flight direction (the compass direction from the point of origin to the last point in each observation) and the estimated wind direction during each observation. Statistics were based on a circular–circular T-linear association test $\hat{\rho}T$ (Fisher 1993, page 151), a correlation index for two circular distributions. The impact of sex, state and location on flight patterns was evaluated by two-way ANOVA, where state (three state-groups: males, virgin females, mated females) and location (three types of locations: hilltop, clear hilltop, nonhilltop locations) were the independent parameters, and the dependent parameters were, first, the average distance between turning points (increment length) and, second, the absolute turning angle (between 0 and π). A Tukey post hoc test was then used to determine the origin of differences between the different groups. Increment lengths were calculated on a horizontal plane because correcting for the true distances moved in three dimensions was marginal over most of the range of inclinations.

During the observations in the field we noted that some individuals, in the presence of other individuals, stayed around the point of release and flew back and forth without leaving the area of release, even if the location was not on a hilltop. To analyse the movement patterns and evaluate whether the tendency to stay around one location was a result of the interactions, we divided the butterflies into two categories, with or without interactions. We then compared butterflies that had interactions with those that had no interactions (two-sample *t* test) for differences in the average increment length (distance between turning points), the average absolute turning angle, the average distance added per flag (the aerial distance added by each movement section to the point of origin), and the proportion of points per observation that were collected further than 10 m from the point of release.

Impact of topography

In the second part of the analysis, we compared flight movements with the available topography. For this we used a Correlated Random Walk (CRW) Simulation to construct landscape-independent random movements, as a null model. In this simulation, 100 virtual butterflies were 'released' at five release points and 'flew' randomly,

based on the characteristics of flight patterns (increment length between turns and turning angles) evaluated from the first part of the analysis. We used the following parameters: the number of turning points ('flags') ranged uniformly between 6 and 18; turning angles distributed normally around a mean direction $\pm$ SD of -0.33 ± 1.664 radians, and truncated by $-\pi$ and π; increment lengths distributed log normally, where the log of flight distances were distributed normally around a mean $\pm$ SD of 0.696 ± 0.467, truncated by 0 and 150 m.

In this analysis, the direction taken at a given point along the path was compared with the available topography at that point, using a Digital Elevation Model (DEM) of the study area, a matrix of elevations with a cell size of 5×5 m that was produced for the purpose of the study (Mapping Technologies Ltd, Ramat-Gan, Israel). To obtain data on the topography along the whole movement trail of all butterflies, we divided each segment between turning points into 3-m segments, with the remainder added to the last segment. The reasoning behind this segmentation was that if topography changes and a butterfly does not change its movement direction, this could be regarded as a decision not to turn. The data points resulting from this segmentation were termed 'no-turning' points, as opposed to 'turning' points (flagged points). This segmentation enabled analysis of the movement patterns along the entire path, while taking into account the continuous changes in topography. It also weights the length of movements between turns, because long movements are described by more data points. The elevation of all data points (both 'turning' and 'no-turning' points) was then calculated using a cubic interpolation from the elevation matrix of the DEM (Matlab 2001). The actual inclination at the direction taken by a butterfly at each point (hereafter, 'slope taken') was calculated from the difference in elevation between that point and the elevation 3 m ahead on the butterfly's flight path. We then calculated the slopes that were available at each location using the elevations at a distance of 3 m in a sample of 16 evenly distributed directions on a compass rosette. This approach allowed us to evaluate the slopes taken during the flight, relative to the slopes that were available at each point.

Initial orientation phase

When butterflies are placed in a totally unknown landscape, their initial movements may be random because of the release effect caused by their need to investigate their surroundings. To see if such an orientation phase exists, we regressed the slope taken at each point against the distance from the origin for each butterfly. If a butterfly flies immediately upwards, which we predicted for males and virgin females, or downwards, as we predicted for mated females, the constant would be positive or negative, respectively, but the slope of the regression would not be significant. However, if a butterfly starts with a random flight (an orientation phase) and then shifts to a directional flight, the constant would not differ from zero, while the slope of the regression would be positive or negative. The analysis was based on counting

the cases where the slopes of the regression line and the constants were positive or negative, regardless of the line's significance. If no trend exists, the number of positive and negative cases should not differ. Since our goal was to determine the behaviour of the butterflies subsequent to the orientation phase, we used a graphical approach to determine the threshold distance below which disoriented movements occur. We created a bar diagram of the proportion of cases in which butterflies moved upwards, pooled over all individuals, and divided the diagram into classes of increasing distances from the origin. We evaluated the tendency to fly upwards (percentage of the movements upwards) for each distance class, for the males, the virgin females and the mated females. We then compared it to the corresponding tendency for the virtual butterflies in the CRW simulation. We validated the results of these two analyses by a repeated measure analysis, in which we tested the effect of time, location, state and location $\times$ state on the slope taken at each point. For this we analysed the first 5, 10, 15 and 20 data points.

Tendency and consistency of upward and downward flight

The number of movements upwards was compared to the number of movements downwards for each butterfly. This proportion was compared to an expected proportion, based on a count of the number of options to move upwards out of 16 possible directions at each data point. A similar comparison between the number of movements upwards and the counted possibilities to move upwards was performed with the data produced by the CRW simulation. We also evaluated the proportional distance that each individual moved upwards versus downwards. Flight consistency was defined as the probability of an upward or downward movement being followed by another upward or downward movement, respectively. We calculated the consistency upwards and the consistency downwards for each butterfly and then compared them using a paired-sample t test. A similar comparison was performed within the CRW simulation's data set.

We compared the slope taken with the available range of options at each point by plotting the slope taken against the maximal slope available at that point, for males, virgin females, mated females and the CRW simulation. This analysis was performed for the pooled data of each group of butterflies, the assumption being that each data point represents an independent decision. This assumption was supported by the consistency of the results when repeating the analysis with other, more conservative methods (see below).

Factors affecting the slope taken

We tested how butterfly movement decisions (expressed by the slopes taken) are affected by their state (males, virgin females or mated females), the location of the release point, and the landscape-specific factors at each point (maximal slope available). We also tested whether the movement decisions were different for turning points versus no-turning points. We needed to take into account

that the range of options from which a butterfly could choose at each point affects the slope taken. To assess the impact of the immediate surroundings on the slope taken, we used a relative index that accounts for the relation between the slope taken by the butterflies and the range of slopes available at each point. We termed this index 'Relative Choice' (RC):

$$RC = 1 - (Max - Taken)/(Max - Min)$$

where Max = maximal slope available at a point (out of 16 options), Min = minimal slope available, and Taken is the slope at the direction taken by the butterfly (slope taken). The RC index ranges mostly between 0 and 1, where 1 represents a slope close to the maximum available and 0 represents a slope close to the minimum available at a given point. Values greater than 1 or less than 0 were obtained in 8% of the cases, because the slopes taken were calculated based on the real direction, whereas the ranges of options were calculated based on 16 bearings. We then performed an ANOVA to test the effect of location (three categories: hilltop, cleared hilltop and nonhilltop locations) and state (three state-groups: males, virgin females, mated females) on the average RC of each butterfly. Since mated females were not released on the cleared hilltop, we conducted an unbalanced-design ANOVA, followed by a similar analysis for males and virgin females alone. We then compared the RC between turning and no-turning points for each state-group (paired-sample t test).

What induces butterflies to turn: slope or distance?

To test which cues induce butterflies to turn, we used only the data for males and virgin females from nonhill-top release points. We compared the slope taken at each turning point to the slope that would have been taken if the butterfly had continued in the same direction (paired-sample t test). A second method of analysis was based on the frequency of movement length between turning points. If butterflies turn at constant intervals regardless of the topography, or if they perform some long movements and some very short orientation movements, the frequency histogram of increment lengths would be significantly different from that predicted from the parallel histogram based on a Poisson distribution. To answer this question, we evaluated the number of turning points for movements of males and virgin females, and summed the total distance moved along their entire flight. We then created random increment lengths by dividing the complete flight interval of each butterfly into the same number of movement segments at random points ('broken stick' model), creating a Poisson distribution. The histogram of flight distance frequency based on the random segmentation was then compared to the observed one using a chi-square goodness-of-fit test.

Evaluating the response range

Since the goal of males and virgin females is to reach a summit, the direction selected should be towards the maximum slope within their range of perception. Given a collection of peaks at varying distances and directions, we can assume that the peak towards which a butterfly flies is the highest peak within the range from which butterflies respond to topography (and, necessarily, also within their range of perception). Thus, if a butterfly flies towards a local summit and disregards another, more distant and taller summit, we can conclude that the distant summit is beyond this range (or possibly even beyond its perceptual range). Naturally, such a comparison can be done only when the direction to the two summits differs considerably.

For this analysis we used only data on males and virgin females, and omitted all releases on the hilltop. At each data point (butterfly location) we delineated concentric circles at increasing radii from 8 to 64 m at intervals of 8 m, and radii from 64 to 144 m at intervals of 16 m. Within each circle, we identified the highest location in the landscape, and derived the bearing from the data point to this maximum. We also included a close-range circle of 3 m. Since there are fewer DEM-elevation points in the smaller circles, the ability to identify the precise bearing of a peak declines with the size of the circle. Thus, at closer ranges we considered nearer and further peaks to be discernable if their bearings differed by more than 21°, while allowing a smaller difference at greater radii, down to a minimum of 6°. We then compared the bearings to the highest location in a circle of a given radius and the circle next in size. For those comparisons where the bearings differed by more than the threshold value, we noted whether the butterfly flew towards the nearer or the more distant peak. We then summarized the proportion of cases in which the closer peak was preferred to the more distant one for all data points, for each pair of radii. If there is an optimal distance on which butterflies base their decision, in closer pairs of circles the movement direction would be towards the distant summit (hereafter, a 'preference' for the distant summit), whereas in distant pairs, the movement direction would be towards the closer summit (hereafter, a 'preference' for the closer summit). The optimal distance itself would be at the point with equal preferences (50%). This analysis approach takes into account the real elevation of any part of the landscape, and disregards the impact of the animals' viewpoint on the visibility of summits or their relative height.

RESULTS

Analysis of Flight Patterns

We found no correlation between wind direction and the net direction of flight when analysing it for males alone (excluding hilltop observations; $\hat{\rho}T = -0.034$, $N = 14$, NS), or for mated females alone ($\hat{\rho}T = 0.044$, $N = 13$, NS). Virgin females (excluding hilltop observations) showed a significant tendency to fly downwind, but it accounted for only 8.6% of the variance in flight direction ($\hat{\rho}T = 0.086$, $N = 19$, $P < 0.05$). We obtained similar results when analysing the correlation between wind direction and the direction of the last leg of movement of males, virgin females and mated females (namely, the impact of wind was significant but marginal for virgin females). In addition, we analysed the last flight

direction of seven males and four virgin females that disappeared at the beginning of the observations, and whose routes were not mapped. We found that these individuals tended to fly downwind ($\hat{\rho}T = 0.278$, $N = 11$, $P < 0.001$).

We did not find an impact of wing wear (four categories), capture method (wild-caught versus reared individuals) and wind velocity (six categories) on the total distance passed from the beginning to the end of the observation, the mean distance between turning points, or the average turning angle. We found, however, an impact of state (ANOVA: $F_{2,52} = 8.327$, $P = 0.001$) but not of location $\times$ state ($F_{4,52} = 1.977$, $P = 0.112$), on the average distance between turning points (the increment length; Fig. 2a). When we repeated the analysis for males and virgin females alone, the impact of location $\times$ state became significant ($F_{2,42} = 3.399$, $P = 0.043$). The longest increment length was observed in the flight of mated females, regardless of location. Males made shortest flight increments on the (uncleared) hilltop, where they encountered other individuals, whereas virgin females made

the shortest flight increments on the cleared hilltop (Fig. 2a).

There was a significant impact of state on the absolute mean turning angle (ANOVA: $F_{2,56} = 11.937$, $P < 0.001$), where males had sharper turning angles than virgin females at all locations, and mated females had a flat turning angle at all locations (i.e. high consistency in one direction; Fig. 2b). We did not find a significant impact of location or location $\times$ state, perhaps because of the small sample size, and the tendency of many males and virgin females to stay around their release point and fly back and forth for a while after release, regardless of the location (often due to interactions with other butterflies).

The average distance added per flag (i.e. increase in net distance to the release point) decreased from 4.92 m/flag for males without interactions to only 1.64 m/flag for males with interactions (two-sample t test: $t_{10.6} = 2.59$, $P = 0.026$). Turning angles became sharper, increasing from 77° without to 124° with interactions ($t_{18} = 1.972$, $P = 0.032$). Furthermore, the percentage of data points at distances greater than 10 m from the origin decreased
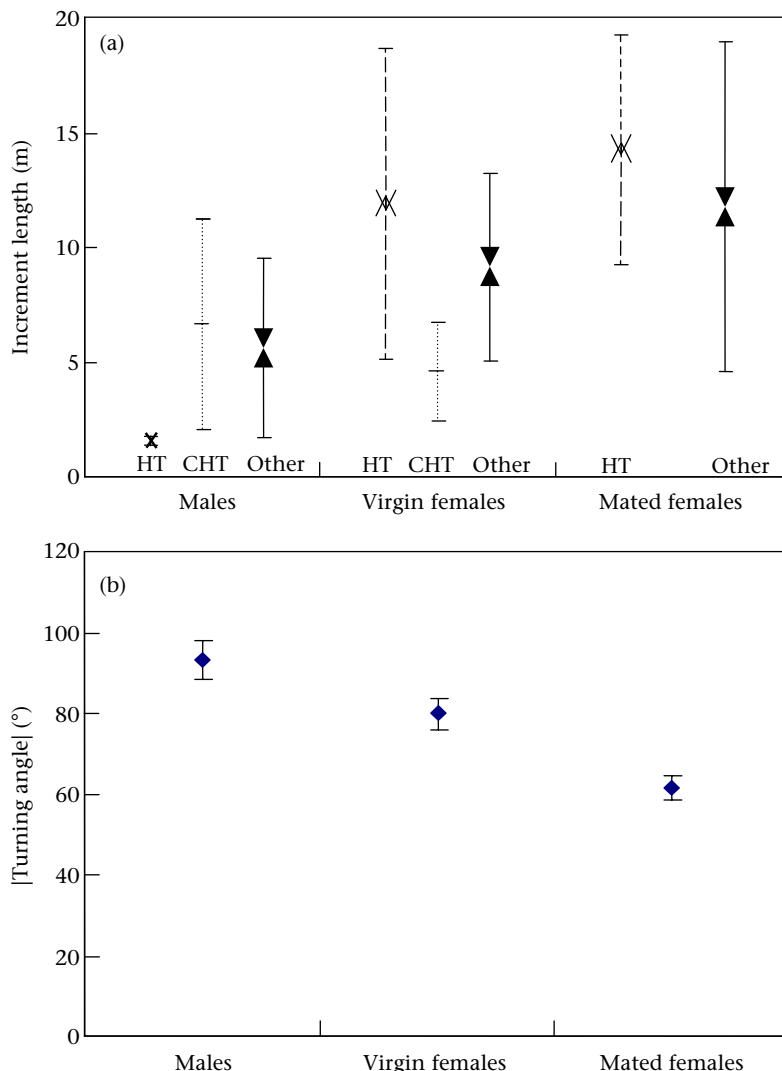

Figure 2. (a) Effect of release location and butterfly state on the average increment length $\pm$ SE. (b) The absolute average turning angle $\pm$ SE. HT: hilltop; CHT: cleared hilltop.

from 63.1% without to 19.4% with interactions ($t_{10.3} = 3.659$, $P < 0.005$). Thus, males tended to stay longer near the origin when they were interacting with other butterflies. Virgin females did not alter flight behaviour while interacting with conspecifics, either the distance added per flag or the percentage of distant data points per observation (60.6% with versus 58.4% without interactions; $t_{12.3} = 0.145$, NS). Mated females also did not alter their flight in response to interactions (88.3% with versus 75.8% without interactions; $t_{12} = 1.703$, NS). However, we observed interactions of mated females with other butterflies in only two of 13 cases, and a pooled variance t test for the mated females did find that the proportion of distant points per observation decreased with interactions ($t_{11} = 2.249$, $P < 0.05$). Virgin females and mated females did not show a difference in the average turning angle with or without interactions. Both virgin and mated females interacted only with conspecifics.

Landscape-associated Analysis

Initial orientation phase

In most males and virgin females we found a positive correlation between the slope taken and distance from the origin (Table 2), although the proportion of males with a positive correlation did not differ significantly from 0.5. The proportion of positive constants did not differ significantly from 0.5. These findings indicate the existence of an orientation phase. Based on visual examination of the diagram resulting from the pooled analysis of the proportion of up- versus downward movements (Fig. 3), we determined that below a threshold distance of 10 m from the origin the movements of males and virgin females were not determined solely by topography, and therefore this reflects an orientation phase. Thus, all data points of males and virgin females that were less than 10 m from the point of release were excluded from any further analyses. After the exclusion process, the slope was nonsignificant (Table 2), indicating that the impact of the orientation phase was removed. The constant was positive in both males and virgin females. However, although the proportion of positive constants was similar for both sexes, this was significant only for virgin females (Table 2). This is due to the small number of males remaining after the exclusion, since the exclusion process removed

Table 2. The proportion of cases with positive values of the constant and the slope derived from linear regressions of the slope taken on the distance from the origin for each individual

	Males	Virgin females	Mated females
Constant	0.55 (20)	0.58 (26)	0.54 (13)
Slope	0.60 (20)	0.69 (26)*	0.38 (13)
Constant after exclusion	0.75 (12)	0.76 (17)*	
Slope after exclusion	0.58 (12)	0.47 (17)	

The analysis was repeated after excluding data points less than 10 m from the origin for males and virgin females. Numbers in parentheses are sample sizes (i.e. the number of individual butterfly regressions).*$P < 0.05$; exact binomial test.

the entire observations of eight males and nine virgin females. This indicated that these individuals remained within 10 m of the release point throughout the observation. Some of these individuals were released on the hilltop, whereas others remained around the release point because of interactions with other individuals. Thus, the exclusion of data points less than 10 m from the origin removed many of the disoriented movements that occurred, in part, because of the orientation phase, as well as other reasons such as adhering to the hilltop and interacting with other individuals. This exclusion was supported by a repeated measures analysis, in which the impact of time was highly significant in males and virgin females before the exclusion and nonsignificant thereafter (results not shown).

Tendency and consistency of upward and downward flight

Table 3 summarizes the flight tendencies with respect to topography (i.e. proportion of movements upwards and downwards), and the consistency to move upwards and downwards (i.e. the likelihood of a movement upwards to be followed by another move upwards). Hilltop releases were included in the analysis only for mated females. For males and virgin females the average proportions of movements revealed a significant tendency upwards (males: 77.5%; $t_8 = 3.45$, $P = 0.009$; virgin females: 81.8%; $t_{16} = 7.31$, $P < 0.0001$). The consistency upwards was higher than the consistency downwards (males: 62.9% versus 56.2%; paired-sample t test: $t_6 = 2.254$, $P = 0.065$; virgin females: 71.0% versus 59.4%; $t_{13} = 4.045$, $P = 0.001$). Mated females flew upwards in only 44.3% of the movements (NS). The consistency downwards was not significantly different from upwards (86.8% versus 73.3%; $t_{12} = 1.486$, $P = 0.163$). Between states, the proportion of movements upwards was significantly higher in virgin females than in males or mated females. The difference between males and mated females was only near significant (LSD post hoc analysis). After we excluded hilltop releases, six of 16 males and three of 22 virgin females consistently flew upwards without any movement downwards. Thus, the tendency to move upwards was 75–90% for most butterflies, and only rarely reached 100%.

Factors affecting the slope taken

Males and virgin females most often moved upwards, towards the maximal slope (Fig. 4a, b). For the mated females, the proportion of points with negative slopes taken was slightly higher than 50% (Fig. 4c), but the tendency did not seem different from the randomly created movements of the CRW simulation (Fig. 4d). There was a significant influence of location on the RC (ANOVA: $F_{2,50} = 17.716$, $P < 0.001$; no-turning points: $F_{2,48} = 19.773$, $P < 0.001$) with a high RC taken on nonhilltop locations relative to HT and CHT. In the no-turning points, there was also a near-significant effect of state ($F_{2,48} = 2.718$, $P = 0.076$), caused by the higher RC of virgin females than that of males, and the high RC of males relative to that of mated females. The lack of
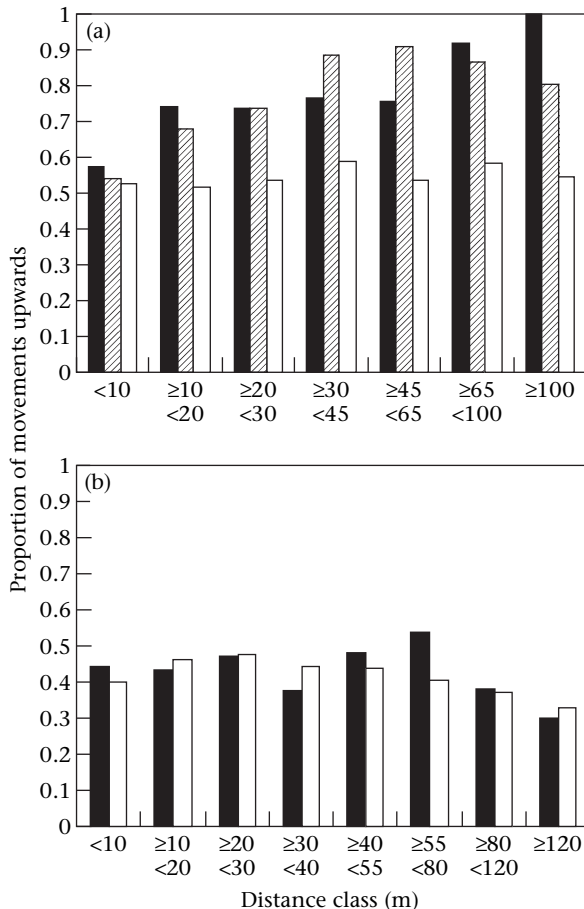
Figure 3. (a) Observed proportion of movements upwards at increasing distances from the point of origin for males (■) and virgin females (▨), compared to that from a Correlated Random Walk simulation (□). Hilltop releases are excluded. Based on a visual inspection of the graph, we excluded data points less than 10 m from all further analyses, as these were not directed by topography. (b) The preference for mated females to move upwards (■) was compared to the Correlated Random Walk (□) based on three release points.

males and virgin females, mated females took more positive slopes at nonhilltop locations, but this tendency did not differ from random (Fig. 3b). A paired sample t test between the average RC in turning and in no-turning points found no significant difference for both males and mated females (males: $t_{13} = 0.424$, $P = 0.679$; mated females: $t_{12} = -0.791$, $P = 0.445$). For virgin females, the RC in turning points was significantly higher than in no-turning points ($t_{25} = 2.598$, $P = 0.015$), a result that remained significant after Bonferroni adjustment for the number of tests.

What induces butterflies to turn: slope or distance?

Pooling all data points of all males and virgin females (excluding hilltop observations), we compared the slope actually taken to the slope that would have been taken if the butterflies had continued at the bearing prior to turning (hereafter, the 'slope not taken'). We found no significant difference between the slope taken and the slope not taken (t_{184} test $= -0.129$, $P = 0.898$). We also counted the cases (=butterflies) where the slope taken exceeded the slope not taken in more than 50% of the turning points. This occurred in only nine of 16 virgin females and two of 10 males. When comparing the frequency histogram of increment lengths (distances between turning points) of males and virgin females with that of the null hypothesis (the broken stick model), we did not find any significant difference (χ^2_6 test $= 8.625$, $P = 0.196$). Thus, neither the slope at the immediate surroundings nor the distances passed from the last turning were associated with the locations where turnings took place.

Evaluating the response range

When we excluded the closest pair of maxima (3 versus 8 m), the preference for the closer summit increased linearly with the size of the assumed perceptual range circle ($R^2 = 0.736$, $N = 10$, $P < 0.005$; Fig. 5). That is, the preference for the closer summits was less than 50% at close-distance circles (a preference for the distant maxima), and higher than 50% at large-distance circles (preference for the closer maxima). Around the 50-m circles the preference was 50% (i.e. no preference), suggesting that this is the range of response. However, when we considered the closest pair of maxima (i.e. 3–8 m maxima), the butterflies showed a strong preference for the closer maximum. Thus, the response range of the butterflies involves a response to both the very near surroundings and

a location × state interaction (ANOVA: $F_{3,46} = 0.093$, $P = 0.963$; no-turning points: $F_{2,46} = 0.990$, $P = 0.379$ was probably the result of low statistical power stemming from lack of data points for males on the hilltops (owing to the excluding procedure), as well as the fact that, like

Table 3. Flight tendencies ($\overline{X} \pm SD$) of males, virgin females and mated females

State	Proportion upwards	Expected upwards	Consistency upwards	Consistency downwards
Males	0.775±0.214	0.527±0.044**	0.629±0.278	0.562±0.251
Virgin females	0.818±0.175	0.490±0.017***	0.710±0.283	0.594±0.220***
Mated females	0.443±0.273	0.498±0.017	0.733±0.267	0.868±0.127

The proportion of movements upwards was compared to the proportion expected to move upwards based on the available slopes around each data point. The consistency upwards, i.e. the probability that a movement upwards was followed by another movement upwards, was compared to the consistency downwards for each butterfly. All cases were tested using a paired-sample t test. Results for males and virgin females exclude observations on the hilltop, data points <10 m from the origin, and two cases affected by strong wind.**$P < 0.01$; ***$P < 0.001$.
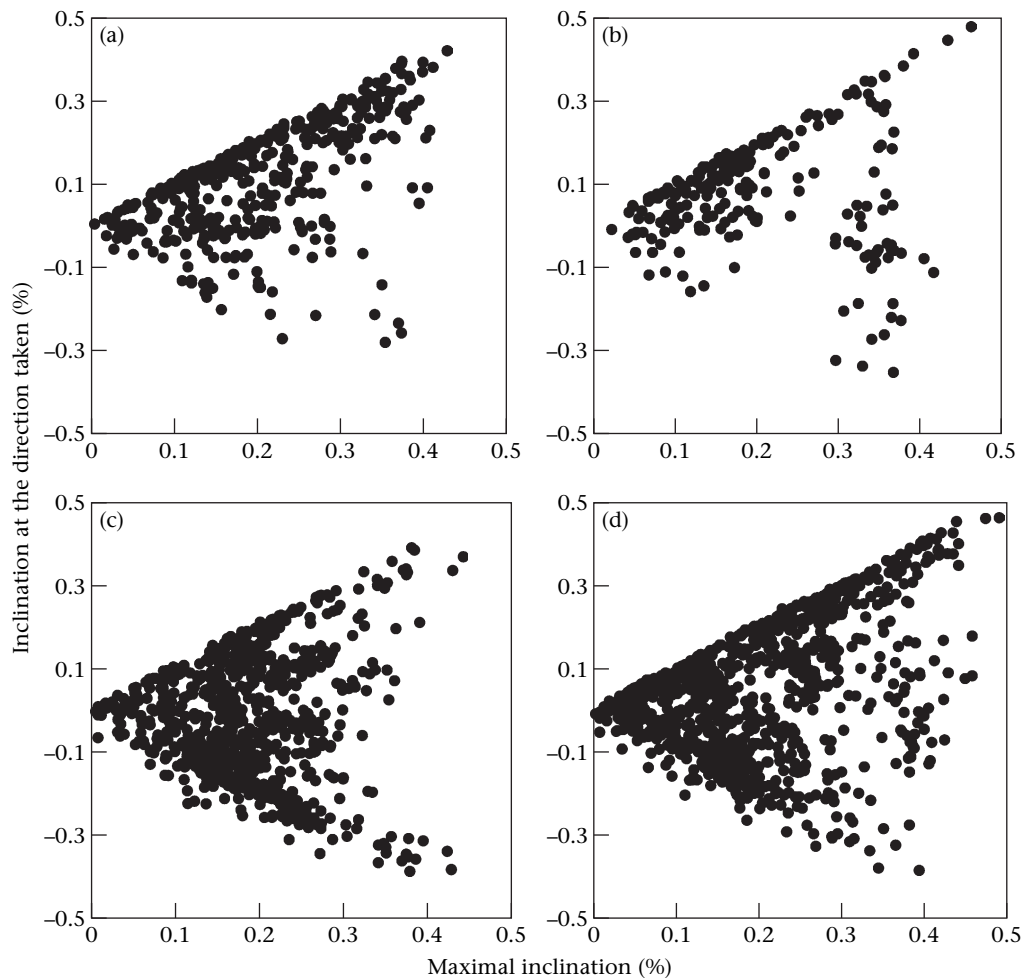
Figure 4. Inclination taken versus the maximal inclination available at each point along butterflies' movement paths for (a) males, (b) virgin females, (c) mated females and (d) Correlated Random Walk simulation. Hilltop releases and data points <10 m from the origin are excluded. Each point represents one data point.

a distant maximum at a range of 50 m. We repeated the analysis by comparing successively the bearing to the maximum in a 3-m-radius circle to the bearing found by each of the more distant maxima. The result revealed a preference for the 3-m maximum to the 8-m maximum, and a preference for the 50-m maximum to the 3-m one (Fig. 6). At distances greater than 60 m, and between 24 and 40 m, no preference was identified. This result suggests that the butterflies orient themselves based on two separate orientation cues: the immediate inclination and the maximum within a range of 50 m, with the more distant maximum preferred.

DISCUSSION

Butterfly Response to Landscape Cues

The movements of *M. trivia* were governed by simple movement rules in response to topography, probably based on visual topographical cues. The uphill movement was directed by two cues: the highest location within

a distance of around 50 m, and the immediate slopes available to the butterfly at its current location. The former was dominant over the latter, so that the preference for the closest maximum was evident only when comparing it to the closest response circles (3 versus 8 m). These findings seem to explain our 'failure' to recognize the cue that induces butterflies to turn, since the decision to turn was not determined only by the immediate surroundings. We postulate that this divided response reflects two forces that orient animals. First, animals need a reliable orientation cue towards the highest maximum, which allows them to avoid local maxima. This requires a long response range (towards the 50-m summits), perhaps limited by the perceptual range of the butterflies. However, local maxima should not be completely avoided, as they might serve as secondary meeting points which, given their proximity, are worth investigating. Thus, we suggest that some preference for the very near surroundings should be expected when animals are located near a local maximum, as well as when the perceptual range is limited by the landscape. For instance, it would make sense to orient towards the highest summit
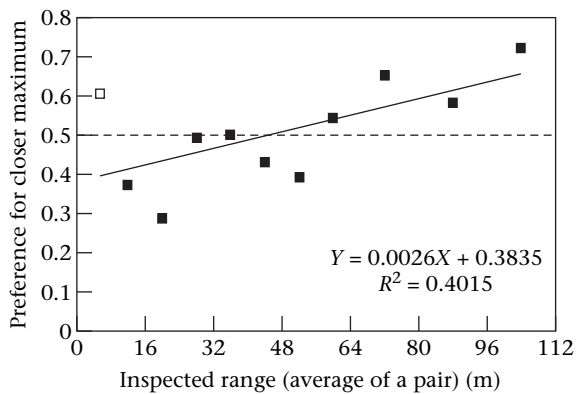
Figure 5. Evaluation of the response range based on the preference for the closer of two maxima within given radii (proportion of moves). X-axis values represent the mean of the two radii (e.g. 8 versus 16 = 12). □: Closest pair of maxima (3 versus 8 m). Dashed line represents a threshold where no preference is seen. Above it, a higher proportion of moves was made towards the closer maximum.

using the 50-m radii response range until this is approached, and then respond to the immediate surroundings. At the larger scale, orientation cues must be far enough away to allow reliable decisions within the limits of the animal's perceptual range.

Although wind is a directional element, which commonly affects the movements of insects searching for conspecifics and host plants (Compton et al. 2000; Marchand & McNeil 2000) as well as during dispersal and migration (Schmidt-Koenig 1993; Bellamy & Byrne 2001; Srygley & Oliveira 2001; Srygley 2003), we found little effect of wind direction on butterfly flight directionality, except during initial movements. This we explain by the observed tendency of butterflies to avoid activity when the wind is strong, as well as by the low height of their flight (usually <1 m off the ground). This result is consistent with field observations on *Maniola jurtina*, in
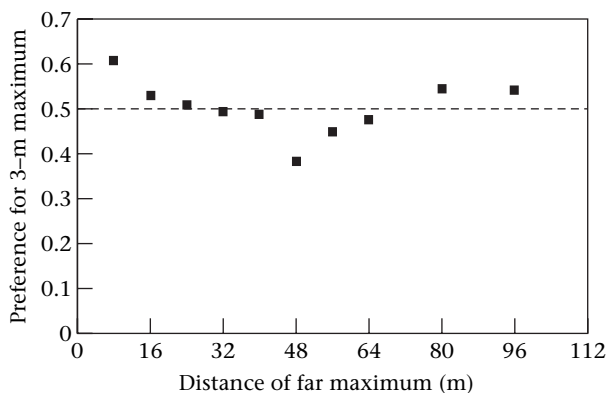
which butterflies showed a clearly directed movement towards patches, but wind direction did not explain flight directionality (Conradt et al. 2000). Thus, visual cues appear to be a key factor directing butterfly movements. More importantly, the lack of response to wind direction suggests that topography is a major external element invoking directional movements on these scales of interest. Another cue that directs movement across the landscape is vegetation (Boone & Hunter 1996; Haddad 1999a; Palomares et al. 2000; Roland et al. 2000; Bélisle & St. Clair 2001; Ricketts 2001). However, in this study we were unable to evaluate the impact of vegetation because we deliberately chose landscape with homogeneous vegetation, to confine the study to the impact of topography alone. We believe that the dispersal patterns of a wide range of organisms, once they have left their habitat patches and moved through the 'matrix', are affected by two main attributes of the landscape: topography and vegetation structures.

Ecological Insights on Hilltopping

Our observations support previous studies on hilltopping behaviour, suggesting that hilltopping is a strategy used to locate potential mates in easily recognized sites (Shields 1967; Lederhouse 1982; Queller 1987; Wickman 1988). We did not aim at understanding the reasons for hilltopping or estimating the successfulness of this behaviour. Nevertheless, the detailed quantification of movement parameters has provided new insights into the ecological meaning of this behaviour.

Males and virgin females of hilltopping butterflies showed a strong tendency to fly uphill. However, in most cases flying uphill was not totally consistent, and movements downwards were common. This randomness may be important for avoiding local summits on the way to more regional summits (Pe'er 2003). Males adhered strongly to the summits, and were often recaptured several hours later (one male was found dead on the hilltop 3 weeks after its release). In contrast, virgin females did not seem to adhere as strongly to the summits. Since females disperse from the summits after mating, males probably contribute less than females to population dynamics within patches. However, the contribution of hilltopping to genetic 'mixing' between populations may be of great ecological importance (see below).

The differences in behaviour between males and virgin females (such as the difference in turning angles, increment length, response to topography and response to conspecifics) possibly represent a certain asymmetry in the mate-searching strategy between genders. This asymmetry may improve the mate-searching 'algorithm', by increasing the chances of meeting along the way (Motro 1991, 1994; Sandell & Libero 1992). For instance, the difference in increment length between males and virgin females indicates that virgin females perform little search for males if not on the summits, whereas males search for conspecifics everywhere. On the summits, virgin females seem to perform searching behaviour if they do not encounter males. Most females were quickly spotted by

Figure 6. Preference for the 3-m maximum (proportion of moves) over each of the more distant maxima. Dashed line represents a threshold where no preference is seen. Above it, a higher proportion of moves was made towards the closer maximum.

males and copulated when they arrived at, or were released on to, the noncleared summit. Furthermore, virgin females did not refuse males encountered in other locations, and copulation soon took place. The strong tendency of butterflies to remain at the site of release when interacting with other individuals implies that hilltopping behaviour is beneficial only when adults are sparsely distributed in space and time, that is, if no potential mates are recognized close by. This is ecologically sound since adult butterflies should naturally hatch in patches of suitable habitat. Our observations suggest that, indeed, butterflies first search for conspecifics within their immediate surroundings (in natural cases, patches), and leave the site only if the search was not successful. The strong impact of interactions on the behaviour of males and virgin females contrasts with findings on the hilltopping butterfly *Lasiommata megera* (Wickman 1988) for which no impact of interactions was noted. The difference may be caused by the difference in methodology, since Wickman (1988) used transect observations instead of the individual-based ones we used in this study. We believe that direct observation methodologies, such as ours, are more appropriate than indirect ones for the purpose of describing and understanding animal behaviour (Osborne et al. 2002).

The movement patterns of mated females could be generally described as highly consistent, with relatively long distances between turning points and with shallow turning angles. We found no tendency to fly downwards, in agreement with Wickman (1988) and in contrast to our prediction that mated females would avoid hilltops and fly downwards to avoid male harassment (Shields 1967). This is further emphasized by the fact that our butterflies originated from desert habitats, where vegetation is normally confined to dry stream beds. Failing to identify a downward tendency may be a result of the small sample, an artefact of our method of obtaining mated females (namely, capturing them in patches), or a result of other ecological factors that this study did not address.

From Directing Elements to Modelling Dispersal

We focused on the movement rules of hilltopping behaviour, using direct observations of individual butterflies moving through a topographically complex landscape. Although the ecological function of this movement is finding a mate and not dispersal per se, it is comparable to dispersal in several aspects. First, hilltopping behaviour leads animals out of their habitat patches and directs them through the so-called hostile matrix. Second, it influences the extent, as well as the spatial patterns, of the exchanges of individuals and genes between populations. Two possible mechanisms are the probability that individuals, originating from two or more distinct populations, would meet at the summits, and the shifting of mated females away from habitat patches, to disperse in search of host plants. Third, once animals initiate a hilltopping movement, they may persistently fly upwards and cover large distances (several kilometres or even tens of kilometres;

Shields 1967; O. Benyamini, unpublished data). Similar patterns have been identified in studies of dispersal, where animals altered their movement behaviour upon leaving their habitats and moved persistently in straight trajectories (e.g. Schultz 1998 and references therein; Schultz & Crone 2001; Bulger et al. 2003). Finally, the spatial scale of hilltopping seems comparable to long-distance dispersal of various animals and plants, as obtained from empirical studies (Harrison 1989; Hill et al. 1996; Bullock & Clarke 2000; Cain et al. 2000; Baguette 2003; Gómez 2003). When applying the results of this study to 'real' dispersal behaviours (or to other species), one should consider the characteristics of the directing element, as well as the resolution of animal perception, along with the behaviour of interest.

Understanding the factors that direct animal movements between populations is crucial for improving models of connectivity and metapopulations. Such models usually assume that the matrix is either homogeneous (Fahrig 1992; Adler & Nuernberger 1994; Hanski et al. 1994; Bascompte & Sole 1996; Frank & Wissel 1998), or changes abruptly, presenting several discrete types of habitats (Gustafson & Gardner 1996; Schippers et al. 1996; Akçakaya & Atwood 1997; Moilanen & Hanski 1998; Morales & Ellner 2002; Schadt et al. 2002). To improve such models, it is necessary to know the mechanisms that direct dispersal in gradually changing landscapes, at the individual level. Therefore, our study addresses topographical heterogeneity, a source of landscape heterogeneity that cannot be tackled by most of the present models of dispersal in heterogeneous landscapes.

Our individual-based approach enabled the identification of clear decision rules. However, even simple movement rules can produce complex movement patterns across the landscape (Wolfram 2002; Pe'er 2003). This is due to the complexity of topographically heterogeneous landscapes, as well as the combination of two distinct movement steps (i.e. the hilltopping process and the postmating movement of females). Therefore, the movement patterns of animals over topographically complex landscapes should be analysed with the aid of individual-based simulation models, with realistic landscape representation. The movement rules obtained from this study serve as a firm basis to develop such a model for the hilltopping behaviour, and a conceptual basis for modelling the dispersal of animals across gradually changing landscapes (Pe'er 2003). Such models, in turn, can be used to analyse the consequences of directional movements on movement patterns and on connectivity in a variety of complex landscapes.

Prospect for Further Studies

Our investigation provides innovative approaches and methodologies for analysing the rules of response to landscape heterogeneity from the animals' point of view. However, the sample size enabled us to address only a limited number of spatial and behavioural factors that determine animal movements. With a larger sample size,

additional factors may be addressed that affect butterfly movements. These include spatial patterns of nectar source, vegetation patterns and biological factors that affect butterflies' behaviour. Longer observations could reveal possible alterations in behaviour on larger spatio-temporal scales. Repeating such an experiment on a variety of landscapes may also reveal the limits of animals' perception for topography.

Acknowledgments

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