Spatial and Behavioral Determinants of Butterfly Movement Patterns in Topographically Complex Landscapes

Thesis submitted in partial fulfillment
of the requirements for the degree of
"DOCTOR OF PHILOSOPHY"

By

GUY PE'ER

**Submitted to the Senate of
Ben-Gurion University of the Negev**

December 2003

BE'ER SHEVA, ISRAEL

This work was carried out under the supervision of

Prof. David Saltz

Prof. Uzi Motro

In the Department of Life Sciences
Faculty of Natural Sciences
Ben-Gurion University of the Negev
Israel

"…Simple rules can produce behavior of great complexity"

Stephen Wolfram (2002)

"A New Kind of Science"

ACKNOWLEDGEMENTS

ii

The two main players in the ecological game: *Melitaea trivia* (left) and me (right…).

CONTENTS

ABSTRACT

The loss of natural habitats and their fragmentation by human activities impose a great threat to biodiversity worldwide. As animal populations become restricted to small and fragmented patches of natural habitat, their viability becomes increasingly dependent upon the arrival of emigrants from elsewhere. Dispersal – the movement of animals away from their original habitat – is thus fundamental to the viability of populations and metapopulations in fragmented landscapes. Ecologists and conservationists seek to understand the processes that determine dispersal patterns, in order to better maintain connectivity between populations. However, dispersal may take complex routes depending on the specific attributes of the landscape and the response of animals to different features of it. Consequently, our ability to predict movement patterns is often limited by a lack of empirical knowledge on animal decision-making processes during dispersal, as well as by the inability to model the varied responses of animals to landscape heterogeneity. This study addressed both problems. I studied movement patterns from a mechanistic, individual-based approach, and developed generalizations on directional movement patterns in heterogeneous landscapes. I focused on topographical heterogeneity, a major source of landscape heterogeneity which receives little attention in the context of dispersal. As a behavioral case-study I examined hilltopping behavior in butterflies. Hilltopping animals seek topographic summits where they meet and mate. Thereafter, mated females descend from summits in search of host plants. Hilltopping is therefore a dispersal-like behavior which leads animals out of habitat patches and directs their movement through the landscape.

I developed a systematic, hierarchical approach to investigating directed movements through topographically heterogeneous landscapes. I started at the individual level, using field observations on the hilltopping butterfly *Melitaea trivia* to deduce the response mechanisms to topography. I then used the results to construct an Individual-Based Model (IBM) of hilltopping, and analyzed movement patterns in virtual and realistic landscapes of increasing complexity. Finally, I validated the model with another field experiment, which assessed the ability of the model to predict movement patterns in a realistic, complex landscape.

The first field study yielded simple decision rules, suggesting that a simple model could suffice for delineating hilltopping movement patterns in a variety of landscapes. Some of the movement rules were then used for developing 'the Hilltopping Model'.

Using the model, I obtained a comprehensive understanding of the consequences of animal response to topography on movement patterns in various landscapes. It indicated that the response to topography canalizes animal movements into specific routes, which I termed 'Virtual Corridors'. Further investigations showed that the structure of Virtual Corridors cannot be intuitively predicted over realistic, complex landscapes. This is because the movement patterns depend on the spatial configuration of the landscape, the location of the patches, and the behavioral parameters. I deduced that landscape-specific predictions of animal movement paths can only be obtained with the use of IBMs.

I developed a novel methodology for identifying and quantifying canalized movement patterns. I analyzed 'accessibility patterns' to summits – the probability of arriving at various summits in a landscape given their distance from a starting point. I revealed that general patterns emerge even in complex landscapes. That is, canalized movements gave rise to distinctive 'accessibility patterns', despite the variety of landscape configurations inspected. Additionally, I found that canalized movement patterns are induced even by a slight response to topography, and prevail through a wide range of behavioral and spatial parameters. Hence, directed movements and Virtual Corridors may be expected in various landscapes and within a variety of movement behaviors.

I then expanded my study and focused on the two-step process of hilltopping, including the hilltopping itself and the consequent dispersal of mated females. I searched for the movement behaviors that optimize mating success and the arrival of mated females to patches. Model results were obtained independently of the field observations, and then compared to the observed behavioral parameters. I found very strong similarity between the optimal behavior in the model and the observed behavior, suggesting that the model is capable of replicating the real behavioral parameters successfully. However, results were inconsistent with respect to the optimal behavior of mated females.

Lastly, I evaluated model performance in the field by a Mark-Release-Recapture (MRR) study. I used the model to predict the recapture pattern, and compared the expected and the observed patterns. Additionally, I tried to elucidate the behavioral parameters of mated females. The model predicted the recapture patterns of males and

virgin females successfully. It provided rare evidence, both theoretical and empirical, that the recapture probability may not decay with the distance if animals respond to landscape heterogeneity. Mated females were not recaptured. However, several results of this research seem to indicate that they either respond weakly to topography, or not at all.

This work provides a first systematic study of animal-landscape interactions in the context of movements in topographically complex landscapes. It demonstrates the importance of topography as a directing agent of animal movements. It suggest that the response of animals to topography *per se* needs to be more carefully addressed in further studies of dispersal, connectivity, and population dynamics in fragmented landscapes. It demonstrates that directed movement patterns evolve when animals respond to topographical gradients. Since many sources of landscape heterogeneity present gradual changes, I hypothesize that directional movements and Virtual Corridors occur whenever animals use gradients to direct their movements during their dispersal. I note that current models of connectivity use maps with discrete habitat types rather than maps with gradients. Thus, current techniques of modeling habitat connectivity tend to underestimate the proportion of non-random movements taken by animals. This work provides novel tools and approaches to tackle this weakness, and re-examine the frequency of directed movements in heterogeneous landscapes. These tools may improve our ability to predict the specific routes that animals are using during their dispersal. In this way, we can better identify corridors and barriers to dispersal, and establish better conservation and landscape-management plans for preserving or enhancing connectivity in fragmented landscapes.

This work demonstrates the power of combining fieldwork and modeling for generating and testing ecological theories. It suggests that a simple model, which is based on good knowledge of animal behavior, can be used both for obtaining theoretic understandings and for applicable purposes. In this way, this study balances two contrasting needs: the scientific need to understand nature on the one hand, and the urgent need to apply this knowledge to conservation practices on the other hand.

Keywords: Topography, hilltopping, butterflies, dispersal, directed movement, connectivity, landscape-heterogeneity, individual-based model, virtual corridors, gradients.

1. INTRODUCTION

1.1 DISPERSAL, CONNECTIVITY, AND METAPOPULATIONS

Human-induced loss and the fragmentation of habitats impose a great threat to biodiversity worldwide (Meffe & Carrol 1997; Hunter 2001). As animal populations become restricted to small and fragmented patches of natural habitat, their viability becomes increasingly dependent upon the arrival of emigrants from elsewhere. Dispersal – the movement of animals through landscapes that are unknown to them, for the purpose of establishing themselves in an area other than their point of origin – is thus fundamental to the viability of populations in fragmented landscapes (Levins 1970; Opdam 1990; Hanski et al. 1994; Hess 1996; Anderson & Danielson 1997; Frank & Wissel 1998; Thomas 2000). It promotes population sustainability (Kareiva 1990; Harrison 1991; Andren 1994), and may rescue populations from extinction (Brown & Kodric-Brown 1977) or bring about the recolonization of suitable patches where extirpation has occurred.

With the growing interest in understanding animal movement between habitat patches, an increasing number of studies indicate that dispersal movement across various landscapes are not random (Beier 1995; Conradt et al. 2000; Palomares et al. 2000; Roland et al. 2000; Shkedy & Saltz 2000; Clobert et al. 2001; Lowe 2003) Animals respond to various sources of habitat heterogeneity, for instance by adhering to some habitat types while avoiding others. The interaction between landscape attributes and the response of organisms to these, directs animals' movements, forming barriers and corridors to dispersal (Wiens et al. 1993; Gustafson & Gardner 1996; Ricketts 2001; Ries & Debinski 2001). 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, animal response to landscape heterogeneity at the individual level is a key to understanding and predicting the large-scale and long-term dynamics of spatially structured populations.

Spatial population models often assume that dispersal between populations takes place in a homogeneous, hostile landscape, and is hence random (Fahrig 1992; Adler & Nuernberger 1994; Hanski et al. 1994; Bascompte & Sole 1996; Gustafson & Gardner

1996; Hanski et al. 1996a; Hanski et al. 1996b; Kuussaari et al. 1996; Frank & Wissel 1998). One reason for assuming that the landscape is homogeneous is the complexity of modeling movements in heterogeneous landscapes. This complexity often results in detailed models, which provide system-specific predictions but lack generality and flexibility (Grimm 1999). Another reason for assuming landscape homogeneity is the lack of knowledge as to the rules that govern animal decisions during dispersal (South et al. 2002). This study addresses both problems, by studying movement patterns from a mechanistic approach and developing generalizations about directional movement patterns in complex landscapes.

<u>1.2 RESEARCH GOALS</u>

This study focuses on the so-called 'hostile matrix', with the aim of understanding the processes that direct dispersal in heterogeneous landscapes, and the effect on connectivity. Specifically, my goal was to delineate the impact of topography on dispersal patterns. Topographical heterogeneity is a major source of landscape heterogeneity, which exists in many terrestrial landscapes and on many spatial scales. Furthermore, it is often directional (e.g. river basins, mountain ranges). 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; Akcakaya & Atwood 1997; Roland et al. 2000; Shkedy & Saltz 2000; Gillespie 2001), migration routes (e.g. Beebe 1949; Beebe 1950a; Beebe 1950b; 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). A variety of 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). However, due to the difficulties with experimenting on dispersing animals (Zollner & Lima 1999; Nathan 2001; Williamson 2002), it is rare for mechanisms of response to be experimentally addressed. Thus, little is known about the decision-making processes

involved in responses to topography, and the consequent movement patterns and connectivity patterns in topographically complex landscapes. Additionally, topographical attributes often change gradually, unlike other sources of habitat heterogeneity that are often assumed to change discretely. Thus, a source of heterogeneity is presented that cannot be tackled by most of the present models of dispersal in heterogeneous landscapes.

In light of the complexity of topographical patterns and regimes, and the further complexity imposed by the various possible movement behaviors, this study seeks generality. I have attempted to gain a comprehensive understanding of the consequences of responding to topography on movement patterns in various landscapes, quantifying these effects, and assessing how strongly directed movements could affect connectivity patterns.

1.3 HILLTOPPING AS A BEHAVIORAL CASE STUDY

In this research, I have chosen to investigate a relatively simple behavioral case study, in which animals are known to respond to topography and are directed by it. I have studied hilltopping behavior in butterflies, a common mate-searching strategy that occurs among various insects (Benyamini 1990; Tennent 1995). In hilltopping species, males and virgin or multiple-mating females seek topographic summits for the purpose of mating (Shields 1967; Ehrlich & Wheye 1988; Singer & Thomas 1992; Tennent 1995). Males tend to stay on the summit and form 'leks' (see Alexander 1975; Lederhouse 1982; Thornhill & Alcock 1983; Queller 1987), while females leave the summit immediately after mating to search for host plants. Hilltops can be considered unsuitable habitats, as they may provide no host plants for the larvae to develop on. Thus, hilltopping behavior serves as a dispersal-like behavior, by driving animals out of habitat patches, facilitating and directing their movements through non-habitable landscapes. I use hilltopping behavior to understand the mechanisms that direct animal movement in non-habitat landscapes, and to investigate the spatiotemporal consequences of these movements. I note that even in this relatively simple behavior, delineating the movement patterns may not be straightforward, since the movement patterns of hilltopping species comprise two very distinctive movement steps: ascending to mountain summits for the purpose of mating, and the consequent dispersal of mated females in search of suitable habitats for oviposition.

1.4 RESEARCH APPROACH AND STRUCTURE OF THE THESIS

The study is based on a hierarchical, "bottom up" approach, in which decision rules made at the individual level serve as a basis for understanding processes at the landscape level. I started at the individual level, using field observations to delineate response mechanisms to topography. I then used the results to construct an individual-based simulation model of hilltopping in topographically heterogeneous landscapes, and analyzed movement patterns in virtual and realistic landscapes of increasing complexity. Finally, I validated the model with another field experiment, which assessed the ability of the model to predict connectivity patterns in a realistic, complex landscape. This hierarchical approach is represented by the detailed structure of chapters 2-7, the aims and descriptions of which are delineated hereafter.

Chapter 2 aims to derive a set of simple behavioral rules and parameters that dictate the movement decisions of butterflies while hilltopping, using direct observations in the field. I also tried to recognize the cues that direct the decision-making process. This knowledge was crucial for developing the individual-based model later on.

In chapter 3 I present an individual-based simulation model, which enabled the analysis of movement patterns of hilltopping butterflies over topographically complex landscapes. The model was qualitatively, but not quantitatively, based on the fieldwork results. In this chapter I focused only on the first movement step (ascending to the hilltops), in order to obtain an initial understanding of the consequences of hilltopping on movement patterns. The main outcome of the chapter is the concept of 'Virtual Corridors'.

In chapter 4, I use the model to obtain qualitative and quantitative generalizations on the effect of topography on movement patterns. Still exploring only the first movement step, I examined the probability of reaching specific targets (the summits) as a function of the distance from a source-point. This indirect approach allowed the development of a systematic methodology for identifying and analyzing canalized movement patterns in a variety of landscapes.

Chapter 5 aims to explore the model more systematically, and to address higher levels of complexity in terms of the behavioral and spatial parameters. I looked at the

combination of two movement steps, namely the ascendance of males and virgin females to the summits and the subsequent dispersal of mated females away from the summits. I optimized the movement behavior upon a simple landscape, independently of the observed behavior in the field. Using this exploration I demonstrated the importance of randomness in animal behavior, and compared the optimization processes of the model with various optimization algorithms.

The goal of <u>Chapter 6</u> was to examine the movement parameters of both movement steps more exhaustively, in a variety of landscapes. I paid special attention to the behavior of mated females. I then compared the results of the optimization results with the observed, realistic behavior. I also discuss the ecological and evolutionary implications of different optimization approaches.

In <u>Chapter 7</u>, I show how I used the simulation model to design and execute a large-scale field experiment. The goals were, firstly, to assess the ability of the model to predict movement patterns in realistic landscapes and large spatiotemporal scales, and secondly, to assess the movement parameters of mated females. I have used this final experiment to discuss the power and limitations of the model, as well as the combination of field observations and individual-based simulation modeling.

A unifying discussion (Chapter 8) is followed by two appendices, the first providing a sensitivity analysis of several parameters which have not been addressed in other chapters, and the second providing a full description of the model.

2. CHARACTERIZING THE RESPONSE TO TOPOGRAPHY IN THE HILLTOPPING BUTTERFLY *MELITAEA TRIVIA*

2.1 INTRODUCTION

The process of dispersal through non-habitat 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 which direct dispersal have concentrated mainly on the behavior of animals when leaving their habitat patches (Hanski et al. 1996; Moilanen & Hanski 1998; Schultz 1998; Schultz & Crone 2001), and responses to barriers during dispersal (Haddad 1999a,b; Bélisle & St. Clair 2001). Another approach taken in studying the forces that direct dispersal is to deduce the movement preference of animals while moving between habitat patches (Beier 1995; Pither & Taylor 1998; Palomares et al. 2000; Shkedy & Saltz 2000; Palomares 2001), with little understanding of the actual mechanisms that direct animals while moving. This understanding is crucial for predicting the actual route taken by a dispersing animal (Bakker 2002). Furthermore, directional movements seem to occur even within landscapes which may seem to be uniform (Conradt et al. 2000,2001), implying that the forces that direct such movements are poorly understood. This is especially true with respect to gradual changes in the landscape, as opposed to the more commonly studied situation of clear and abrupt changes between habitats.

In this chapter, I investigate the response to topography in a hilltopping butterfly *Melitaea trivia* (Nymphalidae). Knowing the aim of the hilltopping process (to find mates), the object of this study was to investigate the mechanisms of the hilltopping process. I ascertained and quantified the behavioral parameters that dictate the movement decisions of a hilltopping species when moving between habitat patches, from the animals' point of view. I was specifically interested in the behavioral rules that direct males and virgin females while moving toward the summits, as well as the post-mating movement patterns of the females. I tried to recognize the topographical elements to which butterflies respond, the perceptual range of this response, and the consistency of

this behavior through time and distance. I attempted to describe the initiation of the hilltopping behavior, its *en-route* process and the performance upon reaching a summit. I also re-examined the perception that females actively descend from the summits after copulation (Shields 1967), hypothesizing that the post-copulation movement away from summits may occur as passive diffusion (Wickman 1988).

2.2 METHODS

2.2.1 FIELD OBSERVATIONS

Melitaea trivia is a small butterfly (wingspan 15-23mm) that exhibits strong hilltopping behavior (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 behavior may serve as part of the dispersal mechanism between habitat patches.

Field observations were conducted 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 20km north of Be'er Sheva (31º25'N 34º50'E, annual precipitation ≈ 300mm). It is characterized by high topographical complexity and a relatively uniform vegetation of semi-arid scrubland (with plants up to 50cm in height)(Fig. 1a). Thus, I have assumed that vegetation structure has no impact on butterfly behavior.

Most of the butterflies were collected as larvae and grown in captivity for the purpose of the study. I fed the larvae on *Verbascum fruticulosum* plants, which I placed in net-cages inside a greenhouse. I placed the adults in cooling boxes immediately after hatching, in order to avoid mating events. I collected some of the males and all mated females as adults in the field, using a sweeping net. Mated females were recognized as such by oviposition events, refusing males and/or typical searching flight around host plants. All butterflies were placed in cooling boxes during daytime until release, and in no case were they held for more than four days. I then released them in areas that contained no larval host plants for the subject species, in order to induce the hilltopping behavior (following the approach taken by Schultz 1998; Conradt et al. 2000). All butterflies still

in hold at the end of the experiments were released within close proximity to suitable habitat patches.

Nearly one hundred butterflies were released individually at one of five different release points located in five different 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 due to the strong influence of interactions with other individuals on butterfly behavior, observed on hilltops. In this treatment, releases were carried out 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. I then tracked their movements while keeping a distance of at least one meter from the butterflies, positioning myself so that my shadow would fall away from the butterflies, and changing my relative direction during observation to ensure that no disturbances, such as herding, occurred (Turchin et al. 1991). During observations, I flagged the movement trails with numbered flags, which I placed at each turning point and landing location. At the end of each observation, I determined the spatial coordinates of each flag by triangulating back to a 'baseline' using a compass (following Turchin et al. 1991; Schultz 1998). In addition, if a fast-flying butterfly disappeared from sight during an observation, I 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), I followed them for up to four more turning events, and mapped their movements 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, I found no difference in flight pattern between the different methods and between short and long observations. Therefore, I used all data in my analysis.

I performed the observations between 1000-1500 hours on clear or hot days (up to 60% cloud cover unless the temperature was above 25°C), and only when the sun was not hidden by clouds. For each observation I 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 the aid of a compass, where a sweeping net was used as a 'wind-sock' at 2m above ground. In choosing the measuring height I considered that at lower heights wind direction became less consistent through time due to boundary layer effects. This decision was conservative since *M. trivia* fly most of the time at a height <1m above the ground. I also recorded wind intensity (six categories, from 0=no wind to 5=very strong wind), cloud cover (%), and observed inter- and intra-specific interactions which may have influenced flight directionality. Observations lasted up to 15 flags or up to 15 minutes (whichever came last). If inactive, I recollected the butterflies and the observations were not used. Also, if lost within four movements or less, butterfly route was not recorded. Under the conservative limitations for conducting observations and accepting their data for analysis, I typically collected 3-5 movement routes in each observation day. I recorded and analyzed the movement paths of 59 butterflies: 20 males, 26 virgin females, and 13 mated females (Table 1), totaling 732 turning-points (12.4 flags/butterfly). In these observations, butterflies moved a total distance ranging between 11-374m (median= 84.7m), and displacing from the point of release by 3-211m (median= 51.8m). The movement trajectories of males and virgin females in two sample locations are depicted in Figs. 1b,c. I note that this investigation was directed towards understanding the general mechanisms that direct flight movement, and not towards evaluating dispersal rates. Therefore I analyzed movement-decisions made during flight, and left out analyses relating to flight speed. For data relating to dispersal-rates see Chapter 7.

2.2.2 FLIGHT ANALYSIS

I 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 20-35cm. Movement patterns and movement decisions were analyzed in two steps. In the first, I explored the general factors that influence flight patterns apart from topography: i.e. wind conditions, animal characteristics, and the presence of conspecifics. In the second step I explored the impact of topography on the process of decision-making itself.

2.2.2.1 Analysis of flight patterns excluding topography

The impact of wind direction on flight direction was estimated using a comparison between 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, p.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 (3 state-groups: males, virgin females, mated females) and location (3 types of locations: Hilltop, clear hilltop, non-hilltop 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.

During the observations in the field I noticed that some individuals, in the presence of other individuals, stayed around the point of release and displayed back-and-forth flights without leaving the area of release, even if the location was not on a hilltop. To analyze the movement patterns and recognize whether the tendency to stay around one location was a result of the interactions, I divided the butterflies into two categories, with or without interactions. I then compared butterflies that had interactions to butterflies 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 which were collected at distances greater than 10m from the point of release.

2.2.2.2 Impact of topography

In the second part of the analysis, I compared flight movements with the available topography. For this I used a Correlated Random Walk (CRW) simulation to construct landscape-independent random movements, as a null model. In this simulation, one hundred virtual butterflies were 'released' at five different 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. I used the following parameters: the number of turning points ('flags') ranged uniformly between 6 and 18;

turning angles distributed normally around a mean direction of -0.33 ± 1.664 radians (mean±SD), and truncated by $-\pi$ and π; increment lengths distributed log-normally, where the log of flight-distances distributed normally around 0.696 ± 0.467 meters (Mean±SD), truncated by 0 and 150 meters.

In this analysis, the direction taken at a given point along the path was compared to 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 5×5m that was produced for the purpose of the study (Mapping Technologies Ltd.). To obtain data on the topography along the whole movement trail of all butterflies, I divided each segment between turning points into 3m 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 3m ahead on the butterfly's flight path. I then calculated the slopes that were available at each location using the elevations at a distance of 3m in a sample of sixteen evenly distributed directions on a compass rosette. This approach allowed me to evaluate the slopes taken during the flight, relative to the slopes that were available at each point.

2.2.2.3 Initial orientation phase

When setting butterflies in a totally unknown landscape, the initial movements may be random due to the release effect caused by the animals' need to investigate their surroundings. To see if such an orientation phase exists, I regressed the slope taken at each point against the distance from the origin for each butterfly. If a butterfly flies immediately upward, which I predicted for males and virgin females, or downward, as I 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 (which could be interpreted as 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 number of cases where the slopes of the regression line and the constants are positive or negative, regardless of the line's significance. If no trend exists, the number of positive and negative cases should not differ. Since my goal was to determine the behavior of the butterflies subsequent to the orientation phase, I used a graphical approach to determine the threshold distance below which disoriented movements occur. I created a bar diagram of the proportion of cases in which butterflies moved upward, pooled over all individuals, and divided the diagram into classes of increasing distances from the origin. I evaluated the tendency to fly upwards (% of the movements upward) for each distance class, for the males, the virgin females, and the mated females. I then compared it to the corresponding tendency for the virtual butterflies in the CRW simulation. I validated the results of these two analyses by a repeated measure analysis, in which I tested the effect of time, location, state, and location×state on the slope taken at each point. For this, I analyzed the first 5, 10, 15, and 20 data-points.

2.2.2.4 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 then compared to an expected proportion, based on a count of the number of options to move upwards out of sixteen possible directions at each data-point. A similar comparison between the number of movements up and the counted possibilities to move up was performed with the data produced by the CRW simulation. I also evaluated the proportional distance that each individual moved up vs. down. Flight consistency was defined as the probability of an upward or downward movement to be followed by another upward or downward movement, respectively. I 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 data set.

I 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).

2.2.2.5 Factors affecting the slope taken

I tested how butterfly movement decisions (expressed by the slopes taken) are affected by their state (males, virgin females or mated females), the location of release-point, and the landscape-specific factors at each point (maximal slope available). Additionally, I tested whether the movement decisions were different for turning points vs. no-turning points. I needed to take into account that the range of options a butterfly had to choose from at each point affects the slope taken. To assess the impact of the immediate surroundings on the taken slope, I 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. I termed this index 'Relative Choice' (*RC*):

$$RC \ = \ 1\text{-}(Max\text{-}Taken)/(Max\text{-}Min) \tag{1}$$

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, while the ranges of options were calculated based on 16 bearings. I then performed an ANOVA to test the effect of location (3 categories: hilltop, cleared hilltop, and non-hilltop locations) and state (3 state-groups: males, virgin females, mated females) on the average *RC* of each butterfly, and then compared the *RC* between turning and no-turning points for each state-group (paired-sample t-test).

2.2.2.6 What induces butterflies to turn – slope or distance?

To test what the cues are, that induce butterflies to turn, I used only the data of males and virgin females from non-hilltop release points. I 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 the frequency histogram of random increment lengths. In order to perform this comparison, I evaluated the number of turning points for movements of males and virgin females, and summed up the total distance moved along this part of their flight. I then created random increment lengths by dividing each complete flight interval into the same number of 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 χ^2 goodness-of-fit test.

2.2.2.7 Evaluating the response range

Since the goal of males and virgin females is to reach a summit, the direction selected should be toward the maximum slope within their range of perception. Given a collection of peaks at varying distances and directions, I can assume that the peak toward 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 toward a local summit and disregards another, more distant and taller summit, I can conclude that the distant summit is beyond this range (or possibly even beyond its perceptual range). Naturally, such a comparison can only be done when the direction to the two summits differs considerably.

For this analysis I used only data on males and virgin females, and omitted all releases on the hilltop. At each data-point (butterfly location) I delineated concentric circles at increasing radii from 8m up to 64m at intervals of 8m, and radii from 64m up to 144m at intervals of 16m. Within each circle, I identified the highest location in the landscape, and derived the bearing from the data-point to this maximum. I also included a close-range circle of 3 meters. 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 I considered the nearer and farther 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°. I 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, I noted whether the butterfly flew toward the nearer or the more distant peak. I then summarized the proportion of cases in which the closer peak was preferred over 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 most often be towards the distant summit (hereafter, a 'preference' to the distant summit), whereas in distant pairs, movement directions would usually be towards the closer summit (hereafter, a 'preference' toward the closer summit). The optimal distance itself would be at the point with equal preferences (50%). I note that this analysis approach takes into account the real elevation of any part of the landscape, and disregards the impact of animals' view-point on the visibility of summits or their relative height.

2.3 RESULTS

2.3.1 ANALYSIS OF FLIGHT PATTERNS

I found no correlation between wind direction and the net direction of flight when analyzing it for mated females alone ($\hat{\rho}T$ =0.044, n=13, P>0.1), nor for males alone (excluding hilltop observations; $\hat{\rho}T$ =-0.034, n=14, P>0.05). Virgin females (excluding hilltop observations) showed a significant tendency to fly along the wind, but it accounted for only 8.6% of the variance in flight direction ($\hat{\rho}T$ =0.086, n=19, P<0.05). Similar results were obtained when analyzing 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, I analyzed the last flight direction of seven males and four virgin females who disappeared at the beginning of the observations, and whose routes were not mapped. I found that these individuals tended to fly with the wind ($\hat{\rho}T$ =0.278, n=11, P<0.001).

I did not find an impact of wing wear (four categories), capture method (wild caught vs. reared individuals), and wind velocity (six categories, 0-5), 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. I found, however, an impact of state (ANOVA, P=0.001) and a near-significant impact of location×state (ANOVA, P=0.11) on the average distance between turning points (the increment length)(Fig. 2a). When excluding the mated females from this analysis, the impact of location×state became significant (P<0.05). The longest increment length was observed in the flight of mated females, regardless of location. Males made shortest flight increments on the (un-cleared) hilltop, where they encountered other individuals, while virgin females had the shortest increment length on the cleared hilltop (Fig. 2a).

There was a significant impact of state on the absolute mean turning angle (ANOVA, 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 three locations (i.e. high consistency in one direction)(Fig. 2b). Despite the back and forth flights of males and virgin females on the hilltop, I did not find a significant impact of location or location×state. I explain this by the small sample size, as well as the tendency of many males and virgin females to stay around their release-point and perform back and forth flights for at least some certain time 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 ($t_{10.6}$=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 10m from the origin decreased from 63.1% without- to 19.4% with interactions ($t_{10.3}$=3.659, P<0.005). Thus males tended to stay longer at close proximity to the origin when they were interacting with other butterflies. Virgin females did not show an alteration of flight behavior while interacting with conspecifics, neither in the distance added per flag nor in the percentage of distant data-points per observation (60.6% with vs. 58.4% without interactions, $t_{12.3}$=0.145, n.s.). Mated females also did not alter their flight in response to interactions (88.3% vs. 75.8% of the distant data points, with vs. without interactions, t_{12}=1.703, n.s.). However, I note that I only observed interactions of mated females with other butterflies in 2 out 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.

2.3.2 LANDSCAPE-ASSOCIATED ANALYSIS

2.3.2.1 Initial orientation phase

In most males and virgin females I found a positive correlation between the slope taken and distance from the origin (Table 2), although the proportion of males exhibiting 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 frequency of upward vs. downward movements (Fig. 3), I determined that below a threshold distance of 10m from the origin the movements of males and virgin females were not determined solely by topography, and therefore this indicates an initial (orientation) phase. Thus, all data points of males and virgin females that were less than 10m from the point of release were excluded from any further analyses. After exclusion, the constant was significantly positive in both males and virgin females, and the slope was insignificant (Table 2), i.e. the impact of the orientation phase was removed. The exclusion process removed the entire observations of eight males and nine virgin females. That indicated that these individuals remained within 10m of the release point throughout the observation. Some of these individuals were released on the hilltop, while others remained around the release point due to interactions with other individuals. Thus, the exclusion of data-points <10m from the origin removed disoriented movements that occurred due, in part, to the orientation phase, as well as other reasons such as adhering to the hilltop and interacting with other individuals. The efficiency of excluding data-points <10m from the origin 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 insignificant thereafter.

2.3.2.2 Tendency and consistency of upward and downward flight

Table 3 summarizes the flight tendencies with respect to topography (i.e. % movements up and down), and the consistency up and down (i.e. the likelihood of a movement up to be followed by another move upward). 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 upward (males: 77.5%, t_8=3.45, P=0.009; virgin females: 81.8%, t_{16}=7.31, P<0.0001). The consistency upward was higher than the consistency downwards (males: 62.9% vs. 56.2%, t_6=2.254, P=0.065 n.s.; virgin females 71.0% vs. 59.4%, t_{13}=4.045, P=0.001). Mated females flew upward only in 44.3% of the movements (n.s.). The consistency downward was not significantly different from upward (86.8% vs. 73.3%). Between states, the proportion of movements up was significantly higher in virgin females than in males or mated females. The difference between males and mated females was only non-significant (Tukey Post hoc analysis). I also note that, after excluding hilltop releases, 6 out of 16 males and 3 out of 22 virgin females performed a 100% consistent flight upward without any movement downward. Thus, the tendency to move upward was between 75-90% for most butterflies, and only rarely reached 100%.

2.3.2.3 Factors affecting the slope taken

Males and virgin females most often took positive slopes, which tended toward the maximal slope (Figs. 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). ANOVA test for the effect of location and state on the average 'Relative Choice' (RC) of each butterfly found a significant influence of location on the RC, with a high RC taken on non-hilltop locations relative to HT and CHT. This was evident both for turning points and no-turning points. In the turning points, there was also a near-significant effect of state, due to higher RC by virgin females in comparison to males, and the high RC of males relative to mated females (Table 4a,b). The lack of a location×state interaction was probably the result of low statistical power stemming from lack of data-points for males on the hilltops (due to the excluding procedure), as well as the fact that, like males and virgin females, mated females took more positive slopes at non-hilltop locations – but this tendency did not differ from random (see 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 (t_{13}=0.424, P=0.679, and t_{12}=-0.791, P=0.445, respectively). 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 also after Bonferoni adjustment for the number of tests.

2.3.2.4 What induces butterflies to turn – slope or distance?

Pooling all data-points of all males and virgin females (excluding hilltop observations), I 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'). I found no significant difference between the slope taken and the slope not taken (t-test = -0.129, df =184, P=0.898). I also counted the number of cases (=butterflies) where the slope taken exceeded the slope not taken in more than 50% of the turning points. This occurred in only 9 out of 16 virgin females and 2 out of 10 males. When comparing the frequency histogram of increment lengths (distances between turning points) between that of the males and the virgin females, and that of the null hypothesis (the broken stick model), I did not find any significant difference (χ^2 test=8.625, df=6, 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.

2.3.2.5 Evaluating the response range

Excluding the closest pair of maxima (3m vs. 8m), the preference towards the closer summit increased linearly with the size of the perceptual range circle (R^2=0.736, n=10, P<0.005)(Fig. 5). That is, the preference toward the closer summits was less than 50% at close-distance circles (a preference toward the more distant maxima), and higher than 50% at large-distance circles (preference toward the closer maxima). Around the 50m circles the preference was 50% (i.e. no preference), suggesting that this is the range of response. However, when comparing the closest maximum to the second closest one (i.e. 3m to 8m maxima), the butterflies showed a strong preference toward the closest maximum. Thus, the response range of the butterflies involves both a response to the very near surrounding and to a distant maximum at a range of 50m. I repeated the analysis by comparing successively the bearing to the maximum in a 3m-radius circle to the bearing found by each of the more distant maxima. The result revealed a strong preference for the 3m maximum over the 8m maximum, and a preference of the 50m maximum over the 3m one (Fig. 6). At distances greater than 60m, and between 24-40m, no preference was identified. This result suggests that the butterflies orient themselves based on two

separate orientation cues, i.e. the immediate inclination and the maximum within a range of 50m. Furthermore, the more distant maximum is preferred over the immediate surroundings. These results seem to explain those presented in section 2.3.2.4, since the decision to turn is determined not only by the immediate surroundings.

2.4 DISCUSSION

2.4.1 BUTTERFLY RESPONSE TO LANDSCAPE CUES

The movements of *Melitaea trivia* are governed by simple movement rules in response to topography, probably based on visual topographic cues. The uphill movement is directed by two cues: the highest location within a distance of around 50m, 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 (3m vs. 8m). I postulate that this dichotomy reflects two forces that orient animals. First, animals need a reliable orientation cue toward the highest maximum, which allows them to avoid local maxima (see chapter 5). This requires a long response-range (toward the 50m 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, I suggest that some preference toward 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.

Though wind is a directional element, which commonly affects insect movements while searching for conspecifics and host-plants (Compton et al. 2000; Marchand & McNeil 2000) as well as during dispersal and migration (Schmidt 1993; Bellamy & Byrne 2001; Srygley & Oliveira 2001; Srygley 2003), I found only little effect of wind direction on butterfly flight directionality, except during initial movements. This I 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 <1m off the ground). This result is consistent with field observations on *Maniola jurtina*, in which butterflies showed a clearly directed movement toward 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 in topographically heterogeneous landscapes. More importantly, the lack of response to wind direction and other external factors (such as nectar sources at the study site) suggests that topography is a major external element invoking directional movements in these scales of interest. Another major 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 chapter I was unable to evaluate the impact of vegetation because the landscape for this study was relatively homogeneous in vegetation, specifically chosen to confine the study to the impact of topography alone. I believe that the dispersal patterns of a wide range of organisms, once leaving their habitat patches and moving through the 'matrix', are affected by two main attributes of the landscape: topography and vegetation structures.

2.4.2 ECOLOGICAL INSIGHTS ON HILLTOPPING

My observations support previous studies on hilltopping behavior, suggesting that hilltopping is a strategy used to locate potential mates in easily recognized sites (Shields 1967; Lederhouse 1982; Queller 1987; Wickman 1988). This fieldwork was not aimed at understanding the reasons for hilltopping or estimating the successfulness of this behavior, but only towards describing its behavioral rules. Nevertheless, the detailed quantification of movement parameters provides new insights into the ecological meaning of this behavior.

Males and virgin females 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 play an important role in avoiding local summits on the way to more regional summits, as elaborated in Chapter 4.

Males adhered strongly to the summits, and were often recaptured several hours later (one male was found dead on the hilltop 3 weeks subsequent to its release). On the other hand, virgin females did not seem to adhere as strongly to the summits. Since females also disperse from the summits after mating, males probably contribute less than females to population dynamics within patches. However, the genetic contribution of this behavior to 'mixing' between populations may be of great ecological importance.

The differences in behavior between males and virgin females (such as the difference in turning angles, increment length, response to topography, and response to

interactions) possibly represent a certain asymmetry in the mate-searching strategy between genders. Such asymmetry may serve in optimizing the mate-searching 'algorithm', by increasing the chances of meeting along the way (Motro 1991; Sandell & Libero 1992; Motro 1994). For instance, the difference in increment length between males and virgin females implies that virgin females perform little search for males if not on the summits, while males search for conspecifics everywhere. On the summits, virgin females seem to activate a searching behavior if not encountered by males. It is noteworthy that most females were quickly encountered by males and copulated when arriving at, or released onto, the non-cleared summit. Furthermore, virgin females did not refuse males if 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 behavior is only beneficial when adults are sparsely distributed in space and time, i.e. if no potential mates are recognized in close proximity. This is ecologically sound since adult butterflies should naturally hatch in patches of suitable habitat. My observations suggest that, indeed, butterflies first search for conspecifics within their near surroundings (in natural cases – patches), and then leave the site only if these are not located. I note that the strong impact of interactions on the behavior of males and virgin females contradicts findings on the hilltopping butterfly *Lasiommata megera* (Wickman 1988). The difference may be due to the difference in approaches, since Wickman (1988) used transect observations instead of individual-based ones as used in this study. I believe that direct observation methodologies, like the one undertaken in this study, are more appropriate than indirect ones for the purpose of describing and understanding animal behavior (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. I found only a slight and insignificant tendency to fly downwards, in agreement with Wickman (1988) and in contrast with my prediction that mated females would avoid hilltops and fly strongly downwards in order to avoid male harassment (see Shields 1967). This is further emphasized by the fact that my 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 artifact of my method of

obtaining mated females (namely, capturing them in patches), or a result of ecological factors that this study did not address.

2.4.3 FROM BEHAVIORAL RULES TO SIMULATING HILLTOPPING

This chapter has focused on understanding the movement rules of hilltopping behavior, using direct observations in individual butterflies moving through a topographically complex landscape. Better understanding of the factors that direct movements while moving between populations is crucial for improving models of connectivity and metapopulations. For this, it is necessary to know the mechanisms that direct animal movements in gradually-changing landscapes, at the individual level. This field study addressed this issue, where the source of landscape heterogeneity was topography. The individual-based approach of this fieldwork demonstrates that, despite the seemingly small sample size and the short-term observations, clear decision rules can be obtained. The movement rules obtained from this study serve as a firm basis for developing an individual-based simulation model of hilltopping, with realistic landscape representation. This model, as will be shown in the following chapters, can be used to analyze the consequences of directional movements on movement patterns and on connectivity in a variety of complex landscapes.

Table 1: Locations of butterfly releases. Due to the small number of mated females, they were not released in the wadi-fork or on the slope.

Topographical formation	Number of successful observations		
	♂♂	Virgin ♀♀	Mated ♀♀
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

Table 2: The proportion of cases with positive values of the constant and the slope derived from linear regressions of the taken slope on the distance from the origin for each individual. The analysis was repeated after excluding data-points less than 10m from the origin for males and virgin females. Numbers in brackets are sample size (i.e. the number of individual butterfly regressions).

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

* $P<0.05$ (χ^2-test)

Table 3: Flight tendencies (mean±SD) of males, virgin females and mated females. The proportion of movements upward was compared to the proportion expected to move upwards based on the available slopes around each data point. The consistency upward, i.e. the probability that a movement upward was followed by another movement up, was compared to the consistency downward for each butterfly. All cases were tested using paired-sample t-test. Results for males and virgin females exclude observations on the hilltop, data-points <10m of origin, and two cases affected by strong wind.

State	Prop. up	Expected up	Consistency up	Consistency down
♂♂	0.775±0.214	0.527±0.044 **	0.880±0.145	0.482±0.39 ns
virgin ♀♀	0.818±0.175	0.490±0.017 ***	0.926±0.078	0.631±0.255 ***
mated ♀♀	0.443±0.273	0.498±0.017 ns	0.733±0.267	0.868±0.127 ns

* P<0.05; ** P<0.01; *** P<0.001

Table 4: ANOVA for the impact of location and state on the Relative Choice of slope out of the available range of slopes at each point. a – 'turning' points; b – 'no-turning' points.

a

Source	ss	df	ms	F-ratio	P
STATE	0.172	2	0.086	2.718	0.076
LOCATION	1.248	2	0.624	19.773	<0.001
Error	1.515	48	0.032		

b

Source	ss	df	ms	F-ratio	P
LOCATION	0.447	2	0.224	17.716	<0.001
Error	0.631	50	0.013		

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 330-401m within the study area. Contour lines represent 10m changes in elevation. Rectangles represent two sections of the map, depicting the movement trajectories of males and virgin females when released in the Wadi (b) and in the Saddle (c). Note that short trajectories are obscured due to the scale.
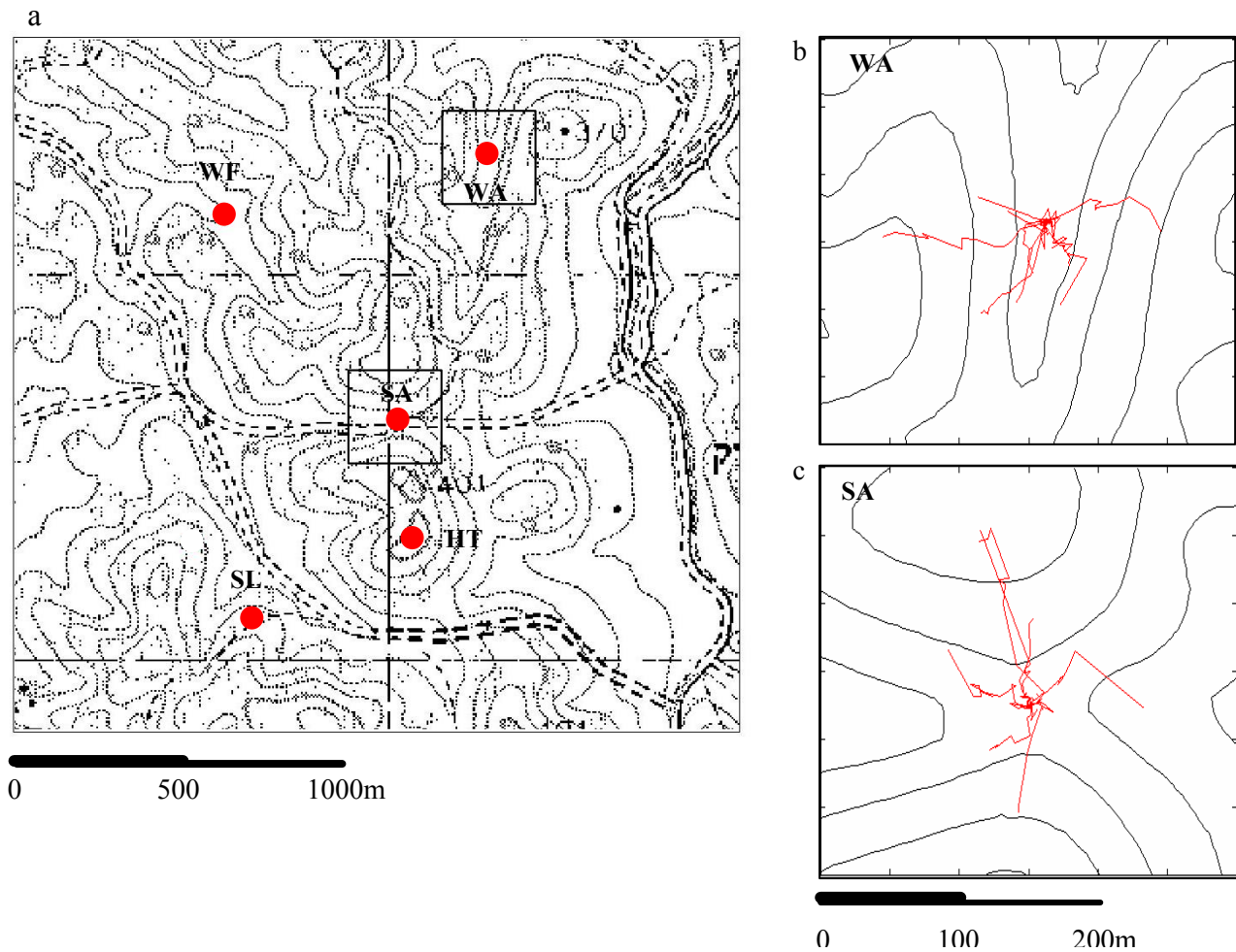
Figure 2: (a) Effect of release location and butterfly state on the average increment length (Mean±SE). (b) The absolute average turning angle (Mean±SE) was affected only by state. HT=Hilltop, SA=Saddle, WF=Wadi fork, WA=Wadi bottom, SL=Slope, CHT=Cleared hilltop. M=males, VF=Virgin females, MF=Mated females.
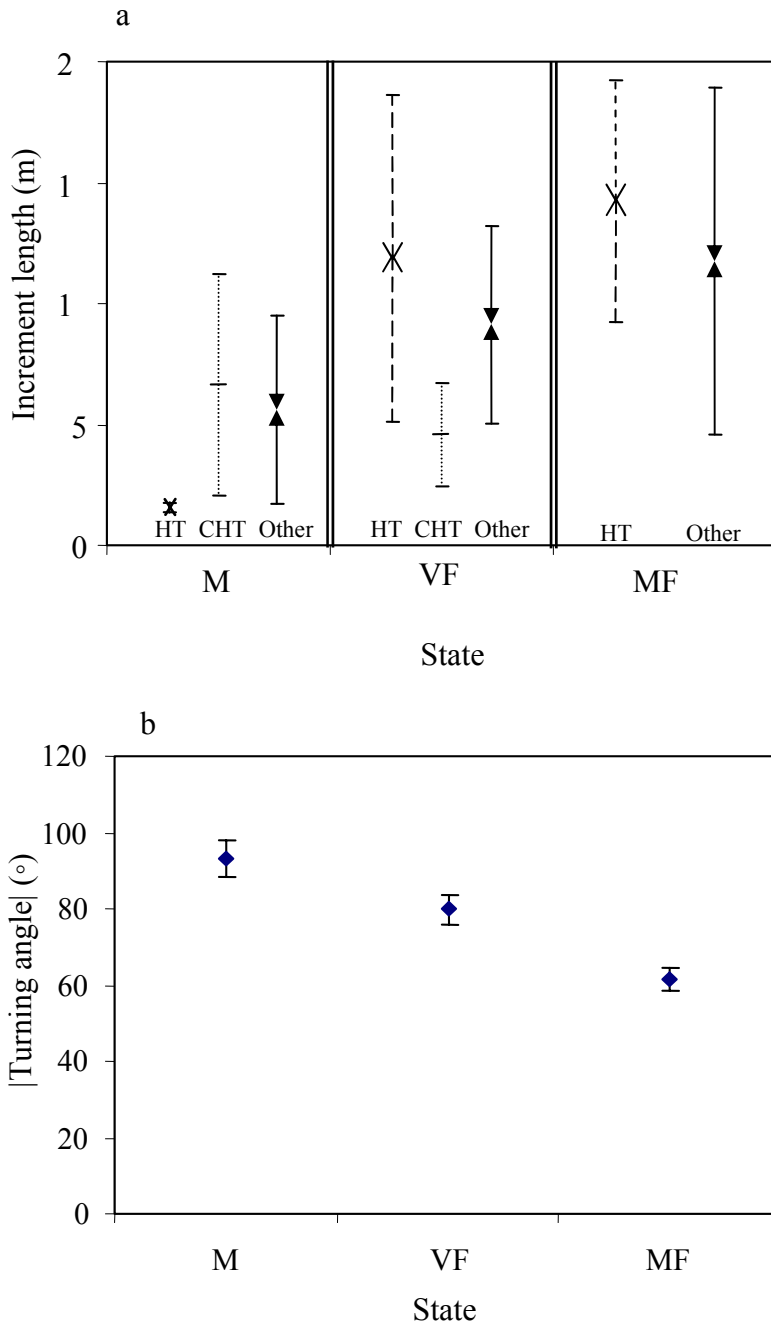
Figure 3: (a) Observed preference to move upward at increasing distances from flight origin for males (black) and virgin females (stripes), compared to that from a Correlated Random Walk simulation (white). Hilltop releases are excluded. The tendency to move upward clearly increased with distance from the point of origin. Based on a visual inspection of the graph, I excluded data-points less than 10m from all further analyses, as these were not directed by topography. (b) The preference for mated females to move upward (black) was compared to the Correlated Random Walk (white) that was based on three release points. I found no preference to move other than random.
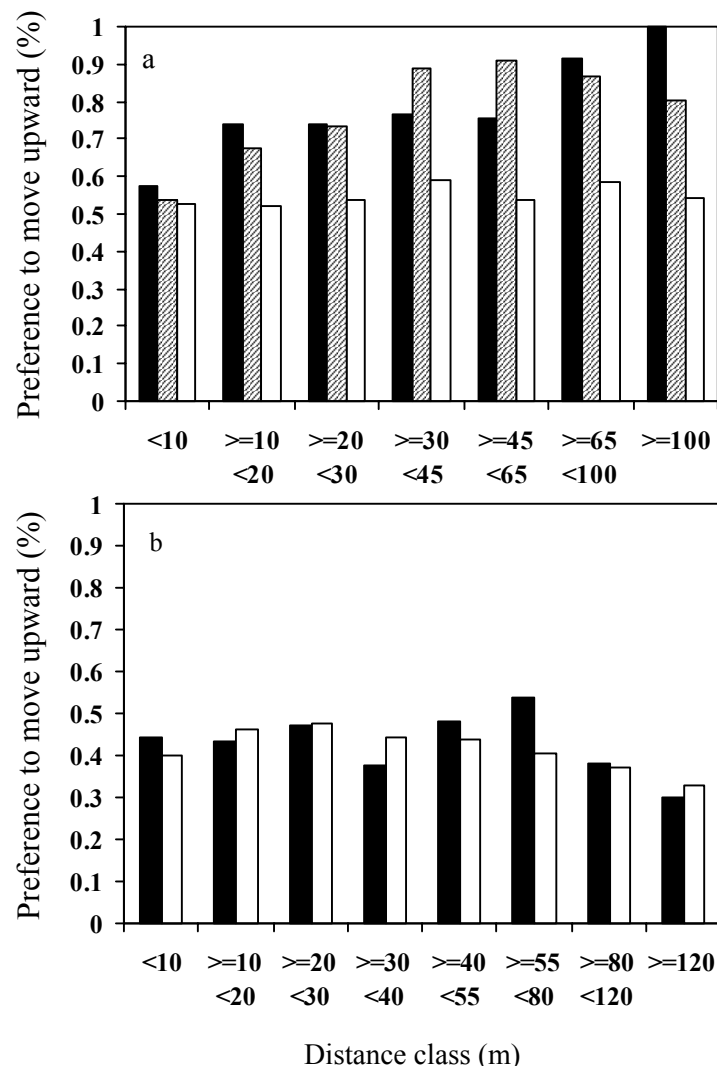
Figure 4: Slope taken vs. the maximal slope available at each point along butterflies' movement paths for a - males, b - virgin females, c - mated females, and d - Correlated Random Walk simulation. Hilltop releases and data-points <10m of the origin are excluded. Each point represents one data-point. Males and virgin females clearly fly toward the maximum. The tendency of mated females to fly downward does not differ from the corresponding tendency produced by the Random Walk simulation model.
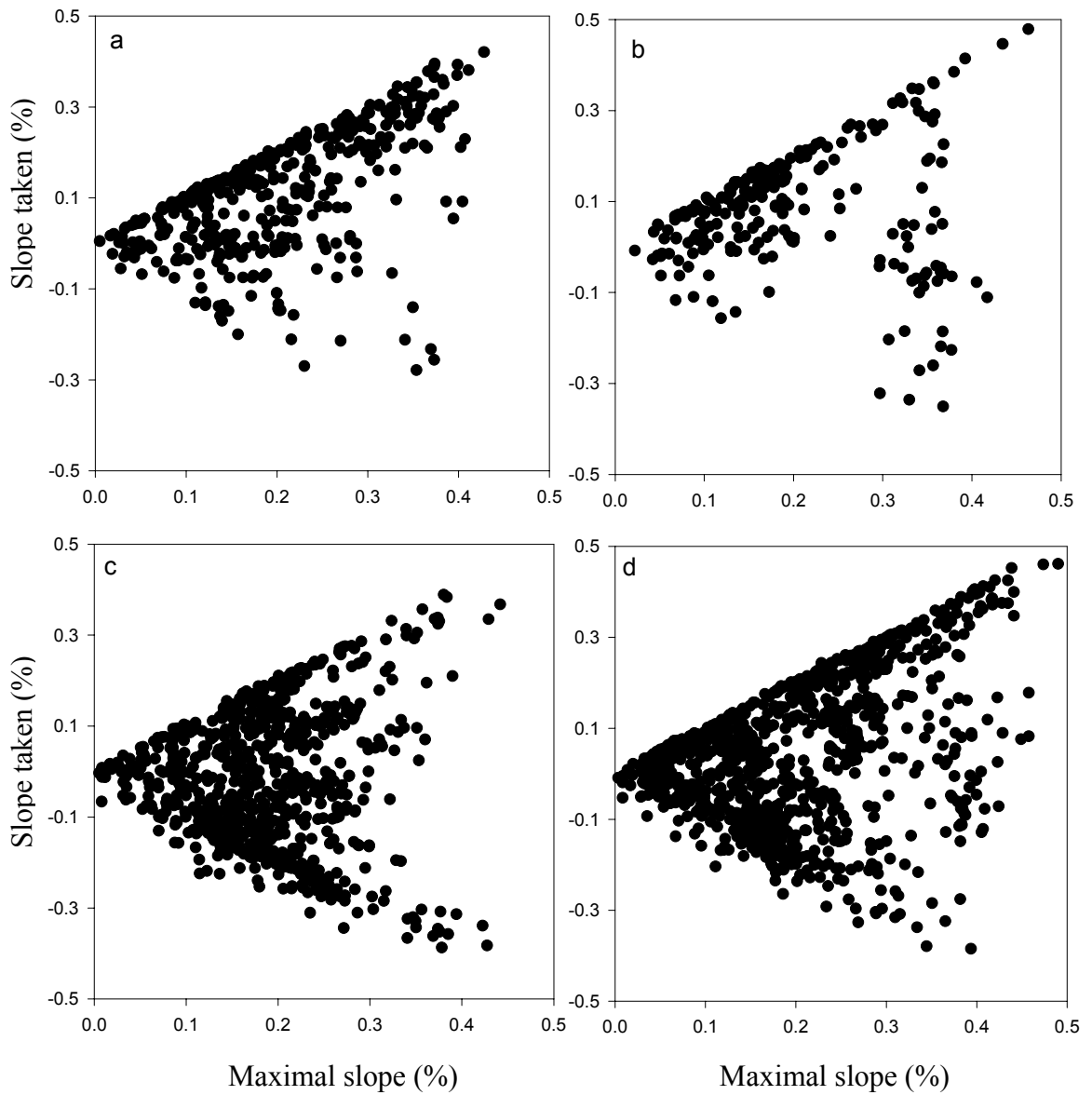
Figure 5: Evaluation of the response-range based on the preference toward the closer of two maxima within given radii. X-axis values represent the mean of the two radii (e.g. 8 vs. 16 =12). Excluding the closest pair of maxima (3m vs. 8m, empty square), the preference toward the closer summit increases linearly with the radii (the perceptual range), with a preference toward the more distant maxima at close-distance radii, and a preference toward the closer maximum at large-distance radii. Thus, the response range of the butterflies seems to involve both a response to the very near surrounding and to a distant maximum at a range of 50m.

$$y = 0.0026x + 0.3835$$
$$R^2 = 0.4015$$
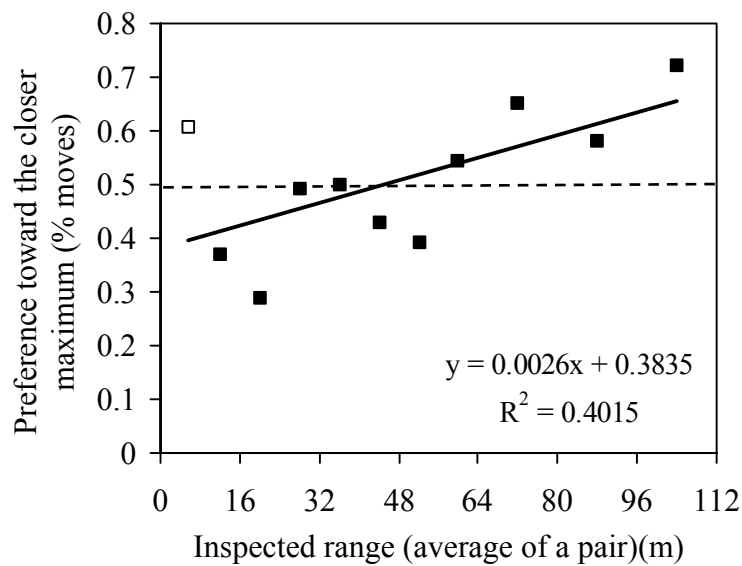
Figure 6: Preference toward the 3m maximum (% moves) over each of the more distant maxima. The graph shows a strong preference to the 3m maximum over the 8m maximum, and a preference for the 50m maximum over the 3m one. At distances higher than 60m, and between 24-40m, no preference can be identified. This suggests that the butterflies orient themselves based on the immediate inclination and the maximum within a range of 50m, where the more distant maximum is preferred over the immediate surrounding.

3. A MODEL FOR HILLTOPPING AND THE CONCEPT OF 'VIRTUAL CORRIDORS'

3.1 INTRODUCTION

The sustainability of many animal populations in fragmented landscapes depends on the attributes of the landscape and on the landscape management in the surrounding human-dominated areas (Bennet 1999), due to the great impact of the 'matrix' on the connectivity between the remaining habitat patches. When animal movements between populations seem to be too scarce, conservationists are interested in enhancing them artificially. One of the approaches for achieving this goal is to secure or provide corridors. Corridors are classically perceived as visible linear habitats that connect two or more larger blocks of habitat and enable animal movement between habitats. This concept embraces a variety of landscape elements, which may be natural or artificial, protected or reclaimed habitats (Hay 1991; Noss & Cooperrider 1994; Hill et al. 1995; Meffe & Carrol 1997; Rosenberg et al. 1997; Beier & Noss 1998; Hunter 2001). The various definitions and descriptions of corridors generally assume that corridors have easily recognized attributes. For instance, corridors are assumed to differ from their surrounding matrix either from one direction (e.g. fences, cliffs), or from both (e.g. roads, strips of forest within open landscapes, or vice versa). In addition, the concept of habitat corridors implicitly assumes that in their absence, movement across the matrix is primarily random. This is despite growing evidence that dispersal is rarely random, even when a directing element cannot be recognized (Conradt et al. 2000,2001).

In this chapter I demonstrate that animal movement can be canalized even in the absence of clear physical corridors. I show that the specific response of animals to certain aspects of landscape heterogeneity, such as topography, can canalize their movements into specific routes. These may not differ from their surroundings, and therefore can be interpreted as 'Virtual Corridors'. In the context of topography, linear topographic elements are often recognized as corridors. For instance, long chains of cliffs provide possible corridors for the dispersal of the Nubian ibex (Shkedy & Saltz 2000), while river basins may provide corridors for the dispersal of butterflies (Nève et al. 1996). I

demonstrate that the response to topography can canalize animals into corridors that are not necessarily self evident, and do not have clear attributes. Furthermore, Virtual Corridors may be formed even when the topography is not directional.

I present an individual-based model of the hilltopping behavior, which I call 'the Hilltopping Model'. The model enables the analysis of movement patterns and connectivity in topographically complex landscapes in the case of hilltopping behavior. Here it is used to investigate the first movement step in the hilltopping process (namely, ascending toward summits). I deduce the preconditions for the occurrence of Virtual Corridors in terms of the response of animals to topography. I analyze the structure of Virtual Corridors within a wide range of behavioral parameters, to identify whether generalizations can be made about the movement patterns of hilltopping butterflies over topographically complex landscapes. I show that, though the concept of Virtual Corridors may be intuitive, their structure may be complex. Therefore, an individual-based modeling approach should be used for obtaining landscape-specific predictions of the structure of Virtual Corridors.

3.2 METHODS

3.2.1 MODEL DESCRIPTION

'The Hilltopping Model' model was developed for the purpose of understanding the mechanisms that drive hilltopping behavior and the consequences of this behavior on movement patterns, patch colonization, and connectivity patterns. It is spatially explicit, individual-based, and rule-based. That is, it simulates the movements of individual animals over topographical maps on a grid base, and the movement decisions are based on simple behavioral rules. In the model, hilltopping butterflies are 'released' individually in the matrix, to seek a topographical summit for the purpose of mating. Mated females then descend from summits in search of patches of host plant.

The movement rules derive from field observations (Chapter 2), yet some simplifying assumptions were made to produce a generalized model for hilltopping. Response to topography is probabilistic in terms of the tendency to move upward: at each step, a butterfly can move upward with a probability q or move randomly with a probability $1-q$. q can range from 0 (a random movement) to 1 (moving 100% of the time

toward the steepest slope). In each simulation run, all butterflies have the same level of response to topography (q). The main assumptions of the model are:

- Movement directionality results only from response to topography, with no self-avoidance (i.e. butterflies have no memory).

- Topography is perceived only within a distance of one cell (response to the 4 direct and 4 diagonal neighbors).

- Simulated butterflies move one cell at a time (constant speed) and make a decision every time-step.

- Butterflies do not respond to the presence of other individuals (see Appendix II for further exploration of this assumption).

- Despite some observed differences between the behaviors of males and virgin females, it is assumed that they react similarly to topography by flying toward the maximal slope, and their movement parameter (q) is similar.

3.2.2 LANDSCAPE AND SIMULATION CHARACTERISTICS

The model includes a landscape generator to create virtual landscapes on a grid base, but it is also capable of using realistic elevation maps derived from Digital Elevation Models (matrices of elevations). The creation of virtual landscapes is based on three stages: firstly, the number of summits and their location is determined. Secondly, the elevation of each cell is calculated, based on its distance to the closest summit. For this purpose, a Gaussian function is used to create 'bell-shaped' hills. Lastly, additional landscape variability ('noise') is added to each cell independently, as a random value with a normal distribution around 0. The magnitude of the variability is determined as a percentage of the summit elevation (for instance, a standard deviation of 2% of summit height).

The parameterization processes presented in this chapter were not species specific, and did not try to imitate true data. Instead, I explored the movement patterns with varying values of q along its range. In each simulation, all butterflies started in one random location, comparable to an uninhabitable 'source patch' in the landscape, and moved across the landscape in search of summits. To obtain a first impression of the hilltopping movement pattern and characterize the structure of Virtual Corridors, I focused on two types of landscapes, and correspondingly analyzed two properties of Virtual Corridors. The first landscape type was a virtual 200×200cell matrix, with one

source patch and one randomly located mountain. Cell side-length was 5m, summit elevation was arbitrarily determined as 10,000 units, and landscape noise was 2% of summit elevation. In this simple case, where only one Virtual Corridor could be formed, I estimated corridor width as an indicator of the level of canalization. This was done by counting the number of cells visited by 500 individuals that moved 1000 steps, and dividing it by the distance between the source patch and the summit (under the simplifying assumption that corridor width is constant over its whole length). I then altered the response to topography (q) systematically from 0.1-1 and calculated the average corridor width of 20 simulations for each value of q.

The second landscape type was a realistic landscape map with complex topography. I used a 300×300cell map (cell side-length = 25m), of a section of the Negev desert (Ef'e ridge, Dimona; 31º05'N, 35º03'E). The elevations in this landscape range between ca. 300-650m. Preliminary simulations on this landscape revealed that individuals often take more than one route and end up on different summits. Hence, for this case, corridor width could not provide a descriptive index. Instead, I characterized the dispersion of individuals throughout the landscape at the end of the simulations, as follows: I allowed 500 individuals to move for 1000 steps, in order to provide sufficient time for them to end up on or near summits. When the final location of two or more individuals was less than 4 cells from each other, I considered them as a single clump, which I termed 'End Location'. I then compared the number of distinct End Locations between various simulations, with q ranging from 0.1-1 and 5 repeats for each value of q. The term End Location refers to the fact that, as a function of q, individuals did not always reach a summit within the 1000 time steps.

3.3 RESULTS

By simulating butterfly movement on the simple, one-summit-one-patch landscape, a Virtual Corridor was formed between the source patch and the summit, which became narrower as q increased (Fig. 7). A systematic analysis of the change in corridor width with q revealed a strong decline in corridor width, especially in low values of q (Fig. 8). This exponential-like decline leveled off when the response to topography

was high, until a sharp fall occurred when q increased from 0.9 to 1. The latter indicated the formation of a deterministic path, one cell in width.

In the one-summit-one-patch landscape, the spatial orientation of the Virtual Corridor was self-evident, while its structure (here, corridor width) depended on the movement parameter. When the topographic attributes became complex, the structure of Virtual Corridors was no longer self-evident. Simulating butterfly movements over the realistic landscape may result in several virtual-corridors, their number depending on q (Fig. 9). While individuals distribute over several summits, several other summits, that seemingly could be reached, were not reached at all. This can be viewed as 'competition' between summits, in which one or several summits intercept the movements of individuals (see Chapter 4).

The number of distinct End Locations declined strongly with increasing q, leveling off at moderate to strong values (Fig. 10). The very high number of End Locations at low q values indicated that many individuals did not reach a summit within the given time horizon of 1000 time-steps. In moderate to strong values of q, most of the End Locations were summits, but still the number of End Locations was high (for instance, even at $q=0.8$ a few dozens of summits were reached). This indicated that in the given example, even a strong response to topography resulted in several movement routes, hence several Virtual Corridors. Only when $q=1$ did all animals arrive at one End Location (a summit). Interestingly, the pattern of diminishing numbers of End Locations with q increasing was similar to the decline in corridor-width with increasing q in the one-summit-one-patch case. This suggests that increasing directedness results in the canalization of more and more individuals into one narrow route. To summarize, in complex landscapes it is not only corridor width but also the number of Virtual Corridors and their structure that depend on the level of directedness.

3.4 DISCUSSION

3.4.1 THE ATTRIBUTES OF VIRTUAL CORRIDORS

In this chapter I have introduced 'the Hilltopping Model', an Individual-Based simulation Model (IBM) of hilltopping. With the aid of this model I have demonstrated that the response to topographical heterogeneity canalizes animal movements and creates Virtual

Corridors. Even from the over-simplified case of a one-summit landscape, two rules-of-thumb can be derived: first, a Virtual Corridor forms in a line connecting the source-population and the summit; second, corridor width is determined by the intensity of response to topography (q). This example also demonstrates that Virtual Corridors may not differ from their surroundings, and in contrast to the common perception of corridors, they are not formed along a visible directional landscape element. From the more complex case of the realistic, topographically complex landscape, I conclude that the number of movement routes, and thus the number of Virtual Corridor and their structure, may be complex.

Due to the possible complexity of Virtual Corridors, and their dependence on a specific landscape and the movement parameters, IBMs should be used for predicting the movement paths of individuals, in order to recognize both corridors and barriers to dispersal. Given the complexity and over-specificity of most IBMs (Grimm 1999), the results of my research suggest that even a generic and limited IBM, with a small number of parameters, could be useful to provide landscape-specific predictions of the patterns of landscape usage by animals. Such predictions necessitate only the parameterization of animal behavior, and the landscape variables affecting these parameters (in this case, topography).

Since topographical heterogeneity is characterized by gradual changes, I hypothesize that Virtual Corridors can exist whenever animals respond to gradients of change in the landscape. Consequently, canalized movements, and correspondingly, Virtual Corridors, may be present in a variety of landscapes and as a result of various sources of landscape heterogeneity. This hypothesis, which has broad implications for conservation and landscape management, is further examined in Chapter 4.

3.4.2 A MECHANISM-BASED DEFINITION OF CORRIDORS

I suggest expanding the definition of corridors, to reflect the interaction between an animal's behavior and the landscape. A broader definition of corridors could be based on a common underlying mechanism. Several authors have suggested that effective corridors are characterized by the strong response of an animal to corridor boundaries. If animals 'bounce' back into the corridor, they remain within the corridor and are not lost to the matrix (Wiens et al. 1993; Tischendorf & Wissel 1997; Haddad 1999; Schultz & Crone 2001). The mechanism that directs animals into Virtual Corridors is essentially the same:

in the case of topography, the avoidance of negative slopes 'reflects' the animals back toward one route. Therefore, I suggest defining corridors as any specific path which has a high potential for being utilized by dispersing animals while moving between habitat patches. Animals can be canalized into the path either by their response to its edges, or by their specific response to the attributes of the landscape.

Figure 7: The trajectories of 100 individuals moving 1000 time-steps from a single source patch (empty circles) towards the mountain summit, with different probabilities to move upward (q)= 0.2 (a); 0.5 (b); and 0.8 (c), demonstrates that increasing the response to topography results in reducing the width of the Virtual Corridor. Landscape Size = 200×200 cells.

Figure 8: Corridor width (± SE) declines with increased response to topography (q) in an exponential-like pattern. Corridor width is evaluated as the number of visited cells divided by the distance from the 'source patch' to the summit. Each value is the average of 20 simulations, each with 500 individuals moving 1000 steps. Results are shown for a single location of the source-patch, but represent a consistent qualitative pattern.

Figure 9: The movement trajectories of 100 butterflies moving for 1000 movement steps, on a realistic landscapes 7.5×7.5km in size (cell side-length=25m). (a) Probability to move upward q=0.2; (b) q=0.5; (c) q=0.8. In the given location of the release point, complex Virtual Corridors are formed. Animals distribute between several summits, while not arriving at several others. The number of End Locations depends on the response to topography and the time horizon.

Figure 10: The number of distinct End Locations declines with increasing response to topography (q) in an exponential-like pattern, demonstrating that the number of summits that are reached depends on the movement parameter. Simulations are for 500 individuals moving 1000 steps each on the realistic, 7.5×7.5km landscape.

3. A MODEL FOR HILLTOPPING AND THE CONCEPT OF 'VIRTUAL CORRIDORS'

3.1 INTRODUCTION

The sustainability of many animal populations in fragmented landscapes depends on the attributes of the landscape and on the landscape management in the surrounding human-dominated areas (Bennet 1999), due to the great impact of the 'matrix' on the connectivity between the remaining habitat patches. When animal movements between populations seem to be too scarce, conservationists are interested in enhancing them artificially. One of the approaches for achieving this goal is to secure or provide corridors. Corridors are classically perceived as visible linear habitats that connect two or more larger blocks of habitat and enable animal movement between habitats. This concept embraces a variety of landscape elements, which may be natural or artificial, protected or reclaimed habitats (Hay 1991; Noss & Cooperrider 1994; Hill et al. 1995; Meffe & Carrol 1997; Rosenberg et al. 1997; Beier & Noss 1998; Hunter 2001). The various definitions and descriptions of corridors generally assume that corridors have easily recognized attributes. For instance, corridors are assumed to differ from their surrounding matrix either from one direction (e.g. fences, cliffs), or from both (e.g. roads, strips of forest within open landscapes, or vice versa). In addition, the concept of habitat corridors implicitly assumes that in their absence, movement across the matrix is primarily random. This is despite growing evidence that dispersal is rarely random, even when a directing element cannot be recognized (Conradt et al. 2000,2001).

In this chapter I demonstrate that animal movement can be canalized even in the absence of clear physical corridors. I show that the specific response of animals to certain aspects of landscape heterogeneity, such as topography, can canalize their movements into specific routes. These may not differ from their surroundings, and therefore can be interpreted as 'Virtual Corridors'. In the context of topography, linear topographic elements are often recognized as corridors. For instance, long chains of cliffs provide possible corridors for the dispersal of the Nubian ibex (Shkedy & Saltz 2000), while river basins may provide corridors for the dispersal of butterflies (Nève et al. 1996). I

demonstrate that the response to topography can canalize animals into corridors that are not necessarily self evident, and do not have clear attributes. Furthermore, Virtual Corridors may be formed even when the topography is not directional.

I present an individual-based model of the hilltopping behavior, which I call 'the Hilltopping Model'. The model enables the analysis of movement patterns and connectivity in topographically complex landscapes in the case of hilltopping behavior. Here it is used to investigate the first movement step in the hilltopping process (namely, ascending toward summits). I deduce the preconditions for the occurrence of Virtual Corridors in terms of the response of animals to topography. I analyze the structure of Virtual Corridors within a wide range of behavioral parameters, to identify whether generalizations can be made about the movement patterns of hilltopping butterflies over topographically complex landscapes. I show that, though the concept of Virtual Corridors may be intuitive, their structure may be complex. Therefore, an individual-based modeling approach should be used for obtaining landscape-specific predictions of the structure of Virtual Corridors.

3.2 METHODS

3.2.1 MODEL DESCRIPTION

'The Hilltopping Model' model was developed for the purpose of understanding the mechanisms that drive hilltopping behavior and the consequences of this behavior on movement patterns, patch colonization, and connectivity patterns. It is spatially explicit, individual-based, and rule-based. That is, it simulates the movements of individual animals over topographical maps on a grid base, and the movement decisions are based on simple behavioral rules. In the model, hilltopping butterflies are 'released' individually in the matrix, to seek a topographical summit for the purpose of mating. Mated females then descend from summits in search of patches of host plant.

The movement rules derive from field observations (Chapter 2), yet some simplifying assumptions were made to produce a generalized model for hilltopping. Response to topography is probabilistic in terms of the tendency to move upward: at each step, a butterfly can move upward with a probability q or move randomly with a probability $1-q$. q can range from 0 (a random movement) to 1 (moving 100% of the time

toward the steepest slope). In each simulation run, all butterflies have the same level of response to topography (q). The main assumptions of the model are:

- Movement directionality results only from response to topography, with no self-avoidance (i.e. butterflies have no memory).

- Topography is perceived only within a distance of one cell (response to the 4 direct and 4 diagonal neighbors).

- Simulated butterflies move one cell at a time (constant speed) and make a decision every time-step.

- Butterflies do not respond to the presence of other individuals (see Appendix II for further exploration of this assumption).

- Despite some observed differences between the behaviors of males and virgin females, it is assumed that they react similarly to topography by flying toward the maximal slope, and their movement parameter (q) is similar.

3.2.2 LANDSCAPE AND SIMULATION CHARACTERISTICS

The model includes a landscape generator to create virtual landscapes on a grid base, but it is also capable of using realistic elevation maps derived from Digital Elevation Models (matrices of elevations). The creation of virtual landscapes is based on three stages: firstly, the number of summits and their location is determined. Secondly, the elevation of each cell is calculated, based on its distance to the closest summit. For this purpose, a Gaussian function is used to create 'bell-shaped' hills. Lastly, additional landscape variability ('noise') is added to each cell independently, as a random value with a normal distribution around 0. The magnitude of the variability is determined as a percentage of the summit elevation (for instance, a standard deviation of 2% of summit height).

The parameterization processes presented in this chapter were not species specific, and did not try to imitate true data. Instead, I explored the movement patterns with varying values of q along its range. In each simulation, all butterflies started in one random location, comparable to an uninhabitable 'source patch' in the landscape, and moved across the landscape in search of summits. To obtain a first impression of the hilltopping movement pattern and characterize the structure of Virtual Corridors, I focused on two types of landscapes, and correspondingly analyzed two properties of Virtual Corridors. The first landscape type was a virtual 200×200cell matrix, with one

source patch and one randomly located mountain. Cell side-length was 5m, summit elevation was arbitrarily determined as 10,000 units, and landscape noise was 2% of summit elevation. In this simple case, where only one Virtual Corridor could be formed, I estimated corridor width as an indicator of the level of canalization. This was done by counting the number of cells visited by 500 individuals that moved 1000 steps, and dividing it by the distance between the source patch and the summit (under the simplifying assumption that corridor width is constant over its whole length). I then altered the response to topography (q) systematically from 0.1-1 and calculated the average corridor width of 20 simulations for each value of q.

The second landscape type was a realistic landscape map with complex topography. I used a 300×300cell map (cell side-length = 25m), of a section of the Negev desert (Ef'e ridge, Dimona; 31º05'N, 35º03'E). The elevations in this landscape range between ca. 300-650m. Preliminary simulations on this landscape revealed that individuals often take more than one route and end up on different summits. Hence, for this case, corridor width could not provide a descriptive index. Instead, I characterized the dispersion of individuals throughout the landscape at the end of the simulations, as follows: I allowed 500 individuals to move for 1000 steps, in order to provide sufficient time for them to end up on or near summits. When the final location of two or more individuals was less than 4 cells from each other, I considered them as a single clump, which I termed 'End Location'. I then compared the number of distinct End Locations between various simulations, with q ranging from 0.1-1 and 5 repeats for each value of q. The term End Location refers to the fact that, as a function of q, individuals did not always reach a summit within the 1000 time steps.

3.3 RESULTS

By simulating butterfly movement on the simple, one-summit-one-patch landscape, a Virtual Corridor was formed between the source patch and the summit, which became narrower as q increased (Fig. 7). A systematic analysis of the change in corridor width with q revealed a strong decline in corridor width, especially in low values of q (Fig. 8). This exponential-like decline leveled off when the response to topography

was high, until a sharp fall occurred when q increased from 0.9 to 1. The latter indicated the formation of a deterministic path, one cell in width.

In the one-summit-one-patch landscape, the spatial orientation of the Virtual Corridor was self-evident, while its structure (here, corridor width) depended on the movement parameter. When the topographic attributes became complex, the structure of Virtual Corridors was no longer self-evident. Simulating butterfly movements over the realistic landscape may result in several virtual-corridors, their number depending on q (Fig. 9). While individuals distribute over several summits, several other summits, that seemingly could be reached, were not reached at all. This can be viewed as 'competition' between summits, in which one or several summits intercept the movements of individuals (see Chapter 4).

The number of distinct End Locations declined strongly with increasing q, leveling off at moderate to strong values (Fig. 10). The very high number of End Locations at low q values indicated that many individuals did not reach a summit within the given time horizon of 1000 time-steps. In moderate to strong values of q, most of the End Locations were summits, but still the number of End Locations was high (for instance, even at $q=0.8$ a few dozens of summits were reached). This indicated that in the given example, even a strong response to topography resulted in several movement routes, hence several Virtual Corridors. Only when $q=1$ did all animals arrive at one End Location (a summit). Interestingly, the pattern of diminishing numbers of End Locations with q increasing was similar to the decline in corridor-width with increasing q in the one-summit-one-patch case. This suggests that increasing directedness results in the canalization of more and more individuals into one narrow route. To summarize, in complex landscapes it is not only corridor width but also the number of Virtual Corridors and their structure that depend on the level of directedness.

3.4 DISCUSSION

3.4.1 THE ATTRIBUTES OF VIRTUAL CORRIDORS
In this chapter I have introduced 'the Hilltopping Model', an Individual-Based simulation Model (IBM) of hilltopping. With the aid of this model I have demonstrated that the response to topographical heterogeneity canalizes animal movements and creates Virtual

Corridors. Even from the over-simplified case of a one-summit landscape, two rules-of-thumb can be derived: first, a Virtual Corridor forms in a line connecting the source-population and the summit; second, corridor width is determined by the intensity of response to topography (q). This example also demonstrates that Virtual Corridors may not differ from their surroundings, and in contrast to the common perception of corridors, they are not formed along a visible directional landscape element. From the more complex case of the realistic, topographically complex landscape, I conclude that the number of movement routes, and thus the number of Virtual Corridor and their structure, may be complex.

Due to the possible complexity of Virtual Corridors, and their dependence on a specific landscape and the movement parameters, IBMs should be used for predicting the movement paths of individuals, in order to recognize both corridors and barriers to dispersal. Given the complexity and over-specificity of most IBMs (Grimm 1999), the results of my research suggest that even a generic and limited IBM, with a small number of parameters, could be useful to provide landscape-specific predictions of the patterns of landscape usage by animals. Such predictions necessitate only the parameterization of animal behavior, and the landscape variables affecting these parameters (in this case, topography).

Since topographical heterogeneity is characterized by gradual changes, I hypothesize that Virtual Corridors can exist whenever animals respond to gradients of change in the landscape. Consequently, canalized movements, and correspondingly, Virtual Corridors, may be present in a variety of landscapes and as a result of various sources of landscape heterogeneity. This hypothesis, which has broad implications for conservation and landscape management, is further examined in Chapter 4.

3.4.2 A MECHANISM-BASED DEFINITION OF CORRIDORS

I suggest expanding the definition of corridors, to reflect the interaction between an animal's behavior and the landscape. A broader definition of corridors could be based on a common underlying mechanism. Several authors have suggested that effective corridors are characterized by the strong response of an animal to corridor boundaries. If animals 'bounce' back into the corridor, they remain within the corridor and are not lost to the matrix (Wiens et al. 1993; Tischendorf & Wissel 1997; Haddad 1999; Schultz & Crone 2001). The mechanism that directs animals into Virtual Corridors is essentially the same:

in the case of topography, the avoidance of negative slopes 'reflects' the animals back toward one route. Therefore, I suggest defining corridors as any specific path which has a high potential for being utilized by dispersing animals while moving between habitat patches. Animals can be canalized into the path either by their response to its edges, or by their specific response to the attributes of the landscape.

Figure 7: The trajectories of 100 individuals moving 1000 time-steps from a single source patch (empty circles) towards the mountain summit, with different probabilities to move upward (q)= 0.2 (a); 0.5 (b); and 0.8 (c), demonstrates that increasing the response to topography results in reducing the width of the Virtual Corridor. Landscape Size = 200×200 cells.

Figure 8: Corridor width (± SE) declines with increased response to topography (q) in an exponential-like pattern. Corridor width is evaluated as the number of visited cells divided by the distance from the 'source patch' to the summit. Each value is the average of 20 simulations, each with 500 individuals moving 1000 steps. Results are shown for a single location of the source-patch, but represent a consistent qualitative pattern.

Figure 9: The movement trajectories of 100 butterflies moving for 1000 movement steps, on a realistic landscapes 7.5×7.5km in size (cell side-length=25m). (a) Probability to move upward q=0.2; (b) q=0.5; (c) q=0.8. In the given location of the release point, complex Virtual Corridors are formed. Animals distribute between several summits, while not arriving at several others. The number of End Locations depends on the response to topography and the time horizon.

Figure 10: The number of distinct End Locations declines with increasing response to topography (q) in an exponential-like pattern, demonstrating that the number of summits that are reached depends on the movement parameter. Simulations are for 500 individuals moving 1000 steps each on the realistic, 7.5×7.5km landscape.

4. QUANTIFYING DIRECTED MOVEMENTS THROUGH ACCESSIBILITY PATTERNS

4.1 INTRODUCTION

The complexity of modeling animal movements in heterogeneous landscapes often results in the loss of model generality (Grimm 1999). Consequently, ecologists seek general schemes for connecting the variety of possible landscapes and the variety of animal behaviors. An indirect approach for generalizing movement patterns in complex landscapes is to analyze the probability that emigrants reach certain patches in the landscape as a function of the distance. I refer to these functions as "accessibility functions". Accessibility functions enable analysis of the contribution of dispersers to the dynamics of populations under fragmentation (Fahrig 1992; Hanski 1994, Adler and Nuernberger 1994; Hanski et al. 1996b; Vos et al. 2001; Frank and Wissel 2002), given the behavioral parameters and the distance from the animals' starting point.

In this chapter I present a systematic approach for investigating the effects of topography on the movement patterns of individuals, using accessibility functions as a main tool. I still focus on the first movement part, namely the ascendance of males and virgin females to the summits. I predict their success in reaching different summits in topographically heterogeneous landscapes (referred to as 'summit accessibility'), given the strength of the animals' response to topography and the clarity of the topographical signal. The approach presented consists of three elements: the individual-based model for simulating individual movements through virtual, topographically heterogeneous landscapes ('the Hilltopping Model'); a formula for the accessibility of patches in topographically homogeneous landscapes developed by Heinz et al. (in press); and a graphical analysis of a special derivation of the accessibility plots. As a result of the analyses, which I performed in collaboration with S. Heinz and K. Frank (UFZ, Leipzig), I show that two main types of movement patterns can arise in the face of topographical heterogeneity: 'effectively homogeneous' or 'canalized'. The intensity of the response of individuals to topography, and the level of landscape variability, determine which of the movement types emerges. I show that a shift from topographically homogeneous to

heterogeneous landscapes results not in a loss, but rather in a change of the accessibility pattern. Furthermore, I present qualitative and quantitative tools for predicting the accessibility of summits in the topographically heterogeneous case. Lastly, I demonstrate that the formula for the accessibilities (Heinz et al. in press), which was originally developed for predicting patch accessibility in homogeneous matrices, is also applicable to some extent in the topographically heterogeneous case.

4.2 METHODS

4.2.1 THE MODELING FRAMEWORK

4.2.1.1 The Landscape

I used the landscape generator of 'the Hilltopping model' to create virtual landscapes of 200×200 cells in size, which included either one or six summits. All the summits were randomly placed, and their elevation was arbitrarily determined as 10,000 units. The elevation of each cell was calculated based on its distance to the closest summit, using a Gaussian function to create 'bell-shaped' hills with additional landscape variability ('noise')(see Chapter 3). After the landscape was created, a single point was randomly selected as a starting point for the movements of all individuals (a 'source patch'). To reduce edge effects, I restricted the location of summits and the source patch to the middle 100×100 cells (See Fig. 11). Consequently, when animals responded to the landscape they tended to move upward (towards the middle area of the landscape), and their likelihood of getting lost on the edges became marginal.

4.2.1.2 Animal behavior

Butterfly movement behavior was modeled as described in Chapter 3, so that the response to topography was simulated by a probability to move toward the maximal slope (q). Individuals were assumed to recognize a summit (the peak) from each of its eight neighboring cells. Upon spotting one, they moved towards it and stayed there until the end of the simulation. In this respect, summits functioned as 'sinks', 'trapping' the individuals. The assumption that animals stay on the summits is biologically sound because males of hilltopping butterflies are known to adhere to summits for long periods

of time (Shields 1967; Wickman 1988; see also Chapter 2). In addition, preliminary simulations indicated that relieving the assumption that summits function as sinks does not have a marked effect on simulation results.

4.2.1.3 Simulation Runs

In each simulation, 500 butterflies were released from a randomly located 'source patch'. Butterflies moved through the landscape according to the movement rules until they died or reached a summit. Each butterfly had a life expectancy of ca. 1,000 steps, its probability of dying in each step being 0.001. This method of incorporating mortality (in contrast to chapter 3, where butterflies had a fixed life span), was used in order to employ similar parameters to Heinz et al. (in press) as used in their analyses. Preliminary simulations indicated that this difference in incorporating mortality was marginal to the results presented in this chapter.

For every parameter value, I repeated the simulations 200 times. Each simulation ran on a different landscape configuration and with the source patch in a different position. I recorded both the accessibility of each summit (the proportion of individuals arriving at it) and the distance between each summit and the 'source patch'.

4.2.2 A FORMULA FOR PATCH ACCESSIBILITY

The central aim of this investigation was to obtain generalizations on how topography affects movement patterns and accessibility patterns. One way of investigating the effect of a particular factor is to compare the results when the factor is either included or excluded. In this case, excluding topography meant assuming matrix homogeneity. For the latter, there are powerful methods for analyzing movement patterns and patch accessibility. One of them is to analyze 'accessibility functions'.

To analyze accessibility functions, I adopted the approach of Heinz et al. (in press), who used an individual-based simulation model and derived an approximation formula for patch accessibility in homogeneous, patchy landscapes for cases whereby dispersers stay at the first patch they reach. They showed that the probability r_{ij} of a certain patch j of being reached by a disperser starting from a certain patch i can be approximated as follows:

$$r_{ij} \approx R_{ij} \cdot W_{ij} \tag{2}$$

where

$$R_{ij} = R(d_{ij}) = 1 - e^{-a \cdot e^{-b \cdot d_{ij}}} \tag{3}$$

and

$$W_{ij} = \frac{R_{ij}{}^{N-1}}{\sum\limits_{k(\neq i)} R_{ik}{}^{N-1}} \tag{4}$$

where d_{ij} is the distance between patches i and j, and a and b are two fitting parameters.

The function $R(d)$ indicates the potential accessibility of a patch in a landscape with two patches (start and target patch) in relation to the distance d between them. The two parameters a and b determine the shape of function $R(d)$ and summarize the effects of all the different aspects of a given movement behavior which are relevant for the potential accessibility of the patches (e.g. movement mortality, step length, etc.).

The expression W_{ij} is a correction term needed for landscapes with more than two patches. In such landscapes, individuals are intercepted by the first patch reached and cannot reach any other patch. As a result, patches 'compete' for the number of individuals arriving at each patch (Hanski et al. 2000), and the actual accessibility of patches is scattered below the potential accessibility R_{ij}. This competition effect is described by the correction term W_{ij}, which depends on the potential accessibilities R_{ij} of the target patch j, weighted against the potential accessibilities R_{ik} of all possible target patches k competing for dispersers from patch i, and a power given by the number N of patches in the landscape.

The overall formula (2) merely contains the number of patches (N), the distances between them (d_{ik}), and two parameters (a and b) summarizing the effects of the movement behavior. Despite its simplicity, it was found to have a high predictive power for a variety of movement patterns in patchy landscapes with a homogeneous matrix: random walk, correlated random walk as well as Archimedian spirals (Dusenbery 1992; Zollner and Lima 1999), and loop-like movement patterns (Hoffmann 1983; Bell 1985, Müller and Wehner 1994; Durier and Rivault 1999; in the context of dispersal: Conradt et al. 2000,2001). An indicator for this power can be obtained by plotting the accessibility values resulting from simulations with the model, r_{sim}, against the values calculated with

the aid of formula (2), r_{calc}. The closer the scattering of points in the r_{sim} vs. r_{calc} plot is to the 'identity line' ($x = y$), the better the formula is at predicting patch accessibility.

Heinz et al. (in press) used the following approach to determine the parameters a and b. They fitted the potential accessibility function (3) against a plot of *rij-dij* values which result from simulating 1000 individual movements in 100 randomly determined landscapes of two patches, where the same movement pattern is assumed throughout the analysis.

4.2.3 THE ANALYSIS APPROACH

Since the approach developed by Heinz et al. (in press) was very successful in addressing the effect of movement behavior and patch configuration on patch accessibility in homogeneous matrices, I adopted this approach to analyze the additional effect of topography. I hypothesized that topographical heterogeneity alters the movement patterns of individuals and posed the following two questions: (a) How can the resulting movement patterns be characterized?, and (b) To what extent can formula (2), originally developed for homogeneous matrices, be used to predict summit accessibility in the topographically heterogeneous case?

I started by simulating individual movement in topographically heterogeneous landscapes with one source patch and one summit (equivalent to the two-patch landscapes in the homogeneous case). I used the resulting *r-d* plot to fit the potential accessibility function (3) and determined the parameters a and b (as above). In a second step, I repeated the simulations in landscapes with one source patch and six summits, and evaluated the ability of the formula to tackle the multi-summit case. When plotting the simulated values of the summit accessibility (r_{sim}) against the values resulting from calculation with the accessibility formula (2) (r_{calc}), the resulting r_{sim} vs. r_{calc} plot enabled a classification of the movement pattern caused by topography: the closeness of the overall plot to the identity line ($x = y$) indicated that the movement pattern lies in the range of applicability of formula (2) for patch accessibility in homogeneous matrices. This meant that the resulting movement pattern was equivalent to a movement pattern which was possible in the homogeneous case. Therefore it could be interpreted as being 'effectively homogeneous'. Any deviation from the identity line could be taken as an indicator of an effect of topography, and required further analysis.

In this chapter I have explored two elements that may influence the effect of topography on movement patterns. In the first part I have examined the impact of the intensity of the individuals' response to topography (q) on the accessibility functions, by varying q systematically from 0 (random movement) to 0.6 (strong response to topography). This upper limit was chosen based on preliminary simulations, in which it was observed to create a highly directed movement. Furthermore, it was biologically sound, based on the field observations presented in Chapter 2 (see also Chapter 6, section 6.4.2). In the second part I have analyzed the impact of landscape variability on the accessibility function by varying the degree of landscape variability (noise) from 0 (clear topography) to 10% of summit elevation (highly obscured). In both parts I have used a hierarchical approach to analyze the results. Firstly, I visually analyzed the resulting accessibility patterns consisting of two components: the accessibility vs. distance (r_{sim} vs. d) plot and the simulated vs. calculated plot (r_{sim} vs. r_{calc}). This was done in order to obtain an initial impression of the effect of topography on movement patterns. Then I performed a systematic analysis, to quantify the alteration of the movement patterns.

4.3 RESULTS

4.3.1 INDIVIDUALS' RESPONSE TO TOPOGRAPHY

4.3.1.1 Graphical analysis of the effect on the individuals' movement patterns

The following results present the analysis of the effect of topography on movement patterns in a landscape with six summits and without noise. I compared the results for three different intensities of the individuals' response to topography q: 'no response' ($q=0$), 'medium response' ($q=0.1$), and 'strong response' ($q=0.3$). As evident from Figs. 12a, 12c, and 12e, an increase in the response to topography changed the shape of the r_{sim} vs. d plots from exponential ($q=0$) to increasingly negative-sigmoidal ($q=0.1$ and $q=0.3$) with accessibility values $r_{sim} \approx 1$ at short distances and values $r_{sim} \approx 0$ at larger distances. However, the latter pattern was strongly scattered due to the 'competition' effect between summits as explained above (corresponding to the competition between patches in a homogeneous matrix). A more structural insight was provided by the r_{sim} vs. r_{calc} plot (Figs. 12b, 12d, 12f). In the case of 'no response' ($q=0$), the plot points were closely scattered around the identity line ($R^2=0.886$, Fig. 12b). This indicated that the movement

pattern was effectively homogeneous. Increasing response to topography q, however, was accompanied by increasing deviation from the identity line, indicating the emergence of an effect of topography. The r_{sim} vs. r_{calc} plots became increasingly positive-sigmoidal (q=0.1, Fig. 12d) and then approach a 'step-function-like' pattern with two ranges of almost constant r_{sim} values ($r_{sim} \approx 0$ and $r_{sim} \approx 1$), and a certain overlap in the range of medium r_{calc} values (Fig. 12f). Additionally, few r_{sim} values were scattered between 0 and 1. This pattern indicated that the r_{sim} values lie partly above and partly below the corresponding r_{calc} values. The open circles in Figs. 12d and 12f indicate that the high accessibility values $r_{sim} \approx 1$ corresponded to the closest summit to the source-patch out of six summits in most of the simulations.

All these arguments point to the conclusion that the main effect of topography on the individual movement patterns is canalization toward the nearest summit. This canalization intensifies the competition between the summits for migrants relative to the competition in a homogeneous matrix. The strength of the canalization effect strongly depends on the intensity of individuals' response to topography.

4.3.1.2 Quantitative analysis of the effect of topography

So far, I have identified the emergence of two types of movement patterns ('effectively homogeneous', 'canalized') in the face of topographical heterogeneity merely by visually analyzing the r_{sim} vs. r_{calc} plots. In order to quantify closeness to these two movement patterns, I derived three indices which were characteristic of the shapes of the r_{sim} vs. r_{calc} plots.

The first index measured the closeness of the r_{sim} vs. r_{calc} plot to the identity line ($x = y$). A suitable quantifier in this context was the R^2 value of a linear regression analysis. 'Effectively homogeneous' movement could be indicated by high R^2 values, while small values indicated the *emergence* of extra effects of topography. The second and third indices were based on the visual notion that a 'canalized' movement pattern is indicated by the emergence of a typical step-function pattern in the r_{sim} vs. r_{calc} plot. I described and quantified this pattern by two characteristics: the existence of a certain overlap of the two regions of extreme r_{sim} values 0 and 1, and the sharpness of the step-function pattern. To quantify the emergence and extent of the overlap, I defined an index of overlap Δr_{calc} which measured the difference between the highest r_{calc} with r_{sim}<0.1

and the lowest r_{calc} value with $r_{sim}>0.9$. To ensure that outliers in the graphs do not affect the index of overlap, I excluded both the lowest 5% of the points in the upper region ($r_{sim}>0.9$) and the highest 5% in the lower region ($r_{sim}<0.1$). Δr_{calc} could take values between 1 and -1, where positive values indicated the existence of an overlap and quantified its extent, while negative values indicated no overlap and, hence, no canalization. The sharpness of the step-function pattern in the r_{sim} vs. r_{calc} plot was given by the percentage of simulations that result in plot points which exclusively belong to the two regions of extreme r_{sim} values. To quantify this percentage, I counted the total number of points with $r_{sim}>0.9$ and divided it by the total number of simulations; the resulting proportion I_{SH} was termed 'the index of sharpness'. The logic behind this calculation was as follows: a value of $r_{sim}>0.9$ for a certain summit in a certain simulation indicated that 90% of the individuals or more arrived at this summit. Therefore, only 10% of the individuals or less could arrive at the other summits, so that necessarily $r_{sim}<0.1$ for all other summits. Hence, such a simulation would contribute to a 'sharp' pattern.

In the following, the three indices R^2, Δr_{calc}, and I_{SH} are analyzed with respect to the intensity of the individuals' response to topography q (note that, for $q=0$, Δr_{calc} could not be calculated because r_{sim} was always <0.9). Evidently, there was a critical value $q \approx$ 0.1 below which $R^2>0.9$ (Fig. 13a), the index of overlap Δr_{calc} was negative (Fig. 13b), and the sharpness index I_{SH} was very low (Fig. 13c). All these findings indicated that the corresponding movement pattern was 'effectively homogeneous'. Above this threshold value, however, R^2 rapidly decreased, Δr_{calc} reached an almost constant positive value ($\approx$ 0.3), and I_{SH} gradually increased towards 1. This showed that there was a threshold-like emergence of canalized movement (q>0.1), whereas the strength of the canalization effect increased gradually. Interestingly, once the overlap pattern was formed, its extent was independent of the individuals' response to topography in this range (Δr_{calc} was constant). Finding an ecological explanation for this effect, however, is beyond the scope of this study.

4.3.2 EFFECT OF LANDSCAPE VARIABILITY

In the second part of my investigation, I addressed the impact of landscape variability (noise) on the movement patterns and the summit accessibility. For the purpose of this analysis, I fixed the individuals' response to topography to $q=0.6$ (recall that, with no noise, this response created a highly canalized movement pattern). I varied the noise from

0 to 10% of summit elevation, fixing an upper limit of 10% which is far higher than in most realistic landscapes. I then analyzed the simulations with the same procedure as above, starting with a visual analysis and ending with a systematic analysis of the r_{sim} vs. r_{calc} plots. The results are given in Figs. 14 and 15.

The shapes of the r_{sim} vs. r_{calc} plots revealed that incorporating landscape variability shifted the pattern from 'step-function-like' (Fig. 14a), via 'sigmoidal' (Fig. 14b), back towards 'close to identity line' (Fig. 14c) with the increase in landscape variability. This indicated a shift from 'canalized' to 'effectively homogeneous' movement. A systematic analysis of the three measures R^2, Δr_{calc}, and I_{SH} in relation to landscape variability demonstrated that, as long as landscape variability was low, R^2 was very low (Fig. 15a), the overlap index Δr_{calc} was >0 (Fig. 15b), and the index of sharpness I_{SH} was ≈ 1 (Fig. 15c) – indicating a distinctly canalized movement. Increasing landscape variability led to a gradual increase in R^2 and a gradual decrease in Δr_{calc} and I_{SH}. Above a critical variability of 8%, Δr_{calc} fell below zero and R^2 exceeded 0.9. This revealed a loss of overlap and canalization, and the emergence of 'effectively homogeneous' movement despite the strong response of individuals to topography.

To summarize, increasing landscape variability counteracted the canalizing effect of an increasing response to topography in a topographically heterogeneous landscape. The originally *'canalized'* movement pattern was shifted back to an 'effectively homogeneous' one, due to the loss of the topographic signal. However, the effect of topography could only be masked by very high values of landscape variability.

4.4 DISCUSSION

4.4.1 EFFECT OF TOPOGRAPHY ON MOVEMENT PATTERNS

A central aim of the analysis presented in this chapter was to obtain a comprehensive understanding of how topography affects movement patterns and the resulting summit accessibility in the case of hilltopping behavior. One major finding is that topographical heterogeneity induces two main movement patterns: 'effectively homogeneous' and 'canalized' movement, with only a small transitional area between the two. Which of the two movement patterns emerges depended on the topographic structure, the strength of the individuals' response to topography, and the degree of landscape variability (which

determined the reliability of the landscape signal). The clear shift between the two distinct movement patterns can be condensed into two rules of thumb:

1. As long as the response to topography is low or landscape variability is high, topographical heterogeneity results in a movement pattern that is effectively homogeneous.

2. If the response to topography is medium or high and landscape variability is low or medium, then topographical heterogeneity results in a canalization of movement to the nearest summit. In consequence, the competition between the summits for dispersers is amplified compared to the competition between patches in homogeneous matrices.

Another important finding of this chapter is that the 'canalized' movement patterns emerge even in cases where the behavioral parameters seem to be only weakly directional. Therefore movement canalization, and hence Virtual Corridors, can be expected for a wide range of behavioral and spatial parameters. Additionally, as demonstrated also in Chapter 3, the topographical gradients induced a canalization effect even though the topographical structure itself was not directional.

4.4.2 THE METHODOLOGY OF ANALYZING MOVEMENT PATTERNS AND PREDICTING ACCESSIBILITY

I have presented a powerful approach for analyzing the effect of topographical heterogeneity and landscape variability on movement patterns, and investigating the role of the individuals' behavior in this context. This approach consisted of three components: the individual-based simulation model presented, the formula for patch accessibility in patchy landscapes with homogeneous matrix by Heinz et al. (in press), and an analysis of the simulation-based (r_{sim}) vs. formula-based (r_{calc}) accessibility plots. As demonstrated, the r_{sim} vs. r_{calc} plots always show a certain characteristic pattern. A shift from topographically homogeneous to heterogeneous landscapes merely led to a change in the shape of this pattern, coding important information about the movement patterns resulting in the face of topography. I offered two ways of investigating the shape of the r_{sim} vs. r_{calc} plots. The first was a visual test for 'closeness to identity line' (indicator of effectively homogeneous movement) or 'closeness to step-function with overlap' (indicator of

canalized movement). The second was a systematic, quantitative analysis of three indices that quantified the closeness to these two patterns. These indices were the regression value R^2, the extent of overlap Δr_{calc} and the sharpness index I_{SH}, the two latter indices representing the existence of a canalization effect and quantifying its strength.

An additional aim of this chapter was to develop tools for quantitatively predicting the accessibility of summits in topographically heterogeneous landscapes. The results indicated that, for each of the possible types of movement pattern, a specific tool could be provided. In the case of 'effectively homogeneous' movement patterns, closeness to an identity line was found to be characteristic of the r_{sim} vs. r_{calc} plots. This indicates that the formula used by Heinz et al. (in press) can be used to predict the accessibility of summits in this case. Thus, the applicability can be partly extended to topographically heterogeneous landscapes. In the case of 'canalized movements', the r_{sim} vs. r_{calc} plot was characterized by the polarization of the r_{sim} values to 0 and 1. High values referred to the summits that were closest to the source patch. Due to the overlap between the two regions of the graph, no function or formula will be able to cover this effect. In this case, the summit accessibility can be predicted by the rule of thumb that "all individuals arrive at the nearest summit".

4.4.3 PROSPECTS FOR FURTHER RESEARCH

The tools described above are still far from having a practical value for real applications, as this investigation provided only a first understanding of the threshold-type shift between effectively homogeneous and canalized movements. Further research is necessary to identify the conditions for this shift in a systematic analysis of the parameter space and a wide variety of landscape types. This is especially important in light of the results of Chapter 3: when hilltopping movements are simulated in realistic complex landscapes, animals may move along more than one route and consequently arrive at several summits, even if the response to topography is strong. Therefore, simple rules of thumb (such as "animals move to the nearest summit") cannot replace the use of individual-based simulation models to predict accessibility values in a landscape-specific context.

Figure 11: Examples of virtual landscapes used, with 1 summit (a) or with 6 summits (b). Adding landscape variability, e.g. 4% of summit elevation (c), reduces the reliability of the topographic cue in directing animals toward the summits. Landscape size is 200×200 cells, with all the summits and the source patches (red circles) restricted to the central 100×100 cells to reduce edge effects.
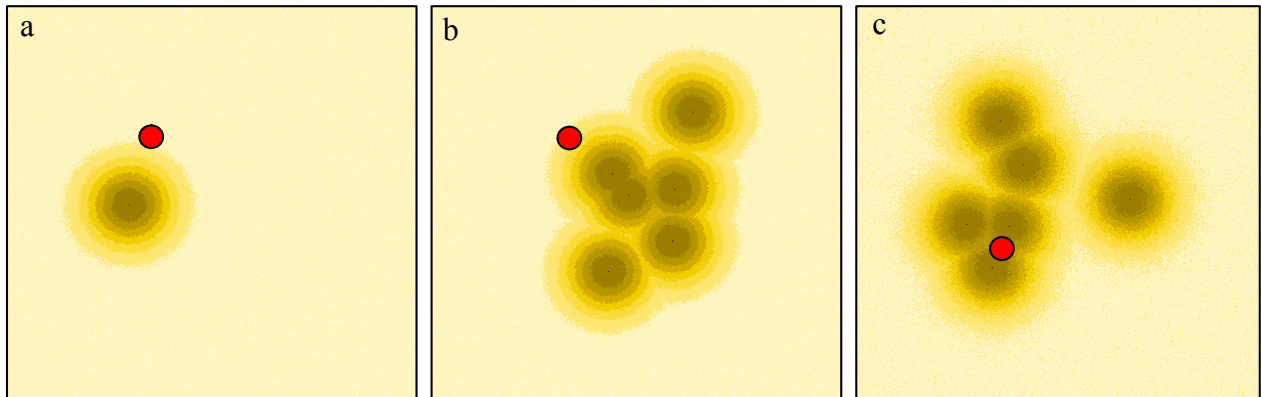
Figure 12 (next page): (a, c, e): Simulated accessibility (r_{sim}) to summits vs. distance from source patch with response to topography $q = 0$ (random movement; a), $q = 0.1$ (c), and $q = 0.3$ (e). (b, d, f): Summit accessibility simulated with the model (r_{sim}) vs. calculated with the formula (r_{calc}; see text) for the 6-summit case and each of the response values: $q = 0$ (b), $q = 0.1$ (d), and $q = 0.3$ (f). Each point in the graphs represents the proportion of individuals to arrive at a given summit (out of 6) in one simulation. Each graph contains 1200 points derived from 200 simulations. The accessibility of the summit closest to the source patch in each simulation is depicted by empty circles in b, d, and f.
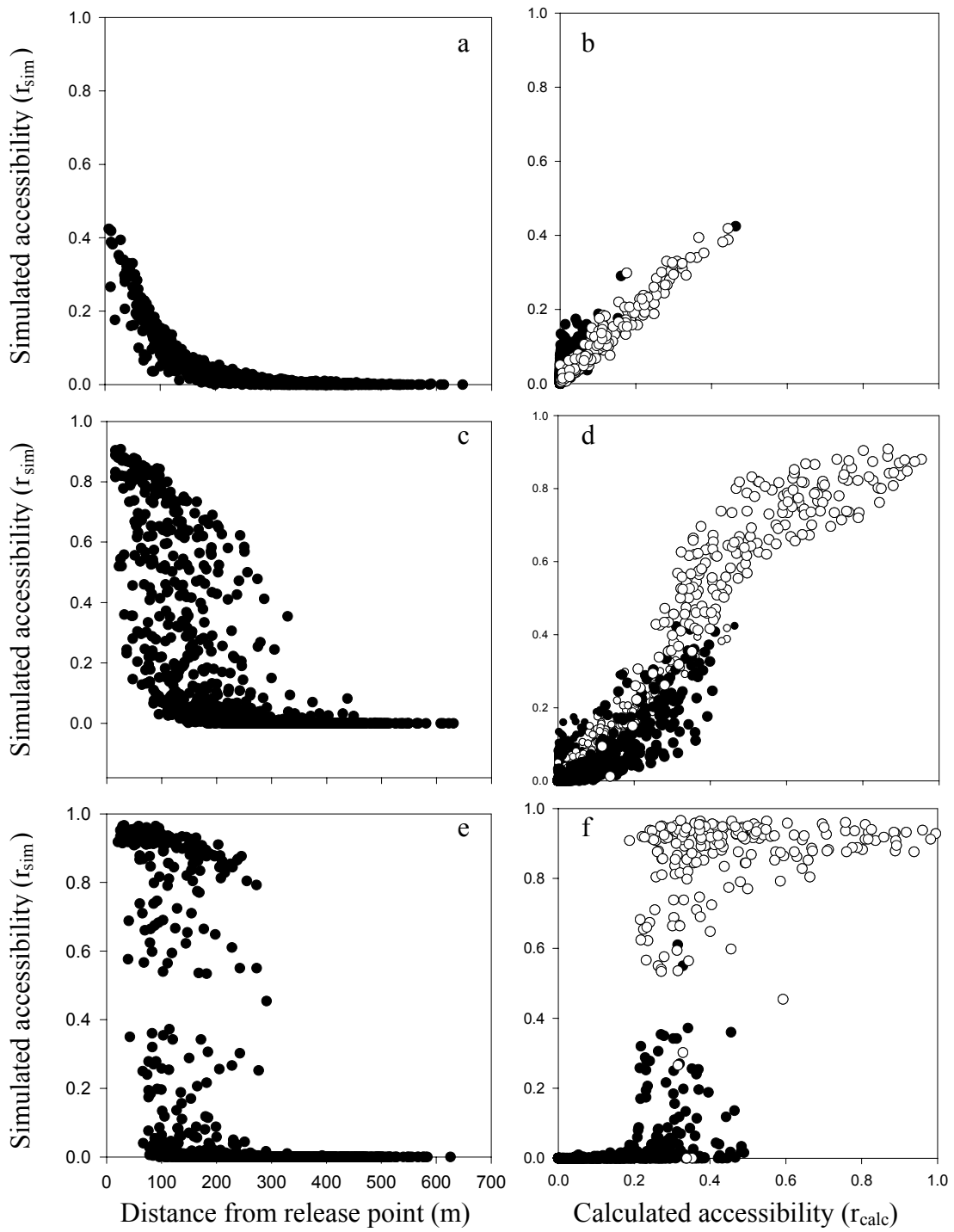
Figure 13: Three indices for quantifying closeness to 'effectively homogenous' and 'canalized' movements in the r_{sim} vs. r_{calc} plots (see text) vs. the response to topography (q): R^2 of a linear regression (a), Index of Overlap Δr_{calc} (b), and Index of Sharpness I_{SH} (c). Full circles in (b) represent all data-points; open circles represent data-points after the exclusion of outliers.
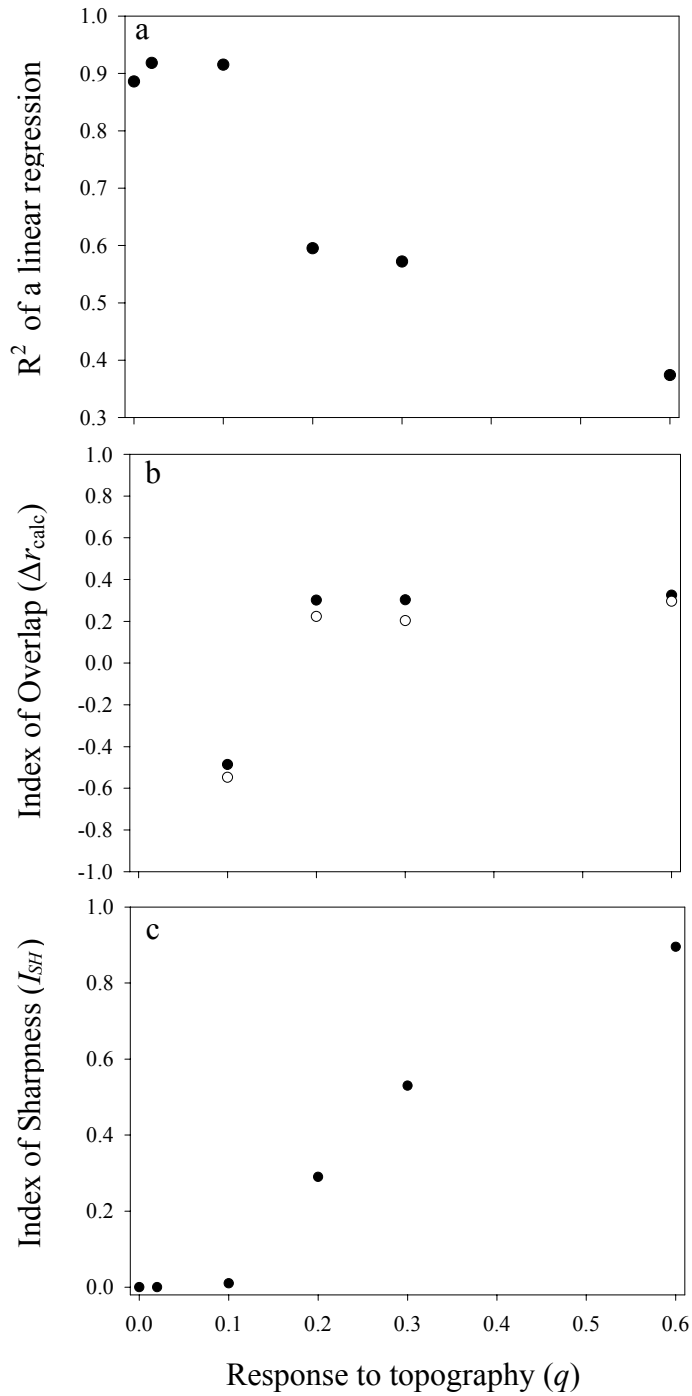
Figure 14: Simulated accessibility (r_{sim}) vs. calculated accessibility (r_{calc}) with different values of landscape variability (noise): 0% (a), 4% (b), and 10% of summit elevation (c). The accessibility to the summit closest to the source patch is depicted by empty circles. In all simulations the response to topography $q = 0.6$

.
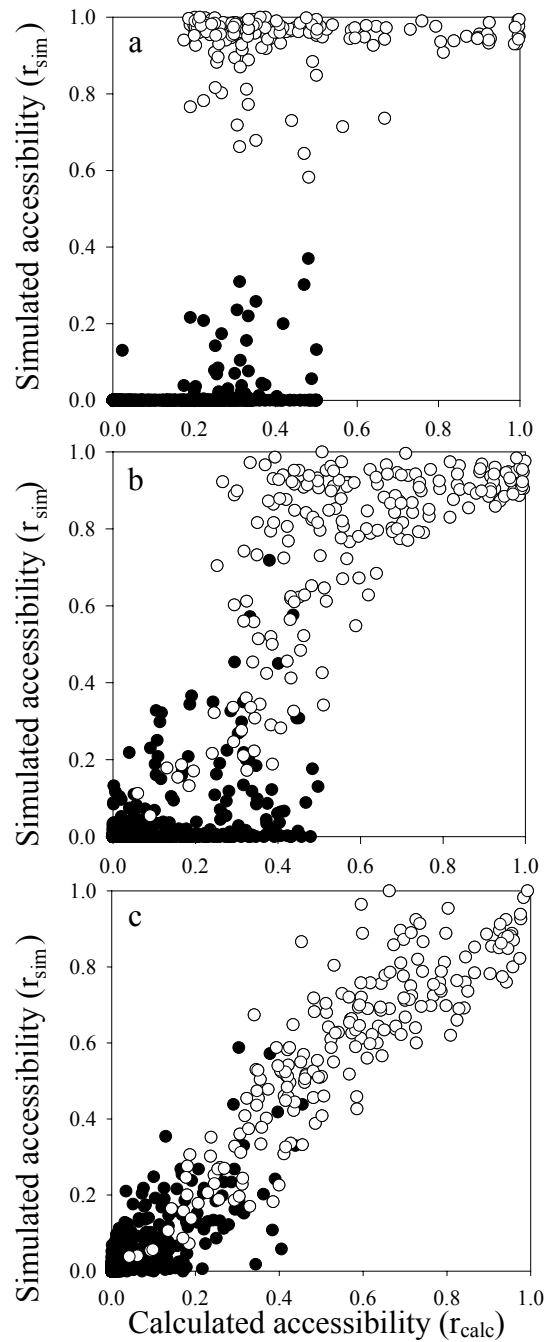
Figure 15: The same three indices as in Fig. 13 vs. the landscape variability (noise): R^2 of a linear regression (a), Index of Overlap Δr_{calc} (b), and Index of Sharpness I_{SH} (c). Open circles in b: after the exclusion of outliers.
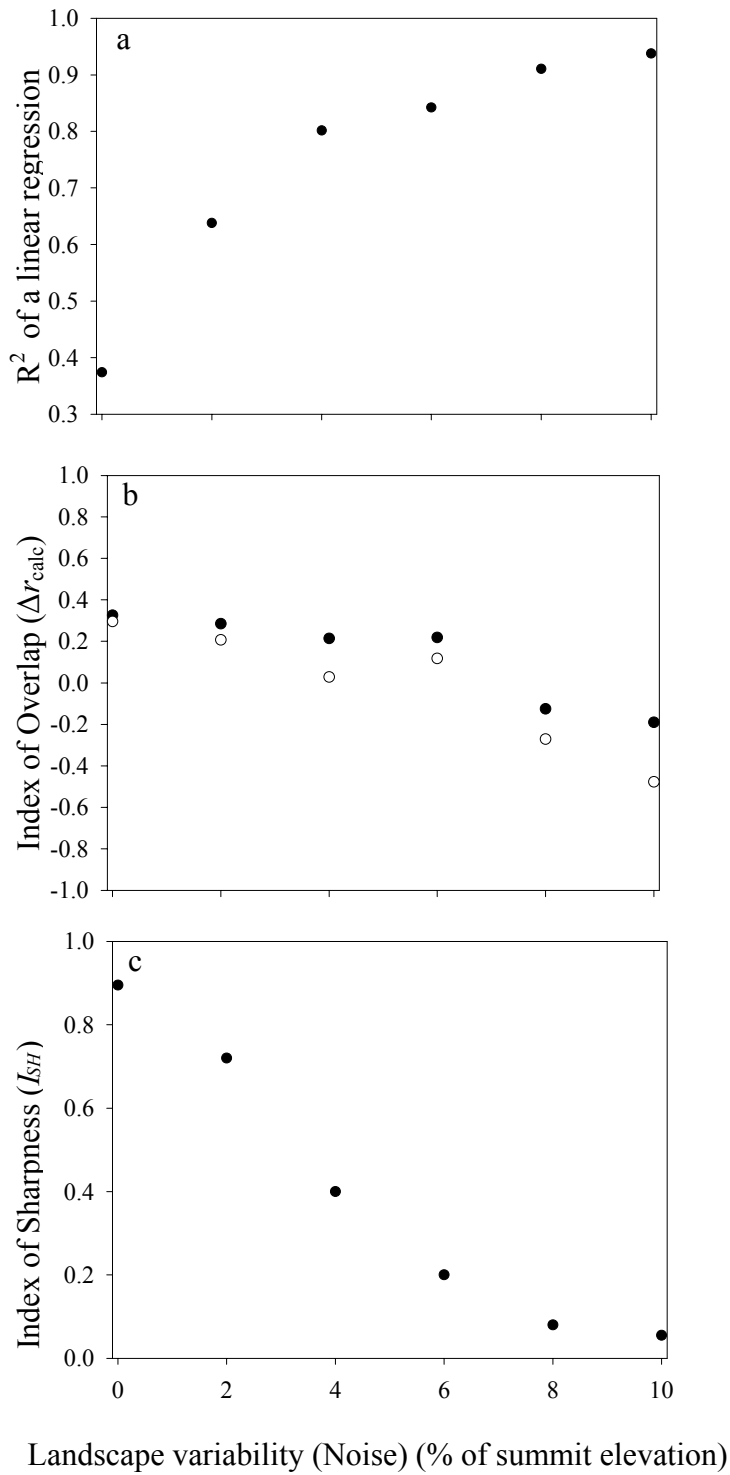
5. OPTIMIZING MOVEMENT PARAMETERS AND LESSONS ON THE IMPORTANCE OF RANDOMNESS

5.1 INTRODUCTION

The process of ascending to mountain summits, and the consequent process of patch-searching by mated females, can be perceived as a searching 'algorithm' in complex landscapes: the tendency of hilltopping butterflies to leave their habitat patches in favor of mating habitats may only be advantageous if butterflies can congregate at a small number of easily recognized meeting points, i.e. the highest possible hilltops, within a short time and at a minimal distance. Once the mated females leave the summits, efficient searching strategies are probably adopted to find host-plant patches. The first movement strategy (moving toward summits) can be achieved either by recognizing the summits from a far distance, or, if the perceptual range is small, by optimizing a search strategy for 'hill-climbing'. Field observations presented in Chapter 2 suggested that the perceptual range of butterflies with regards to topography is fairly small – around 50m, and affected by their immediate surroundings. Thus, the hilltops probably cannot be recognized by butterflies from their starting points. Assuming a short perceptual range for topography, hilltopping butterflies should have developed a simple but efficient search strategy to locate the highest peaks ("global maxima") in a variety of landscapes, and overcome landscape variability which may 'trap' individuals on local maxima. Optimizing search strategies in a complex landscape is comparable to a wide group of searching algorithms, which are used for searching optimal solutions in complex 'landscapes' of parameters or possibilities in many fields of science, business, and engineering (Devroye & Krzyzak 2002). Many of these optimization algorithms rely on a certain degree of randomness. Therefore, I hypothesize that the optimal search strategies of hilltopping butterflies should comprise a certain degree of directedness, along with certain randomness.

In the field of animal behavior, some authors recognize that non-random, 'perfect' behavior is not always the optimal one. For instance, Stephens & Krebs (1986) and Jager & Tyler (2001) have shown that random movements to low-quality patches

might be rewarded if and when these movements provide information about the landscape, thus reducing uncertainty. Keasar et al. (1996) have suggested that imperfect long-term memory could be advantageous when the habitat changes temporally. Boyd & Lorberbaum (1987) and Boyd (1989) have shown that imperfect behavior might allow a highly profitable evolutionary stable strategy (ESS) in the repeated prisoner's dilemma. However, in the context of animal movement and dispersal, rules of thumb which predict what level of directedness is required for optimizing movement strategies are lacking. Consequently, models of animal dispersal have to determine the level of directedness (or the level of randomness) either arbitrarily or based on empirical data which may be species-specific.

In this chapter I optimize the movement behavior of the two movement strategies involved in the hilltopping process – toward the summits and then away from them. I elucidate the behavioral parameters that optimize mating success and the consequent patch-location success in topographically complex landscapes. This methodology enables the quantification of the necessary level of movement directedness (or randomness) in light of the different levels of variability (and consequently unreliability) of the landscape signal. By doing this I aim to achieve two goals: Firstly, to investigate 'the Hilltopping Model' more thoroughly and address a greater number of relevant parameters. In this way I progressively increase model complexity. Secondly, I demonstrate that 'suboptimality' in animal behavior may be an optimal behavior in a wide range of cases where the directing cue is not totally reliable. On the one hand I stress the significance of directed dispersal, and, on the other hand, the importance of a certain amount of randomness. I show that the balance between directedness and randomness is affected by two main components: the response to certain landscape characteristics as directing elements, and the reliability of these elements in directing the movements toward an aim.

The optimization processes presented herein are performed independently of the data collected in the field. This is in order to obtain a better general understanding of the mechanisms that direct the movement, and the factors that determine the level of directedness of animal movements in heterogeneous landscapes. Finally, I compare the hilltopping movement algorithm used in my model to optimizing algorithms used in other fields of science, and discuss the possible advantages and disadvantages of the model in light of these differences.

5.2 METHODS

5.2.1 LANDSCAPE AND PATCH CONFIGURATION

To optimize the two step process of hilltopping, I used an oversimplified landscape configuration with one mountain and two patches at constant locations. The landscape was an 80×80 cell grid, with a cell side-length of 5m and a summit elevation of 10,000 units. One bell-shaped hill (see Chapter 3) was located south of the butterflies' starting point (the 'source patch'), half way between the starting point and one of the two patches (hereafter, P_{south}). A second patch was located to the east of the release point, at the same distance from the starting point as the first patch (hereafter, P_{east})(Fig. 16). The two patches were cells in the landscape which resembled concentrations of host plants for the butterflies' larvae. Each patch was single cell in size, yet patch size could be altered implicitly by defining the distance from which butterflies were capable of recognizing the patches. Here, I determined the recognition distance to be 15 meters.

5.2.2 MOVEMENT RULES

In this chapter the movement rules of the butterflies were expanded to incorporate two behavioral parameters. The direction taken at each movement step of each butterfly was determined by two consequent probabilities. First, a butterfly had a certain probability to continue forward in the same direction as its previous movement (p). This probability is hereby defined as 'Consistency'. If the next movement was not consistent with the previous (with a probability of $1-p$), an individual could either respond to topography by moving toward the steepest slope with a probability q, or choose a totally random direction with probability $1-q$. The probability q was determined separately for males + virgin females (hereafter q_{m+v}, tendency to move toward the maximal slope), and for mated females (hereafter q_f, tendency toward the minimal slope). The probability p was similar for all three states, in order to keep the number of parameters small (This simplifying condition is relaxed in Chapter 6). The three probabilities p, q_{m+v}, and q_f were determined *a priori* for each simulation run and applied to all butterflies of a given state.

5.2.3 MODEL ASSUMPTIONS

Some of the underlying assumptions of 'the Hilltopping Model' were presented in Chapter 3 (section 3.2.1). Some more assumptions, which are of relevance to this chapter, are hereby presented:

- When arriving at a recognition distance from a patch, butterflies move into the patch and stay there until their death. Patch dynamics, such as mating events within the patches, are irrelevant to the model.

- Virgin females, having five or more encounters with males, become mated females (several males may be encountered in one given cell, and a male can be encountered twice). This is under the assumption that females only mate once during their lifetime, and only when arriving at a concentration of males (a 'lekking' behavior; see Lederhouse 1982; Queller 1987).

5.2.4 SIMULATION RUNS AND PARAMETER EXPLORATION

In each simulation run, 500 butterflies were released, each with a maximal life span of 1000 time steps. All butterflies started at the same 'source patch' in the landscape, with a gap of 10 time steps between releases to prevent immediate mating at the release location. For each parameter combination I performed 30 repetitions, each with newly created landscapes to avoid artifacts caused by the locally added noise. I systematically examined several parameters to assess their impact on mating success and on the success of mated females in locating patches (see Table 5). In this way I performed a parameter exploration which was not species specific, and which was independent of data collected in the field.

   In the first stage, I addressed the importance of the simulated behavioral parameter q with respect to fitness. I used two measures that depend on the response to topography of males and virgin females (q_{m+v}):

   (1) *Mating success*, the percentage of females which became "mated".

   (2) *Time until mating*, namely the mean number of time-steps before virgin females became mated females (excluding females that failed to mate).

Two further measures depended both on the response to topography of males+virgins and that of the mated females (q_{m+v} and q_f, respectively):

   (3) *Arrival success of mated females*, the total number of mated females that reached any patch.

(4) *Optimal responses*, the pair of probabilities of response to topography (*$*q_{m+v}$, *$*q_f$) that maximized the number of arrivals of mated females, i.e. which produced the highest value for (3).

In these simulations, the consistency (*p*) was set to 0 (i.e., no tendency to continue in the same direction), and the landscape variability (noise) was 2% of summit elevation.

In the second stage of the analyses, I analyzed the importance of the behavioral parameter 'consistency' through changes in the four above measures along with increasing values of consistency. Similarly, I explored the spatial parameter 'noise'. In these analyses I determined the optimal responses (*$*q_{m+v}$, *$*q_f$, measure (4)) separately for each of five blocks of six simulations, and determined the optimal responses as the average between the five simulation-blocks. This was done in order to allow a continuum of changes in *$*q_{m+v}$ *$*q_f$ with the changes in *p* or in the noise.

In the last set of simulations I explored the impact of consistency on the values of the optimal responses *$*q_{m+v}$ and *$*q_f$, but this time with random release of each individual. Releasing each individual at a random point in the landscape imitated a situation where individuals were originally sparse over the landscape. The respective exploration of the 'random release'-scenario was compared to the 'one-release-point'-scenario, while exploring the three behavioral parameters: *p*, q_{m+v} and q_f . Again, I used the four measures described above: mating success, time until mating, arrival success, and optimal response to topography. These simulations were performed only for a landscape noise of 2%. Additionally in these simulations, the temporal gap between two releases was reduced to five time-steps (instead of ten), to compensate for the reduction in mating success when individuals are sparsely distributed over the landscape.

5.3 RESULTS

5.3.1 RESPONSE TO TOPOGRAPHY

In order to explore the two measures of response to topography (q_{m+v}, q_f), I first analyzed simulation results under the reference scenario (i.e. *p*=0; noise=2%; fixed release point). For a random movement of males and virgin females (q_{m+v}=0), mating success was low. Mating success increased rapidly with increasing q_{m+v} (Fig. 17a), reaching 100% success when q_{m+v} exceeded 0.3. The time until mating did not change

for q_{m+v} below 0.1. It then shortened with increasing q_{m+v}, in a "diminishing return" pattern (Fig. 17b), so that beyond $\approx$ 50% response to topography, additional reduction in the time until mating was marginal. Therefore, moderate response to topography in males and virgin females was sufficient to maximize mating success and the time until mating.

After successful mating the individuals have to succeed in finding a patch. Thus I plotted the arrival success of mated females against the different values of both q_{m+v} and q_f (Fig. 17c; note that the number of arrivals is represented by color). For any value of q_f the number of arrivals was a unimodal function with respect to q_{m+v}. The peaks, namely the maximal number of successful arrivals, were at $q_{m+v} \approx 0.6$. Maximizing the arrivals with respect to q_f revealed that the optimal response of mated females to topography was weak but consistently above zero. Thus for the reference scenario ($p=0$; noise=2%; fixed release), the optimal response was determined as ($*q_{m+v}=0.6$, $*q_f=0.1$). To explain the optimal mated female behavior $*q_f=0.1$, I plotted the percentage of mated females reaching P_{south} out of the total number of arrivals (to both patches)(Fig. 17d). Clearly, the preference toward P_{east} or P_{south} was determined primarily by q_f. When $q_f<0.1$, a random dispersal favors the arrival of mated females only to P_{south} (all females die before arriving at P_{east}). When $q_f>0.1$, P_{east} was favored (Bias to $P_{south} \approx 0.1$-0.3), but most females did not detect any of the patches (see Fid. 17c for parallel values of q_{m+v} & q_f).

To summarize, medium response to topography in males and virgin females, combined with the weak response to topography of mated females, maximized the number of successful arrivals in patches in the specific landscape and patch configuration.

5.3.2 FIRST INTERPRETATION OF THE RESULTS

The impact of q_{m+v} on the arrival of mated females at the patches is twofold. When $q_{m+v}<0.4$, mating success and mating time determined the number of mated females in the system. Above this value, the limiting factor is the location of the mating event. A strong response increases the chance that the mating event will take place on a local maximum. Given that mated females move downwards, mating on a local peak turns the hill into a barrier for mated female dispersal, and reduces the chances of reaching certain patches (see Fig. 18a). Consequently, a moderate $*q_{m+v}$ allows most mating

events to take place on the hilltop, and the mated females start seeking the patches when halfway to P_{south}. This favors the arrival of mated females to P_{south} when the movement is random (Fig. 18b). However, P_{south} is located on the slope of the hill, while P_{east} is located on the plateau. As a result, a strong response of mated females increases the probability of missing P_{south}. When arriving at the plateau, the directional cue becomes obscure and a more random movement pattern takes place (Fig. 18c), favoring the detection of P_{east} despite its larger distance from the summit (Fig. 17d in corresponding values). The weak $*q_f$ allows mated females to arrive at both patches, so that the bias toward P_{south} is only marginal (63.7% of the arrivals occur at P_{south}). Correspondingly to this interpretation, when optimizing the arrivals of mated females to each of the patches separately, the optimal response to topography was $*q_f = 0$ for P_{south} and $*q_f = 0.5$ for arriving to P_{east}. That the overall optimum was at 0.1, reflects the dominancy of P_{south} in terms of accessibility.

5.3.3 MOVEMENT CONSISTENCY

In the following paragraph, I repeated the analysis described above with different values of p, and followed the changes in the above four measures of mating success and arrival success to patches.

For a given response value of males and virgin females (q_{m+v}), increasing consistency worsened the outcome, i.e. mating success was reduced (Fig. 19a) and the time until mating was prolonged (Fig. 19b). However, the qualitative dynamics of both measures with respect to q_{m+v} did not change: increasing response to topography increased mating success and reduced the time until mating; even for relatively high consistency ($p=0.4$), increasing the response to topography above 0.6 did not yield further improvement in mating success or the time until mating.

The value of q_{m+v} which maximized arrival success increased with increasing consistency (Fig. 19c). Thus, response to topography should be more precise to compensate for the misleading effect of the strong tendency to continue forward with respect to mating success (Note that increased movement consistency (p) reduces the response to the landscape and increases movement randomness, since the probability that animals respond to topography is $q \cdot (1-p)$). When consistency exceeded 0.6, the "mulish" forward movement could no longer be compensated by a stronger response to topography. Hence, butterflies failed in mating and the number of mated females that

arrived at patches decreased markedly (Fig. 19d). The maximizing value of q_f remained low as long as p did not exceed 0.6, and then increased with further amplification of p. Therefore, as long as consistency (i.e. the tendency to continue straight irrespective of any cues) remained low or moderate, maximization of the outcome of the hilltopping movement was achieved by medium response to topography of males and virgin females, and weak response to topography of mated females.

Since p, q_{m+v}, and q_f, are all behavioral parameters, the optimal movement behavior can be presented as a combination of the three parameters which maximizes the number of successful arrivals (in Fig. 19d): (*$p=0.5$, *$q_{m+v}=0.8$, *$q_{f,}=0.1$). Remember that the actual response to topography is $*q \cdot (1-*p)$. Importantly, the optimal behavior comprises a high level of consistency. This demonstrates that the seemingly "misleading effect" of consistent movements (as seen in Figs. 19a,b) has an over all positive effect on the arrival probability to the summit and the patches.

5.3.4 EFFECT OF LANDSCAPE VARIABILITY (NOISE)

In the absence of noise, the topographical gradients directed the animals toward the summit (or away from it) from every point in the landscape (remember that the virtual topography is created by a Poisson distribution). Accordingly, the mating success could reach 100% even when the response to topography was low. When noise was incorporated, the topographical cue was weakened, mating success was reduced, and the time until mating increased (Figs. 20a,b). Consequently, the optimal response value *q_{m+v} decreased with the increase in noise (Fig. 20c), compensating for the 'misleading' effect of landscape randomness (noise) and assuring the arrival at the global maximum. On the other hand, the optimal response value *q_f increased sharply when the landscape noise increased from 2% to 4%, but thereafter remained rather constant (Fig. 20c). That is explained by a need to retain a minimum use of the topographical cue. The overall impact of increasing the noise was a reduction in the number of successful arrivals of mated females at the patches at the optimal response values *q_{m+v} and *q_f (Fig. 20d). This reflected a diminishing success in patch finding with the reduced reliability of the topographical signal as a directing element.

5.3.5 RANDOM RELEASE

When each individual started at a random point, mating success never reached 100%, and a perfect response to topography ($q_{m+v}=1$) was clearly suboptimal, as it led to the trapping of individuals on local maxima and diminished mating success (Fig. 21a). The overall patterns remained similar to the one-release-point case: increasing male and virgin female response to topography increased mating success and reduced mating time, both in a diminishing-return pattern (Figs. 21a,b). When analyzing the change in *q_{m+v} and *q_f vs. consistency (p) in the random-release case, a relatively high q_{m+v} value (with a certain level of randomness) and low q_f value were necessary for optimizing the success of mated females in locating the patches. The optimal behavior with respect to all three parameters was *p ≈ 0.1-0.4 (there was no clear optimum; Fig. 21c), *q_{m+v} ≈ 0.85-0.95, *q_f ≈ 0.1-0.2. Thus, the qualitative results were similar to those of the one-release-point case – a partially random behavior of males and virgin females *(q·(1-p) ≈ 0.57-0.77)*, and a strongly random behavior of the mated females *(q·(1-p) ≈ 0.09-0.12)*, were optimal. However, these simulations revealed an intriguing spatial phenomenon. The relatively high *q_{m+v} led those individuals that started close to the summit to mate on its top, but those who were too far tended to stay on the plateau and mate on local maxima. Therefore, the optimal behavior led to a dichotomy in the type of mating location.

5.4 DISCUSSION

In this chapter I utilized 'the Hilltopping Model' to examine optimal movement behaviors in a simple topographically-heterogeneous landscape, and to deduce the consequences of various movement and landscape parameters on mating success and on patch detection success. Model results showed that as long as noise exists in the landscape, the optimizations of both mating success and the patch recognition process require an imperfect response to topography. The necessary randomness increased when the landscape randomness was amplified, demonstrating that a moderate response to topography allows hilltopping individuals to overcome landscape variability and reach the true summit (global maximum). For males and virgin females, randomness allowed individuals to utilize a partly reliable cue (topography) for directing their movement

toward a meeting point (hilltop). Mated females exhibited only a weak response to topography, in response to the need to locate two patches that differed in their configuration with respect to the mountain. It directed the females away from the summit, generally downwards, while creating a wide searching path.

The contrasting movement strategies of the mated females vs. the males and virgin females, demonstrate that the optimal combination between directed movements and random ones might vary strongly based on the need for a directing cue and the reliability of that cue. However in both cases, a 'pure strategy' (either completely directed or completely random) was suboptimal to a mixed one in most cases (see also Boyd & Lorberbaum 1987). These results may be affected by the assumption that all butterflies behave similarly. Namely, a mixed strategy in a population can either be achieved by all individuals behaving "imperfectly" (a monomorphism of mixed strategies), or by the prevalence of two different strategies within a given population (polymorphism of pure strategies). Investigating the consequences of a mixed-strategy within the population could provide new insights on the evolution of animal movements, yet this is beyond the scope of this study.

The optimal movement-strategy of males and virgin females could lead them either to the real summit alone (in the case of one starting point) or to both the local summits and the global summit (in the case of multiple starting-points). Consequently, local maxima may serve as meeting points when the global maximum is too far. This intriguing result suggests that the same behavioral rule can direct animals towards meeting at two distinct types of points. This reflects high performance of one strategy under different scales of landscape heterogeneity.

For the mated females, the optimal behavior revealed by these simulations was determined by the need to arrive at two distinct areas of the landscape. Consequently, the optimal response consistently differed from a random one. These results, though landscape specific, may suggest that in some cases a slight response may be the optimal movement strategy.

5.4.1 A COMMENT ON THE METHODOLOGY OF INCORPORATING NOISE

When exploring the impact of landscape variability (noise), I introduced the noise by a random number which was incorporated into each cell independently. Consequently, the noise could not direct animals away from the summit, but mainly obstructed their way

toward the summit. In reality, spatial noise may be "spatially correlated", so that the altitude of a given parcel of the landscape depends on its neighbors. In these cases, noise may impede the arrival at summits more strongly, but local summits can serve as secondary mating-points more efficiently. In preliminary simulations I created a spatially-correlated noise. I used a 3×3cell square which 'moved' across the landscape, copying the noise from each cell to its eight neighbors. However, simulations performed on landscapes with spatially-correlated noise yielded qualitatively similar results to those with random-noise. Namely, the optimal behavior of the butterflies, in terms of the three behavioral parameters, showed a qualitatively similar pattern − a moderate response of males and virgin females, and a weak response of the mated females. (*p=0.6, *q_{m+v}=0.8, *q_m=0.1 − compared to 0.5,0.9,0.1, respectively, in the random noise scenario). The main difference between the random-noise and spatially-correlated case was that the latter resulted in lower mating success and consequently a lower number of total arrivals at the patches. These results indicated only that the landscape signal was poorer in the spatially-auto-correlated case, necessitating a stronger behavioral randomness to compensate for the noise. Thus, I conclude that the method of incorporating noise does not affect the qualitative results of the model.

5.4.2 THE HILLTOPPING MODEL AND 'HILL-CLIMBING' ALGORITHMS

The lack of past information for a butterfly while moving through an unknown landscape, as well as the unreliability of the landscape, makes behavioral randomness a necessary component of directed dispersal. The study of situations that are characterized by such uncertainty is frequently addressed by stochastic programming (Gottfried & Weisman 1973). A variety of optimization algorithms can be used for stochastic programming, including *Simulated annealing* (Laarhoven & Aarts 1987), *Genetic algorithms* (Goldberg 1989), *Tabu search* (Glover & Laguna 1997), *Levy flight* (Viswanathan et al. 2000), *Random Walk* and *Directed Random Walk* for Monte Carlo simulations (Rubinstein 1986), and others (see Devroye & Krzyzak 2002). All these algorithms require a certain level of stochasticity for optimizing performance in environments typified by uncertainty and a given time constraint.

I hereby present a brief description of three groups of commonly used optimizing algorithms, one of which is comparable to the hilltopping algorithm. I

discuss the advantages and disadvantages of choosing one of these algorithms or another, in light of the underlying assumptions of my modeling approach.

The movement behavior used in 'the Hilltopping Model' can be categorized within a group of algorithms that are often named 'hill-climbing' algorithms. They seek the global maximum using a local-scope search, namely the gradients in the immediate neighborhood of each current point, and then "climb" in the steepest permissible direction (Goldberg 1989). Typically, 'hill-climbing' algorithms are memoryless, and therefore they exhibit no learning processes (Glover & Laguna 1997). Their main advantage is their simplicity.

Simulated annealing algorithms rely on learning rules and on memory of the environment (Laarhoven & Aarts 1987; Whittle 1998). Commonly used in many fields of science and technology, *Simulated annealing* algorithms start with high level of randomness (high "temperature"), which reduces with time. Although these algorithms are highly effective in recognizing the global optimum, it is important to remember that my model showed that local maxima may serve as secondary mating points. Furthermore, the change in "temperature" over time requires a more complicated movement algorithm than the one used by my model.

Tabu Search algorithms also use memory and adaptive memory, based on concepts from artificial intelligence and optimization (Glover & Laguna 1997). They are often used for decision-making processes and for optimizing combinatorial solutions. *Tabu search* algorithms avoid "wrong" movements or locations that have been previously visited, achieving 'self avoidance' strategies that are often incorporated to prevent animals from oscillating between two cells (Stanley 1986; Bunde & Havlin 1991; Gustafson & Gardner 1996). Combining the hill-climbing algorithm of my model with *tabu search* methods may provide a highly efficient optimizing algorithm, on account of model simplicity.

The main difference between 'the Hilltopping Model' and both *Simulated annealing* and *Tabu Search* algorithms, is the assumption that butterfly behavior is constant over time and space. In my model, I assumed that animals have no memory and no ability to learn the topographic environment. This was done mainly to keep the model simple and general, since the addition of learning capability requires the use of several parameters, which may be species-specific. Additionally, my assumption was based on the low chances that individuals move through any landscape more than once

during their life-time, and the limited knowledge of learning processes during hilltopping movements. In fact, although learning processes may be highly optimal for the optimization of animal behavior (Ollason 1980), empirical works are lacking to point at learning processes exhibited by animals during dispersal.

Although I did not investigate memory and learning processes in my fieldwork, I did observe time-dependent behaviors to take place. For instance, field observations indicated that the initiation of hilltopping does not occur immediately after their release, while further observations have suggested that their behavior may change depending on the time spent on summits (see Chapter 2 and 7). The importance of time-dependent processes in the model is further discussed in Chapter 7.

This chapter presented a systematic methodology for analyzing the consequences of animal response to landscape heterogeneity on their resulting success in patch detection. However, these first results were derived from simulations relying on a simple virtual landscape. Thus, the results of this exploration cannot be interpreted in light of realistic behavioral parameters. For this, it is necessary to simulate butterfly movement in complex, realistic landscapes, using the methodology presented above. This is addressed in the following chapter.

Table 5: The behavioral and spatial parameters explored in this chapter.

Parameter	Range	Step Width
Response to topography – males and virgins (q_{m+v})	0.0 - 1.0	0.1
Response to topography – mated females (q_f)	0.0 - 1.0	0.1
Probability of flying consistently (p)	0.0 - 1.0	0.1
Noise (% of summit elevation)	0% - 10% [A]	1%
Source patch	One location vs. Sparse [B]	

[A] additional noise seems unreliable for most existing realistic landscape

[B] Namely, each individual starts at a random point in the landscape

Figure 16: A map of the landscape used for the simulation. Landscape size=80×80 cells. The locations of the release point (red) and the patches (blue), as well as summit location, are constant. The summit is located half way between release point and P_{south}, so that P_{east} is on a plateau and P_{south} is on the slope of the hill. The degree of landscape variability (noise) is independent in each cell.
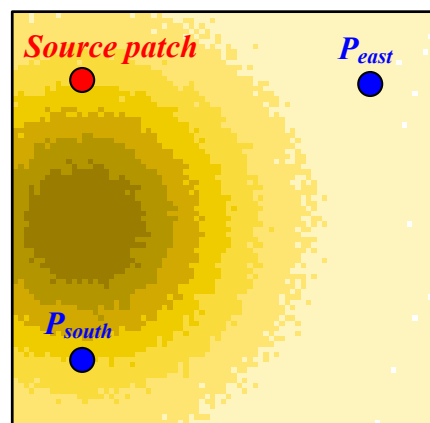
Figure 17: The effect of varying the response to topography of males and virgin females (q_{m+v}) on mating success of the females (a) and the time until mating (b). The number of arrivals of mated females at patches is depicted against both q_{m+v} (males and virgin females) and q_f (mated females), so that the number is represented by color (c). Similarly, the bias towards P_{south} is depicted against q_{m+v} and q_f and represented by color (d). Moderate q_{m+v} guaranteed highest mating success and shortest time until mating (a,b), and maximized the number of arrivals (c). Low but non-zero q_f vales induced a high arrival success, along with relatively balanced arrivals to both patches (d). Higher values of q_f resulted in a string bias toward P_{east}.
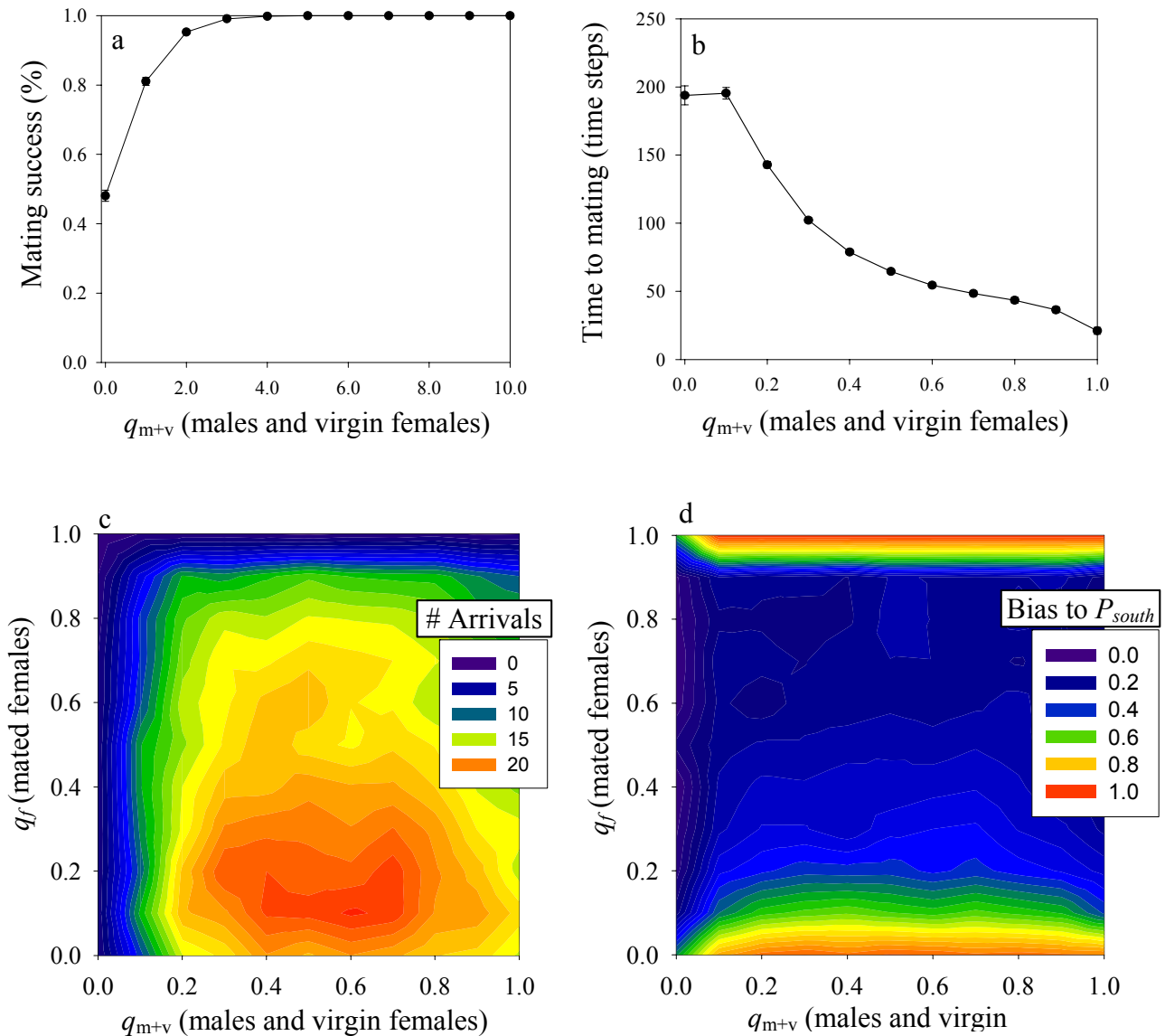
Figure 18: Representative paths of 5 butterflies, differing in parameters of response to topography. Male and virgin female movements are depicted in black, mated female movements in blue. a - $q_{m+v} = 100\%$, $q_f = 50\%$. Males and virgin females are trapped by local maxima, the hill acts as a barrier for the dispersal of mated females. b - $q_{m+v} = 50\%$, $q_f = 0\%$. P_{south} is easily detected by a random-walk pattern. c - $q_{m+v} = 50\%$, $q_f = 50\%$. P_{south} is missed by the mated females while P_{east} is easily detected.

a

b

c
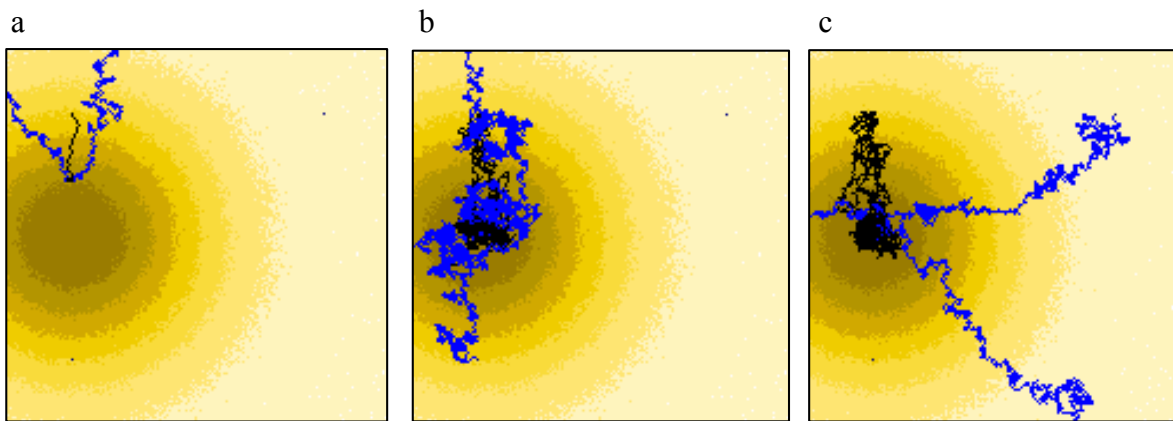
Figure 19: The effect of increasing consistency ($p=0$, $p=0.2$ and $p=0.4$) on: (a) mating success and (b) time until mating. (c) Optimal response ($*q_{m+v}$, in full circles, $*qf$ in empty circles) depending on different values for consistency (p). See methods for determination of the optimal response measure. (d) The arrival success of mated females according to the selected optimal response as function of consistency (p). Confidence Intervals for (c) and (d) represent 6 repeats of 5 simulation runs each.
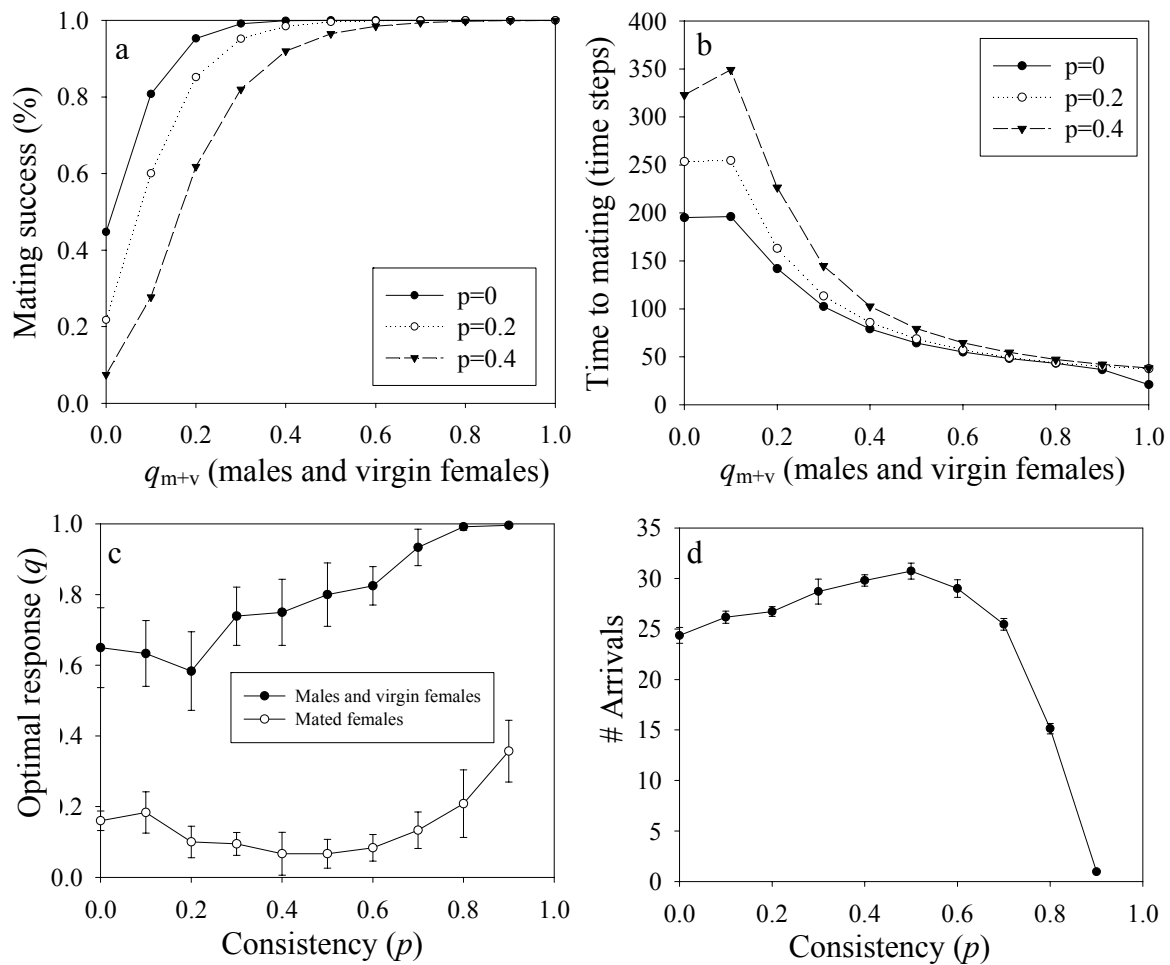
Figure 20: The impact of landscape variability (noise = 0%; 1%; 5%; 10% of summit elevation, respectively) on the correlation between the response to topography and mating success (a) and time until mating (b). Also shown are the optimal responses (*q_{m+v}, full circles and *q_f, empty circles) vs. landscape variability (c) (see methods for determination of the optimal response measure), and the number of arrivals of mated females at the patches at the optimal response vs. landscape variability (d).
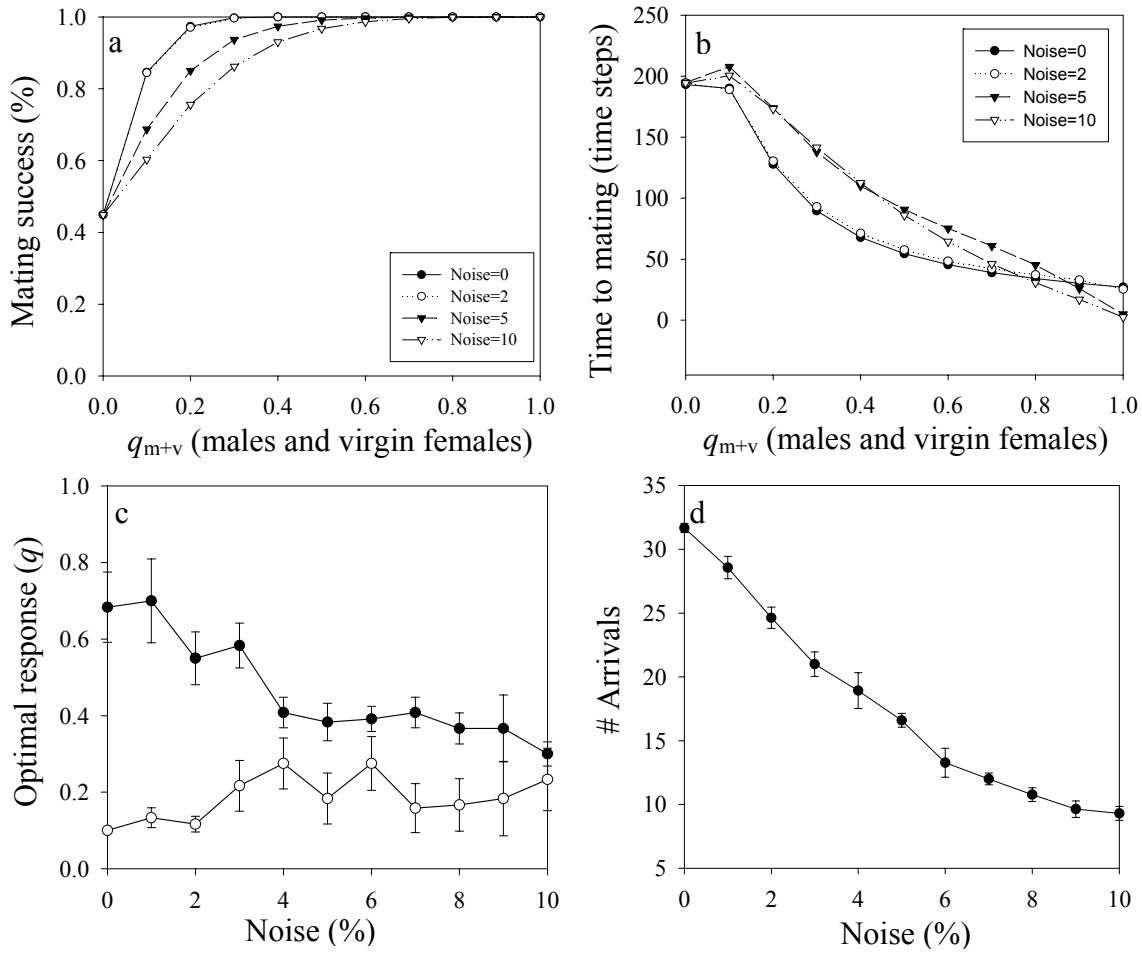
Figure 21: The effect of releasing butterflies throughout the landscape on: mating muccess vs. q_{m+v} (a); Optimal q_{m+v} (full circles), and the optimal q_f (empty circles) vs. consistency (p) (b), and the total number of mated female arrivals vs. consistency (c).
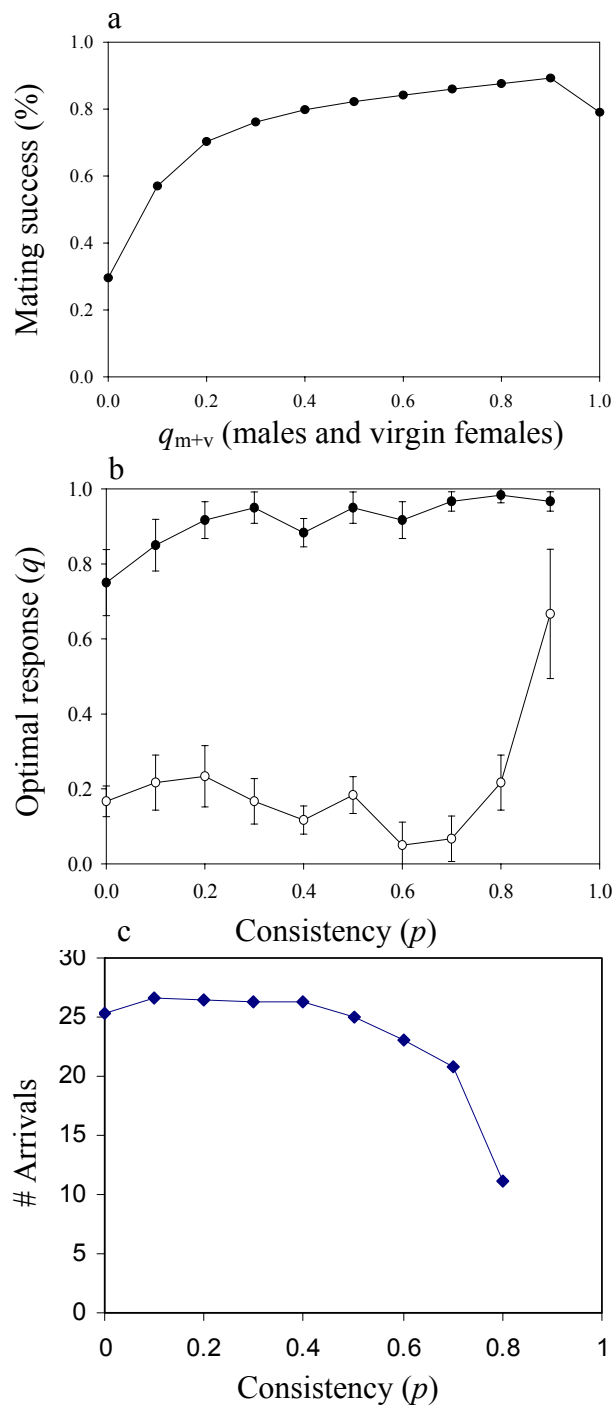
6. HOW REALISTIC IS THE MODEL?

6.1 INTRODUCTION

Hilltopping behavior brings males and virgin females out of their original habitat patches. Mated females then have to search for patches of suitable habitat. These patches, especially in arid environments, may be found along stream beds. Since mated females may also wish to avoid male harassment on hilltops, I hypothesized that a certain tendency to move downwards would be advantageous for mated females while moving in topographically complex landscapes. However, studies that addressed the movement parameters of mated females obtained inconsistent results. Shields (1967) observed that females descend from mountains, while Wickman (1988) concluded that mated females do not respond to topography. In my fieldwork I could not recognize a significant tendency to fly downwards (Chapter 2), yet various simulations indicated, repeatedly, that a slight tendency to fly downwards may optimize their success in finding patches (Chapter 5). I obtained these results by simulating animal movements over a simple virtual landscape, with a single topographic configuration and a fixed location of the patches. Therefore, it is necessary to repeat the same optimization processes presented in Chapter 5 in realistic landscapes, and evaluate whether the results are valid also for such landscapes. Another limitation of the simulations described in Chapter 5 was that the 'consistency' (p) was equal for butterflies at all states (males, virgin females and mated females), in spite of field observations that indicated that the flight of mated females is more consistently straight than males and virgin females (Chapter 2). Given that mated females start their searching movements on summits, it is possible that the parameter p can direct the mated females away from the summits, without any response to topography. Therefore, it is necessary to determine whether the response to topography of mated females (q_f) is necessary for optimizing the movements of mated females, or flying consistently (high p_f) can replace q_f as a directing element of their movement.

In this chapter I increase the complexity of the spatial and behavioral parameters in use by 'the Hilltopping Model'. In the first part of this chapter I address the need to adapt the life-span of the butterflies to the landscape in use. Then, in the second part I

explore two behavioral parameters, p (consistency) and q (the response to topography) for each of the two investigated states – males+virgin females, and mated females. I further address the sensitivity of the model results to the optimizing approach taken. Specifically, I incorporate indices of 'success' that take into account time limitations and intraspecific competition within habitat patches. I then discuss the ecological and evolutionary sense of different optimization approaches, and utilize the results to speculate on the ecological and evolutionary processes that determine the actual behavior of animals in the 'real world'. Finally, I evaluate the ability of the model to reproduce the 'correct' behavioral parameters. For this I suggest a simple conversion of the model parameters p and q into variables that are measurable in the field, I compare between them, and discuss the quantitative validity of the model.

6.2 METHODS

6.2.1 OPTIMIZING MOVEMENTS OVER VARIOUS LANDSCAPES

In the first part of this chapter, I aimed to develop a reliable methodology of repeating the optimization processes, as presented in Chapter 5, in a variety of realistic landscapes. In preliminary simulations with different landscapes I noticed that the optimal behavior of butterflies is affected by the time-horizon that butterflies have for moving, with respect to extent of the landscape in use. Therefore, in this part I explored the impact of butterflies' life span and the landscape size on the simulation outcomes in several realistic landscapes. I ran simulations over three different realistic topographic maps, all derived from DEMs of landscapes in Israel. The three maps differ in extent, topographical complexity, and cell size: 'Lahav', a semi-arid region north of the city of Be'er Sheva (31º25'N 34º50'E; see Chapter 2); 'Halukim' ridge, a hyper-arid region west of Sde-Boqer (30º53'N 34º46'E); and 'Dimona', a map of E'fe ridge, a hyper-arid region north-east of the city of Dimona (31º05'N, 35º03'E; see Chapter 7). For each landscape I ran the simulations with several different life spans of the butterflies. Further details on the landscapes in use and the butterflies' life-spans in these simulations are given in Table 6.

As in Chapter 5, in this analysis I determined the consistency (p) together for butterflies of all states. I varied p from 0-0.8 in steps of 0.2. Each parameter combination

(p, q_{m+v}, q_f) was repeated 30 times. In each repeat, ten patches were randomly distributed across the landscape. The optimal responses to topography ($*q_{m+v}$, $*q_f$) was then determined for each simulation set. The optimization index was the number of mated females that successfully arrived at the ten patches. I then plotted $*q_{m+v}$ and $*q_f$ against the ratio t/A, where t is the butterflies' maximal life span (in time-steps) and A is the landscape size (i.e. the total number of cells in the matrix).

6.2.2 FOUR-PARAMETER OPTIMIZATION

In the second part, I optimized four behavioral parameters: the response to topography of males and virgin females (q_{m+v}) varied between 0.5-1, the response to topography of mated females (q_f) varied between 0-0.5, the consistency of males and virgin females (p_{m+v}) and the consistency of mated females (p_f), both in the range of 0-0.7. All four parameters were varied in steps of 0.1. I simulated all the possible combinations of parameters (hereafter, a 'set'), and selected the combination of all four parameters ($*p_{m+v}$, $*q_{m+v}$, $*p_f$, $*q_f$), which maximized the butterflies' success in arriving to patches. This I repeated 30 times, and calculated the average optimal behavior for each of the four behavioral parameters. In this analysis, I maximized three different indices of the butterflies' success, each presenting a slightly different optimization approach:

(a) '*Arrivals*' – the maximal number of mated females arriving at any patch. Optimizing the number of arrivals summarizes both movement steps (toward the summits and then away from them), because the number of mated females depends firstly on mating success and the time until mating (see Chapter 5).

(b) '*Arrivals/Time*' – the number of mated females arriving, divided by the (log) average number of time-steps to arrive at the patches. This optimization approach emphasizes the fact that animals often have limited time to search for habitat patches.

(c) '*Arrivals·D*' – the number of females that arrive at the patches, multiplied by an index that describes their distribution between patches. Indirectly, this optimization approach takes into consideration intra-patch competition. I assumed that under intra-specific competition, the reproductive-success of females increases if they are evenly distributed over a large numbers of patches. To evaluate the distribution of individuals among patches I used the Simpson index for diversity (D):

$$D = \frac{1}{\sum \vartheta_i^2}$$
(5)

where ϑ_i is the proportion of individuals arriving at each of the patches. D takes a maximal value (D=number of patches) if individuals are equally distributed among all patches, and a minimal value (D=1) if all females arrive at the same patch.

Due to the high number of explored variables, these simulations required huge computation capacity (each set of parameter combinations required 2304 simulations). Consequently, I could only run a limited number of simulations, over relatively small landscape matrices. I therefore focused on three different landscapes – one virtual and two realistic landscapes:

1. The virtual landscape had one summit, its location similar to that in Chapter 5 (but recall that the starting point and the patches were now randomly distributed). I used two maps of this topographic configuration, differing in their extent: one had 100×100 cells (hill-width = 25 cells), and the second with 120×120 cells (hill-width = 30 cells).

2. 'Halukim', a realistic landscape with high topographic complexity, 200×200 cells in size (similar to the map used in the first analysis).

3. 'DimonaS' landscape, a section of 'Dimona' landscape used in the first analysis, 120×120 cells in size. This map was to be used later on in the field validation of the model (Chapter 7).

In order to decrease the impact of landscape size on simulation outcomes, I performed three simulation sets (one with each landscape type) with a constant ratio between the life span of the butterflies and the landscape size (t/A ≈ 0.07). I then ran one additional simulation set for each of the three landscapes, with a slightly smaller or slightly larger *t/A* ratio. Further details on the landscapes, the number of patches and the butterflies' life spans are given in Table 7. Other simulation attributes were: 500 butterflies, a gap of 10 time-steps between releases, and 5 encounters necessary before mating. All butterflies started in one randomly located starting point (a 'source patch').

A third and last analysis aimed to inspect the simulation outcomes when the distribution of patches is deliberately correlated with topography. The simulations for

the analysis were performed over the virtual one-summit landscape (100×100 cells). In the first set of simulations, the five patches were randomly distributed, yet confined only to the lower third of the range of elevations ($0 \leq x \leq$ ⅓S, where S=summit elevation). This distribution of patches corresponded to the location of P_{east} in Chapter 5, since the patches were located on the plateau. In the second set of simulations the patches were distributed on the middle third of the elevation range (⅓S $\leq x \leq$ ⅔S). This scenario was parallel to the location of P_{south} in Chapter 5, in the sense that patches were on the slopes of the hill. The analysis was similar to the above procedure, seeking the combination of four behavioral parameters (p_{m+v}, q_{m+v}, p_f, q_f) that maximized each of the three indices of success.

6.3 RESULTS

6.3.1 EXPLORING THE BUTTERFLIES' LIFE-SPAN

The optimal response to topography of males and virgin females (*q_{m+v}) increased mildly with increasing t/A, either by increasing their life span or decreasing landscape size, until reaching 1 (Fig. 22a). This trend occurred only for low values of p (<0.4). Above that, when $p \geq 0.4$, *$q_{m+v} \approx$ 0.9-1 (Fig. 22b). The optimal response to topography of mated females (*q_f) decreased with increasing t/A, until reaching 0. This trend was not affected by the values of p (Figs. 22a,b). In effort to summarize all the simulations (for all values of p), I pooled all the *q_{m+v} values for all simulation sets, and searched for the best terms which explain the variability in *q_{m+v}. I repeated this procedure with *q_f. *q_{m+v} was best explained by the term:

$$\log\left(\frac{t}{A^{\sqrt{1-p}}}\right) \tag{6}$$

where t is the butterflies' life span (number of time steps), A is the landscape size (total number of cells), and p is consistency (Fig. 23a; R^2=0.6216, n=43, P<0.0001). I note that a correlation analysis was statistically more appropriate in this case because p is not a predictor of q. However, a regression was necessary here for deriving equation (6).

For mated females, adding p to the ratio t/A only reduced the explanatory power of the regression. That is, $*q_f$ was best explained simply by the term: $-\log(t/A)$ (Fig. 23b; $R^2=0.4525$, n=43, P<0.005). Note that, when the butterflies' life-span was short and the landscape was effectively large, $*q_f$ could reach values as high as 1.

6.3.2 OPTIMIZING FOUR PARAMETERS

When optimizing the number of mated females that arrive to patches ('*Arrivals*') as a function of t/A, $*p_{m+v}$, $*q_{m+v}$, and $*p_f$ seemed to obtain consistent values over the simulations, while $*q_f$ varied more strongly (Fig. 24a). In all four parameters, the variability when t/A was fixed seemed to be of the same magnitude as the variability when t/A was not fixed. Kruskal-Wallis Tests for the impact of landscape on each of the four behavioral parameters were all insignificant. Linear regressions for the impact of the t/A ratio on the values of the four parameters were insignificant as well. Similar results were obtained for the two other optimization indices, *Arrivals·D* and *Arrivals/T* (results not shown).

Fig. 24b summarizes the optimization results of the four behavioral parameters, for the three different optimization indices. On average, $*p_{m+v}=0.28$, $*q_{m+v}=0.84$, $*p_f$ $=0.53$, and $*q_f =0.14$. The values of the optimal behavior differed depending on the behavioral parameter of interest (ANOVA, df=3, F=260.546, P<0.0001). Each of the optimal behaviors differed significantly from all three others (Bonferoni Post-hoc analysis), despite the relatively high variability in $*q_f$. I hereby summarize the main findings for each of the four behavioral parameters, with respect to three factors that could affect them: the optimization index, the landscape, and the value of the ratio t/A.

- $*p_{m+v}$: The average consistency was half of that of mated females, demonstrating the need to separate the two variables. Results for the *Arrivals·D* index were significantly higher than the two other indices (Kruskal-Wallis Test = 7.709, df=2, P=0.021). $*p_{m+v}$ did not change between the three Landscapes in use and the values of t/A.

- $*q_{m+v}$: I found no significant difference between the three optimization indices or the landscapes in use in terms of $*q_{m+v}$. However, note that the *Arrivals·D* index had slightly lower response values and higher variability.

- *p_f : I found a significant impact of the index on the optimal consistency (Kruskal-Wallis Test = 8.609, df=2, P=0.014), where the values of *p_f were lower for the *Arrivals* index.

- *q_f : Results were highly variable. I found a significant impact of the landscape in use on the values of *q_f (Kruskal-Wallis Test = 7.161, df=2, P=0.028), with highest values obtained in 'DimonaS'. Although the index in use did not have a significant effect on the results, note that the lowest *q_f values were obtained by the *Arrivals* index – as in *p_f. Additionally, I note that for each group of 30 simulation repeats, *q_f varied strongly and ranged from 0-0.5. The proportion of simulations in which 0 was the optimal response (out of 30 repeats) ranged from 16-73% between different groups of simulations.

In the one-summit landscape when the patches were distributed over the lower third of the elevations, the optimal behaviors were: very low *p_{m+v}, very high *q_{m+v}, moderate *p_f, and a weak to moderate *q_f (depending on optimization index)(Table 8). Again, the results with respect to mated females were inconsistent, and this time clearly affected by the optimization index in use. Note that the use of the optimization index *Arrivals* resulted in the lowest values of *q_f, as in the simulations described above. When patches were in the middle third of the landscape, *p_{m+v} was higher, *q_{m+v} was inconsistent, *p_f was slightly higher, and *q_f was 0. This was the only case in which *q_f obtained a consistent result.

6.4 DISCUSSION

In this chapter I tested whether the optimization of both movement steps (toward the summits and then away from them) can yield consistent results in both virtual and realistic landscapes. I found that the major source of 'landscape specific' results is the extent of the map in use, and not the topographic configuration *per se*. I therefore compensated for the extent of the maps by increasing the life span of butterflies and using relatively small maps, so that the ratio *t/A* took high values (see Fig. 22). Doing this, I obtained highly robust results for three of the four behavioral parameters – the

consistency of males and virgin females ($*p_{m+v}$), their response to topography ($*q_{m+v}$), and the consistency of mated females ($*p_f$). I found that $*p_f$ was persistently higher than $*p_{m+v}$, and the response to topography of males and virgin females was high. These results demonstrate that general patterns and results can be obtained despite the use of different landscapes that are different in extent, topographic complexity and even in cell-size.

With respect to the response of mated females to topography ($*q_f$), results were less conclusive and ranged from 0 to ≈0.4. These results require special attention given the high values of the t/A ratio. For the selected values, the optimal response of mated females was expected to fix on its lowest value ($*q_f = 0$; see Fig. 22). However, the average optimal response of $*q_f = 0.14$ was obtained despite the 'conservative' value of *t/A*. Interestingly, this result is also consistent with the results obtained in chapter 5, which suggested that a weak response to topography may be an optimal behavior. Therefore, I conclude that the optimal movement behavior of mated females may comprise a weak but important component of response to topography.

Due to the small number of simulations it is impossible to establish the reasons for the highly variable behavior of mated females. I suggest two hypotheses for the source of this variability. The first is that the response of mated females has little effect on the simulation outcome, and therefore the optimal response ranges 'freely' between various values. The second option is that the simulation outcome depends on the specific configuration of the patches in each of the simulation runs. This is supported by the different optimal behaviors that were obtained when the patches were distributed either in the lower third or the middle third of the landscape. Further simulations may be necessary to inspect which of the two hypotheses, if any, is valid.

6.4.1 THE PROCESSES THAT DETERMINE THE OPTIMAL BEHAVIOR

A major outcome of my simulations is that the optimal movement behavior of males and virgin females is affected by different factors than the behavior of mated females. This was manifested in several aspects:

1. The term that best explained the optimal response to topography was different for the two movement steps. While the optimal response of males and virgin females was partly explained by *p* (equation 6), the term *t/A* alone was a better predictor of the optimal response to topography in mated females. However, since *p* at that

stage was equal for all states, this can only indicate that the optimal value of p is mainly determined by the first movement stage, in which males and mated females need to seek summits.

2. The optimal behaviors of males+virgin females and of mated females were affected by the optimization index in use, but in different ways. While the use of the *Arrival·D* index resulted in significantly higher values of $*p_{m+v}$ and lower values of $*q_{m+v}$, the *Arrivals* index was the index that yielded significantly different values of the optimal behavior of the mated females (lower $*p_f$). I elaborate on the possible meaning of such differences below.

3. In the analysis of four-parameters, only the behavior of mated females was significantly affected by the landscape. This may indicate that the specific topographic configuration can have an important impact on movement strategy which is taken by animals. Further simulations are necessary to establish what the specific impact of the landscape is.

The use of three different optimization indices brings about interesting possibilities for linking between the behavioral parameters and the ecological and evolutionary factors that determine these behaviors. For instance, the index *Arrivals·D* did not seem to be the best index for optimizing the behavior of males and virgin females. Since the optimization of this index spreads individuals over the landscape, one can deduce that dispersing across the landscape is less important at that stage of the movement. This is biologically sound since the major goal of the hilltopping process is simply to find mates, and this is best done when animals concentrate in small number of places. On the other hand, *Arrivals* seemed a lesser index for optimizing the behavior of mated females. Unlike the two other indices, *Arrivals* does not explicitly incorporate spatiotemporal limitations on dispersal. Therefore, I can deduce that the behavior of mated females is strongly affected by the need to disperse efficiently over the landscape, in terms of their limited time and the need to cover the landscape efficiently in search for patches. This conclusion can be partially supported by the high consistency of their flight.

The use of different optimization approaches might also be important for understanding evolutionary processes. For instance, if animals are shown to optimize the *Arrival·D*, it can be indicative of two possible mechanisms. The first mechanism is

intraspecific competition. If individuals concentrate in a small number of patches, the competition between them would decrease their reproduction success. The second mechanism could be the long-term sustainability of a metapopulation. In this case, arriving at a large number of patches could decrease the risk of extinction. Naturally, this work is not aimed to test such hypotheses. This example simply points to the possible applicability of the modeling methodology, as presented in this chapter, to testing ecological and evolutionary theories.

6.4.2 OPTIMAL BEHAVIORS AND DIFFUSION RATES

In an effort to derive landscape-independent results with respect to the butterflies' optimal behavior, I used the correction term t/A – the ratio between the butterflies' life span and the landscape size. Interestingly, the units of this term are – time (number of time steps) divided by area (number of cells on each of the matrix's dimensions). These units could be explained in terms of diffusion rates, because they describe the 'efficiency' of spreading over the landscape (Turchin 1998; Okubo & Levin 2001). Thus, it is of no surprise that p had a strong impact on the optimal behavior of males and virgin females: increasing p allows animals to move across the landscape more quickly, and reduce the chances of moving through one cell more than once. This is why p affects equation (6) in opposite direction to A, so that increasing p diminishes the effective extent of the landscape.

Zollner & Lima (1999b) showed that a random walk (totally random movement) is a very effective searching strategy if time is unlimited, while a highly correlated random walk (CRW) becomes more efficient when time is limited (due to the need to cover large areas in a short time). My results with regards to mated females are partially consistent with Zollner & Lima (1999b): When t/A was low, mated females responded more strongly to topography, thereby achieving a strongly directed movement pattern. When t/A increased, mated females had a longer time to search for patches, and the optimal response of mated females decreased until reaching 0 – giving a rise a totally random walk (an efficient search strategy when time is unlimited). I did not find an increase in the optimal p with the decreasing time, seemingly in contrast to Zollner & Lima (1999b). This I explain by the fact that in the first analysis the consistency (p) had equal value for all states (as explained above), so that p did not reflect the optimal behavior of mated females.

However, in the case of males and virgin females, the results are seemingly opposite to Zollner & Lima (1999b) – the optimal response increased with the time horizon for searching, instead of decreasing. This can be explained by the fact that p was incorporated into the explaining term of $*q_{m+v}$ (equation 6). As shown in Chapter 5, the main factor that determines the behavior of males and virgin females is the need to overcome topographic noise. When the time horizon is short, animals should spend less time on local maxima, and a more consistent flight is necessary to avoid the trapping effect of local maxima. When the time horizon is prolonged, animals can respond more strongly to topography and inspect also local maxima (see also Chapter 5), by decreasing p and increasing q. Therefore, although the pattern is seemingly opposite to the one shown by Zollner & Lima (1999b), the overall result is similar.

The impact of t/A on the optimal behaviors has important implications for practical uses. In order to derive species-specific or landscape-specific predictions in the 'real world', one has to take into account the extent of the landscape (and its resolution) from the point of view of the species of interest, as well as the time horizon that animals have for their dispersal. This requires empirical data on the life span of individuals, their survival during dispersal, and their movement rates. Such empirical data is available from a variety of field studies (e.g. Harrison 1989; Turchin et al. 1991; Hanski et al. 1994; Beier 1995; Kuussaari et al. 1996; Schultz 1998; Van Vuren 1998; Palomares et al. 2000; Gillespie 2001; Macdonald & Johnson 2001; Schadt et al. 2002; Wilson & Thomas 2002; Baguette 2003; Lowe in press). In the next Chapter, I collect such empirical data in the context of hilltopping.

6.4.3 TRANSLATING p AND q INTO MEASURABLE VALUES

To compare the results of this chapter with the results of field observations, it is necessary to translate the behavioral parameters of the model into measurable indices. I hereby suggest a simple methodology of converting between these parameters, and then compare the results and evaluate the performance of the model.

6.4.3.1 Converting q

The parameter q in the model (hereafter, q_{model}) describes the proportion of movements in which animals deliberately move upward (males and virgin females) or downwards (mated females). Ideally, this is parallel to the proportion of time that animals are

observed to spend moving upwards or downwards. However, it is necessary to consider that a totally random movement would yield 50% of the movements upward (or downward). Therefore, q_{model} will determine the proportion of directed movements, but 50% of the remaining movements would also show the same tendency. Thus, the observed proportion of directed-movements (q_{obs}) can be represented by

$$q_{obs} = q_{model} + (1 - q_{model})/2 \qquad (7)$$

and therefore

$$q_{model} = q_{obs} \cdot 2 - 1 \qquad (8)$$

However, note that in the model animals first decide whether to continue with the previous direction with a probability p (hereafter, p_{model}). This decision is prominent over the response to topography. Therefore, a more generalized form of equation (8) would be:

$$q_{obs} \cdot 2 - 1 = q_{model} \cdot (1 - p_{model}) \qquad (9)$$

I hereby use equation (9) to compare between the field observations in *M. trivia* and the results of this chapter. In the field, males move upward $q_{obs} = 77.5\%$ of the time, and virgin females move upward $q_{obs} = 81.8\%$ of the time. Using equation (9) $q_{obs} \cdot 2 - 1 = 0.55$ and 0.64 for males and virgin females, respectively (an average of 0.60). In the simulations presented in this chapter, I found that $*p_{m+v} = 0.28$ and $*q_{m+v} = 0.84$, so that $q_{model} \cdot (1 - p_{model}) = 0.60$.

Similarly, mated females in the field moved downwards $q_{obs} = 55.7\%$ of the time, and this translates into $q_{obs} \cdot 2 - 1 = 0.11$. In the model, $*p_f = 0.53$, and $*q_f = 0.14$, so that $q_{model} \cdot (1 - p_{model}) = 0.07$. This comparison reveals that, despite the independence of the optimization process from the results of my fieldwork, the model repeats the observed behavioral parameters with striking robustness, especially for males and virgin females.

6.4.3.2 Converting p

The parameter p in the model (hereafter, p_{model}) can be estimated from observations by comparing the model's cell-size to the observed distances between turning points (the increment lengths). Specifically, one should calculate the probability that animals perform straight movements that exceed cell size. This probability can be calculated directly from the data (using bootstrapping methods), or indirectly, from the distribution of increment lengths. Noteworthy, in grid-cell matrices such as the ones used by this model, each cell is a rectangular with eight neighbors. The use of such maps means that the distance from each cell to its diagonals is $\sqrt{2}$ the distance from a cell to its immediate neighbors. This can be corrected by evaluating p_{obs} twice, once for the side-length of cells and once for the diagonals, and average the two.

Table 9 depicts the calculated probability to exceed cell size of 5m and 25m, as well as the probability to exceed the diagonals based on field data on *M. trivia*. The results demonstrate the problem with converting p between the model and reality. Seemingly, this conversion methodology yields similar results between the optimal p_{m+v} and p_f in the model and p_{obs} for males, virgin females and mated females when the landscape has a cell side-length of 5m. However, for landscapes with cell side-length of 25m the probability to exceed cell-size diminishes to marginal values. Based on these results, one may hypothesize that p should be determined based on the landscape in use. However, the results of this chapter demonstrate that the parameter p has an intrinsic importance in the model irrespective of cell size. I showed that the parameters p and q, for both movement steps, obtain robust values that are landscape-independent. Furthermore, this conversion brings up also the question of field-work methodologies. The measured increment length depends on the tracking method, the time between sampling events, and the animals of interest. Therefore, in further modeling (Chapter 7) I use values of p that are quantitatively based on the model, and only qualitatively based on the observed behavior. Specifically, the males and virgin females have lower consistency than mated females, both in the model and in reality.

To summarize, I provided a simple and straightforward methodology of converting field observations into measures that can be directly incorporated into the model. Nevertheless, the conversion between the observed values of p and the modeled ones require further exploration, which is beyond the scope of this work.

The inconsistent results with respect to the behavior of mated females, and the need to validate the predictive power of the model in the field, are addressed by a field experiment presented in the following chapter (Chapter 7). In the simulations presented in the Chapter 7 I partly rely on the specific results of this chapter with respect to 'DimonaS' landscape: $*p_{m+v}=0.24$, $*q_{m+v}=0.86$, and $*p_f=0.57$. Since the results with respect to q_f were inconsistent, I investigate a range of possible responses to topography.

Table 6: Explored landscapes and the life spans (in time steps), for the first analysis of the optimal response (q_{m+v},q_f) in realistic landscapes.

Landscape	Number of cells	Cell side-length	Life-spans
Lahav	255×360	5m	700,1000,1500,2000
Halukim	200×200	25m	700,1000,2000
Dimona	300×300	25m	1000,2000,2500,3500

Table 7: The landscapes in use and several simulation properties in the second analysis, where all four behavioral parameters were optimized (p_{m+v}, p_f, q_{m+v}, q_f).

	Landscape	Size (# cells)	Life-span	t/A	Patches
1	One summit*	100×100	1000	0.1	5
2	One summit**	120×120	1000	0.069	10
3	Halukim	200×200	2000	0.05	10
4	Halukim	200×200	2780	0.07	10
5	DimonaS1000	120×120	1000	0.069	10
6	DimonaS1200	120×120	1200	0.083	10
7	One summit*	100×100	1000	0.1	5 in lower 1/3
8	One summit*	100×100	1000	0.1	5 in middle 1/3

* Hill-width = 25 cells; ** Hill-width = 30 cells.

Table 8: Results of a four-parameter optimization (p_{m+v}, q_{m+v}, p_f, q_f) for the one-summit landscape, with patches in the lower third and the middle third of the range of elevations. See text for details on the optimization indices.

Patches' distribution	Opt. index	p_{m+v}	q_{m+v}	p_f	q_f
Low third	*Arrivals*	0	0.93	0.43	0.13
	Arrivals·D	0.03	0.83	0.43	0.27
	Arrivals/Time	0	1	0.6	0.47
Middle third	*Arrivals*	0.37	0.97	0.67	0
	Arrivals·D	0.37	0.7	0.63	0
	Arrivals/Time	0.13	0.93	0.67	0

Table 9: The proportion of observed increment lengths *M. trivia* movements that exceed a given cell size (length or diagonal), based on field data (see Chapter 2). First row represents the average increment length (distance between turning points) for males (n=245 flight increments), virgin females (n=249), and mated females (n=209). Recall that the distribution of increment length is log-normal (Chapter 2).

Cell size	Males	Virgin females	Mated females
inc. length (mean±SD)	5.97± 9.31m	8.54±11.25m	11.71±19.42m
5m	0.34	0.55	0.54
7.07m	0.24	0.39	0.40
25m	0.029	0.061	0.11
35.4m	0.016	0.036	0.067

Figure 22: Optimal response to topography in Male and Females (*q_{m+v}; black squares) and in mated females (*q_f; empty squares) vs. the ratio t/A − Life span (# time steps) / landscape size (# cells in the matrix). (a) $p = 0.2$; (b) $p = 0.4$.
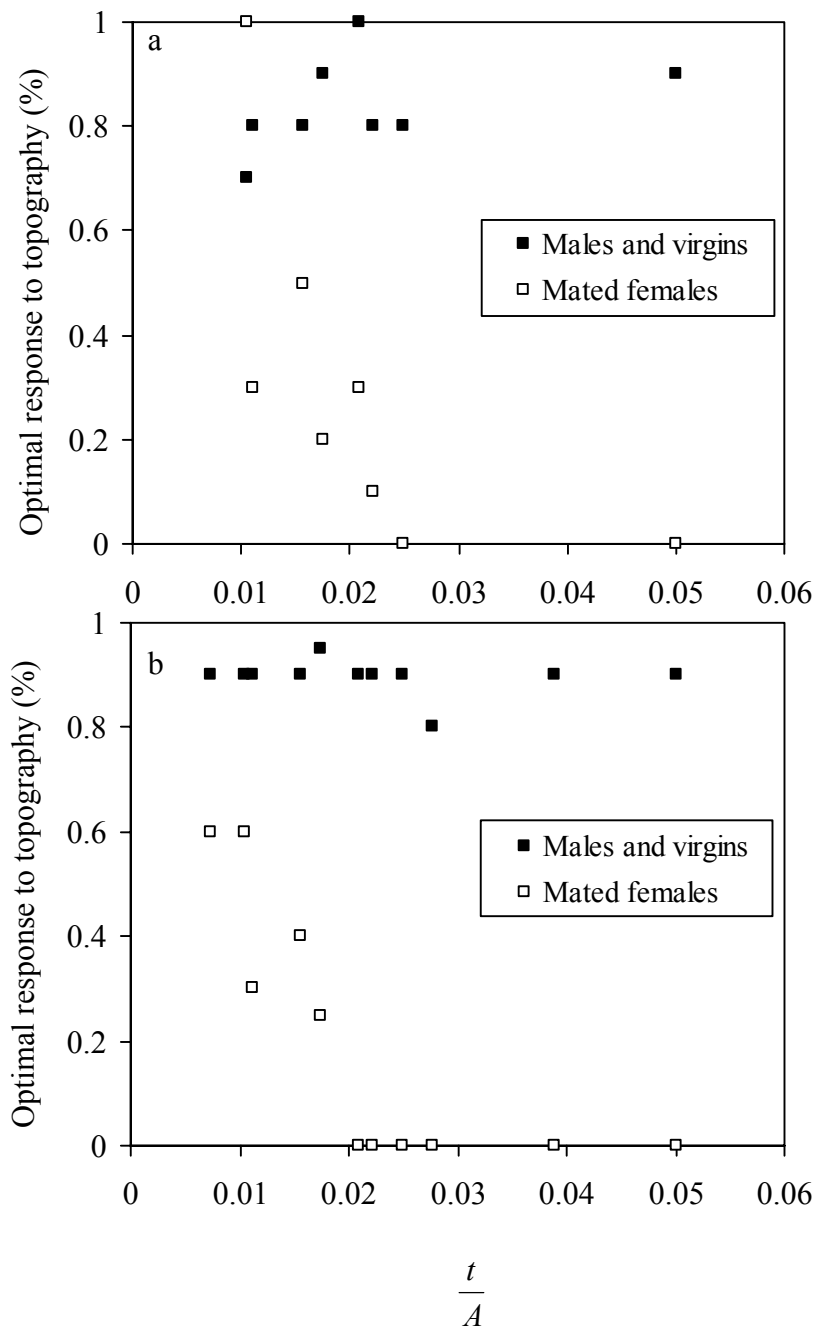
Figure 23: (a) Optimal response to topography of males and virgin females (*q_{m+v}) vs. equation (6): t = butterflies' life-span, A is the total number of cells in the matrix, p is the behavioral parameter consistency. (b) Optimal response to topography of mated females (*q_f) vs. the ratio t/A.

a

Optimal response (q_{m+v})(%)

$y = 0.0507\mathrm{Ln}(x) + 0.9331$

$R^2 = 0.6216$

$\dfrac{t}{A^{\sqrt{1-p}}}$

b

Optimal response (q_f)(%)

$y = -0.3624\mathrm{Ln}(x) - 1.2224$

$R^2 = 0.4526$

$\dfrac{t}{A}$
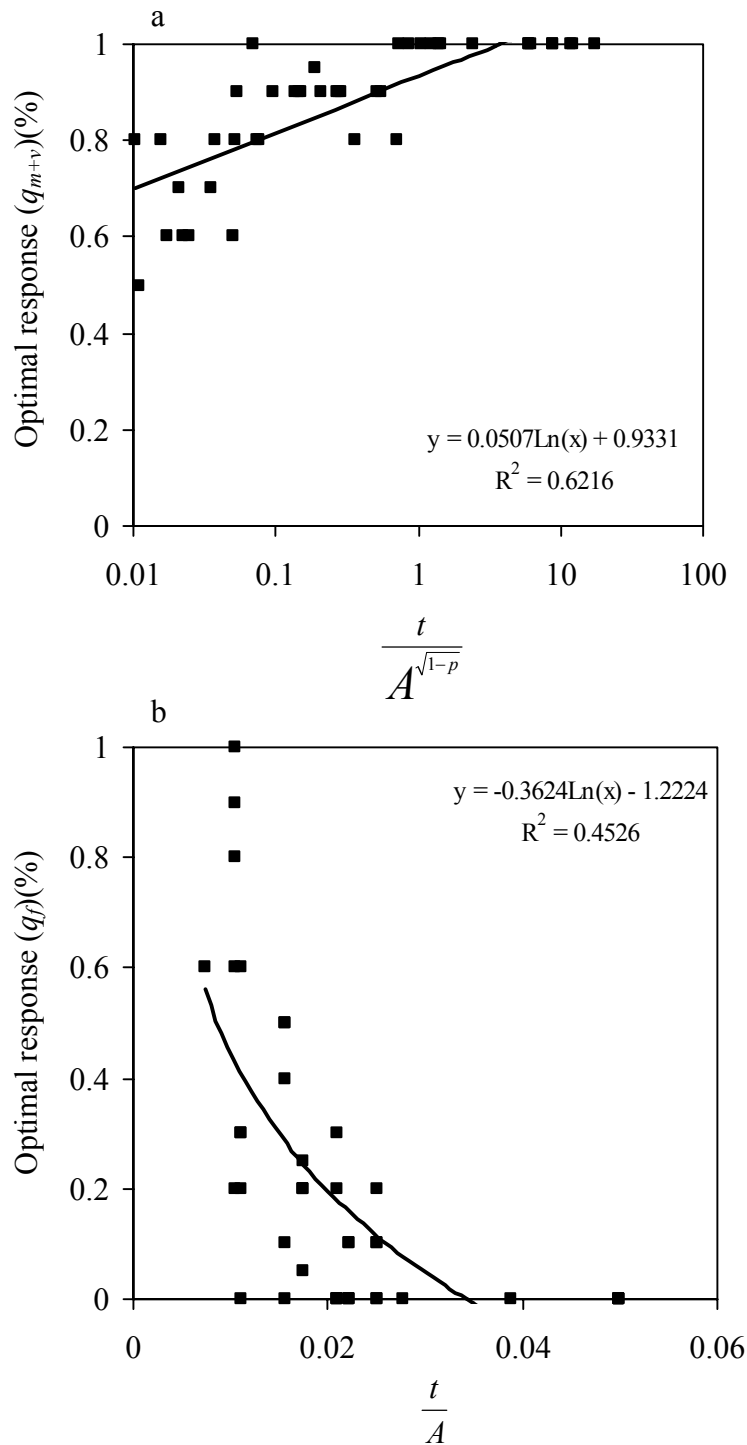
Figure 24: (a) Optimal behavioral parameters ($*p_{m+v}$,$*q_{m+v}$,$*p_f$,$*q_f$) vs. the ratio t/A for the optimization index *Arrivals*. The results for $*p_{m+v}$,$*q_{m+v}$ amd $*p_f$ seem quite consistent over the different landscapes and the inspected range of t/A ratios. Results for $*q_f$ are much less consistent. (b) The average optimal movement behaviors ($*p_{m+v}$,$*q_{m+v}$,$*p_f$,$*q_f$) in the six different sets of simulations (Table 7). Results are divided into the three different optimization indices: Number of arrivals of mated females (*Arrivals*, black), Arrivals multiplied with the diversity index D (*Arrivals·D*, stripes) and Arrivals divided by the (log) average arrival time (*Arrivals/T*, white). Error bars represent one standard deviation.
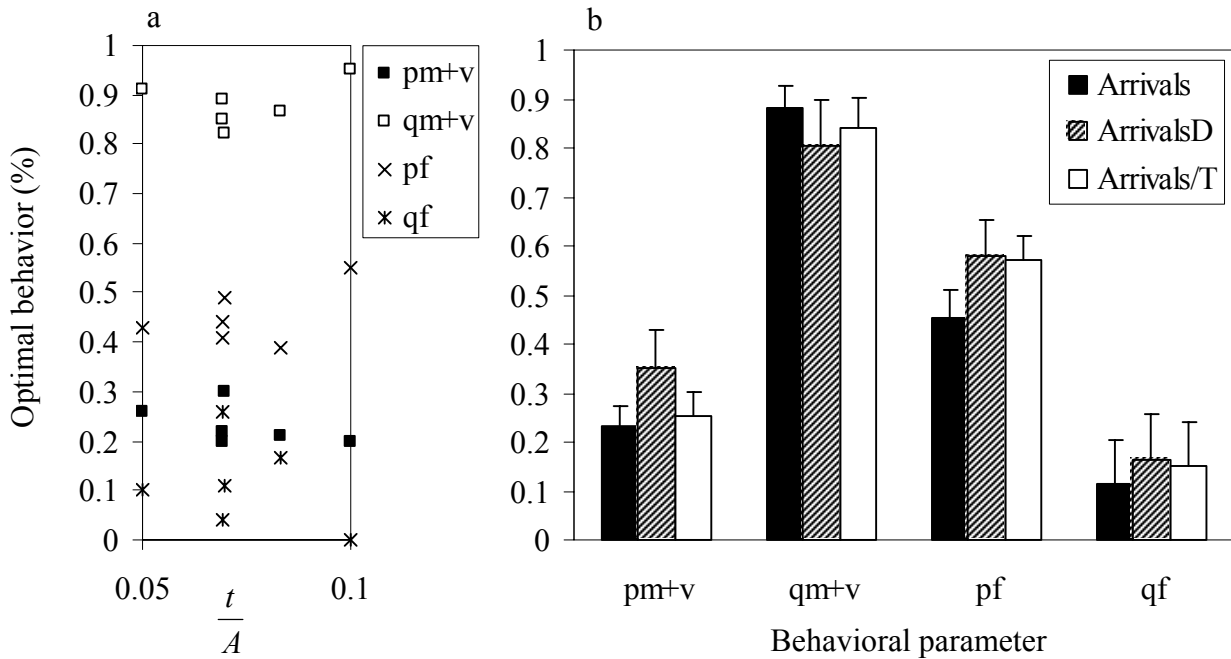
7. FIELD VALIDATION OF THE MODEL AND EVALUATION OF THE MOVEMENT PARAMETERS OF MATED FEMALES

7.1 INTRODUCTION

Mark-Release-Recapture experiments (MRRs) are commonly used in field studies of dispersal (Turchin et al. 1991; Krebs 1998; Turchin 1998; Buckland et al. 2000; Bennetts et al. 2001). MRRs provide a major source of empirical knowledge which can be used for modeling dispersal and connectivity (Turchin 1998; Nathan 2001). However, if animals are not followed individually, animals that perform long-distance movements are often lost. This commonly results in underestimating dispersal distances when long distance dispersal occurs (Turchin 1998; Nathan & Muller-Landau 2000; Gómez 2003). Despite this weakness, MRR experiments provide powerful tools for delineating spatial and temporal patterns, such as the spreading of individuals over a landscape following their release (Turchin 1998). Typically, they indicate that the number of recaptures diminishes rapidly with growing distance from the source point, mainly due to the distribution of movement-distances (Turchin 1998; Williamson 2002). However, the results of previous chapters indicated that different patterns evolve when animals respond to landscape heterogeneity. Therefore, in this chapter I evaluate the effectiveness of MRRs in delineating the spatial patterns that result from the movements of hilltopping butterflies across a topographically complex landscape.

'The Hilltopping Model' was developed for the purpose of analyzing movement patterns of hilltopping butterflies in the context of topographic heterogeneity. It simulates the two distinct movement behaviors that are involved in hilltopping: the hilltopping process itself, where animals move upwards toward mountain summits for the purpose of mating, and the dispersal of mated females away from summits in search of host plants. Using the model, I explored the resulting movement patterns in a wide range of spatial and behavioral parameters. I searched for movement parameters that optimize the success of animals in mating, and consequently in patch-finding, independently of the observed behavior of butterflies in the field (chapters 5 & 6). With respect to the movement behavior of males and virgin females, I obtained very high agreement between the model

results and the real behavioral parameters (Chapter 6). This suggested that the model, despite its simplicity, can provide landscape-specific predictions of butterfly movements in real landscapes. However, the results with respect to mated females were less consistent, ranging from random movement to moderate response to topography. Thus it is necessary to determine what the behavioral parameters of mated females are, for the purpose of predicting the patterns of the over-all, two-step process of hilltopping. In effort to estimate the behavioral parameters of mated females, I combine the model and the MRR experiment. Thus, in this chapter I combine the model with a MRR for two main purposes: to validate the model as a predictive tool in the case of males and virgin females, and to generate and test hypotheses in the case of mated females. In this way, I link between the hilltopping model as a theoretical tool, and MRR methodologies as a measure of the observed spatial patterns. Specifically, in this chapter I pose two questions:

(1)   Given the small spatiotemporal scale of the observations on which the model is based (Chapter 2), and the simple movement rules of the model, can it provide accurate landscape-specific predictions of the movement patterns of over realistic complex landscapes?

(2)   Given the ambiguous model results with respect to the behavior of mated females (Chapter 6), can the combination of the simulation model and a MRR experiment reveal the intensity of the mated female response to topography?

I demonstrate that, due to the response of males and virgin females to topographic heterogeneity, the spatial pattern of recaptures diverges strongly from the diminishing pattern which is predicted for homogeneous landscapes. Using the model as a predictive model, I successfully maintain high recapture rate even at relatively large distances. With respect to mated females, the combination of the model and the field experiment provide only little knowledge. I discuss the power and limitations of the model with regards to the two movement steps, and offer possible improvements to the model for theoretic and applied purposes. Finally, I provide a few insights on MRRs, as well as their combination with modeling.

7.2 METHODS

7.2.1 THE LANDSCAPE

The field experiment took place on Ef'e Ridge, north-east of Dimona, Israel (31º05'N, 35º03'E). This hyper-arid region (annual precipitation ca. 50mm) is typified by low human density, high topographical complexity, and contractile vegetation (i.e. plants are restricted primarily to wadis). With the aid of the model and preliminary field surveys, I selected a section of 3×3km from a Digital Elevation Model (DEM) of the Negev, with a cell side-length of 25m. The range of elevations in the selected area is 480-680m (Fig. 25).

7.2.2 CONCEPTUAL BASIS OF THE ANALYSES

Since the goals with respect to the two movement steps are different, I have adapted two different approaches for analyzing each of them. In the following, I elaborate on these approaches.

7.2.2.1 Males and virgin females

Prior to the fieldwork I performed simulations to determine the location of a single release point in the selected landscape. The specific location of this point was chosen so that males and virgin females would arrive at a major mountain summit from a considerable distance, and mate primarily on it. I decided to locate the release point on a ridge leading to a relatively distinct hill, 602m in elevation. The distance between the release point and the summit (hereafter, S_{602}) was 480m.

With the aid of the model, I performed simulations to determine the expected movement patterns of the males and virgin females towards the summit. To analyze these patterns I needed a methodology of translating the movement patterns that were generated by the model into measurable recapture patterns. For this, I recorded the total number of times that each cell in the landscape was visited by butterflies during a given simulation (following Gustafson & Gardner 1996). Thereby, the number of visits to each cell could be plotted against the distance to the release point, to generate a pattern that can be easily analyzed and quantified (hereafter, 'Visits' Pattern'). The advantage of this approach is exemplified in Fig. 26, where I have plotted the Visits' Pattern for a virtual landscape with one summit. In a case where the movement is random ($q_{m+v} = 0$,

Fig. 26a) the number of visits decreases with distance from the release site in an exponential-like pattern, similar to that which is often obtained in MRR studies of dispersal. Note that, in this case, the pattern is also similar to the 'accessibility pattern' (Chapter 4, Fig. 12a). However, when animals respond to topography (q_{m+v}>0) the number of visits decreases with the distance and then increases markedly around the summit, creating a hump-shaped pattern due to animal adherence to the summit (Figs. 26b,c). In this case, the location of the 'hump' is independent of the distance between the release point and the summit (assuming no mortality along the way), while its altitude depends on the intensity of response to topography (note the y-values in Fig. 26b vs. 26c). The conceptual basis of this approach is that the recapture probability in the field is proportional to the time that butterflies spend at each point. Therefore, I expected the Visits' Pattern to represent the recapture probability across the landscape, under the assumption that the sampling effort is similar over the whole area. The advantage of this approach is that it mimics the results of a single release experiment in terms of the landscape-specific recapture probability at each point in the landscape.

To apply this approach for summarizing the movement pattern over the selected landscape, I performed 10 simulation runs, with 200 butterflies that could move 300 time-steps each. In these simulations, males and virgin females were not allowed to mate. Their behavioral parameters were set to (q_{m+v} = 0.9, p_{m+v} = 0.2), based on the optimization results of Chapter 6. As in previous simulations, individuals recognized the topographical signal only within their immediate proximity, choosing one of eight neighboring cells on each movement step. In this landscape, this translated into a perceptual range of 25-35m (25m to the four direct neighbors and ≈ 35m for the four diagonal ones).

I depicted the average number of visits per cell against the distance from the release point. This resulted in the generation of several 'humps', due to the dispersion of males and virgin females among various summits. The relative size of each hump depended on the movement parameter, the relative height of each summit, and the spatial configuration of the landscape. However, one-dimensional representation of the accessibility pattern condensed all this information into a single parameter (i.e. distance), resulting in the loss of information that was coded by the spatial pattern of arrivals. To avoid this, I plotted the Visits' Pattern on top of the landscape map, instead of plotting it against the distance. The number of visits in each cell was represented by a color (Fig. 27). The resulting pattern provided landscape-specific predictions, which were then tested

in selected locations that could be monitored by a few people (see Fig. 27). These locations included the release point; the main summit (S_{602}); the anticipated path leading from the release point to S_{602}; two local summits along this path (S_{loc1}, S_{loc2}); and two additional summits: The first was expected by the model to receive no individuals despite its close proximity to the release point (S_{mul}), and the second (S_{ptch}) was expected by the model to receive some arrivals despite its large distance from the main ridge ($\approx$ 350m) and the fact that it is separated from this ridge by a relatively deep wadi.

In a first step of the analysis, I depicted the expected Visits' Pattern and compared it to the observed recapture pattern. First I compared the two patterns visually, by plotting both patterns on top of a map of the study area. To take into account the differences in sampling efforts between the summits, I normalized the expected number of visits by the number of observation-hours spent at each of the cells in the selected area (hereafter, the 'sampling effort'). This analysis was followed by a quantitative evaluation of model performance, in which I plotted the number of recaptures at each of six points (the five summits and the release point) against the normalized predicted values (log number of visits, multiplied by the sampling effort). The residuals of the regression line were then plotted against distance from the release point, to inspect whether model performance tends to decrease with distance.

7.2.2.2 Mated females

Simulations performed in previous chapters have indicated that the probability that mated females arrive at patches depends on two main factors: the intensity of their response to topography (q_f), and the distance of the patches from the females' starting point (in this case, S_{602}). In the case of random movement, patches should receive decreasing number of arrivals as their distance from the starting point increases. However, if mated females respond to topography the topographic context becomes a major determinant of their arrival probability. Under these conditions, a patch which is closest to the starting point could receive the lowest number of mated females, whereas a more distant patch could receive higher number of arrivals. Setting a configuration of patches in the field which satisfies these conditions, may serve in evaluating the behavioral parameter of mated females. To achieve this goal, I determined the specific location of three artificial patches, which I later created in the field, in the following way (Fig. 25):

1.   The closest patch to S_{602} (hereafter, P_{SUM}) was located at a distance of 430m west of the summit. I located it ca 50m north of a local yet prominent summit (the local summit is hereafter referred to as S_{ptch}). Butterflies could reach this patch only if they crossed a wadi, i.e. move downhill into it and then uphill out of it.

2.   A second patch (hereafter, P_{SL}) was located 510m north of S_{602}, downhill from the summit towards north. Its name indicates that the patch was located on a slope of the mountain.

3.   The most remote patch, P_{WF}, was located 825m South-Southeast of S_{602}, in a meeting point between two major wadis downstream from the summit.

I then performed simulations to verify that the location of the three patches satisfies the requirements of this investigation for estimating the behavior of mated females. In each simulation, 200 butterflies were released as males and virgin females and moved 300 time steps each. The time-gap between releases was 3 time-steps, and the females were allowed to mate after 8 encounters with males (instead of 5 encounters in previous simulations, in order to reduce the chance of mating along the way in the model). The distance from which patches could be identified was defined as 50m, in accordance with field observations by Harrison (1989) and Benyamini (personal comm.). The behavioral parameters of males and virgin females were set to ($q_{m+v} = 0.9$, $p_{m+v} = 0.2$) as above. The consistency of mated females was set to $p_f = 0.4$, and their response to topography, q_f, varied from 0-0.5 in steps of 0.1. For each value of q_f I performed 30 simulations, in which I determined the arrival success of mated females to each of the three patches.

The results of this systematic analysis showed that, if the movements of mated females were random, the expected probability would depend solely on the distance from S_{602} (Fig. 28). Consequently, recapture success would be highest in P_{SUM}, lower in P_{SL}, and lowest in P_{WF}. Increasing q_f in the model resulted in a rapid increase in the probability of arrival at P_{WF}, and a mild decrease in the probability of arrival at the two other patches (Fig. 28). The overall recapture success was expected to increase with q_f. These qualitative results yielded two simple scenarios for recognizing the behavior of mated females in the field:

(1) The '*low recapture success*' scenario: if mated females fly randomly, low recapture success and a relatively uniform allocation of arrivals between patches is expected (with possible bias toward the patch closest to S_{602}, P_{SUM}).

(2) The '*biased recaptures*' scenario: if, however, mated females respond to topography by flying downwards, a high recapture rate is expected, along with a strong bias toward the remote patch P_{WF}.

7.2.3.1 Plant and butterfly cultivation

As in previous field-work (Chapter 2), the hilltopping butterfly *Melitaea trivia* (Nymphalidae) served as a model organism for the experiment. For this purpose, I collected both butterflies and plants and then cultivated them until the beginning of the study. In January 2003 I collected ca. 150 *Verbascum fruticulosum* plants (Scrophulariaceae), a major host-plant of the butterfly larvae in semi-arid and arid regions in Israel (Benyamini 1990). The plants were collected in Yatir, a region where they grow abundantly by roadsides. I potted them in 10 liter PVC planters, and cultivated them until the onset of the experiment. Most of the plants were used to create the artificial patches in the field, and the rest were used for butterfly cultivation.

The butterflies were collected during March-April 2003. I collected them as eggs in an effort to retrieve a large number of butterflies and avoid 'cultivating' parasitoid insects. The latter lay their eggs into the butterfly larvae immediately after hatching, thus serving as a major cause of butterfly mortality in the wild (Benyamini 1990). By following wild females while depositing eggs, I collected approximately 1200 eggs and reared them in a cultivation-room at a temperature of 20°C. After one month, I increased the temperature to 27°C to enhance synchronized pupating and adult hatching. Unfortunately, the mortality rates were high at all developmental stages due to diseases and cannibalism, and only 120 adult butterflies hatched. I used 100 individuals for the experiment, and released the others back to their original population, near Revivim.

7.2.3.2 Creating artificial patches in the field

Each of the artificial patches comprised 42 plants, arrayed in 14 clumps of three plants each. The clumps were arranged in five rows, with 2,3,4,3, and 2 clumps – creating a hexagonal formation with a diameter of 20m. This design was aimed at mimicking plant configurations in natural habitat patches, where, from my observations, the distribution of plants is often clumped. To ensure butterfly arrival at the artificial patches, I surveyed the study area for wild host plants, *Verbascum* and *Scrophularia* plants (Scrophulariaceae),

and removed their upper canopy (see Fig. 25). In this region the wild host-plants grow mostly along wadis. Therefore, the survey concentrated mostly on these areas.

Since both plant taxa are common in desert habitats where high grazing pressure occurs, I expected that the removing of their upper canopy would have little long-term effect on the host plants. To reduce any possible impact on the local butterfly population, I removed the plant canopy during the adult activity period (when the number of eggs and larvae are minimal). Host-plants downstream from the study area were left untouched, so that mated females would be able to locate these within a short time.

7.2.4 BUTTERFLY RELEASES AND RECAPTURES

The MRR experiment was held from May 20-June 20 2003. The duration of the experiment was constrained by two main factors: Firstly, releases could only be conducted within the short period of peak adult activity, in order to exceed a 'critical mass' of butterflies in the field. During the year 2003, this only occurred twice, in March and in May-June, yet the weather conditions in March were inadequate for consecutive days of work. Secondly, the low viability of the plants when translocated to the study site, as well as disturbances by indigenous nomads, allowed for only a single, short-term field experiment.

All butterflies were collected into cooling boxes immediately after hatching, and marked with sequential numbers on their wings using a permanent marker. I released 23 males and 48 virgin females at the designated release point. Additionally I released 21 males and 8 virgin females 45m south-west of the main summit (S_{602}), to enhance mating success when the density of adult butterflies was low (this occurred mainly in the second half of the experiment, when the activity of wild butterflies in the field decreased markedly). By releasing butterflies at this secondary release point I aimed to increase the chances of retrieving mated females later on. In addition to releasing marked butterflies, I marked wild butterflies that were observed during the experiment. These individuals were marked by letters and/or specific configurations of dots. I marked 35 butterflies on the main summit and 12 butterflies in other locations. In total, the MRR experiment included 147 marked butterflies.

Butterflies were released individually between 0930-1230 hours. Each release occurred after the previously-released butterfly moved at least 10-20m away from the release point, or after 15 minutes (whichever occurred first). If inactive due to weather

conditions or physical damage, the butterflies were recaptured and excluded from the analysis. With the aid of a second surveyor, I recorded the last time a butterfly was observed within a distance <20m of the release point. These data were not regarded as recaptures. Instead, they were used for estimating the time until the onset of hilltopping behavior (see below, section 7.2.5).

Surveys of the landscape and observations in the patches started an hour before the first release on each release-day, and lasted for ca. 30hrs subsequent to the last release (that is, between 0830-1530 hours). I performed transect observations along the predicted movement path from the release point toward S_{602}, between two to six times per day. The main summit (S_{602}) and an area of ca. 20×80m around it were surveyed for at least two hours each day, usually by one or two surveyors. I used three additional assistants for conducting observations in and around the artificial patches. Each surveyor allocated 20-30 minutes of each hour in search of butterfly activity in the patches, and the rest of the time surveying the area adjacent to the patch. These surveys included the summit near P_{SUM} (S_{ptch}) and the wadis adjacent to each patch (see Fig. 25). Additionally, once in every four observation days I performed a thorough transect survey along the entire length of two wadis that flank S_{602} from the west and south.

During the surveys and the observations in patches, each butterfly arrival at a patch was recorded. If not successfully captured, I took a conservative approach and assumed that the butterflies belong to the wild populations. Outside the patches, every butterfly was captured, checked for marks, and marked if necessary. The capture and recapture locations were marked using a GPS (Garmin GPS 12XL), with an accuracy of ca. 5m. I also recorded the location of six mating events. If one or both of the mating individuals were unmarked, I marked them during the mating process while making sure they were not disturbed by the marking process.

7.2.5 ANALYZING DISPERSAL RATES

Another goal of the field experiment is to assess dispersal rates. This information is necessary to include not only landscape-specific but also time-specific predictions in the model (see Chapter 6). I used several sources of data for estimating the movement rates. Firstly, I estimated the time that individuals spent around the release point (<20m of the release point). Secondly, I calculated the time elapsed from the moment of release until the first recapture on the main summit (S_{602}, a distance of 480m). Lastly, in order to obtain

a more accurate estimate of flight speed and dispersal rates I used direct observations of 12 butterflies (including two mated females). In these observations I followed individuals for 2-25 minutes, and recorded their locations every 5-10 meters using a GPS. The time-intervals between records depended on the activity of the butterflies, but were not shorter than one minute. I plotted the calculated flight-speed against the time interval between records, in order to evaluate the maximal movement speed ($\equiv$ flight speed) and the minimal one ($\approx$ low dispersal rate). Data from the 12 individuals were pooled, each pair of records taken as a separate data-point.

Given that a single field experiment was conducted, the following results are aimed primarily towards recognizing the limitations of the model rather than performing a systematic statistical analysis. This is because a more systematic quantitative analysis would require repeating the entire experiment in various locations and landscapes. For this reason, throughout the text, special attention is given to rare events or observations which may contradict the model.

7.3 RESULTS

7.3.1 MALES AND VIRGIN FEMALES

I recaptured 13 of 23 males (56.5%) and 14 of 48 virgin females (29.2%) that were released at the release point, in 49 recapture events. Most of the individuals were recaptured either on S_{602} or on the way to it. Hence, the average recapture distance was 272±204m (mean±SD), and the maximum was 506m. Females that were recaptured were either virgin or observed while copulating. Out of the butterflies that were released near S_{602}, I recaptured 10 of 21 males (47.6%) and 3 of 9 virgin females (33.3%), in 24 recapture events. The average recapture distance was 21.5±21.7m (mean±SD), and the maximal distance was 55.6m. Butterflies that were released near the summit were not observed elsewhere later on. The difference in recapture rates between males and virgin females reflects the strong tendency of males to adhere to summits.

It is noteworthy that two individuals which were released at the release-point were observed at S_{loc} (101m from the release point), and then recaptured again at the release point. One individual was observed at S_{602} and, on the same day, was recaptured again on S_{ptch}, 460m away.

Out of 33 wild males that were marked on S_{602}, 17 (51.5%) were recaptured in 35 recapture events. Fifteen of the males were observed on the summit, two were observed on S_{loc1} and one on S_{loc2}. The average recapture distance was 37.7±97.7m (maximum = 387m). Out of seven males that were marked on other summits, two (28.6%) were recaptured in three events. Both moved away from the summits, and were recaptured at maximal distances of 387m and 414m (the latter in a wadi).

The spatial distribution of recaptures (for reared butterflies only) is depicted in Fig. 29a. Note that most of the recaptures that took place on the 20×80 area surrounding S_{602} were clumped in one cell, as if they took place on the summit itself. This is because animals were in constant movement over the whole of the summit area. The recapture pattern can be compared to the Visits' Pattern predicted by the model (Fig. 29b), as well as to the Visits' Pattern normalized by the sampling effort (Fig. 29c). From a visual comparison between the Visits' Pattern and the recapture pattern, the model successfully predicted the high recapture numbers on S_{602} and around it, the low recaptures on S_{loc1} and the even lower recapture probability at the release point. It also predicted the lack of recaptures at S_{mul}, and the non-zero probability of recaptures on S_{ptch}. The main discrepancies between the predicted and the observed pattern were as follows:

1. The model overestimated the probability of recaptures along the path from the release point to S_{602}, as I observed hardly any individuals along the way (unless following them individually). This overestimation was partly due to the sampling effort along the way (see Fig. 29b vs. 29c).

2. If not corrected for the sampling effort, the model predicted that individuals would stop on S_{loc2} along their way to the main summit (local hump in Fig. 29b). Furthermore, the model did not recognize S_{loc1} as a point of interest. Since S_{loc1} is a local peak, several meters in width and about 1m in height, the coarse resolution of the model did not allow it to be recognized. In contrast, S_{loc2} was almost utterly undetectable in the field, and correspondingly, individuals were hardly observed there (except for one wild butterfly). Although the correction for sampling effort lessens this bias, I note that my sampling effort was also based on the observed behavior of the butterflies, and is not the sole cause of the bias.

3. The model underestimated the number of arrivals at S_{ptch}, and predicted animals would arrive at S_{ptch} only from the release point (see Fig. 30a). However, it should

be noted that three out of the four recaptures on S_{ptch} occurred in a single day, in which exceptional weather conditions prevailed.

4. The model seemed to underestimate the recapture probability at the release point. This is mainly due to the underlying assumption of the model that individuals move immediately away from the release point. In reality, individuals remained around the release point for certain time (see section 7.3.1.1 below), and often flew back towards the release point after an initial flight away.

Despite the above differences, I found a high quantitative agreement between the normalized number of expected visits and the observed number of recaptures (Fig. 30a; adjusted R^2=0.951, P<0.001). The strong correlation remained significant even when S_{602} was excluded from the regression (adjusted R^2=0.809, P<0.05). The residuals of the regression were not explained by distance from the release point (Fig. 30b; adjusted R^2=0.302, P=0.15). This indicates that the discrepancies between the observed and the expected patterns result from model assumptions and are distance-independent, at least at the examined scale and the specific landscape.

7.3.1.1 Butterfly movement rates

After release, 18 males (78.3%) and 28 females (58.3%) were observed a second time or more within 20m of the release point. The average staying time was 20±29 min for males and 15±38 min for virgin females (mean±SD). The maximal staying duration was 102 min for a male and 196 min for a female. The distribution of staying times differed significantly between males and virgin females (Fig. 31; χ^2=19.4, df=7, p<0.01), indicating the shorter time for females to leave the release point and the tendency of males to come back to the point of release after their initial flight.

Six males (26.1%) and eight females (16.7%) were recaptured on the summit after ascending from the release point. All but three butterflies were observed on the summit only on the day following the release (21h58m±06h38m, mean±SD). This translates into a movement rate of ≈ 70m/h (assuming that butterflies were inactive between ≈1600-0700 hours). The minimal time taken to arrive at the summit was 62 minutes for a female (≈460m/hour) and 76 minutes for a male (≈380m/hour). Since my daily observations were

only halted at the end of butterfly activity, these observations suggest that individuals often initiated the uphill movement only in the second day of their activity.

From observations in individuals, I found that the average flight speed for time-intervals of 1min was 0.927km/h (n=21), with a maximal speed of 3.24km/h. The recorded movement rate diminished with the length between recording intervals (Fig. 32, P<0.001), falling to less then 100m/h for longer intervals. Thus, all the three estimation methods yield similar results, indicating a dispersal rate ranging from several tens- to several hundred meters per hour. These results indicate that the time allocation between different activities is the major factor that affects dispersal rates.

7.3.2 MATED FEMALES

No reared females were recaptured after copulating, either in the patches or in the surveys.

Sixteen wild individuals were located in 18 capture and recapture events during surveys along wadis. All but two of these captures were females (Table 10). Only four individuals were observed inside patches, all moving rapidly through the patches. As a result, none of these were captured or identified. It is noteworthy that no *M. trivia* butterflies were observed in P_{SUM} despite the proximity of this patch to a summit (S_{ptch}). The number of butterflies captured along the two major wadis (near P_{WF}) was higher than in other wadis, also after correcting for the relatively high sampling effort in the former (Table 10). This pattern may simply reflect the natural distribution of plants, as well as host-plants, in the experimental area. Namely, deeper stream-beds receive more water and thus support more plants. Out of two wild females that were marked on the S_{602}, one female (a mated one) was recaptured twice – first on the same summit, and then in a wadi at a distance of 699m from it. Out of five wild females that were marked in other locations, one was observed again twice at the point where it was marked (in a wadi).

7.4 DISCUSSION

7.4.1 MALES AND VIRGIN FEMALES

In this chapter I compared the model with the 'real world'. I analyzed the performance of the model in predicting the movement patterns of males and virgin females in a

topographically complex landscape, and the consequent distribution of recaptures over several distances and a range of expected recapture-probabilities. Previous theoretical studies and empirical ones on dispersal have suggested that recapture probabilities should diminish rapidly with distance (Turchin 1998; Clark et al. 1999; Bullock & Clarke 2000; Cain et al. 2000; Wiens 2001; Williamson 2002). In contrast, in this study both the predicted and the observed patterns diverged strongly from this decaying function. Recapture rates remained very high even in fairly large distances ($\approx$ 50%), and occurred in specific locations – mainly, but not exclusively, on summits. I term such points 'recapture hotspots'. These results provide empirical evidence that recapture success becomes less dependent on distance when animal movements are directed by landscape heterogeneity. This is rarely shown in field studies of animal dispersal, although more widely recognized in the field of seed dispersal (Jordano & Schupp 2000; Schupp et al. 2002; Gómez 2003; Wehncke et al. 2003). The qualitative and quantitative ability of the model to predict the location and extent of 'recapture hotspots' may therefore be of great importance to field studies of dispersal in heterogeneous landscapes. Yet further research is required to determine the spatial scales within which the patterns of 'recapture hotspots' prevail. Perhaps, at a certain distance, the impact of distance is greater than the impact of landscape heterogeneity, and a 'diminishing' recapture-success may replace the 'recapture hotspots' pattern.

7.4.1.1 The power and limitations of the model

The model's main power lies in its simplicity. With only two behavioral parameters (the consistency p and the response to topography q), the model yielded accurate predictions of the movement patterns in a specific landscape of a certain complexity. I obtained a general agreement between the *Visits' Pattern* in the model and the observed recapture pattern, both qualitative and quantitative. Moreover, the model successfully predicted the existence of rare events – such as the occasional arrivals of individuals to S_{ptch} – despite the simplifying assumption that animal recognition-distance is limited. However, the divergence between the model and the observed pattern suggests caution. Since the extent and directionality of rare long-distance movements have profound effects on the dynamics of spatially-structured populations (Williamson 2002), predicting long-term and large-scale patterns may require high quantitative accuracy. Hence, the inaccuracies of the

model, as described above, may explain the model's failure in detecting the overall pattern (i.e. the combination of two movement-steps, as it is reflected in the arrival of mated females at patches). This may demonstrate the need for highly accurate quantitative predictions of mating locations, to lessen accumulating spatial errors. In the following section, I discuss the discrepancies between the model and the observed patterns in light of the possible ways in which the modeling approach could be improved, in order to achieve more accurate predictions.

a. The model seemed to underestimate the number of arrivals at summits other than the main one (S_{602}). It overestimated the adherence of males and virgin females to summits, as suggested by several observations of individuals who moved to other summits or even toward the release point and the wadis. One reason for this may be that the perceptual range of butterflies is greater than hitherto assumed. This is suggested by the observation of one individual on S_{602} and later that same day on S_{ptch} (a distance of 460m, through a route which was not predicted by the model), as well as a hilltopping Satyridae butterfly which was observed flying in a straight line from S_{602} toward S_{ptch} until disappearing from sight.

b. The model assumes that animals respond to gradients similarly in all cases, choosing the steepest slope out of the ones available. Consequently, even in seemingly flat landscapes, males and virgin females are expected by the model to seek summits and concentrate at higher points, while in reality they do not respond to the topographic attributes. This was evident by the fact that S_{loc2} was undetectable in the field. Similarly, the area surrounding S_{602} seemed to be nearly flat, while the model recognized it as three distinct summits. A slope-dependent response to gradients should thus be incorporated, so that threshold-like responses can be modeled.

c. The current form of the model makes no predictions as to dispersal rates. The field experiment provided such data, which, if incorporated into the model, would enable the model to make time-specific predictions. This, in turn, would enable searching for the butterflies in the field based on the anticipated time horizon for their arrival at different locations in the landscape. This should take into account the adherence to the release-point and summits, the mating process itself (which I observed to last from 30min to over three hours), and possible differences in movement speeds between different states. Such differences in movement speeds

may also be important since they affect the probability of mating along the way to the summits (e.g. if males and virgin females move at different speeds).

d. Cell size – a local summit was not recognized by the model, while clearly seen by the individuals. Its main feature was a heap of stones that clearly distinguished it from the surrounding terrain and drew the butterflies' attention. The model's sensitivity to cell size seems even greater in the context of mated female behavior. The model evidently overestimated mated female recapture success. A map with smaller cells is effectively larger (Chapter 6), and thus the recapture probability is easily overestimated by models that use coarse, 'effectively small' matrices. The difficulties of selecting a "correct" grid cell size for modeling are broadly discussed by landscape ecologists (e.g. Turner et al. 1989; Cullinan & Thomas 1992; Obeysekera & Rutchey 1997; Farina 1998).

From the weaknesses described above, a major improvement of the model can be achieved by reducing the butterflies' adherence to summits. Preliminary simulations indicated that this could be done simply by increasing consistency (p), but this evidently results in consistency values that are not biologically sound (especially given the map's cell size; see Chapter 6). Alternatively, the consistency can be modified as a function of time. For instance, individuals may leave a summit (perhaps in a straight line) if a certain time has passed without interactions with conspecifics. Another option for reducing the adherence to summits can be to increase the perceptual range of the topographical signal, in accordance with statement (a). However, incorporating this ability into the model might lead simulated butterflies to move between summits whenever recognizing new summits. This may even result in a constant move between summits, which is of course non-optimal and biologically unrealistic (Gruber 2002). Therefore, increased perceptual range could only be incorporated as a function of time. Since both improvements (increased consistency, increased perceptual range) require time-dependent behaviors, I conclude that the major weakness of the model is in its assumption that the behavioral rules are constant over time and space (see also Chapter 5). Incorporating time-dependent behaviors may allow for modeling the movements of various animal species.

7.4.1.2 A comment on the lekking hypothesis

My modeling approach followed Lederhouse's (1982) hypothesis that hilltopping is a lekking behavior – in which males form aggregations that are visited by females for the purpose of mating. Mated females seem to choose males either based on the males' behavior or their relative location to other males in a group (see Alexander 1975; Thornhill 1983; Queller 1987). Correspondingly, in the model I allowed females to mate only after several encounters with males. In reality, I did not observe any virgin female refusing males, either in this field experiment or in the previous one (Chapter 2). This implies that hilltopping females may not actively choose males, and therefore hilltopping cannot be regarded as a clear lekking behavior. Nevertheless, in several cases I observed a male and a virgin female passing each other at a distance of a few meters or less without noticing. Such a low perceptual range for recognizing conspecifics suggests that the mating probability increases with butterfly density, in accordance with the lekking phenomenon. In this respect, the modeling approach is closer to reality: in the model, if a male and a virgin female stay at the same cell for several time-steps, they have an increased chance of mating simply because they repeatedly encounter each other, regardless of butterfly density.

7.4.2 MATED FEMALES

Various reasons can account for the lack of recaptures. Firstly, the low number of butterflies observed in the artificial patches, including the wadi-fork patch (P_{WF}), indicates that the patches did not attract butterflies as expected. Secondly, the model predicted that mating events should take place mainly on S_{602}. Yet the model seems to have overestimated the adherence of males, and probably even more so of virgin females, to summits. Mating events could take place in other locations, shifting the starting point of the movement of mated females from the expected one. Low mating success and/or low survival of the mated females could also explain the lack of mated-female recaptures. However, the lack of mated-female recaptures, and to some extent the distribution of arrivals of (unrecognized) butterflies at two patches, corresponds with the '*low recapture success*' scenario, implying that mated females either respond weakly to topography or do not respond to topography at all. Naturally, the lack of recaptures cannot serve as a conclusive evidence for the behavior of the mated females. Nevertheless, several inconclusive results still lend support to this conclusion:

a. The model predicted low recapture success if the mated females moved randomly.

b. Given the relatively high number of recaptures of other butterflies along the wadis, it is somewhat improbable that mated females in this study flew along the wadis.

c. The results of previous field studies (Wickman 1988, Chapter 2) and several simulation results (Chapters 5 & 6) also indicate that mated females should either fly randomly or respond very weakly to topography.

The results of this fieldwork seem to exclude the possibility that mated females respond moderately to the topographic signal, even in a hyper-arid landscape where plants are distributed along wadis. This is in contrast to the results of Chapter 6, which suggested that mated females should respond moderately to topography if the natural distribution of host plants is along stream-beds. However, based on this study I am unable to determine whether the mated females respond weakly to topography or do not respond to topography at all. Since previous simulation results suggested that a slight response to topography may be an optimal behavior (Chapter 5), and pointed out the importance of such response to connectivity patterns (Chapter 4), it may be important to conduct further experiments to establish what the detailed behavior of the mated females is. This may require a much larger sample size, or the use of further individual-based observations.

7.4.2 WHAT CAN WE LEARN ABOUT MRR EXPERIMENTS?

This chapter has presented the results of an MRR experiment in a topographically complex landscape. I have shown that this approach is effective for depicting spatial patterns and analyzing the movements of males and virgin females in a heterogeneous landscape. However, since mated females were not recaptured, this experimental approach could not predict the overall, two-step movement pattern, as expressed by the arrival of mated females to patches. This is despite the relative simplicity of the experimental design, in which males and virgin females were expected to move along one route and arrive at a single mating point. This may point to the complexity of modeling canalized movement patterns over heterogeneous landscapes, even when the behavioral rules are known to a large extent. It also shows that MRRs may be effective only when a large number of individuals can be obtained for the experiment, and when the movement comprises a single movement behavior (which may or may not be random). In a case where two or more movement steps occur, the success of an MRR may be limited due to accumulating spatial errors and uncertainties. For instance, in the case of hilltopping the

number of mated females and their starting point could not be determined. Thus, spatial errors can only be avoided if the mating locations are predicted with great accuracy.

Another limitation of MRRs is evident already in the results of the preliminary simulations. Namely, this experiment could not elucidate the detailed movement parameters of mated females even if large numbers of butterflies were captured. It could only differentiate between random movement and a moderate response to topography. For the purpose of detailed quantification of behavior, an individual-based approach seems more appropriate, requiring less individuals and, perhaps, less effort (Wiens et al. 1993; Turchin 1998).

Lastly, the results of MRR studies are often summarized by plotting the recapture success against distance from the release point (see e.g. Turchin 1998; Williamson 2002). Although this approach may be useful for understanding spatial patterns, it also tends to over-simplify them. In fact, by averaging many zero results over the landscape, a diminishing pattern is almost inevitably obtained. This simplifying approach results in the loss of vital information which is coded by the landscape, that may be important for both theoretic and applied purposes (see also Schupp et al. 2002). Taking a landscape-specific approach, in which Visits' Patterns are plotted over a two dimensional map, may be of great importance for applied purposes. It enables the identification of 'recapture hotspot' patterns, both through modeling and direct observations. Thus, combining modeling and MRRs could be a highly effective form of analysis.

The experimental approach presented here calls for broader field studies and observations, in order to determine movement patterns and connectivity in more complex landscapes and experimental designs, and within larger spatiotemporal scales.

Table 10: Recaptures in patches and in wadis surveyed around patches. The transect area along wadis near P_{WF} was 600m, but surveys were conducted back and forth.

Patch name	In Patch - unknown	In Patch - Cultivated	In Surveys – wild/unknown	Total Observed
P_{SUM}	0	0	2/300=0.0067	2
P_{SL}	2	0	1/200=0.005	3
P_{WF}	2	0	15/1200=0.013	17

Figure 25: Study area and location of the release point ($\bowtie$) and the three patches ($\otimes$). Solid lines represent main survey paths. Dashed blue lines represent additional areas that were surveyed less regularly. All the surveyed areas were cleared of wild host-plants prior to the onset of the experiment.
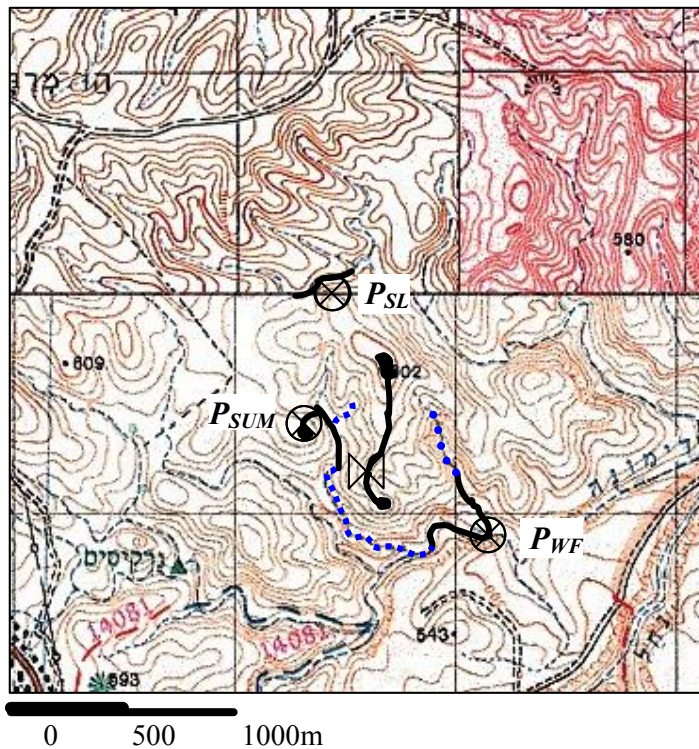
Figure 26: The Visits' Pattern of males and virgin females to each cell in the matrix – the number of visits to each cell vs. its distance from the release point, in a virtual 100×100 cells landscape with one summit at a distance of 180m of the release point (cell side = 5m). The response to topography $q_{m+v} = 0$ (a); 0.1 (b); and 0.3 (c). When animals respond to topography (b,c), a hump-shape pattern is generated around the summit due to animal adherence to it (note the y-axis units).
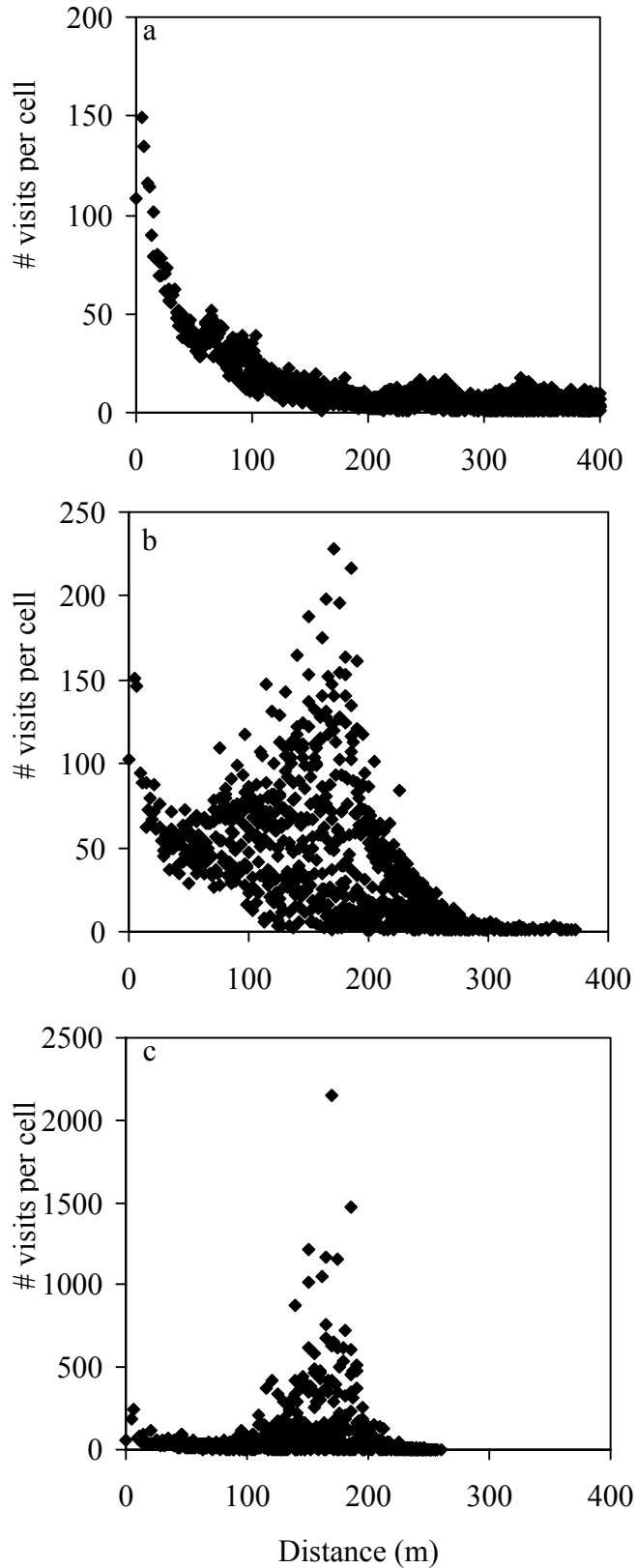
Figure 27: (a) the predicted Visits' Pattern (log(number of expected visits)+1) for the field experiment. Arrows and labels indicate the location of five summits and the release point. Dotted red lines delineate the two main areas that were surveyed. Dashed white lines depict the main areas that were surveyed in the search for mated females. Simulation parameters: p_{m+v}=0.2 and q_{m+v}=0.9, for 200 butterflies and 300 time-steps, in 10 simulation repeats.
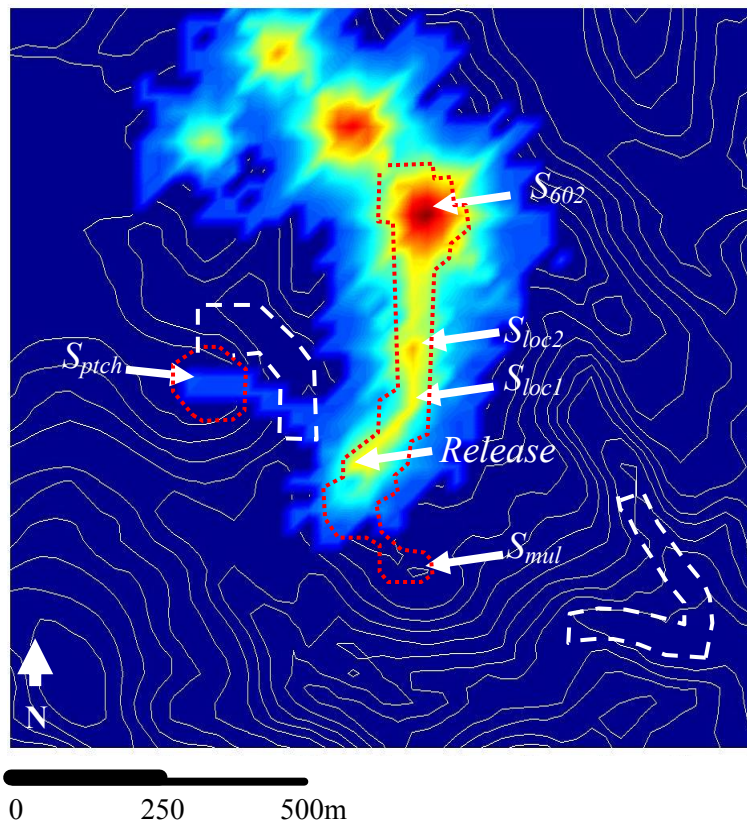
Figure 28: The estimated probability of a mated female to arrive at the three artificial patches vs. the hypothesized movement parameter of the mated females (q_f).
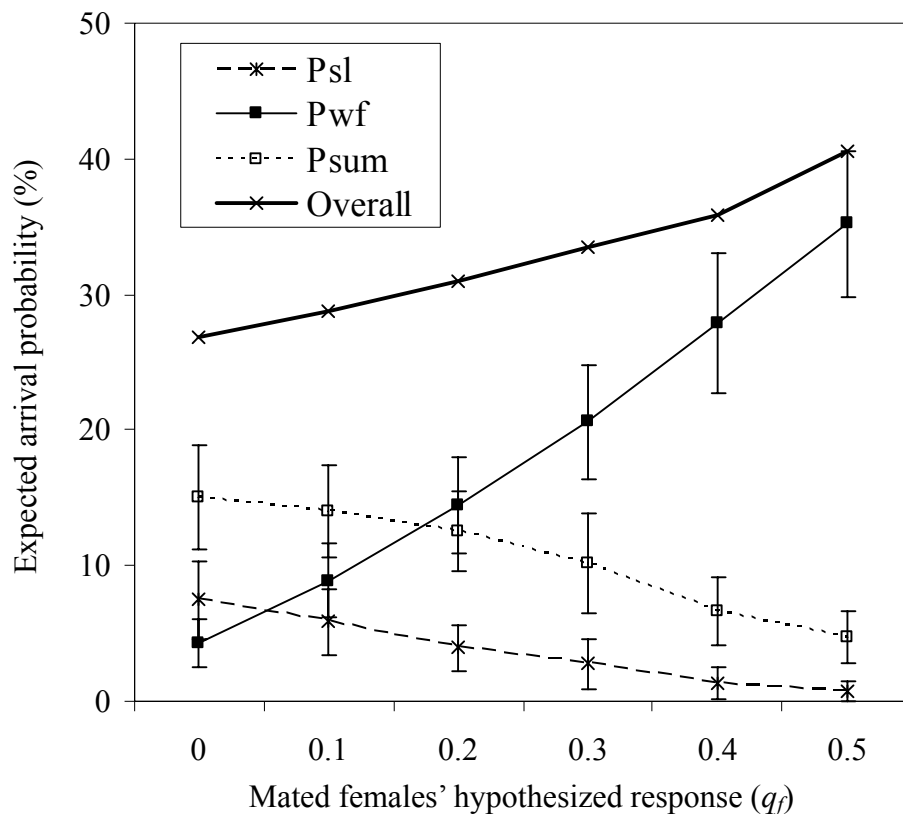
Figure 29: (a) The observed number of recaptures in the sampled area, viewed from West (-90°) with a 70° tilt. White lines depict the surveyed area (red dotted lines in Fig. 27). (b) The Visits' Pattern: similar to Fig. 27, but presents the (log) number of expected visits only for the sampled area. View-point similar to (a). (c) The (log) expected number of visits multiplied by the sampling effort (total number of observation hours).
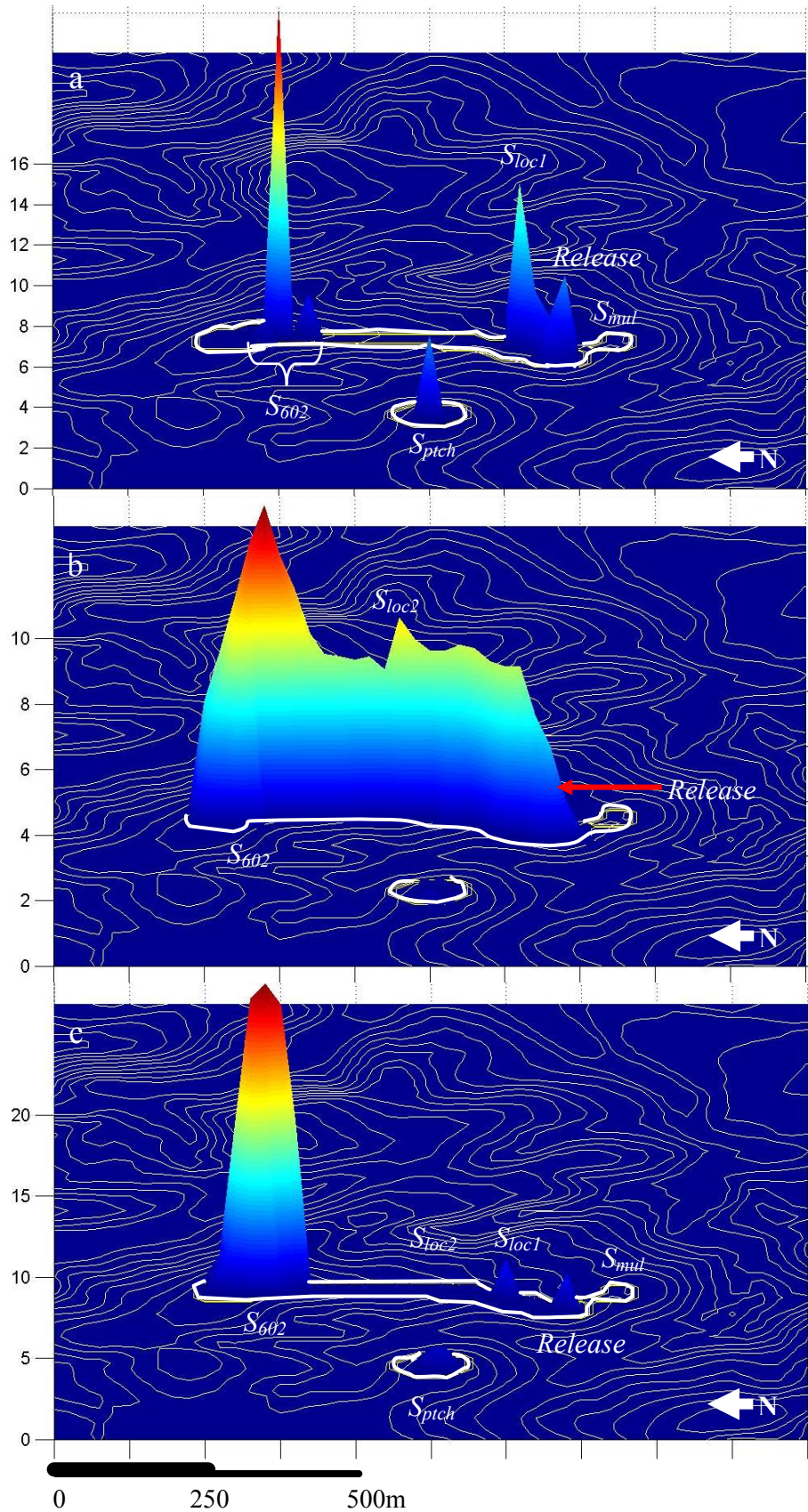
Figure 30: Quantitative evaluation of model accuracy. (a) Number of observations vs. log(number of predicted visits)+1), after normalization by the sampling effort (number of observation hours) at the five summits and the release point. After exclusion of S_{602}, adjusted R^2=0.809. (b) The residuals of the linear regression from (a), plotted against the distance from release point.

a

$y = 4.4938\text{Ln}(x) - 0.8306$

$R^2 = 0.9611$, p<0.001

Number of recaptures

(log(number of visits+1))*samplingeffort

b

$y = -0.0053x + 1.2321$

$R^2 = 0.4415$, n.s.

Residuals

Distance from release (m)
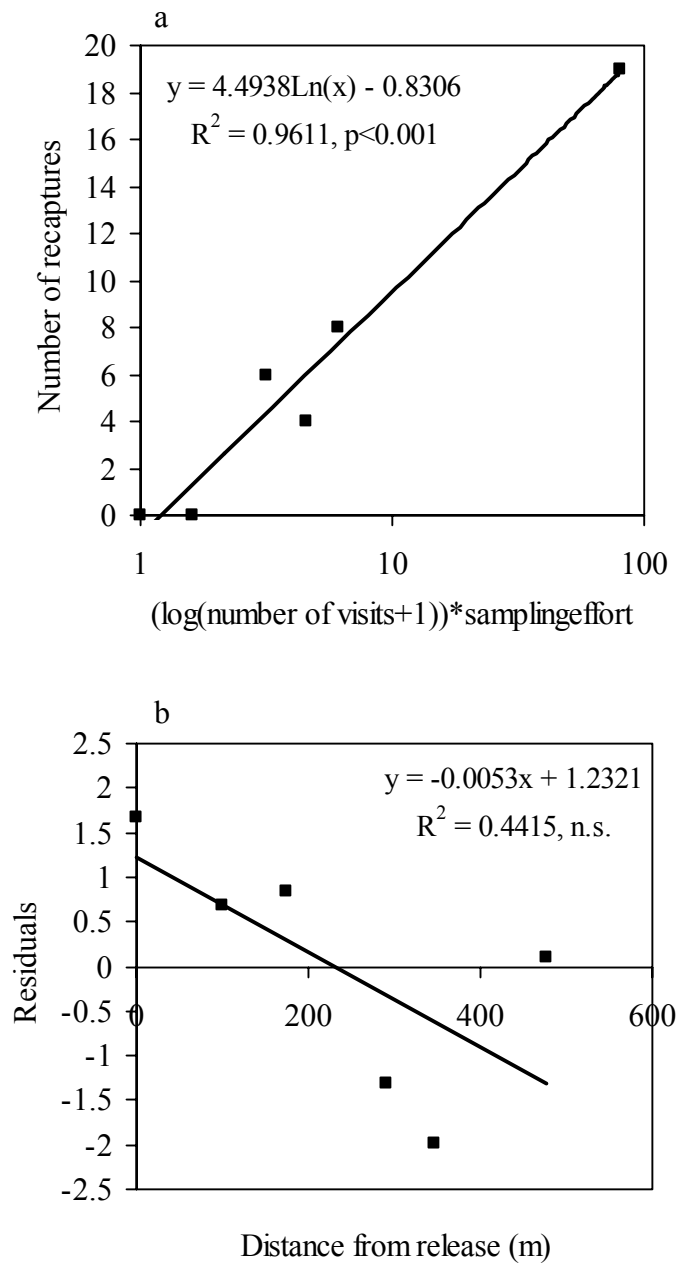
Figure 31: Distribution of staying times at the site of release (<20m of the release point) for males (empty columns) and virgin females (full columns). Males tended to stay longer than virgin females.
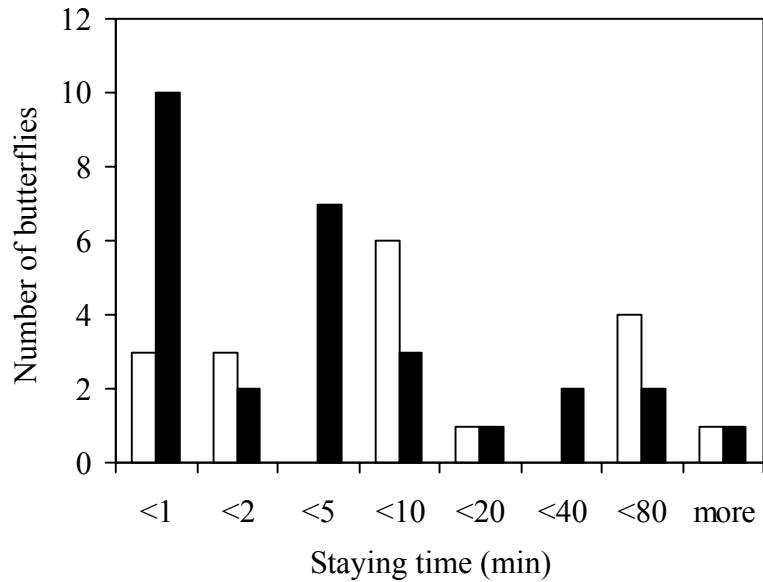
Figure 32: Log(movement speed) vs. log(time interval between records). n=55, from 14 butterflies.
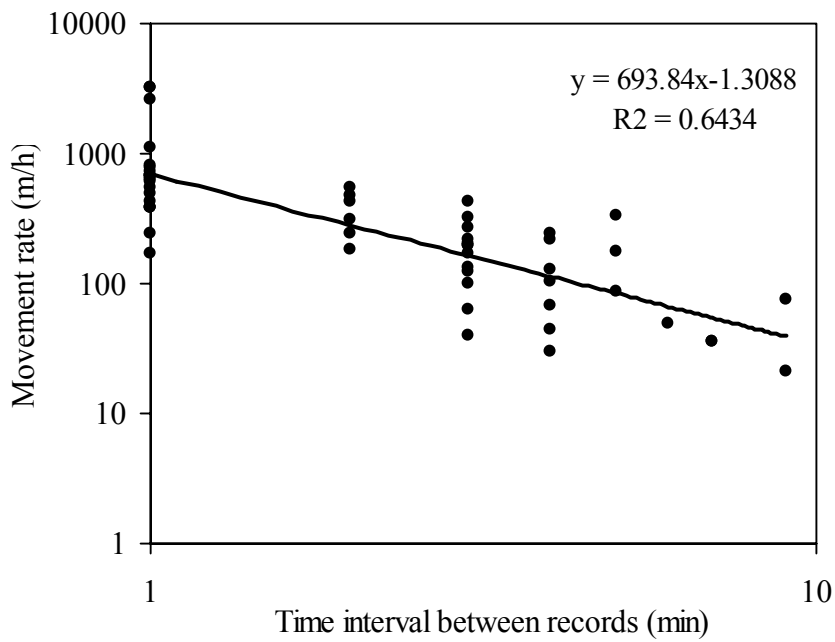
8. DISCUSSION

8.1 MODELING DISPERSAL IN HETEROGENEOUS LANDSCAPES

Animal behavior, and specifically how the landscape is perceived and interpreted by the individual, has recently been established as a major key for studying and understanding dispersal patterns (Wiens et al. 1993; Van Vuren 1998; Nathan 2001; Osborne et al. 2002). Once the behavioral mechanisms are known, they need to be incorporated into a proper modeling framework for determining the specific routes that animals are expected to use, for the recognition of both corridors and barriers to dispersal.

Due to the complexity of modeling dispersal through heterogeneous landscapes, many spatially-explicit models assume that the landscape is effectively homogeneous (Fahrig 1992; Adler & Nuernberger 1994; Hanski et al. 1994,1996a,b; Bascompte & Sole 1996; Frank & Wissel 1998; Hanski 1998). With the recent realization that landscape structure has fundamental effects on connectivity (Ricketts 2001), models increasingly incorporate landscape heterogeneity and evaluate its impact on dispersal, connectivity and population dynamics. However, these models often use maps with several discrete types of habitat, so that changes between habitat types occur abruptly (Gustafson & Gardner 1996; Schippers et al. 1996; Akçakaya & Atwood 1997; Moilanen & Hanski 1998; Morales & Ellner 2002; Schadt et al. 2002). The use of such maps forces the assumption that animal movements within a given habitat type are effectively random, and animal-landscape interactions are confined to the border between habitats (see Wiens et al. 1993; Gustafson & Gardner 1996; Haddad 1999; Malanson & Cramer 1999; Morales & Ellner 2002). In contrast, my study demonstrates that topographic gradients (which may occur within a certain habitat) direct animal movements and canalize them into 'Virtual Corridors' (Chapter 3). I therefore conclude that current techniques of modeling habitat connectivity tend to underestimate the proportion of non-random movements taken by animals. Furthermore, two independent results of this research have indicated that directed movements, and consequently also Virtual Corridors, can be expected in many landscapes and contexts. Firstly, I have found that canalized movement patterns may be induced even by a slight response to topography, and prevail through a wide range of behavioral and spatial parameters (Chapter 4); and secondly, simulations have indicated

that the optimal movement behavior incorporates a significant element of randomness (Chapter 5). In mated females, the optimal movement behavior was found to be almost totally random. These results imply that slight responses to landscape heterogeneity may sometimes be optimal. Since such responses are also enough to evoke canalized movements, I have concluded that field studies can easily fail to recognize canalized movements due to their being obscured by random behavior.

The need to address animal responses to gradients is further emphasized when considering the common definition of 'patches' in current spatial models. Many models assume that patches, like oceanic islands, have discrete borders (With et al. 1997; Farina 1998), and that therefore animals can only perceive patches within a certain distance. However, gradients that are indicative of the location of patches may obscure their borders and increase the ability of animals to identify and colonize patches.

This work demonstrates the importance of topography as a prominent directing element of animal movements. It shows that the response of animals to topography *per se* should be more carefully addressed in studies of dispersal, connectivity, and population dynamics in fragmented landscapes. Especially, I have shown that directed movement patterns evolve due to the response of animals to topographical gradients. However, many other sources of landscape heterogeneity often change gradually across landscapes: habitat suitability, temperatures, soil moisture, humidity, chemical compounds that can be sensed by individuals, and others. These may direct animal movements while searching for elements that are necessary for their survival or reproduction, such as patches of suitable habitats, conspecifics, or essential resources along their route (water, food, or shelter). Therefore, I suggest that directional movements and consequently also Virtual Corridors may evolve whenever animals respond to gradients, in a wide variety of contexts.

The response to gradients is known to play an important role in homing birds (Phillips 1996; Wallraff 2000; Wiltschko & Wiltschko 2003) and in conspecific recognition in insects (Fadamiro et al. 1998; Yamanaka et al. 2003 and references therein). Wiens (1992) discusses aspects of animal behavior on the boundary between landscapes, but this discussion is limited to ecotones. It is surprising that the response to gradients is poorly represented in modeling animal dispersal and patch-recognition processes.

I speculate that new analysis, which fully incorporates animal responses to gradients in heterogeneous landscapes, would elucidate the impact of canalized movements on the structure and sustainability of spatially-structured populations. This work provides novel tools and approaches to tackle this, and re-examines the frequency of directed movements in heterogeneous landscapes.

8.2 A SINGLE MODEL FOR TWO PURPOSES

In this study I used a variety of tools to address non-random movement patterns in topographically complex landscapes. These included individual-based field observations, an individual-based model, and a Mark-Release-Recapture (MRR) experiment. This work demonstrates the power of combining field experiments and modeling work, for generating and testing ecological and evolutionary theorems. By systematically increasing the complexity of the model and the landscapes in use, I have obtained generalizations on the one hand, and derived valid landscape-specific predictions on the other hand. Thus, I have demonstrated that understanding patterns and predicting them are not mutually exclusive.

I first analyzed movement patterns with respect to behavioral and spatial parameters, irrespective of the observed behavior. By doing this I obtained a comprehensive understanding of the outcomes of the response to topography on movement patterns in a variety of landscapes. I have demonstrated that generalizations can be made despite the variety of landscape configurations. By analyzing the accessibility of summits as a function of distance, I revealed that the canalization of movements takes a clear and robust form (Chapter 4). Thus, analyzing accessibility patterns serve as a powerful methodology for recognizing canalized movements and quantifying their extent.

I have shown, however, that the structure and orientation of Virtual Corridors cannot be intuitively predicted over realistic complex landscapes. This is because the movement patterns depend on the spatial configuration of the landscape, the location of the patches, and the behavioral parameters. These results suggest that landscape-specific predictions of animal movement paths can only be obtained with the use of IBMs. The simplicity of my model, in contrast to many of the currently used IBMs (Grimm 1999), implies that even simple and general models can be used for this purpose.

I have further demonstrated that the model is capable of mimicking 'real world' behaviors. Despite its low number of parameters and the simple behavioral rules, it yielded optimal behaviors that were highly equivalent to the behavioral parameters observed in the field (Chapter 6). Furthermore, the model successfully predicted the recapture patterns of males and virgin females in the field (Chapter 7). I obtained rare evidence, both theoretical and empirical, that the recapture probability does not necessarily decay with distance when animals respond to landscape heterogeneity. Instead, a 'recapture hotspots' pattern evolved. Thus, I conclude that the model is also capable of providing landscape-specific predictions of high validity (but see section 8.5 below).

8.3 HILLTOPPING AND DISPERSAL

Due to the difficulties of identifying dispersal events and keeping track of individuals during dispersal, the knowledge of animal behavior during dispersal is still limited (Zollner & Lima 1999; Nathan 2001; Williamson 2002). In order to retrieve sufficient numbers of dispersing animals, researchers often attempt to enhance dispersal by translocating animals out of their habitat patches (Turchin et al. 1991; Schultz 1998; Turchin 1998; Conradt et al. 2000; Haddad 2000; Conradt et al. 2001; Nathan 2001; Gobeil & Villard 2002; Goheen et al. 2003). An alternative approach is to study dispersal-like movement behaviors that may occur more commonly. My field methodology combined both approaches: I displaced individuals out of their habitats, and thereby enhanced a dispersal-like behavior (hilltopping). Although the ecological function of the first stage of hilltopping is finding a mate and not dispersal *per se*, it is comparable to dispersal in several aspects:

1. Hilltopping behavior leads animals out of their habitat patches and directs them through the so-called, hostile matrix.

2. 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.

3. Once animals initiate a hilltopping movement, they may fly persistently upwards and cover large distances (several kilometers or even tens of kilometers; (Shields

1967); Benyamimni, unpublished data). Similar patterns have been identified in studies of dispersal, where animals altered their movement behavior upon leaving their habitats and moved persistently in straight trajectories (e.g. Schultz 1998 and references therein; Schultz & Crone 2001; Bulger et al. 2003).

4. The spatial scale of hilltopping (i.e. moving hundreds of meters and more) 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; Gomez 2003).

I conclude that the similarities between hilltopping and other dispersal behaviors justifies applying the ideas and results of this study to 'real' dispersal behaviors. Yet, naturally, to apply them to other species one should consider the characteristics of the directing element, as well as the resolution of animal perception, along with the behavior of interest.

8.4 FURTHER DEVELOPMENT OF 'THE HILLTOPPING MODEL'

As its name suggests, 'the Hilltopping Model' is so far able to analyze movement patterns for one type of behavior. Its main strength is in its simplicity, achieved by the low number of behavioral parameters. This allows us to gain a general, species independent understanding of animal movements through heterogeneous landscapes. However, even for the hilltopping behavior alone, the predictive power of the model is still limited, especially with respect to the recapture pattern of mated females (Chapter 7). The model's inability to provide predictions for the two step process of hilltopping (as expressed in the arrival of mated females to patches), suggests that further improvements are necessary to predict the mating points and the overall pattern more accurately. I hereby describe several major changes in the model that are necessary for deriving more accurate landscape-specific predictions for applied purposes, as well as to adapt the model for analyzing other behaviors.

8.4.1 Addressing connectivity in its full sense

My study addressed the processes that occur during dispersal itself for the purpose of understanding how landscape heterogeneity affects connectivity. However, I assumed that animals are already dispersing through the matrix, and addressed only the processes that

occur during this stage of the movement. By doing this I followed the concept of 'connectivity' as it was defined by (Taylor et al. 1993): "the degree to which the landscape facilitates or impedes movement among resource patches". However, to provide quantitative predictions of connectivity in the context of population- and metapopulation dynamics, one should address two more processes that could not be addressed within the scope of this study: the tendency to leave habitat patches, and the chances of dispersers to establish themselves successfully in new patches (Harrison 1989; Noss & Cooperrider 1994; Moilanen & Nieminen 2002). Leaving habitat patches may clearly be a directional process by itself, due to the characteristics of habitat boundaries and landscape structure within and around patches (Wiens et al. 1993; Moilanen & Hanski 1998; Matthysen 2002; Schtickzelle & Baguette 2003). More importantly, both processes – leaving habitat patches and settling successfully in others – are largely affected by population densities and by patch-dynamics (see Hanski 2001; Nathan 2001; Sutherland et al. 2002 for reviews). I conclude that two main factors should be incorporated into the model for predicting connectivity: (a) density dependent processes both within and between patches; and (b) the initial directionality of dispersal (i.e. when leaving habitat patches) given the attributes of the landscape within patches and in the area surrounding them. For instance, habitat quality in the "matrix", as well as vegetation structure, may determine the tendency to leave a patch in a certain direction (e.g. Kuussaari et al. 1996).

8.4.2 Incorporating memory and learning

In Chapter 7 I concluded that the main deviations between the model and 'reality' result from the need to incorporate time-dependent behaviors, processes that may occur due to memory and learning. For instance, incorporating memory may be necessary to model the ability of butterflies to return to the point of release after a certain time (see Chapter 7, Conradt et al. 2000; 2001). The need to incorporate learning processes and memory is further emphasized by the high efficiency of many optimizing algorithms that incorporate them (Laarhoven & Aarts 1987; Goldberg 1989; Glover & Laguna 1997; Devroye & Krzyzak 2002 Chapter 5). Adding time-dependent processes to the model should give it the flexibility to fit the behavior of many species, yet result in a more complex model.

8.4.3 Threshold-type responses

The results of chapter 7 further indicated that threshold-like responses should be taken into consideration in modeling animal movement. The model recognized directional movements in places where the topographical attributes seemed unrecognized by individuals, either because the slope was marginal or because other attributes of the landscape were dominant over topography. Threshold-like responses are thus important to avoid overestimating the directionality of movements. Additionally, they are necessary to develop biologically sound movement rules for other species and behaviors. For instance, some animals may be incapable of moving through steep topographies. Naturally, threshold-like behaviors may be species-specific and possibly even landscape- and context-specific. Therefore, adding such parameters may increase model complexity and reduce its generality.

8.5 IMPLICATIONS FOR CONSERVATION

When animal populations are restricted to a small number of habitat patches, the ability to identify Virtual Corridors becomes crucial. Under these conditions, the number of movement paths and their structure become vital for the functioning of the system. While some movement paths could maintain connectivity, others may lead animals away from patches, to die in the 'hostile matrix'. Routes which contribute to connectivity should be recognized and preserved, while the leakage of individuals into the matrix, through 'dead end' routes, should be prevented. Furthermore, patches that are better connected should have higher priority for conservation purposes. However, as demonstrated by this research, such landscape-management decisions require a better understanding of the decision-making processes that animals perform while dispersing. I have shown that, when animals respond to landscape heterogeneity the recognition of these routes may not be intuitive. I have further demonstrated that connectivity between patches cannot be predicted simply from the distance between them. Thus, it is of great importance to identify the major factors that determine connectivity in different species and landscapes, and incorporate them into a proper modeling framework that can accurately predict the routes taken by animals. With better predictive tools, better ways can be found to identify priority areas for conservation, and to find more efficient ways to preserve or enhance animal movements between habitat patches.

My research provided a first systematic, hierarchical study of animal-landscape interactions in the context of topographic heterogeneity. It addressed the need to obtain empirical data on animal behavior during dispersal, as well as the need to use these data in developing individual, behavioral-based modeling frameworks. It provided a comprehensive understanding of the consequences of animal response to topography on dispersal patterns, along with rules of thumb for conservation. In this way I have balanced two contrasting needs: the scientific need to understand nature on the one hand, and the urgent need to apply this knowledge to conservation practices on the other hand.

9. REFERENCES

Adler, F. R. & Nuernberger, B. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology*, **45**, 41-75.

Akçakaya, H. R. & Atwood, J. L. 1997. A habitat based metapopulation model of the California gnatcatcher. *Conservation Biology*, **11**, 422-434.

Alexander, R. D. 1975. Natural selection and specialized chorusing behavior in acoustical insects. In: *Insects, Science, and Society* (Ed. by Pimentel, D.). Academic Press, New York, US, pp. 35-77.

Anderson, G. S. & Danielson, B. J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecology*, **12**, 261-271.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355-366.

Baguette, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. *Ecography*, **26**, 153-160.

Bakker, V. 2002. Scale-dependent movement behavior of red squirrels (*Tamiasciurus hudsonicus*) in logged landscapes. *ESA 87th annual meeting, 4-9 August 2002, Tucson, Arizona*.

Bascompte, J. & Sole, R. V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology*, **65**, 465-473.

Beebe, W. 1949. Migration of Papilionidae at Rancho Grande, north-central Venezuela. *Zoologica*, **34**, 119-126.

Beebe, W. 1950a. Migration of Danaidae, Ithomiidae, Acraeidae and Heliconidae (butterflies) at Rancho Grande, north-central Venezuela. *Zoologica*, **35**, 57-68.

Beebe, W. 1950b. Migration of Pieridae (butterflies) through Portachuelo Pass, Rancho Grande, north-central Venezuela. *Zoologica*, **35**, 189-196.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management*, **59**, 228-237.

Beier, P. & Noss, R. F. 1998. Do habitat corridors provide connectivity? *Conservation Biology*, **12**, 1241-1252.

Bélisle, M. & St. Clair, C. C. 2001. Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology*, **5**, 9. [online] 5 UR - http://www.consecol.org/vol5/iss2/art9.

Bell, W. J. 1985. Source of information controlling motor pattern in arthropod local search orientation. *Journal of Insect Physiology*, **31**, 837-847.

Bellamy, D. E. & Byrne, D. N. 2001. Effects of gender and mating status on self-directed dispersal by the whitefly parasitoid *Eretmocerus eremicus*. *Ecological Entomology*, **26**, 571-577.

Bennet, A. F. 1999. *Linkage in the landscape: the role of corridors and connectivity in wildlife conservation.* IUCN, Gland, Switzerland.

Bennetts, R. E., Nichols, J. D., Lebreton, J. D., Pradel, R., Hines, J. E. & Kitchens, W. M. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. In: *Dispersal* (Ed. by Clobert, J., Nichols, J. D., Danchin, E. & Dhondt, A.). Oxford University Press, Oxford, UK, pp. 3-17.

Benyamini, D. 1990a. *A Field Guide to the Butterflies of Israel, Including of Mt. Hermon and Sinai*. Keter Publishing House, Jerusalem (In Hebrew).

Boone, R. B. & Hunter, M. L. 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. *Landscape Ecology*, **11**, 51-64.

Boyd, R. 1989. Mistakes allow evolutionary stability in the Repeated Prisoner's Dilemma game. *Journal of Theoretical Biology*, **136**, 47-56.

Boyd, R. & Lorberbaum, J. P. 1987. No pure strategy is evolutionary stable in the repeated prisoner's dilemma game. *Nature*, **327**, 58-59.

Brown, J. H. & Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445-449.

Buckland, S. T., Goudie, I. B. J. & Borchers, D. L. 2000. Wildlife population assessment: Past developments and future directions. *Biometrics*, **56**, 1-12.

Bulger, J. B., Scott, N. J. & Seymour, R. B. 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. *Biological Conservation*, **110**, 85-95.

Bullock, J. M. & Clarke, R. T. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia 124*, **124**, 506-521.

Bunde, A. & Havlin, S. 1991. Percolation I. In: *Fractals and Disordered Systems* (Ed. by Halvin, S. & Bunde, A.). Springer-Verlag, Berlin, pp. 83-84.

Bustamante, J., Donazar, J. A., Hiraldo, F., Ceballos, O. & Travaini, A. 1997. Differential habitat selection by immature and adult grey eagle-buzzards *Geranoaetus melanoleucus*. *Ibis*, **139**, 322-330.

Cain, M. L., Milligan, B. G. & Strand, A. E. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany*, **87**, 1217-1227.

Clark, J. S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475-1494.

Compton, S. G., Ellwood, M. D. F., Davis, A. J. & Welch, K. 2000. The flight heights of chalcid wasps (Hymenoptera, Chalcidoidea) in a lowland Bornean rain forest: Fig wasps are the high fliers. *Biotropica*, **32**, 515-522.

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 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.

Cullinan, V. I. & Thomas, J. M. 1992. A comparison of quantitative methods for examining landscape pattern and scale. *Landscape Ecology*, **7**, 211-227.

Devroye, L. & Krzyzak, A. 2002. Random search under additive noise. In: *Modeling Uncertainty, An Examination of Stochastic Theory, Methods, and Applications.* (Ed. by Dror, M., L'ecuyer, P. & Szidarovszky, F.). Kluwer Academic Publishers, Boston, pp. 383-417.

Durier, V. & Rivault, C. 1999. Path integration in cockroach larvae, *Blattella germanica* (L.) (insect : Dictyoptera): Direction and distance estimation. *Animal Learning and Behavior*, **27**, 108-118.

Dusenbery, D. B. 1992. *Sensory ecology: how organisms acquire and respond to information*. W. H. Freeman, New York.

Ehrlich, P. R. & Wheye, A. 1988. Hilltopping butterflies revisited. *American Naturalist*, **132**, 460-461.

Fadamiro, H. Y., Henry, Y., Wyatt, T. D. & Birch, M. C. 1998. Flying beetles respond as moths predict: *Optomotor anemotaxis* to pheromone plumes at different heights. *Journal of Insect Behavior*, **11 (4) .** 549-557.

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology*, **41**, 300-314.

Farina, A. 1998. *Principles and Methods in Landscape Ecology*. Chapman & Hall, London.

Fisher, N. I. 1993. *Statistical analysis of circular data*. Cambridge University Press, Cambridge.

Frank, K. & Wissel, C. 1998. Spatial aspects of metapopulation survival: from model results to rules of thumb for landscape management. *Landscape Ecology*, **13**, 363-379.

Frank, K. & Wissel, C. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. *American Naturalist*, **159**, 530-552.

Fritts, S. H. & Carbyn, L. N. 1995. Population viability, nature reserves, and the outlook for gray wolf conservation in North America. *Restoration Ecology*, **3**, 26-38.

Gillespie, T. W. 2001. Remote sensing of animals. *Progress in Physical Geography*, **25**, 355-362.

Glover, F. & Laguna, M. 1997. *Tabu Search*. Kluwer Academic Publishers, Boston.

Gobeil, J. F. & Villard, M. A. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos*, **98**, 447-458.

Goheen, J. R., Swihart, R. K., Gehring, T. M. & Miller, M. S. 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: Species differences in perceptions of forest connectivity and carrying capacity. *Oikos*, **102**, 95-103.

Goldberg, D. E. 1989. *Genetic Algorithms in Search, Optimization, and Machine Learning*. Addison-Wesley Publishing Company, Reading, Massachusetts.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of Quercus ilex acorns by jays in a heterogeneous landscape. *Ecography*, **26**, 573-584.

Gottfried, B. S. & Weisman, J. 1973. *Introduction to Optimization Theory*. Prentice-Hall, Inc., New Jersey.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling*, **115**, 129-148.

Gruber, B. 2002. *Linking landscape structure to population dynamics - The role of movement in a structured population of the arboreal gecko Gehyra variegata.* PhD Thesis, UFZ-Centre for Environmental Research, Leipzig/Halle.

Gustafson, E. J. & Gardner, R. H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, **77**, 94-107.

Haddad, N. M. 1999a. Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications*, **9**, 612-622.

Haddad, N. M. 1999b. Corridor use predicted from behaviors at habitat boundaries. *American Naturalist*, **153**, 215-227.

Haddad, N. M. 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia. Conservation Biology*, **14**, 738-745.

Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151-162.

Hanski, I. 1998. Metapopulation dynamics. *Nature*, **396**, 41-49.

Hanski, I. 2001. Population dynamic consequences of dispersal in local populations and in metapopulations. In: *Dispersal* (Ed. by Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D.). Oxford University Press, Oxford, pp. 283-298.

Hanski, I., Alho, J. & Moilanen, A. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology*, **81**, 239-251.

Hanski, I., Kuussaari, M. & Nieminen, M. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia. Ecology*, **75**, 747-762.

Hanski, I., Moilanen, A. & Gyllenberg, M. 1996a. Minimum viable metapopulation size. *American Naturalist*, **147**, 527-541.

Hanski, I., Moilanen, A., Pakkala, T. & Kuussaari, M. 1996b. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology*, **10**, 578-590.

Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha byensis. Ecology*, **70**, 1236-1243.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, **42**, 73-88.

Hastie, G. D., Wilson, B. & Thompson, P. M. 2003. Fine-scale habitat selection by coastal bottlenose dolphins: Application of a new land-based video-montage technique. *Canadian Journal of Zoology*, **81**, 469-478.

Hay, K. 1991. Greenways and Biodiversity. In: *Landscape Linkages and Biodiversity* (Ed. by Hudson, W. E.). Island Press, Washington, pp. 162-175.

Heinz, S. K., Conradt, L., Wissel, C. & Frank, K. Dispersal behavior and fragmented landscapes: deriving a formula for patch accessibility. *Landscape Ecology*, in press.

Hess, G. R. 1996. Linking extinction to connectivity and habitat destruction in metapopulation models. *American Naturalist*, **148**, 226-236.

Hill, D. A., Andrews, J., Sotherton, N. & Hawkins, J. 1995. Farmland. In: *Managing habitats for conservation* (Ed. by Sutherland, W. J. & Hill, A.). Cambridge University Press, Cambridge, pp. 230-266.

Hill, J. K., Thomas, C. D. & Lewis, O. T. 1996. Effects of habitat patch size and isolation on dispersal by Hesperia comma butterflies: Implications for metapopulation structure. *Journal of Animal Ecology*, **65**, 725-735.

Hoffmann, G. 1983. The search behaviour of the desert isopod *Hemilepistus reaumuri* as compared with a systematic search. *Behavioral Ecology and Sociobiology*, **13**, 93-106.

Hunter, M. L. 2001. *Fundamentals of Conservation Biology*. Blackwell Science, Inc., Cambridge, MA.

Jager, H. I. & Tyler, J. A. 2001. Discussion on 'Movement rules for individual-based models of stream fish' [S. F. Railsback et al. 123 (1999) 73-89]. *Ecological Modelling*, **143**, 245-248.

Jordano, P. & Schupp, E. W. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**, 591-618.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society London B*, **330**, 175-190.

Keasar, T., Motro, U., Shur, Y. & Shmida, A. 1996. Overnight memory retention of foraging scills by bumblebees is imperfect. *Animal Behaviour*, **52**, 95-104.

Krebs, C. J. 1998. *Ecological Methodology*. Addison-Wesley Educational Publishers, Inc., Menlo Park, CA.

Kuussaari, M., Nieminen, M. & Hanski, I. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology*, **65**, 791-801.

Laarhoven, P. J. M. & Aarts, E. H. L. 1987. *Simulated Annealing: Theory and Applications*. D. Reidel Publishing Company, Dordrecht.

Lederhouse, R. C. 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxense*. *Behavioral Ecology and Sociobiology*, **10**, 109-118.

Levins, R. 1970. Extinction. In: *Some mathematical questions in biology.* (Ed. by Gerstenhaber, M.). American Mathematical Society, Providence, Rhode Island, pp. 75-107.

Lowe, W. 2003. Linking dispersal to local population dynamics: a case study using headwater salamander system. *Ecology*, **84**, 2145–2154.

Macdonald, D. W. & Johnson, D. D. P. 2001. Dispersal in theory and practice: consequences for conservation biology. In: *Dispersal* (Ed. by Clobert, J., Nichols, J. D., Danchin, E. & Dhondt, A.). Oxford University Press, Oxford, pp. 258-372.

Malanson, G. P. & Cramer, B. E. 1999. Landscape heterogeneity, connectivity, and critical landscapes for conservation. *Diversity and Distributions*, **5**, 27-39.

Marchand, D. & McNeil, J. N. 2000. Effects of wind speed and atmospheric pressure on mate searching behavior in the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). *Journal of Insect Behavior*, **13**, 187-200.

Matlab. 2001. *Matlab, the language of technical computing. version 6.1.0 Release 12.1*. The MathWorks, Inc.

Matthysen, E. 2002. Boundary effects on dispersal between habitat patches by forest birds (*Parus major, P. caeruleus*). *Landscape Ecology*, **17**, 509-515.

Meffe, G. K. & Carrol, C. R. 1997. *Principles of Conservation Biology*. Sinauer Associates, Inc., Sundrerland, Massachusetts.

Moilanen, A. & Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology*, **79**, 2503-2515.

Moilanen, A. M. & Nieminen, M. 2002. Simple connectivity measures in spatial ecology. *Ecology*, **83**, 1131-1145.

Morales, J. M. & Ellner, S. P. 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology*, **83**, 2240-2247.

Motro, U. 1991. Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. *American Naturalist*, **137**, 108-115.

Motro, U. 1994. Evolutionary and continuous stability in asymmetric games with continuous strategy sets: the parental investment conflict as an example. *American Naturalist*, **144**, 229-241.

Mueller, M. & Wehner, R. 1994. The hidden spiral-systematic search and path integration in desert ants, *Cataglyphis fortis*. *Journal of Comparative Physiology*, **175**, 525-530.

Mysterud, A., Langvatn, R., Yoccoz, N. G. & Stenseth, N. C. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: The effect of a variable topography. *Journal of Animal Ecology*, **70**, 915-923.

Nathan, R. 2001. The challenges of studying dispersal. *Trends in Ecology & Evolution*, **16**, 481-483.

Nathan, R. & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278-285.

Nève, G., Mousson, L. & Baguette, M. 1996. Adult dispersal and genetic structure of butterfly populations in a fragmented landscape. *Acta Oecologica*, **17**, 621-626.

Noss, R. F. & Cooperrider, A. Y. 1994. *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press, Washington D.C.

Obeysekera, J. & Rutchey, K. 1997. Selection of scale for everglades landscape models. *Landscape Ecology*, **12**, 7-18.

Okubo, A. & Levin, S. A. 2001. *Diffusion and Ecological problems: modern perspectives*. Springer-Verlag, New York.

Ollason, J. G. 1980. Learning to forage - optimally? *Theoretical Population Biology*, **18**, 44-56.

Opdam, P. 1990. Dispersal in fragmented populations: the key to survival. In: *Species dispersal in agricultural habitats* (Ed. by Bunce, R. G. H. & Howard, D. C.). Belhaven Press, London, pp. 3-17.

Osborne, J. L., Loxdale, H. D. & Woiwod, I. P. 2002. Monitoring insect dispersal: methods and approaches. In: *Dispersal Ecology: the 42nd Symposium of the British Ecological Society held at the University of Reading, 2-5 April 2001* (Ed.

by Bullock, J. M., Kenward, R. E. & Hails, R. S.). Blackwell Publishing, Malden, MA, pp. 24-49.

Palomares, F. 2001. Vegetation structure and prey abundance requirements of the Iberian lynx: implications for the design of reserves and corridors. *Journal of Applied Ecology*, **38**, 9-18.

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J. & Revilla, E. 2000. Iberian lynx in a fragmented landscape: Predispersal, dispersal, and postdispersal habitats. *Conservation Biology*, **14**, 809-818.

Peterson, M. A. 1997. Host plant phenology and butterfly dispersal: causes and consequences of uphill movement. *Ecology*, **78**, 167-180.

Phillips, J. B. 1996. Magnetic navigation. *Journal of Theoretical Biology*, **180**, 309-319.

Pither, J. & Taylor, P. D. 1998. An experimental assessment of landscape connectivity. *Oikos*, **83**, 166-174.

Queller, D. C. 1987. The evolution of leks through female choice. *Animal Behaviour*, **35**, 1424-1432.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87-99.

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.

Roland, J., Keyghobadi, N. & Fownes, S. 2000. Alpine Parnassius butterfly dispersal: Effects of landscape and population size. *Ecology*, **81**, 1642-1653.

Rosenberg, D. K., Noon, B. R. & Meslow, E. C. 1997. Biological Corridors: Form, Function, and Efficacy. *Bioscience*, **10**, 677-687.

Rubinstein, R. Y. 1986. *Simulation and the Monte Carlo Method*. John Wiley & Sons, New York.

Sandell, M. & Libero, O. 1992. Roamers and stayers - a model on male mating tactics and mating systems. *American Naturalist*, **139**, 177-189.

Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T. & Trepl, L. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological Applications*, **12**, 1469-1483.

Schippers, P., Verboom, J., Knaapen, J. P. & van Apeldoorn, R. C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography*, **19**, 97-106.

Schmidt-Koenig, K. 1993. Orientation of autumn migration in the monarch butterfly. In: *Biology and Conservation of the Monarch Butterfly* (Ed. by Malcolm, S. B. & Zalucki, M. P.). Natural History Museum of Los-Angeles County Science Series, Los Angeles, CA, pp. 275-283.

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.

Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology*, **12**, 284-292.

Schultz, C. B. & Crone, E. E. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology*, **82**, 1879-1892.

Schupp, E. W., Milleron, T. & Russo, S. E. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forest. In: *Seed dispersal and frugivory: ecological, evolutionary, and conservation issues.* (Ed. by Levey, D. J., Silva, W. & Galetti, M. e.). CABI Publishing, Wallingford, pp. 19-33.

Shamoun, B. J., Leshem, Y., Yom-Tov, Y. & Liechti, O. 2003. Differential use of thermal convection by soaring birds over central Israel. *Condor*, **105**, 208-218.

Shields, O. 1967. Hilltopping: An ecological study of summit congregation behavior of butterflies on a southern California hill. *Journal of Research in Lepidoptera*, **6**, 69-178.

Shkedy, Y. & Saltz, D. 2000. Characterizing core and corridor use by Nubian ibex in the Negev desert, Israel. *Journal of Conservation Biology*, **14**, 200-206.

Singer, M. C. & Thomas, C. D. 1992. The difficulty of deducing behavior from resource use: an example from hilltopping in checkerspot butterflies. *American Naturalist*, **140**, 654-664.

South, A. B., Rushton, S. P., Kenward, R. E. & Macdonald, D. W. 2002. Modelling vertebrate dispersal and demography in real landscapes : how does uncertainty regarding dispersal behaviour influence predictions of spatial population dynamics? In: *Dispersal Ecology: the 42nd Symposium of the British Ecological*

Society held at the University of Reading, 2-5 April 2001 (Ed. by J.M., B., Kenward, R. E. & Hails, R. S.). Blackwell Science, Malden, MA, pp. 327-349.

Srygley, R. B. 2003. Wind drift compensation in migrating dragonflies Pantala (Odonata: Libellulidae). *Journal of Insect Behavior*, **16**, 217-232.

Srygley, R. B. & Oliveira, E. G. 2001. Sun compass and wind drift compensation in migrating butterflies. *Journal of Navigation*, **54**, 405-417.

Stanley, H. E. 1986. Form: an introduction to self-similarity and fractal behavior. In: *On growth and form* (Ed. by Stanley, H. E. & Ostrowski, N.). Martinus Nijhoff, Dordrecht, pp. 5-6.

Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.

Sutherland, W. J., Gill, J. A. & Norris, K. 2002. Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences. In: *Dispersal Ecology: the 42nd Symposium of the British Ecological Society held at the University of Reading 2-5 April 2001* (Ed. by J.M., B., R.E., K. & R.S., H.). Blackwell Publishing, Malden, MA, pp. 134-151.

Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571-573.

Tennent, W. T. 1995. Field observations of the "hilltopping" phenomenon in North-West Africa - and an introduction to "Ravining" (Lep.: Rhopalocera). *Entomologists' Record*, **106**, 57-67.

Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London B*, **267**, 139-145.

Thornhill, R. A. & Alcock, J. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, MS.

Tischendorf, L. & Wissel, C. 1997. Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. *Oikos*, **79**, 603-611.

Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Sunderland.

Turchin, P., Odendaal, F. J. & Rausher, M. D. 1991. Quantifying insect movement in the field. *Environmental Entomology*, **20**, 955-963.

Turner, M. G., O'Neill, R. V., Gardner, R. H. & Milne, B. T. 1989. Effects of changing spatial scale on the analysis of landscape patterns. *Landscape Ecology*, **3**, 153-162.

Van Vuren, D. 1998. Mammalian dispersal and reserve design. In: *Behavioral ecology and conservation biology* (Ed. by Caro, T.). Oxford University Press, Oxford, pp. 369-393.

Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P. & Stanley, H. E. 2000. Levy flights in random searches. *Physica A*, **282**, 1-12.

Vos, C. C., Verboom, J., Opdam, P. F. M. & Ter Braak, C. J. F. 2001. Toward ecologically scaled landscape indices. *American Naturalist*, **183**, 24-41.

Wallraff, H. G. 2000. Simulated navigation based on observed gradients of atmospheric trace gases (models on pigeon homing, part 3). *Journal of Theoretical Biology*, **205**, 133-145.

Wehncke, E. V., Hubbell, S. P., Foster, R. B. & Dalling, J. W. 2003. Seed dispersal patterns produced by white-faced monkeys: Implications for the dispersal limitation of neotropical tree species. *Journal of Ecology*, **91**, 677-685.

Whittle, P. 1998. *Neural Nets and Chaotic Carriers*. John Wiley & Sons, Chchester.

Wickman, P. O. 1988. Dynamics of mate-searching behavior in a hilltopping butterfly, *Lasiommata megera* (L.): the effect of weather and male density. *Zoological Journal of the Linnean Society*, **93**, 357-377.

Wiens, J. A. 1992. Ecological flows across landscape boundaries: a conceptual overview. In: *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows* (Ed. by Hansen, A. J. & di Castri, F.). Springer-Verlag, New York, pp. 217-235.

Wiens, J. A. 2001. The landscape context of dispersal. In: *Dispersal: Individual, Population, and community* (Ed. by Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D.). Oxford University Press, Oxford, UK, pp. 96-109.

Wiens, J. A., Stenseth, N. C. V. & Ims, R. A. 1993. Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369-380.

Williams, T. C., Williams, J. M., Williams, P. G. & Stokstad, P. 2001. Bird migration through a mountain pass studied with high resolution radar, ceilometers, and census. *Auk*, **118**, 389-403.

Williamson, M. 2002. Overview and synthesis: the tale of the tail. In: *Dispersal Ecology: the 42nd Symposium of the British Ecological Society held at the University of Reading 2-5 April 2001.* (Ed. by Bullock, J.M., Kenward, R. E. & Hails, R. S.). Blackwell Publishing, Malden, MA, pp. 431-443.

Wilson, R. J. & Thomas, C. D. 2002. Dispersal and the spatial dynamics of butterfly populations. In: *Dispersal Ecology: the 42nd Symposium of the British Ecological Society held at the University of Reading 2-5 April 2001.* (Ed. by Bullock, J. M., Kenward, R. E. & Hails, R. S.). Blackwell Publishing, Malden, MA, pp. 257-278.

Wiltschko, R. & Wiltschko, W. 2003. Avian navigation: From historical to modern concepts. *Animal Behaviour*, **65**, 257-272.

With, K. A., Gardner, R. H. & Turner, M. G. 1997. Landscape connectivity and population distribution in heterogeneous environments. *Oikos*, **78**, 151-169.

Yamanaka, T., Tatsuki, S. & Shimada, M. 2003. An individual-based model for sex-pheromone-oriented flight patterns of male moths in a local area. *Ecological Modelling*, **161**, 35-51.

Zollner, P. A. & Lima, S. L. 1999. Search strategies for landscape-level inter-patch movements. *Ecology*, **80**, 1019-1030.

APPENDIX I:
SENSITIVITY ANALYSIS AND FURTHER EXPLORATION OF THE MODEL

In the main body of the thesis I presented the investigation of several spatial and behavioral parameters of the model, while some other parameters were used as constants. In this appendix I describe further spatial and behavioral attributes of the model that were explored during preliminary simulations. In these simulations I identified the main parameters of interest, and established these constants. In the first part of this Appendix I present a coarse sensitivity analysis of the impact of six parameters on simulation outcomes. In the second part I systematically explore some of these parameters, as well as several spatial configurations of the virtual, topographic landscape.

1. METHODS

1.1 LANDSCAPE AND SIMULATION ATTRIBUTES

All simulations that are presented hereby used 80×80cells' landscapes, with two patches that were located in their default location (Fig. 33). This configuration ensured that the two patches had a similar distance to the source patch. The default topographic configuration for simulations was a landscape with one summit at half the distance between the source patch and the southern patch (P_{south}; as in Chapter 5), hill-width of 20 cells, and landscape variability (noise) of 2%. The default simulation parameters were: 500 butterflies with a maximal life-span of 1000 time steps; a gap of 10 time-steps between release events; and a minimum of 5 encounters necessary for females to become 'mated females'.

1.2 SENSITIVITY ANALYSIS

In the first analysis, I tried to identify the main factors that affect (a) mating success, (b) the number of arrivals, and (c) the bias between patches in the number of arrivals. This was done by fixing the response to topography (q) to constant values q_{m+v}=0.5 and q_f=0.1,

and altering six parameters arbitrarily in 10,000 simulation runs, each on a different landscape. The six inspected parameters and ranges of change were:

- Consistency (p), varied from 0-1.

- Landscape variability (noise), varied from 0-7%.

- Number of encounters until mating, varied from 1-20.

- Gap between releases, varied from 2-20time steps. It had a similar impact on simulation outcome as the number of necessary encounters. Both the number of encounters and the gap between releases determine the time and location of the mating event (that is, they affect the chances of males and virgin females to meet on their way to the summit).

- Hill width, varied from 5-25 (in number of cells). Recall that the parameter 'hill width' determines the standard deviation of the normal distribution which creates the bell-shaped hill (see Chapter 3). In the specific landscape, this factor determined whether the source patch and P_{south} are located on a plateau or on the slopes of the hill.

- Weight of Interactions, or W in the equation $P_{stay}=W \cdot aX^b$ (see appendix I). This factor may reduce the tendency of individuals to move toward the summits, and affect the mating location. W varied from 0-1, while the other parameters in the function were fixed to $a=0.25$ and $b=1$.

The range of change was varied only within 'logical' values, excluding extremities. For instance, I avoided using consistency above 0.7, since such values diminish mating success and patch finding success very strongly.

I conducted a multiple regression to inspect which of the parameters had the greatest impact on the three above three indices, in terms of partial correlation and significance.

1.3 SYSTEMATIC INVESTIGATION OF SPECIFIC PARAMETERS

The above methodology assumes a linear effect of all parameters on the simulation outcome, which is not the case in many cases. In addition, the above analysis was based on fixing the behavioral parameters q_{m+v} and q_f, while simulation outcomes often depended on the ability of these parameters to change in response to changes in the simulation parameters, resulting in a diminished effect. Therefore, in the second analysis I first determined the optimal response to topography (*q_{m+v}, *q_f) with the change of the

parameters of interest, and only then did I inspect the simulation outcomes in terms of the total number of the number of arrivals to patches and the bias between them. Using this methodology I systematically explored the following parameters: Number of Encounters until Mating; Gap between releases; Weight of Interactions (W); Hill width (Figs. 33a,b); the number of summits (Figs. 33c,d); and the location of the summit (Figs. 33e-h). Increasing the number of summits was done to create a ridge from north to south, i.e. from the source patch toward the southern patch P_{south} (Figs. 33c,d). The location of the summit was explored for two main scenarios. In the first I shifted the hill from its original location eastwards (Figs. 33e,f), and in the second I shifted the summit eastward starting at the release point (Figs. 33g,h). The specific details of the range of exploration of each of the parameters are given in Table 11. For each parameter combination (q_{m+v}, q_f, and the parameter of interest), 30 simulation repeats were conducted, each on a different landscape.

2. RESULTS AND DISCUSSION

2.1 SENSITIVITY ANALYSIS

Results of the multiple-regression are given in Table 12. Evidently, in terms of its effect on the three indices (mating success, number of arrivals, and bias between patches), the most dominant parameter was 'Consistency' (p), followed by the number of encounters needed for mating and the gap between releases. The Weight of Interaction had a significant but marginal contribution (low partial correlation). The latter three parameters are explored and discussed below. The impact of consistency was given extensive notice in Chapters 5 and 6.

2.2 SYSTEMATIC INVESTIGATION OF SPECIFIC PARAMETERS
2.2.1 Number of necessary encounters and gap between releases
A systematic investigation of both factors revealed a similar trend: increasing the gap or the number of necessary encounters increased the total number butterflies arriving to patches, and slightly also the bias toward the southern patch P_{south} (Figs. 34a,b). However, in both cases the range of changes in the total number of arrivals was small (see, e.g. impact of consistency in Fig. 19, Chapter 5). Furthermore, both patterns quickly leveled off – beyond a certain threshold, further increase in each of the

parameters enhanced the total arrival success only marginally, with slight impact on the bias between patches. These results indicated that, beyond these thresholds, individuals arrived successfully at the summit and mated there. I have concluded that, in order to guarantee the arrival of animals to the summit (and consequently to the patches), I only need to set a constant value for the two parameters which is above these thresholds (I also found that setting one parameter beyond a threshold may suffice). In further simulations I used a gap of 10 time steps between releases, and a minimal number of 5 encounters until mating.

2.2.2 Interaction effect

Increasing the response to conspecifics (weight of interactions) seemed to affect the location of the mating event. Males and virgin females tended to stay on local maxima or around the source patch. However, this had little effect on the overall movement patterns of males and virgin females: the total number of arrivals at patches changed only little if the response to conspecifics was mild, and fell dramatically only when the tendency to respond was 100% (Fig. 35). In parallel, the bias between patches was only slightly affected by the tendency to respond to conspecifics. Graphical representations of the simulation results indicated that both effects (on the total number of arrivals and the bias between patches) diminish strongly if the gap between releases is increased. Similarly, increasing the number of necessary encounters or the response to topography (q) compensate for the impact of interactions. Therefore, in further simulations I set the effect of interactions to 0.

2.2.3 Effect of hill width

For a landscape with a small hill, the total number of arrivals was low (Fig. 36a). When hill-width was increased to 10 cells, the number of arrivals at the patches increased markedly and it remained fairly constant with further increase in hill width. This demonstrates that when hill width extended beyond this threshold, it could be easily recognized by individuals. In contrast, the bias toward P_{south} started to decrease when hill-width exceeded 10 cells (Fig. 36a). This indicates that the patch was missed more often by mated females, because it was on the slope of the hill (the bigger the hill, the steeper the slope near P_{south}).

The optimal response of males and virgin females to topography ($*q_{m+v}$) increased with increasing hill-size (Fig. 36b). This indicated that the topographic signal was more readily identified. Consequently, less randomness was necessary to overcome the noise. The mated females' optimal response ($*q_f$) did not change with changes in hill-width. These results indicate that changing hill width is analogous to changing the distance between the hill, the source patch and the habitat patches. This could be addressed by other analyses (see below), as well as by releasing the individuals randomly across the landscape (Chapter 5). Hence, in further simulations I fixed hill width to 20 cells.

2.2.4 Increasing the number of summits to form a ridge

Hypothetically, the ridge could function as a corridor for males and virgin females, who could move between summits until arriving at P_{south}. Therefore, in these simulations I allowed not only mated females, but also males and virgin females, to enter patches.

The number of mated female arrivals at patches diminished strongly with the change from one summit to two (Fig. 37a). Further increasing the number of summits increased the number of mated females' arrivals, reaching a leveling off at around five summits. Beyond four summits, the number of males and virgin females arriving at patches started to increase, until leveling off at around ≈ 7 summits. At that point, the total number of arrivals (by all butterflies) approached the 'original' one-summit case.

Only in the one-summit case did mated females arrive at both patches. Otherwise, mated females arrived only at P_{east}, while males and virgin females arrived only at P_{south} (Fig. 37b). Evidently, the latter could only arrive at P_{south} when the saddles between summits were shallow enough. Since mated females had a higher arrival rate at patches than males and virgin females in all cases (Fig. 37a), the overall bias was always toward P_{east}, except for the one-summit case. Therefore, the ridge performed as a corridor for males and virgins, a complete barrier to mated females, and, over-all, a barrier to dispersal. It is noteworthy that $*q_{m+v}$ was far lower in these simulations than in the one-summit case (≈ 0.3). This was necessary to allow animals to move between summits (results not shown).

2.2.5 Location of the summit

The number of arrivals at patches changed unimodally with shifting the hill from its original location to the east (Fig. 38a). It increased until *shift*=0.5 (half the distance to P_{east}), and then decreased. The high probability to arrive at both patches when the summit was in the middle is explained by the lack of bias between patches, the decreased chances to be lost on the edges, and the fact that, at that point, both patches were effectively on the plateau. Beyond this point, the chances of arriving at the summit decreased since the source patch was on the plateau (that is, the topographic signal could not be easily recognized). Interestingly, the bias between patches was quite weak throughout most of the locations of the summit (Fig. 38a). $*q_{m+v}$ decreased with the shift eastward (Fig. 38b), in response to the higher distance between the source patch and the summit. That is, a higher randomness was required.

Shifting the summit eastward from the point of release (case II) yielded qualitatively similar understanding – the total number of arrivals and the bias between patches reflect the distance between the hill and the three locations of interest (the release point and the two patches). The optimal responses to topography of both states reflected this response to altering the distances between the hills and patches (results not shown).

Table 11: parameters and range of changes in a thorough investigation of each parameter alone.

Parameter	Range	Step width	Comments
Number of encounters until mating	1-19	2	
Gap between releases	2-20	2	
Weight of Interaction (W)	0-1	0.1	
Hill width	5-25	5	
Move summit eastward (case I)	0-1.2	0.1	0=south of release, 1=south of P_{east}
Move summit eastward (case II)	0-1.2	0.1	0=at point of release, 1=at P_{east}
Number of summits in a ridge*	1-15	1	

* Here hill-width was reduced to 15 cells. For details on the calculation of distances between summits, see equation (11), Appendix I.

Table 12: Multiple linear regression (significance and partial correlation) for the effect of different parameters on: the total number of mated females' arrivals, the bias to P2 and mating success. In all simulation runs $q_{m+v}=0.5$, $q_f=0.1$. The strongest impact factors in terms of partial correlation are in bold.

Parameter	Total mate arrivals		Bias to P2		Mating Success	
	P	Part. Corr	P	Part. corr	P	Part. corr.
Constant	P<0.0001		P<0.0001		P<0.0001	
Noise	ns	0.001	ns	-0.002	ns	-0.001
Consistency	P<0.0001	**-0.407**	P<0.0001	0.040	P<0.0001	**-0.755**
# encounters	P<0.0001	0.049	P<0.0001	**0.182**	P<0.0001	**-0.193**
Gap releases	P<0.0001	0.072	P<0.0001	**0.244**	P<0.0001	**-0.253**
Hill width	ns	-0.001	ns	-0.004	ns	-0.006
Interactions	P<0.05	0.025	ns	-0.013	P<0.00001	0.051

Figure 33: Examples of inspected landscape configurations. (a,b) changing hill size. a – hill-width=10 cells; b – hill-width=25. c,d – increasing the number of summits to form a ridge. e,f – moving the summit eastwards (case I) e – *shift*=0.2; f – *shift*=1. g,h – moving the summit eastward starting from the source patch (case II). g – *shift*=0; h – *shift*=0.7. g,h –Red circles: location of the source patch. Blue circles: location of the patches, P_{east} (upper right) and P_{south} (lower left). All landscapes were 80× 80cells in size.
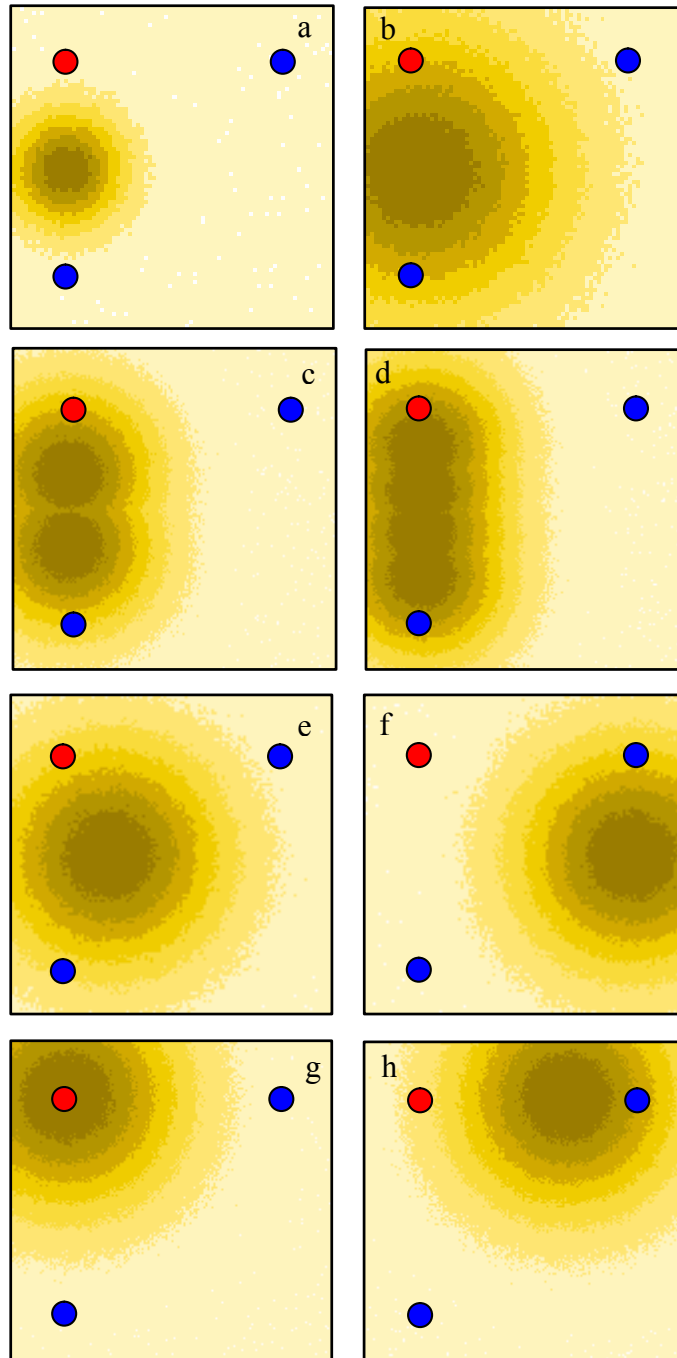
Figure 34: Impact of the minimal number of encounters (a) and the gap between releases (b) on the total number of arrivals to patches (full squares, solid lines) and the bias toward P_{south} (empty squares, dashed lines), both in optimal response to topography ($*q_{m+v}$, $*q_f$). Dashed lines represent moving averages of pairs of points.
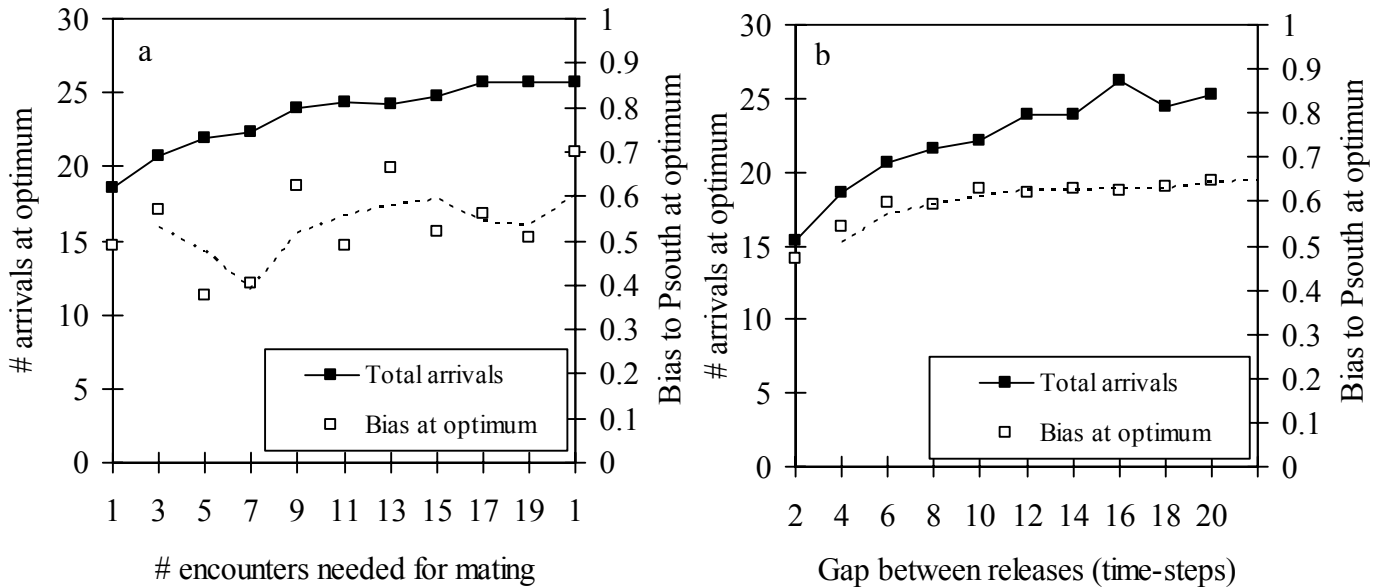
Figure 35: Impact of increasing the Interaction Effect W (the probability to respond to conspecifics) on the total number of arrivals (full squares, solid line) and the bias toward P_{south} (empty squares, dashed line), both at optimal behavior. Dashed line represents moving average of pairs of points. In the interaction equation ($a \cdot x^b$) $a=0.25$ and $b=1$.
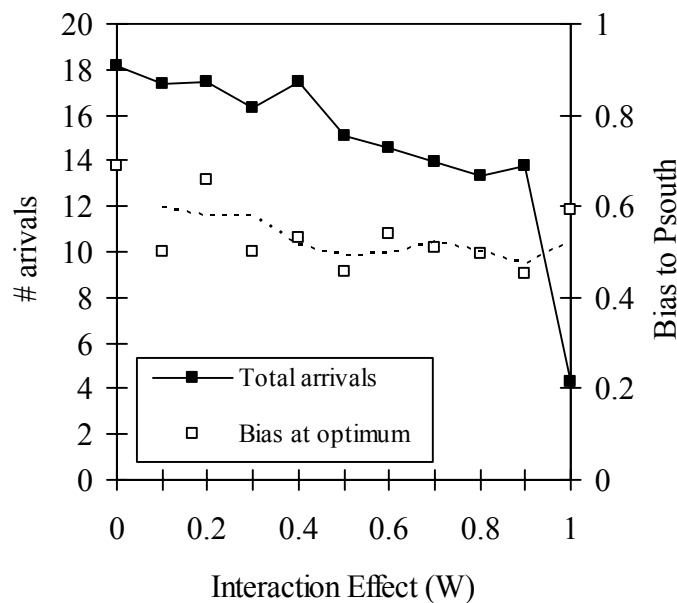
Figure 36: Impact of hill-width on (a) the total number of arrivals (full squares, solid line) and the bias toward P_{south} (empty squares, dashed line) at optimal response. (b) on the values of $*q_{m+v}$ (full squares, solid line), and $*q_f$ (empty squares, dashed line).
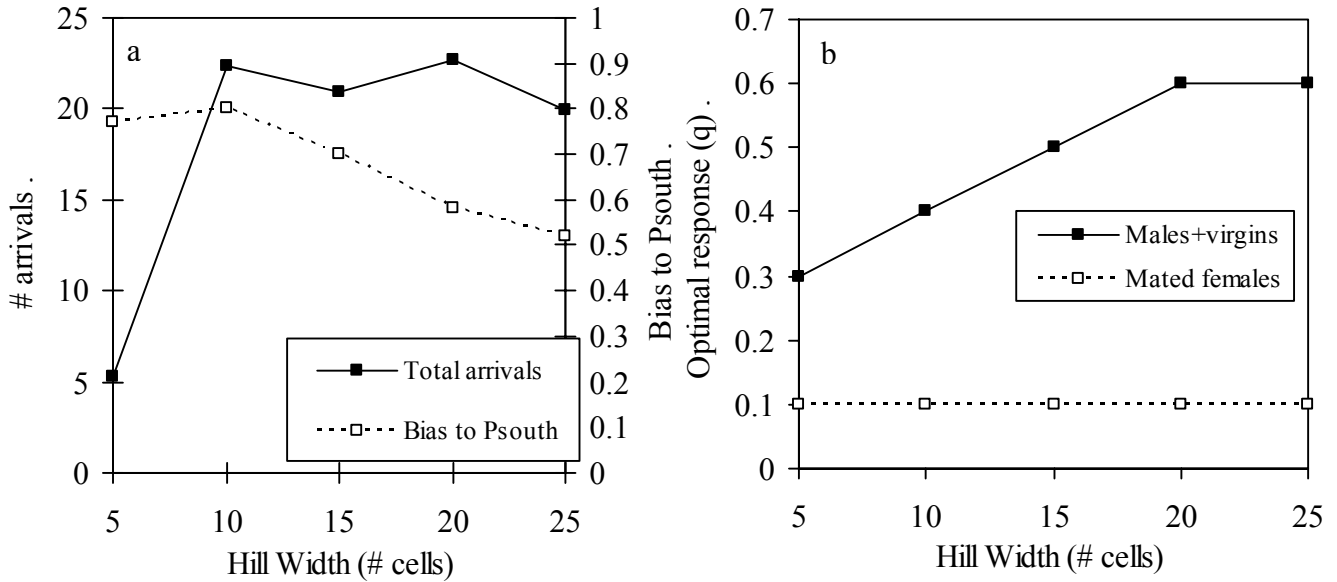
Figure 37: Impact of the number of summits on a ridge, on: (a) the number of arrivals at optimal response; (b) the proportion of arrivals at P_{south} at optimal response. Here I allowed the males and virgin females to enter patches, and differentiated between the arrivals of males+virgin females, mated females, and all individuals.

Figure 38: Impact of shifting the summit eastward (case I, Figs. 33c,d) on (a) the total number of arrivals (full squares, solid line) and the bias toward P_{south} (empty squares, dashed line) at the optimal response; (b) on the values of $*q_{m+v}$ (full squares, solid line), and $*q_f$; empty squares, dashed line). Lines represent running averages of pairs of data-points.
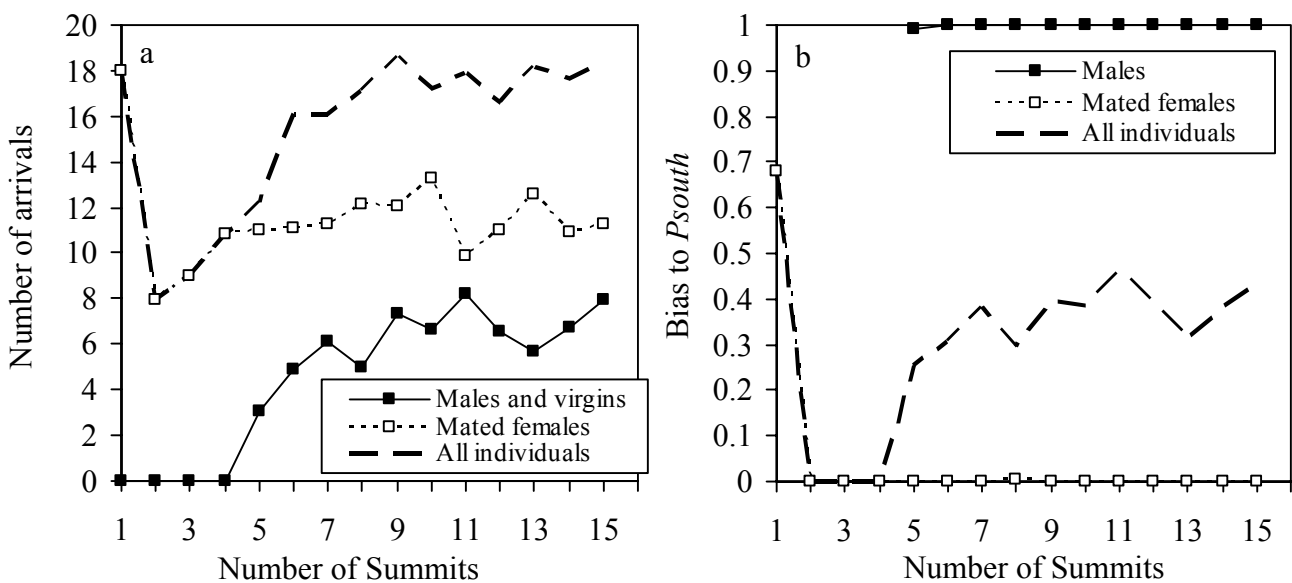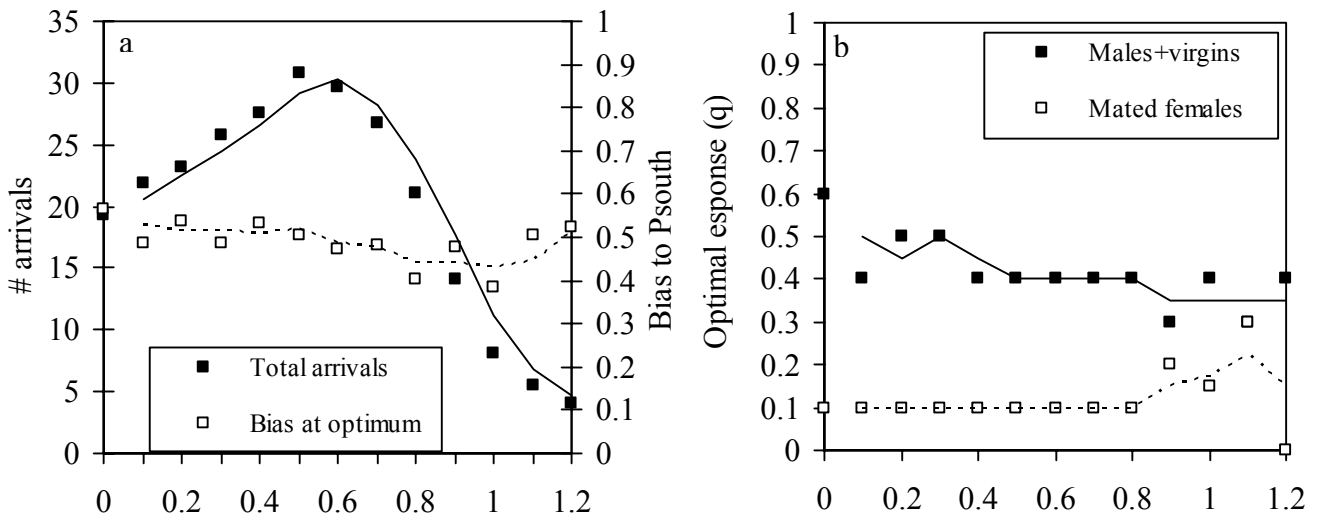
APPENDIX II:

'THE HILLTOPPING MODEL' SOFTWARE PROGRAM – MODEL DESCRIPTION AND USER MANUAL

This appendix aims to provide a transparent description of the model. It is aimed at those who wish to understand the conceptual framework of the model, to replicate it, use it, or access its source-code. It starts with a description of the conceptual framework and the main algorithms of the model. A user manual follows, supplying a full description of the components and parameters of the model, along with operational notes. Lastly, I list the main procedures used in the model. A copy of the program can be downloaded from the internet upon request from the author.

1. MODEL DESCRIPTION AND CONCEPT

'The Hilltopping Model' is a spatially explicit, individual-based, rule-based model. That is, it simulates the movements of individual animals over topographical maps with a grid base, and the movement decisions are based on simplistic behavioral rules. In the model, hilltopping butterflies are 'released' individually in the matrix, to seek topographical summits for the purpose of mating. Mated females then descend from summits in search for patches of host plant. In order to work with topographical landscapes of various complexities, the model includes a landscape generator to create virtual landscapes, and is also capable of using realistic topographic maps (arrays of elevations).

Flow Diagram 1 describes the main algorithm that operates when a single simulation is running. The program retrieves the simulation parameters, creates butterflies, moves them, and finally ends the simulation and summarizes it. Flow Diagram 2 describes the movement algorithm itself, including the decision-making process made by each butterfly at each movement step. This decision-making process involves three stages:

1. Males and virgin females can stay in a cell in response to conspecifics, or leave it with a probability that is determined by:

$$W \cdot (a \cdot x^b) \tag{10}$$

where x is the number of conspecifics in the cell, and a and b allow extensive flexibility to determine a variety of density-dependent responses to conspecifics – both positive and negative. The Interaction Effect (W) determines the probability of following this function.

2. If moving out of a cell, a butterfly may continue flying in the same direction as in the previous movement, with a probability p (termed 'consistency'). This probability is determined separately for males+virgin females (p_{m+v}), and for mated females (p_f) (See Chapter 6).

3. If not flying in the previous direction (with the probability of 1- p), a butterfly either responds to topography (flying toward the maximal or minimal slope) with a probability q (q_{m+v} for males and virgin females; q_f for mated females), or flies randomly with probability 1-q.

These three behavioral rules serve as the core of modeling the butterflies' movements. For further details on the parameters used by the program for determining simulation properties, see the 'User Manual' below

2. USER MANUAL

2.1 GENERAL

The model was developed with Delphi 6.0 – an object-oriented, visual programming environment for rapid application development (RAD), using Object Pascal language (Borland 2001). The user interfaces are friendly and straightforward, and it is activated using simple buttons, check-boxes and menu-driven screens which allow the user to provide inputs for simulation parameters without needing to access the source code.

2.2 COMPONENTS AND PARAMETERS

The model is based on three types of parameters: Landscape parameters, behavioral parameters and the simulation parameters. These are located in five main sections: Landscape; Patches; Butterflies; Release properties; and Simulation Properties.

Operational Note:

- Sections 4 and 5 are accessed through a secondary screen which is made available

  by the button   **More Properties**

A description for each set of parameters follows:

2.2.1 Landscape

The user may choose between several fixed landscapes (virtual or realistic). Alternatively, one may generate virtual landscapes of various levels of complexity. The main **parameters** of such virtual landscapes are as follows:

1. **Landscape Size**: number of cells on one of its two dimensions.

2. **Deviation Around Summits**: determines the width of the hill/s (# of cells). A hill is shaped by a normal distribution of soil around the summit, so that the value is one standard deviation of this distribution (See Chapter 3).

3. **Number of Summits**.

4. **Cell Size**: determines the side-length of the cells (meters). Cell-size is arbitrarily set to 5m, but it changes automatically if any of the realistic maps are used (e.g. Lahav = 5m, Dimona = 25m).

A subsection of the Landscape section determines the parameters of landscape variability (noise) which is added to the landscape on top of the topographical heterogeneity, in order to obscure the topographical signal. The noise is created by a random-number generator, with normal distribution around 0. It can be added independently to each cell in the matrix, or it can be spatially-correlated, by copying the value of the noise that is given to each cell, to its eight immediate neighbors (in a square of 3×3 cells) or to its neighbors in a 5×5 cell area.

5. **Landscape Noise**: determines the standard deviation of the normal distribution of the random-number generator, thereby determining the amount of noise (in % of summit elevation).

6. **Correlate Noise in Space**: determines the proportion of noise which is copied from one cell to its neighbors. Ranges from 0-1, where 0= adding no noise to the neighbors (each cell is independent of its neighbors), and 1=adding the total value of noise from each cell to its neighboring cells.

7. **Correlation Box size**: determines whether the noise is added to the 3×3 or to a 5×5cell area. Relevant only if Correlate Noise in Space >0.

Another subsection of the Landscape section determines the location of summits and their configuration. It allows the user to create either a ridge or a random-distribution arrangement of mountains.

8. **Ridge**: creates a ridge of summits from the release point and 'southward'. The distance (d) between summits is based on the number of summits, using the equation:

$$d=\text{Xsize}\cdot 4/6/(\#\text{summits}+1) \tag{11}$$

where *Xsize* is the side-length of the landscape (number of cells).

9. **Ridge direction**: determines the orientation of the ridge (in degrees), by rotating it around the point of release counter-clockwise. $0^{\circ}=$ 'Southward', from north-west to south-west; $90^{\circ}=$ 'Eastwards', from north-west to north-east.

10. **Shift ridge/cluster**: moves the summit-cluster or the ridge 'eastwards' along the X-axis of the map. The value represents a proportion of the distance from the release point on the west (=0) to the fixed patch (P_{east}; see Chapter 5) on the east (=1). Values between   -0.2 and 1.2 are still within the landscape's limits.

11. **Cluster**: Creates a cluster of random summits, depending on the **clustering coefficient**. A coefficient of 0 will result in a random distribution of summits over the landscape, and a Clustering Coefficient of 1 would distribute the summits around a small area, its length being ca. $\frac{1}{6}$ the length of the landscape.

Operational Notes:

- To open other landscape maps choose 'fixed landscape' and select 'From File'.
- Changing landscape size automatically changes the 'Deviation around summits' in order to preserve the topographic configuration. If you wish to change it, modify landscape size first.

2.2.2 Patch Configuration

Each patch is defined by its *location* (X,Y), the total number of butterflies which *arrived* at it, and the number of *mated females* out of these butterflies.

As a default, landscapes are created with one release point and two patches (or three in the case of realistic landscapes), all in constant locations (e.g. Chapter 5). Alternatively, the user can change the following parameters:

1. **Number of patches**.

2. **Patch-topography**: if this box is checked, the patches will not be randomly located over the whole landscape. Instead, patches can be created on the lowest 1/3 range of elevations, the middle third, or the upper 1/3 of the landscape elevations according to the user's choice.

3. **Put patches on summits**: this option cancels the above two parameters (1,2) and instead creates patches on top of each summit. The number of patches is thus determined by the number of summits. This option is only available for virtual landscapes (this option was used for Chapter 4).

4. **Recognize patch from**: determines the recognition distance of the patches, (in meters).

5. **Create patches manually**: this button enables the design of field experiments by manually determining the location of up to 3 patches and the location of the release point (X,Y values are in number of cells).

Operational Notes:

- The default location of patches ensures that the distance between the release point and all the patches is similar.

- Once determining a configuration of patches which is different from the default, simulations cannot be run unless you first press ▢ Create Landscape ▢ and then ▢ Create Patches ▢

2.2.3 Butterflies and the behavioral parameters

Each butterfly is defined by several properties: *live* & *arrived*: two Boolean values for properties defining whether a butterfly is able to move in a given time-step. *State* (male, virgin female, mated female); *Location* and *Last location* (X,Y); movement *Direction* (1-8, each representing one of 8 neighbors), *Encounters*; and *Time* – which is separately defined for each butterfly. *Location of mating events* (X,Y) is recorded as well.

The 'Butterflies' section includes the following parameters:

1. **Stay if summit**: If, in a given time-step, a males or a virgin female has to choose the maximal slope and all eight slopes are negative, it will remain at that point.

2. **Encounters Needed for Mating**: the minimal number of encounters with males that a virgin female has to have before turning into a 'mated female'.

The following are the behavioral parameters that are used in the decision-making process during butterflies' movements (Flow Diagram 2).

3. The **Interaction Effect** (*W* in equation 10), **Slope (a)** and **Power (b)** are the three parameters that determine the probability that individuals remain in a cell if they interact with *x* other individuals (equation 10). *W* ranges from 0-1, while *a* and *b* are unlimited. Note that under some parameters values equation (10) could yield values >1 or <0. This would simply result in 100% or 0% chances to remain in a cell, respectively.

3. **Consistency males** and **Consistency Mated** determine the probability to continue consistently with the previous direction, for males+virgin females (p_{m+v}), and for mated females (p_f), respectively. Values range from 0-1. If *p*=1 then all movements will follow the same (initial) direction.

4. **males (fly to max)** and **Mated (fly to min)** determine the probabilities to respond to topography, q_{m+v} (males and virgin females) and q_f (mated females). Values range from 0-1. While responding to topography, Males move toward the maximal slope available. Females, however, move toward the minimal slope or to one of the two cells neighboring the cell of that direction.

Operational Notes:

-   The consistency of Males+virgin females (p_{m+v}) is coupled, by default, to the consistency of Mated females (p_f). To uncouple these parameters un-check the box *"Couple male and female consistency"*.
-   As a default, the Interaction Effect is set to 0.
-   Some more parameters that relate to the butterflies, such as the butterflies' **life-span**, are located under 'Simulation properties' (section 2.2.5 below).

Butterflies
☐ Stay if on Summit
Encounters Needed for Mating   5
Behavioral Rules
☑ Couple male and female Consistency

Consistency males (0-1)   0.5
Consistency Mated (0-1)   0.5

Probability to follow slope when not
flying consistently (0=random):
males (fly to Max) (0-1)   0.5
Mated (fly to Min) (0-1)   0.1

Interaction Effect (0-1)   0
Interaction equation (ax^b):
Slope (a) 0.25   Power (b) 1

2.2.4 Release properties

The user can choose between the following options for the release point/s of the butterflies:

1. Release all butterflies at one default release point: either at the upper left area of the landscape in virtual landscapes (1/6 from 'west' and 1/6 from 'north), or, in realistic landscapes, halfway along the Y-axis and $1/6^{th}$ way from the 'west' edge.
2. Release all butterflies at one random point in the landscape.
3. All butterflies can be released on one of the summits.
4. Release each individual at a random point in the landscape.
5. Release each individual randomly at one of the five constant release-points, parallel to their locations during the field experiment in Lahav (Chapter 2).
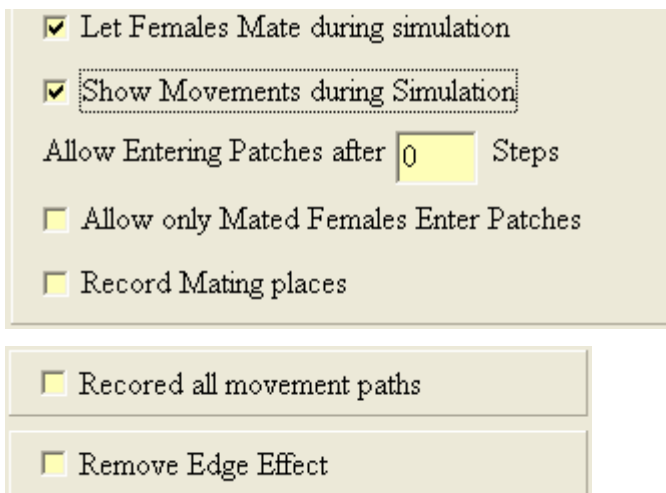
- Operational Notes:
- To choose between release options, activate a secondary screen by pressing

  More Properties

- When the release point is randomly set (option 2), its location will be determined when pressing   **Create Patches**

2.2.5 Simulation properties

This section, to be found in a separate screen, handles parameters and options that are not specific to the behavior of individuals. These parameters are:

1. **Initial butterfly state**: Males, Virgin Females, Mated Females, Males and Virgins together (50% probability for each), or All States (33.3% for each state).

2. **Number of butterflies in each simulation**.

3. **Per-step mortality**: if this option is chosen, this parameter determines the fixed probability of each butterfly to die at each time-step.

4. **Maximal Number of Moves**: determines the maximal life-span of each butterfly. If Per-step mortality is not checked, all butterflies have the same life-span (unless they move out of the landscape and die).

5. **Gap between release events** – determines the number of time-steps between releases (see Flow Chart 1). Indirectly, this parameter affects the chance of mating along the way to summits.

   Other simulation options:

☑ Let Females Mate during simulation

☑ Show Movements during Simulation

Allow Entering Patches after [0] Steps

☐ Allow only Mated Females Enter Patches

☐ Record Mating places

☐ Recored all movement paths

☐ Remove Edge Effect

The last option ('**Remove Edge Effect**') increases the landscape size by ¼ of the length in each direction, while not allowing the summits and the release point to be located at these edges (see Chapter 4 for further details).

Operational Notes:

- To define simulation parameters and properties, activate the secondary screen by pressing **More Properties**

- 'Remove Edge Effect' can only be performed with clusters of summits, not with a ridge.
- As a default, initial butterfly state is 'Males and Virgin females'.

2.2.6 Other functions and operations

After a simulation has ended, you can remove the movement trajectories of the simulated butterflies by pressing: **Re-Draw Landscape** .You can also depict the number of visits that each cell received during the previous simulation - press: **Show Visits**

The map plots the log (# of visits) using seven levels of blue.

You can copy the maps to the clipboard using Copy to Clipboard , save the topographic map by pressing Save Landscape or save the number of visits to each cell by pressing Save visits' map.

To terminate the program, press **Close** .

2.2.7 Running multiple simulations

Multiple simulations can be parameterized and run through a special screen. This screen allows the operator to set a variety of simulation options and parameters without accessing the source code. These parameters are:

1. Number of simulations and number of times for recreating the landscapes and/or the location of the patches.

2. Landscape type (while running multiple simulations on virtual landscapes, the landscape parameters and the patch locations are taken from the main screen. Hence, determining the landscape-parameters in the main screen is sufficient.)

3. Release locations

4. Patch configuration (excluding "patch-topography" option, which should be determined in the main screen).

5. Simulation constants (number of butterflies, life-span etc.). These include an option of preventing animals from entering patches for a certain number of time-steps.

6. Finally, the screen enables a systematic alteration of the main parameters of interest, namely consistency (p_{m+v} & p_f) and the response to topography (q_{m+v} &

q_f). The user can determine the range of these changes and the step-size. For systematic changes of other parameters, source code modifications are required.

After each simulation, results are saved (into a text file). Results include the value of the parameter/s that undergo systematic changes, the number of females released in the simulation, mating success and the time until mating, and the number of arrivals at different patches (all individuals, and mated females out of them). If requested, the distances of the patches from the release point and the summit/s can also be recorded.

- Operational Notes:
- To active the Multiple simulation screen press **Multiple Simulations**

- To run the multiple simulations, press **Run Multiple Simulations**

- To save a description of the multiple-simulation parameters, and further comments about the simulation, press **Record parameters to file**

- The file extension *.txt is not added automatically.
- A progress bar and the behavioral parameters used by each simulation are displayed during multiple simulations.
- To stop the sequence, press **Stop Process** . A warning message will appear. Data saved until the halting point will not be lost.
- When the process is finished, a dialog box will appear to ask you for further instructions.

2.3 REFERENCES

Borland. 2001. *Delphi 6.0 for windows*. Borland Software Corporation, Scotts Valley, CA, USA.

Flow Diagram 1: Main Algorithm

Start

User Input

Initialize Landscape and butterflies

Get parameters ---- User input and/or Multiple Simulation Input

TimeCounter = 0

TimeCounter = TimeCounter+1

NumButterflies < NeededNum? — n / y

TimeCounter/gap = IntegerNum? — n / y ---- Check if remainder = 0

create butterfly

Live = True
Location = X,Y
direction = Random
state = male/virgin

NumButterflies = NumButterflies +1

Initialize movement:
butterfly=0
LiveOnes=0

butterfly=butterfly+1

butterfly <= NumButterflies — y / n

alive = true? — n / y

LiveOnes=LiveOnes+1

Move butterfly **(Diagram 2)**

NumButterflies = NeededNum? — n / y

LiveOnes>0? — y / n

Continue next page

Continue from previous page

LiveOnes>0?

y

n

end simulation

summarize results

Displey mating success, mating time, arrivals to patches

Multiple simulations?

y

n

save paramters + simulation results

SimRepeat = SimRepeat+1

SimRepeat <Needed?

y

n

end multiple simulations

Report menu:
Display visits map
Save visits info
Save map
Copy maps to clipboard

n   terminate?

y

terminate

Legend

Operation / Declaration

Decision

Status

Output

Report

Junction point

Termination of process

---------- explanation of parameter

Flow Diagram 2:
Butterfly Movement Algorithm

From diagram 1

In Patch? — y

n

Time Ends? — y → Live = False

n

state = virgin female? — y → encounters = encounters + # Males in cell

n

state =male? — y → Create RandNum

n

Num > Interaction — n

y

NumOthers = all others in cell

Calculate interaction (equation 1)

Create RandNum

Num > interaction? — y → stay in cell

n

encounters>Needed number? — n

y

state=mated female

Record mating success and mating

Create RandNum

Num>P? — n → keep direction

y

Create RandNum

Num>Q? — n → check 8 slopes

y

direction Random   direction Up

New X,Y

keep direction ← n — Num>P?   (Pm+v or Pf)

y

Create RandNum

check 8 slopes ← n — Num>Q?   (Qm+v or Qf)

y

direction Down   direction Random

New X,Y

Continue next page

Continue from previous page

New X,Y

MVvisits = MVvisits +1
in cell X,Y

Draw Black Line

In land? n

y

Live = False

See a
Patch? n

y

allowed to enter? n

y

Move to Patch

CountArrivalsMV in patch=
CountArrivalsMV+1

Draw Black Line

Butterfly
InPatch

New X,Y

Fvisits = Fvisits +1
in cell X,Y

Draw Blue Line

n In land?

y

See a
Patch? n

y

allowed to enter? n

y

Move to Patch

CountArrivals F in patch=
CountArrivalsF+1

Draw Blue Line

Time = Time+1

To diagram 1

Legend

Operation /
Declaration

Decision

Status

Output

Report

Junction
point

Termination of
process

- - - - - - explanation of parameter

3. PROGRAM CODE DESCRIPTION

The following table describes the main procedures that comprise the model, and demonstrates how to activate these procedures when using the model.

Procedure name	Description	Called by
LandCreateButtonClick	Designs landscapes or open saved virtual landscapes	*RunMultipleClick*
ReadRealMap	Opens saved (realistic) maps	*LandCreateButtonClick*
PatchCreateButtonClick	Create patches	*LandCreateButtonClick, RunMultipleClick*
PlotMap	Plots a designed landscapes	*PatchCreateButtonClick, PlotMapButtonClick*
PlotLahav	Plots any realistic landscape	(Deactivated during multiple simulations)
RunButtonClick	Runs simulation (Flow Diagram 1)	*RunMultipleClick*
CreateButterfly	Creates butterfly (see Flow Diagram 1)	*RunButtonClick*
MoveButterfly	Moves butterfly (see Flow Diagram 2)	*RunButtonClick*
GetSlopes	Finds the slopes to nearest eight neighbors	*MoveButterfly*
GetParameters	Takes input parameters from the active form	*MoveButterfly, SaveParameterClick, RunMultipleClick*
PlotResultButtonClick	Plots # of visits in each cell on a color map	
RunMultipleClick	Runs Multiple simulations	
SaveParameterClick	Records multiple-simulation parameters & comments	
BreakButtonClick	Stops multiple simulations	
CloseButtonClick	Terminates the program	

לחזות את מסלולי התנועה המסוימים שבהם נעים בעלי חיים במהלך ההפצה. כך, ניתן לזהות מסדרונות ומחסומים להפצה, ולהתאים תוכניות שמירת טבע התורמות לשימור, כמו גם לשיפור, הקשר בין אוכלוסיות בעלי חיים בסביבות המקוטעות בידי אדם.

מחקר זה ממחיש את היתרונות והמגבלות שבשילוב מודלים ומחקר-שדה לשם פיתוח של רעיונות אקולוגיים ובחינתם. הוא מראה כי מודלים פשוטים המבוססים על הבנה טובה של התנהגות בעלי חיים יכולים לשמש הן למטרות תיאורטיות והן למטרות יישומיות. על ידי כך, מושג איזון בין העניין המדעי המיועד להבין את הטבע מחד גיסא, והצורך הדחוף ליישם את ההבנות הנרכשות בשמירת טבע הלכה למעשה.

מילות מפתח: טופוגרפיה, העפלה, פרפרים, הפצה, תנועה כיוונית, קישוריות, הטרוגניות סביבתית, מודל מבוסס-פרט, מסדרונות מדומים, גרדיאנטים.

נוסף לכך פיתחתי כלים חדשניים לזיהוי של 'תנועות מתועלות' ולכימותן. זאת באמצעות ניתוח "דפוסי ההגעה" לפסגות (accessibility patterns) – כלומר, סיכויי ההגעה לפסגות שונות במרחב בהינתן מרחק מנקודת המוצא. מצאתי כי ניתן למצוא הכללות על דפוסי התנועה אפילו כאשר הסביבה מורכבת: תנועות מתועלות באו לידי ביטוי ברור ב"דפוסי הגעה" אופייניים, על אף המגוון הרחב של טופוגרפיות אפשריות שנוסו. נוסף לכך, ניתוח זה הראה שאפילו תגובה חלשה לטופוגרפיה מספקת כדי להביא ליצירתם של דפוסי תנועה מתועלים. אי לכך, ניתן לצפות שתנועות כיווניות ו'מסדרונות מדומים' יתקיימו במגוון רחב של סביבות והתנהגויות.

בשלב הבא הרחבתי את האנליזות וניתחתי את שני שלבי התנועה הקשורים ל'העפלה' – תהליך ההעפלה עצמו, ותנועת הנקבות המזווגות מן הפסגות והלאה. חיפשתי את ההתנהגות האופטימלית של פרפרים שתביא להגעת מספר מירבי של נקבות אל כתמי הפונדקאי. התוצאות הושגו ללא תלות בתוצאות הידועות מן השדה, ורק אז הושוו אל התנהגות הפרפרים במציאות. מצאתי דמיון רב בין ההתנהגות האופטימלית שנמצאה במודל לבין ההתנהגות שנצפתה בשדה. מכאן שהמודל מסוגל לשחזר את הפרמטרים ההתנהגותיים בהצלחה. עם זאת, התוצאות באשר לנקבות הבתולות לא היו קונסיסטנטיות.

לבסוף, הערכתי את יכולותיו של המודל באמצעות ניסוי בשדה, המבוסס על שיחרור ולכידות חוזרות (Mark-Release-Recapture). באמצעות המודל ניסיתי לנבא את דפוסי הלכידה החוזרת של פרפרים המשוחררים בשדה, והשוויתי בין תוצאות המודל לתוצאות שהתקבלו בניסוי עצמו. בנוסף לכך, ניסיתי לקבוע את התנהגותן של הנקבות המזווגות. המודל ניבא בהצלחה את דגמי התנועה של זכרים ונקבות בתולות.

הן המודל והן עבודת השדה הראו כי הסיכוי ללכידות החוזרות אינו יורד בהכרח עם המרחק מנקודת המוצא כאשר בעלי חיים מגיבים להטרוגניות סביבתית (במקרה זה טופוגרפיה). נקבות מזווגות לא נלכדו, מה שהראה את הבעייתיות של ניסויי שיחרור ולכידות חוזרות במקרים בהם כמות הפרטים מעטה. העדויות המצטברות מכלל המחקר, כולל ניסוי זה, מרמזות כי הנקבות המזווגות מגיבות חלש לטופוגרפיה או אינן מגיבות כלל.

זהו מחקר שיטתי ראשון הבוחן את התוצאות של יחסי הגומלין בין בעלי חיים לסביבתם בהקשר של תנועה בסביבות בעלות טופוגרפיה מורכבת. המחקר מדגים את החשיבות המכרעת של הטופוגרפיה כגורם המכוון את תנועתם של בעלי חיים. הוא ממחיש את הצורך לתת משקל רב יותר לטופוגרפיה במחקרים העוסקים בהפצה, בקשר בין בתי גידול ובדינמיקה של אוכלוסיות בסביבות המקוטעות בידי אדם. המחקר מראה כי תנועות כיווניות נוצרות בשל תגובת בעלי חיים לגרדיאנטים טופוגרפיים. היות ששינויים הדרגתיים בסביבה קיימים בהקשרים רבים ובסביבות רבות, אני מסיק שתנועות כיווניות ו'מסדרונות מדומים' קיימים בהקשרים רבים בהם בעלי חיים נעים בהתאם לשינויים הדרגתיים בסביבה. חשוב לציין כי מודלים רבים של הפצה וקישוריות עושים שימוש במפות שבהן קיים מספר מסויים של בתי גידול, כשהמעבר בין בתי הגידול הוא חד. לכן, השיטות הנוכחיות לניבוי דגמים של הפצה ושל קשר בין אוכלוסיות, שאינן מתייחסות לגרדיאנטים, נוטות להמעיט בניפוצתן ובחשיבותן של תנועות כיווניות של בעלי חיים בסביבות הטרוגניות. מחקר זה מציב גישות וכלים לטיפול בבעייה זו, לשם בחינה מחודשת של תנועות כיווניות בסביבות הטרוגניות. כלים אלה עשויים לשפר את יכולתנו

תקציר

הרס בתי גידול וקיטועם בידי אדם, מסכנים את המגוון הביולוגי בכל רחבי העולם. אוכלוסיות בעלי חיים הולכות ומצטמצמות אל בתי גידול קטנים ומקוטעים. קיומן של אוכלוסיות כאלו הופך תלוי בהגעתם של פרטים חדשים מחוץ לאותן אוכלוסיות. על כן, ישנה חשיבות מכרעת לתהליכי הפצה לשרידותן של אוכלוסיות ואוכלוסיות-על בבתי גידול מקוטעים. אקולוגים ומומחים בשמירת טבע מנסים להבין תהליכים המשפיעים על דפוסי ההפצה, על-מנת לשמר את הקשר בין אוכלוסיות בעלי חיים ('קישוריות'). הקושי העיקרי הוא במורכבות הרבה של דפוסי ההפצה. מסלול התנועה שבעלי חיים בוחרים בו תלוי בתנאי השטח ובאופן שבו מגיבים בעלי חיים מסויימים למאפיינים השונים של השטח. כתוצאה מכך, היכולת לנבא את המסלולים שבהם נעים בעלי חיים בתנועתם בין אוכלוסיות, מוגבלת עקב מיעוט הידע האמפירי ועקב המורכבות הרבה של מודלים, המנסים לתאר את התגובות השונות של בעלי חיים לסביבות הטרוגניות.

מחקר זה בא לטפל בשתי הבעיות כאחת. חקרתי דגמי תנועה של בעלי חיים בגישה מיכאניסטית, המבוססת על התנהגות הפרט הבודד, ומכאן הגעתי להכללות על דגמים של תנועות כיווניות בסביבות הטרוגניות. הטרוגניות טופוגרפית הינה גורם מרכזי של הטרוגניות, שאינו נחקר דיו בהקשר עם מחקרים בהפצה, ועל כן התמקדתי בהשפעת הטופוגרפיה על דגמי תנועה. כמקרה מחקר התנהגותי בחרתי לבחון 'העפלה' של פרפרים. מינים 'מעפילים' עולים לפסגות הרים למטרת מפגש והזדווגות. הנקבות המזווגות ממשיכות לאחר מכן הלאה בחיפוש אחר צמחים פונדקאים שעליהם הן מטילות את ביציהן. התנהגות 'העפלה' דומה להתנהגות הפצה בכך שהיא גורמת לבעלי חיים לעזוב את בית גידולם, אך כאן ידוע לנו כי תנועתם במרחב מושפעת על ידי הסביבה.

כדי לחקור תנועות כיווניות במרחבים בעלי טופוגרפיה מורכבת, נקטתי בגישת מחקר שיטתית והיארכית. התחלתי ברמת הפרט, ע"י תצפיות בתנועתם של פרפרי נמפית הבוצין בשדה. מתצפיות אלה למדתי כיצד מגיבים הפרפרים לטופוגרפיה ותיארתי את חוקי התנועה. התוצאות שימשו אותי לבניית מודל מבוסס-פרט (individual-based model) המחקה את התנהגות ההעפלה. באמצעות המודל ניתחתי דגמי תנועה על פני מפות טופוגרפיות מדומות ואמיתיות בעלות מורכבות טופוגרפית הולכת וגדלה. לבסוף, אימתתי את המודל ע"י ניסוי שדה נוסף, שבו אמדתי את יכולת המודל לנבא דפוסי תנועה בסביבה אמיתית ומורכבת.

עונת המחקר הראשונה הניבה חוקי תנועה פשוטים וברורים, מהם הסקתי כי מודל פשוט עשוי לתאר בהצלחה את דפוסי התנועה של בעלי חיים המעפילים לפסגות, בסביבות רבות ומגוונות. חלק מחוקי התנועה הללו שימשו לבניית 'מודל ההעפלה'.

המודל איפשר להגיע להבנה מעמיקה של מאפייני התגובה לטופוגרפיה מבחינת דפוסי התנועה במגוון רחב של סביבות. המודל הצביע על כך שהתגובה לטופוגרפיה "מתעלת" את תנועתם של בעלי חיים אל מסלולי תנועה מסוימים, אותם כיניתי 'מסדרונות מדומים' (Virtual Corridors). סימולציות נוספות הראו שהמבנה של מסדרונות מדומים אינו ניתן לחיזוי אינטואיטיבי מתוך הסתכלות במפות טופוגרפיות. זאת משום שדפוסי התנועה מושפעים על ידי המבנה הטופוגרפי המסוים, מיקום הכתמים וכן הפרמטרים ההתנהגותיים. מכאן הסקתי שמודלים מבוססי-פרט, כמו זה שמוצג במחקר זה, דרושים לניבוי מסלולי התנועה של בעלי חיים במרחבים אמיתיים ומורכבים.

העבודה נעשתה בהדרכת :

פרופ׳ דייויד זלץ

פרופ׳ עוזי מוטרו

במחלקה למדעי החיים
הפקולטה למדעי הטבע
אוניברסיטת בן-גוריון בנגב

גורמים מרחביים והתנהגותיים הקובעים דפוסי תנועה
של פרפרים בסביבות בעלות טופוגרפיה מורכבת

מחקר לשם מילוי חלקי של הדרישות
לקבלת תואר ״דוקטור לפילוסופיה״

מאת

גיא פאר

הוגש לסינאט אוניברסיטת בן-גוריון בנגב
אושר ביולי 2004

כסלו התשס״ד   דצמבר 2003

באר שבע