

Dispersal in fragmented landscapes: from individual dispersal behaviour to metapopulation dynamics

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Introduction

1. Background

One of the most beloved paradigms in chaos theory is that a butterfly's wing flap in Leipzig can cause a storm in Hong Kong. This thesis does NOT deal with verifying or falsifying this theory. However, the question addressed here concerns a similar jump in scales: This thesis deals with the impact of the dispersal behaviour of individuals (for example, a butterfly) on the connectivity of landscapes and the viability of metapopulations.

For most people, it is quite clear why we need a weather forecast. The importance of studying the dynamics of metapopulations is less obvious. So, let us start with some words about that.

Habitat fragmentation is one of the main factors in the present increase in species vulnerability and extinction (Wilcove *et al.* 1986, Andren 1994). Fragmentation implies that a species habitat is dissected into smaller units separated by for the species unsuitable or even hostile strips of land, called matrix. It occurs in natural systems through disturbances like fire, windfall, flooding or soil erosions. However, the most menacing and large-scale cause of habitat fragmentation is the current expansion and intensification of human land use (Burgess & Sharpe 1981).

In fragmented landscapes, each habitat fragment, called patch, may contain a population of the species considered, but local extinction may cause (temporal) vacancies. This is especially the case for very small patches, where local populations may become extinct purely by stochastic processes. Immigration from other patches can lead to recolonisation of the empty patch. Thus, the whole set of such populations, the “population of populations”, can potentially persist if these recolonisations outweigh the extinction of local populations. This concept of a species regional persistence in a fragmented landscape being driven by the colonisation and extinction of subpopulations is called metapopulation concept. The term metapopulation was introduced first in the work of Levins (1970), although its roots may be found in earlier work (Wright 1940, Andrewartha & Birch 1954, Huffaker 1958, Den Boer 1968, Levins 1969). After nearly 20 years of recess, it has been widely applied in the last years in the research of spatially structured population (Quinn & Hastings 1987, Merriam 1988, Harrison & Quinn 1989, Gilpin & Hanski 1991, Hanski 1994, Drechsler & Wissel 1997, Hanski & Gilpin 1997, Stelter *et al.* 1997, Frank & Wissel 1998).

The metapopulation dynamics is the results of the combined dynamics of the subpopulations and the between-patch dispersal flow. Therefore, dispersal – the spreading of individuals

away from each other (Begon *et al.* 1990) - is seen as a key determinant of the viability of spatially structured populations (Den Boer 1970, Opdam 1990, Hanski *et al.* 1994, Hess 1996, Anderson & Danielson 1997, Frank & Wissel 1998, Thomas 2000, Johst *et al.* 2002). In metapopulation theory, it is not only crucial that an emigrant starting at a certain patch i successfully reaches any other patch in the landscape, but also which patch it reaches. Or, to formulate it from the perspective of a patch: it is important with which probability a certain patch j is reached by an emigrant starting at a certain patch i (referred to as patch accessibility). This patch accessibility is an important determinant of patch recolonisation. On the landscape level, it can be also used as a measure of landscape functional connectivity, i.e. the degree to which a landscape facilitates or impedes animals' movement (Taylor *et al.* 1993).

Whether an individual reaches patch j depends on the landscape structure and the individuals' movement behaviour (King & With 2002). The second factor is especially true for animals' dispersal behaviour since most animals can disperse actively through the matrix. The path an animal takes through the matrix, depends on a variety of factors such as landscape elements functioning as corridors (Merriam 1991, Haddad 1999, Neve *et al.* 1996) or barriers (Ricketts 2001, Roland *et al.* 2000), the distance from which animals can detect habitat patches (referred to as perceptual range) (Zollner & Lima 1997) or a specific systematic movement pattern of the animals (Dusenbery 1992). Such systematic movement patterns were found for a variety of animals in the context of homing behaviour (Hoffmann 1983, Bell 1985, Müller & Wehner 1994, Durier & Rivault 1999), as well as for some butterflies in context of dispersal (Conradt *et al.* 2000, Conradt *et al.* 2001). The existence of a perceptual range has been observed for a variety of animals as well (Zollner & Lima 1997, Zollner & Lima 1999a, Yeomans 1995, Conradt *et al.* 2000).

2. The approach

The reason why meteorologists did not yet include the wing flaps of butterflies in their predictions, can be seen in the fact that it would cost immense calculating time to consider each wing flap of all butterflies in the world explicitly (and just don't think of the turbulence caused by bumble bees, fruit flies and wasps). The same problem appears in this thesis: how can we condense the individual behaviour in a simple form without losing important information?

Non-random dispersal behaviour is likely to have an important impact on patch accessibility and therefore on landscape functional connectivity and metapopulation dynamics (Keitt *et al.* 1997, Wiens, Schooley & Weeks 1997, Pither & Taylor 1998, Wiens 1997). This thesis deals with the problem of how to link the specific movement behaviours of individuals with the complex dynamics of spatially structured populations. The goal is to analyse the consequences of non-random dispersal behaviour on metapopulation dynamics. To tackle this problem, we have first to deal with the question of how the effect of individual movement behaviour can be incorporated in metapopulation dynamics. The consequences of dispersal for population dynamics are often analysed using models (Verboom *et al.* 1993). In most metapopulation models, the underlying process of dispersal is assumed to be random (Fahrig 1992, Hanski 1994, Adler & Nuernberger 1994, Vos *et al.* 2001, Frank & Wissel 2002). Non-random dispersal behaviour, like systematic search strategies or the existence of a perceptual range, are scarcely considered. Therefore, a focal point of this thesis will be to develop a modelling framework that allows the effect of individual dispersal behaviour to be studied in a simple way. By means of an individual based simulation model, a formula is derived that describes the effect of individual dispersal behaviour and landscape structure on patch accessibility in a simple way. This formula is inserted in an already existing software for metapopulation analysis to investigate the effect of individual dispersal behaviour on metapopulation viability. Before starting with the model, a field study is performed that gives a first impression of how animals disperse in the field. This field study should illustrate how dispersal behaviour of individuals can be measured and analysed, and furthermore it should give us – the readers as well as the author - a feeling of the subject to be modelled.

3. Thesis overview

The thesis consists of 4 chapters and is divided into 3 parts. Each part is intended to be readable for itself, each chapter is intended to be submitted independently to journals for publication. Therefore, it is unavoidable that some sections are repeated in the different chapters. A chapter presenting not only ideas for continuative studies, but also some first results, completes the thesis.

The parts are arranged in the order of organisation levels: We start at the individual level where the movement behaviour of individuals is analysed (Part I). The consequences of individual dispersal behaviour on patch accessibility and landscape connectivity are addressed in Part II. Part III deals with the effects of individual behaviour on the metapopulation level.

The different questions addressed in the three different parts necessitate the use of different methods. In Part I, I applied field work and statistical analysis, in Part II, I developed and analysed an individual-based simulation model and in Part III an already existing software for metapopulation analysis is combined with the formula derived in Part II.

Part I

In Part I, we investigated how individuals disperse in the matrix. A small case study, taking the bog fritillary butterfly *Proclossiana eunomia* (Esper) as an example, demonstrates not only how individuals move in the field, but also how the movement of individuals can be measured and analysed. We released individual bog fritillary butterflies into an unsuitable habitat to force them to disperse and then mapped their flight paths. We focused on two aspects of the dispersal behaviour: we wanted to identify the distance from which *P. eunomia* can detect habitat patches (perceptual range), and we wanted to determine whether (if no habitat patch lies within the perceptual range) the butterflies move randomly or employ non-random systematic dispersal strategies. To tackle the second aspect, we compared observed flight paths to a model of correlated random walk using net square displacement analysis (Turchin 1998). The part closes by discussing the implications of dispersal behaviour for landscape connectivity and metapopulation dynamics.

Part II

Part II approaches the problem of how the effect of individual movement behaviour can be incorporated in metapopulation models.

In the first chapter of this part (Chapter 3), we address the question whether and how the effect of individual dispersal behaviour and landscape structure on patch accessibility can be described in one simple formula. One crucial aspect in studying the consequences of dispersal is predicting the probability r_{ij} of a certain patch j being reached by individuals starting at another patch i (called patch accessibility). This patch accessibility r_{ij} depends on both the landscape structure and the individuals' dispersal behaviour (King & With 2002). To investigate the effects of these factors on r_{ij} , we developed a simulation model focusing on animal dispersal. The model analyses show that there is an important intrinsic effect of the interplay between landscape structure and dispersal behaviour on patch accessibility: the competition between patches for migrants. We derive a formula for patch accessibility. Although this formula is very simple, it is able to cover effects such as the competition for migrants. The formula was found to have high predictive power for a variety of movement

behaviours (loops, random walk with various degrees of correlation and Archimedean spirals) in any given landscape. The formula can be interpreted as a generic function for patch accessibility for further population dynamical analyses. It also delivers insights into the consequences of dispersal in fragmented landscapes. We complete this part by discussing the formula's practical value as a tool for decision-support.

In the second chapter of Part II (Chapter 4), we investigated the effect of movement behaviour on the formula derived. The relationship between the aggregated parameters of this formula and all the relevant movement details were analysed. Using the individual-based simulation model, we wanted to derive fitting functions for the functional relationship between the parameters of the dispersal function and several details of the movement behaviour. Moreover, we were looking for an ecological interpretation of such relationships. Although the study addresses a particular movement behaviour observed in nature by way of an example, the approach presented of integrating movement behaviour into dispersal functions is general and can be applied to a wide range of movement patterns.

Part III

In Part III, the effect of individual dispersal behaviour on the viability of metapopulations is investigated.

Metapopulation models are a useful tool to assess fragmented landscapes regarding their ability of carrying viable metapopulations (review by Verboom *et al.* 1993, Hanski 1999). In such models, the processes that determine metapopulation viability are often modelled in a simple way. Animals' dispersal between habitat fragments is mostly taken into account by using a simple dispersal function that assumes the underlying process of dispersal to be random movement (Fahrig 1992, Hanski 1994, Adler & Nuernberger 1994, Vos *et al.* 2001, Frank & Wissel 2002). Species-specific dispersal behaviour as for example a systematic search for habitat patches is likely to influence the viability of a metapopulation (Wiens 1997, Ims & Yoccoz 1997). We investigate whether such specific dispersal behaviour affects the predictions of ranking orders of landscapes ranked regarding their ability of carrying viable metapopulations. We compare metapopulation viability of different landscape configurations taking different underlying dispersal behaviours into account. This is done by using META-X (Frank, *et al.* 2002), a software for metapopulation viability analysis. To incorporate dispersal behaviour in META-X, we use a submodel for the colonisation rates which utilises the formula for the accessibility of patches derived in Part II and allows different movement patterns to be considered. Landscape ranks were given by comparing for each movement

pattern (random walk with various degrees of correlation, loops) the resulting mean metapopulation lifetime T_m of different landscape configurations. The results show that landscape ranks change considerably between different movement patterns. We furthermore analyse under which circumstances such an inversion of landscape ranks can happen. We discuss implications for metapopulation modelling, planning and conservation.

Where to go from here: possible directions and first results

This chapter does not only provide ideas for prospective research, but also some first investigations and results how these ideas can be implemented. These ideas cannot be completely covered by this thesis and therefore need to be investigated more thoroughly in future studies.

Additional landscape heterogeneity, like e. g. heterogeneous sized patches (Hill *et al.* 1996, Kuussaari *et al.* 1996, Bender *et al.* 2003) or a heterogeneous matrix (Gustafson & Gardner 1996, Haddad & Baum 1999, Merriam 1991, Roland *et al.* 2000, Jonsen *et al.* 2001, Ricketts 2001, Ries & Debinski 2001, Vandermeer & Carvajal 2001), is likely to change patch accessibility. I present several approaches of investigating the applicability of the formula derived in Part II in landscapes with additional landscape heterogeneity. In these approaches, the effect of heterogeneously sized patches or heterogeneous matrix structures as barriers and topography on patch accessibility is investigated.

Furthermore, I discuss how the formula's results can be compared with field data and I show exemplarily how models can help to estimate the structure of unknown parameters.

Finally, I call into question whether the incidence pattern of patches can be used as an indicator of a change in landscape ranks under different underlying dispersal behaviours. I compare the mean lifetimes T_m resulting of different underlying dispersal behaviours for a given landscape with the corresponding patch incidence pattern.

Part I

On the individuals' level



Non-random dispersal behaviour of individuals in fragmented landscapes: the bog fritillary butterfly

Proclassiana eunomia

1 Introduction

Animals' ability to disperse between habitat fragments is a key determinant of the viability of spatially structured populations (Levins 1970, Opdam 1990, Hanski *et al.* 1994, Anderson & Danielson 1997, Frank & Wissel 1998, Thomas 2000). The consequences of dispersal for population dynamics are often analysed using models. In most metapopulation models, the underlying process of dispersal is assumed to be random movement (purely or correlated random walk) (Fahrig 1992, Hanski 1994, Frank & Wissel 2002). However, several studies have shown that animals' movement is not totally random (Odendaal, Turchin & Stermitz 1989, Matter & Roland 2002). Conradt *et al.* (2000, 2001) investigated the dispersal behaviour of two butterfly species, the meadow brown butterfly *Maniola jurtina* and the gatekeeper butterfly *Pyronia tithonus*. Their studies revealed systematic dispersal behaviour different from a random movement with the individuals flying in large ellipses in a succession of petal-like loops around their starting-point. Another deviation from random movement occurs due to animals' ability to detect distant habitat patches and then head for them, known as the "perceptual range" (Zollner & Lima 1997). This perceptual range has been observed in a variety of animals (Harrison 1989, Yeomans 1995, Zollner & Lima 1997, Zollner & Lima 1999a). The type of dispersal behaviour (random or systematic) could influence the functional connectivity of the landscape and therefore affect the whole spatio-temporal dynamics of (meta-) populations. For example, a recent modelling study found a systematic search strategy more efficient than random walk in a landscape with a clumped distribution of habitat patches (Conradt *et al.* 2003). However, detailed information about how individuals disperse in the field is limited because of the difficulties of keeping track of dispersing individuals in the field (Nathan 2001). Most investigations rely on mark-release-recapture studies, partly combined with modelling studies (e.g. (Brakefield 1982, Dover 1996, Hill, Thomas & Lewis 1996, Petit *et al.* 2001, Wahlberg *et al.* 2002), but these do not provide information about the individuals' actual dispersal path.

The first step to shedding light on the role of movement behaviour within landscape connectivity and metapopulation viability is therefore to expand on our hitherto limited knowledge of the dispersal movement of individuals. Hence we studied the dispersal behaviour of the threatened bog fritillary butterfly, *Proclossiana eunomia* (Esper), whose population dynamics are well investigated (Baguette & Neve 1994, Baguette *et al.* 1996, Baguette *et al.* 1998, Schtickzelle & Baguette in press). This butterfly is a non-migratory species living in fragmented habitat networks whose natural patchiness is increasing due to human impact (Baguette *et al.* in press). In order to simulate dispersal in a field experiment (Harrison 1989, Zollner & Lima 1997, Conrath *et al.* 2000), we released individual butterflies into an unsuitable habitat in order to force them to disperse and mapped their flight paths. We focused on two aspects of the dispersal behaviour: we wanted to identify the distance from which *P. eunomia* can detect habitat patches (perceptual range), and we wanted to determine whether (if no habitat patch lies within the perceptual range) the butterflies move randomly or employ non-random systematic dispersal strategies. To tackle the second aspect, we compared observed flight paths to a model of correlated random walk using net square displacement analysis (Turchin 1998). The paper closes with a discussion of the implications of movement behaviour for landscape functional connectivity and metapopulation dynamics.

2 Methods

2.1 Study organism

The bog fritillary butterfly, *Proclossiana eunomia* (Fig. 2.1), is a glacial relict occurring in scattered population islands all over Europe (Ebert 1991). The species is restricted to wet meadows and peat bogs where the only larval food plant and the nectar source of the adults, the bistort *Polygonum bistorta*, can be found (Baguette & Neve 1994). These wet meadows are early successional stages created in the past by agricultural use and nowadays mostly maintained by extensive management. Due to anthropogenic changes (the abandonment of mowing and grazing), the natural patchiness of such habitats has increased. As a result, *P. eunomia* is contained in the Red List of Threatened Species in some European countries such as Belgium (Baguette *et al.* 1998) and Germany (Pretschner 1998).

The bog fritillary is a univoltine Nymphalid flying for about one month between the end of May and the beginning of July. Male butterflies emerge earlier than females. The mating system is polygynous and male mate-locating behaviour is patrolling (Baguette *et al.* 1996).

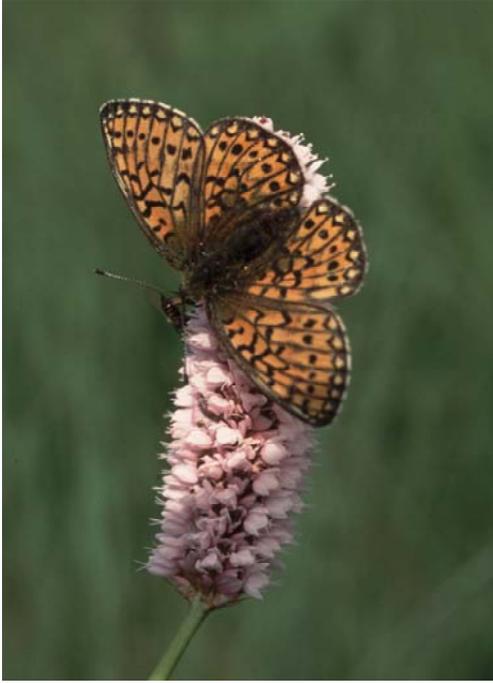


Figure 2.1 A female bog fritillary butterfly, *Proclossiana eunomia*, on its food plant, the bistort *Polygonum bistorta*

2.2 Study site

The experiment was performed during June 2002 at two different release sites in the Belgian Ardennes.

One study site, Prés de la Lienne, was located on the Lienne river (50°18' N, 5°49' E). Small habitat patches of unfertilised wet meadow with *Polygonum bistorta* were situated on both sides of the river. The release site was located east of these habitat patches, separated from the habitat by a fragmentary tree line. It was an extensively used meadow with no stands of *Polygonum bistorta*, making it an unsuitable habitat for the bog fritillary butterfly.

The other site was located at the Pisserotte nature reserve (50°13' N, 5°47' E). Stands of *Polygonum bistorta* were scattered over a peat bog surrounded by pine trees (Fig. 2.2a). Fig. 2.2b demonstrates the wetness of this peat bog. The release site – again an extensively used meadow without *Polygonum bistorta* – was situated in the south of the bog. Pictures of both sites are shown by Schtickzelle & Baguette (2003).

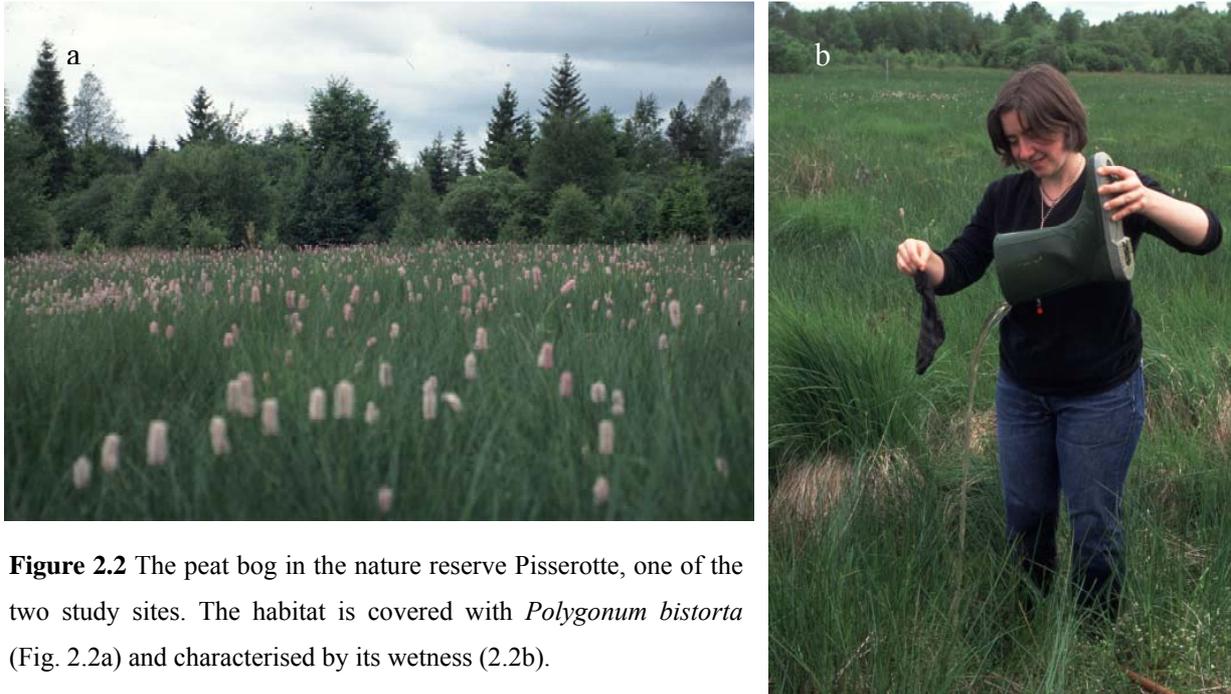


Figure 2.2 The peat bog in the nature reserve Pisserotte, one of the two study sites. The habitat is covered with *Polygonum bistorta* (Fig. 2.2a) and characterised by its wetness (2.2b).

2.3 Experiments

Butterflies were captured in one of the population's habitat patches. They were sexed, marked (Baguette & Neve 1994), and male butterflies were immediately moved to the release site ($n=58$ in total) in a nylon meshed transport box (18 x 18 x 30 cm) covered with a black bag. Only male butterflies were used for releases in order to reduce the impact on the population. The release sites, which constituted unsuitable habitats, were at distances of 50, 70, 100, 250 and 300 m away from the nearest habitat patch (the other habitat patches being considerably further away). Butterflies were transferred to a release box (18 x 18 x 30 cm) covered in fine nylon mesh and were given 3 minutes to settle. Then they were released (always one butterfly at a time) by opening the release box with a string pulled by an observer standing 5 m away (Fig. 2.3). The observer's position was changed between different releases to avoid a bias in data due to the observer's presence. Nevertheless, the position of the observer did not seem to influence the subsequent flight pattern. The observer followed each butterfly (from a distance of >10 m) until it either found the habitat patch or was lost from view.



Figure 2.3 The release box opened by a string.

2.4 Data collection

The butterflies' paths were mapped by placing flags at every point the butterfly turned. Additionally, one flag each was placed at the point where the animals crossed a circle with a radius of 10 m around the release point (crossing point). This information was used to measure the diverging angle between the shortest possible route to the habitat patch and the route to the actual crossing point (i. e. start direction, Fig. 2.4). With this quantity the initial orientation of the butterflies could be assessed. This ability to orient towards the patch was taken as an indication of the bog fritillary butterfly's perceptual abilities, as has already been done in the literature for a variety of animals (Yeomans 1995, Zollner & Lima 1997, Conradt *et al.* 2000).

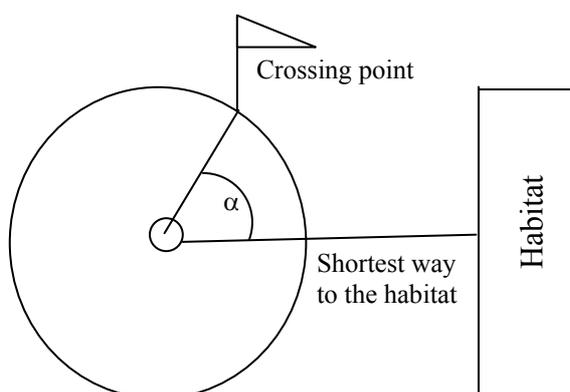


Figure 2.4 The butterflies' ability to orient towards the patch is determined by measuring the starting angle α . This is done by placing one flag at the point where the individual crosses a circle with a radius of 10 m around the release point (crossing point). The starting angle α is calculated by the divergence between the shortest possible route to the habitat patch and the route to the actual crossing point.

For all the butterflies released at 250 and 300 m, the flight path was recorded ($n=33$). This was done by determining the exact positions of the flags by measuring the distances between the flags and three fixed points each. The positions of these fixed points were obtained by GPS, and the exact positions of the flags were calculated by triangulation. From the positions of the flags, we determined the straight move length between two flags and the associated turning angle. The overall path of an animal can therefore be described by a sequence of moves (distance between two flags) and turning angles (change in direction between two moves). Note that the definition of moves in this context diverges from the definition of Turchin (1998), where a move is defined as the distance between two stopping points. As butterflies rarely stopped in the matrix, this definition could not be applied here. Instead, move is defined here as the straight distance between two turning points. According to Turchin (1998), this wider definition of the term move could entail serial correlation in data analysis, which can be solved by using a moving block bootstrap (see data analysis).

We also noted the number of butterflies which returned to the habitat patch. This was determined either directly by following them until they found a patch or their subsequent recapture in the patch. Additionally, we measured the following environmental factors for each release: temperature, wind speed, wind direction and cloud cover.

2.5 Data analysis

Perceptual abilities

The orientation of the butterflies towards the patch measured in terms of the starting angle was analysed using a standard circular statistical test (Batschelet 1981, Fisher 1993). We used the Rayleigh V -test, which is considered more powerful than Rayleigh's z when a predicted direction is known. This was done in order to test whether the orientation differs from a uniform distribution and has a specific mean direction (Zar 1999). To test whether there is a correlation between starting angles and the environmental factors temperature, wind speed and cloud cover, we used an angular–linear correlation test; for wind direction we used an angular–angular correlation test (Zar 1999).

Turning angles and move lengths

Because the data of flight paths were taken from two different locations and two different release distances (250 m in Prés de la Lienne and 300 m in Pisserotte), they were analysed separately. The sample size of the data from Prés de la Lienne ($n=7$) was not high enough to test for differences between sites.

The flight paths were analysed regarding the move lengths and turning angles of the paths. The mean and standard deviation of the turning angles was calculated using circular methods (Fisher 1993). After graphical inspection of the distribution of turning angles (in order to confirm unimodality), we tested whether the mean angle is orientated towards 0° as is typical of turning angles (Turchin 1998) using the Rayleigh V -test (Zar 1999). We also examined the data for correlation between consecutive turning angles using a parametric angular–angular test (Zar 1999). To obtain significance we resampled the angular–angular correlation coefficient r_{aa} n times, each time eliminating a different pair of consecutive turning angles, and then obtained the 95% confidence interval of the statistic for the null hypothesis of no correlation ($r_{aa} = 0$). The r_{aa} of the angular–angular test corresponds to the correlation coefficient Pearson’s r for linear data, also referred to as “Pearson product-moment correlation coefficient”. If $r = 0$, there is no correlation between variables; for $r = 1$ and $r = -1$ the data are 100% correlated. We also tested for correlation between turning angles and move length using an angular–linear correlation test (Zar 1999). The move lengths between turns were analysed regarding their distribution using a Kolmogorov-Smirnov test. We examined the data for correlation between consecutive moves using Pearson’s r and a Spearman’s rank correlation for not normally distributed cases. Whether there is a correlation between consecutive turning angles or move lengths needs to be known in order to determine whether a moving block bootstrap (see analyses of paths) has to be used.

Analyses of paths

The overall paths were analysed according to Turchin (1998). To check whether the movement can be described by a correlated random walk, the theoretical net square displacement was calculated (Kareiva & Shigesada 1983) and compared with the observed one. In order to determine whether the deviation between observed and theoretical net square displacement R_n^2 is statistically significant, we performed a bootstrap (Turchin 1998). For this analysis, all the turning angles and move lengths of one site were pooled. A large number of pseudopaths ($n = 1000$) was simulated by drawing random move lengths and turning angles out of the empirical distribution. From the pseudopaths, the R_n^2 was calculated and the resulting values were sorted in ascending order. The 95 % confidence interval was estimated for each move by taking the 26th and 975th values of the sorted list as the end of the 95 % confidence interval. If the observed R_n^2 lies within the 95% confidence interval, the path can be described with a model of correlated random walk (CRW). Because there were only a few

observed paths with more than 15 moves, the average for each move $n > 15$ was calculated using the displacement after the first 15 moves (Turchin 1998). Since there was an autocorrelation in the turning angles and move lengths of the paths from Pisserotte, a moving block bootstrap was used for these path data (Efron & Tibshirani 1993). For this moving block bootstrap, data were pooled in blocks of three (e.g. 1-3, 2-4, 3-5, ...) because there was no third-order autocorrelation. This analysis was only performed for paths with 6 or more moves, and so we analysed a total of 27 paths (thereof 20 paths from Pisserotte).

Paths with a more systematic movement

To characterise the paths which displayed a pattern different from correlated random walk, we analysed them in the following way: First, we tried to find out whether there is a preference to retain the orientation of one step in the next step. This was done by placing all possible turning angles into one of two categories: (1) turns in the same orientation and (2) turns in the opposite orientation. Deviation from a random distribution can then be assessed by a χ^2 test. Second, we tested whether there are high-order autocorrelations (1 to 8 lags) between the turning angles of all the paths with a low R_n^2 using the above-described parametric angular–angular correlation test (Zar 1999).

The linear statistics were calculated with SPSS. The circular statistics, net square displacement and bootstrapping were programmed in C++.

3 Results

3.1 Perceptual abilities and return rate

Fig. 2.5 shows the angular orientation of butterflies 10 m away from the release point. There was no correlation between the starting angle and the environmental factors investigated (for wind speed and cloud cover: angular–linear correlation test, for wind direction: angular–angular correlation test, $P > 0.05$). While for butterflies released at 50, 70 and 100 m most of the starting angles lay within 90° of the shortest route to the habitat patch, the butterflies released at 250 and 300 m seemed to be less orientated. However, in statistical terms there was no significant orientation towards the habitat for butterflies released at 50 m (V -test, $u = 0.887$, $P > 0.05$, $n = 7$). Butterflies released at 70 and 100 m were significantly orientated towards the habitat patch (V -test, $u = 2.583$, $P < 0.005$, $n = 9$; and $u = 1.782$, $P < 0.05$, $n = 7$). In contrast, there was again no significant orientation for butterflies released at 250 and 300 m (V -test, $u = -1.586$, $P > 0.05$, $n = 6$; and $u = 1.379$, $P > 0.05$, $n = 29$).

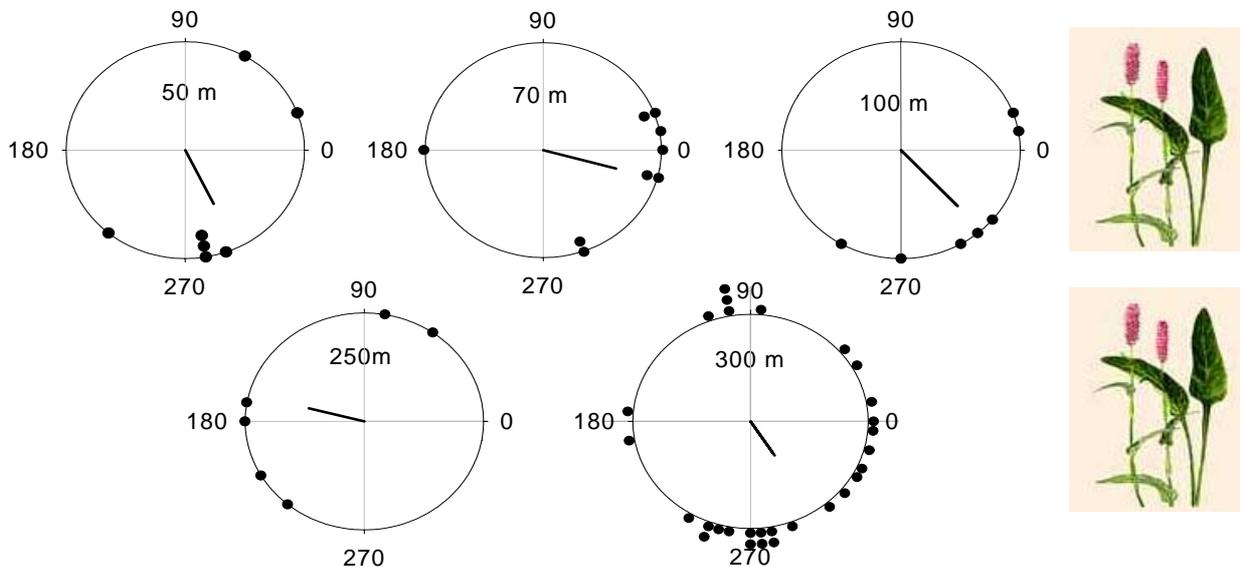


Figure 2.5 The angular orientation of butterflies at 10 m from the release point. Data are given for butterflies released at 50, 70, 100, 250 and 300 m from the habitat patch. Each point represents one individual. The point of the habitat closest to the release point (symbolised by the bistort) was defined as 0° for each release point. The vectors indicate the average angle and the mean vector length.

100% of those butterflies released at 50 and 100 m and 86 % of those released at 70 m were found to have returned to the habitat. Of the butterflies released at 250 m or more (the data from 250 m and 300 m being combined), only 61 % returned.

3.2 Analysis of dispersal behaviour

Turning angles and move lengths

For both sites, the turning angles were significantly orientated towards 0° (Rayleigh's V -test; Prés de la Lienne: $u=4.958$, $P<0.0005$; Pisserotte: $u=10.94$, $P<0.0005$). In Prés de la Lienne, the mean angle (\pm SD) was $10.47^\circ \pm 10.56^\circ$; in Pisserotte it was $8.28^\circ \pm 4.34^\circ$. For Prés de la Lienne, there was only a weak correlation between consecutive turning angles separated by one lag (i.e. a first-order autocorrelation, angular–angular correlation $r_{aa}=0.091$, $n=31$ [the 95 % confidence interval of all the r_{aa} presented here did not include 0]). For Pisserotte, there was a slightly stronger correlation between consecutive turning angles, separated by one lag (angular–angular correlation $r_{aa}=0.21$, $n=202$) and by two lags (i.e. a second-order autocorrelation, $r_{aa}=0.16$, $n=183$). Separated by three lags, the correlation between turning

angles becomes weaker ($r_{aa}=0.08$, $n=164$). For both sites, there was no correlation between turning angle and the associated move length (Pearson's r ; Prés de la Lienne: $r=0.57$, $P>0.05$, $n=48$; Pisserotte: $r=0.54$, $P>0.05$, $n=237$).

The distribution of move length followed a normal distribution in Lienne (Kolmogorov-Smirnov $d=0.132$, $P>0.05$, $n=48$) but not in Pisserotte ($d=0.188$, $P<0.01$, $n=237$). The mean move length (\pm SD) was $19.4\text{ m} \pm 11.9\text{ m}$ in Lienne and $11.3\text{ m} \pm 10.2\text{ m}$ in Pisserotte. For Prés de la Lienne, no correlation between consecutive move lengths was detected (Pearson's $r=0.05$, $P>0.05$, $n=39$). In Pisserotte, a correlation was found between consecutive moves for moves separated by one (Spearman's rank $r_s=0.19$, $P<0.01$, $n=209$) or two lags ($r_s=0.19$, $P<0.01$, $n=185$), but not for a higher-order correlation ($r_s=0.07$, $P>0.05$, $n=162$).

Analyses of paths

In order to assess whether a model of correlated random walk (CRW) can describe the path data appropriately, the overall paths were analysed by comparing the theoretical net square displacement R_n^2 for all moves n with the observed one (Kareiva & Shigesada 1983). An observed R_n^2 exceeding the predicted one indicates the paths are more direct than would be suggested by CRW. The opposite pattern, an observed R_n^2 lying below the predicted one, is less common and occurs in data sets where a more systematic search is found (e.g. Mexican bean beetles *Epilachna varivestis* (Turchin 1998)).

In the first step, we perform this analysis by pooling the turning angles and move lengths of all paths to calculate the predicted net square displacement R_n^2 . Exemplarily, the results of this analysis of the Pisserotte data are shown in Fig. 2.6. As long as the observed R_n^2 values are averaged over all paths, the following picture occurs: the mean R_n^2 observed for each move n lies after 9 moves close to the calculated R_n^2 and well within the 95% confidence interval. However, considering each observed path separately, almost all of the paths lies outside the 95% confidence interval. From all 27 paths, the observed R_n^2 of 13 paths increases significantly faster with increasing step number n as predicted. In contrast, the observed R_n^2 of 10 paths increases (compared with the predicted R_n^2) significantly slower. This can be also seen in Fig. 2.6, where the R_n^2 of two paths with the described properties are shown as an example. This result indicates that there are great differences in turning angles

and move length of different paths. The good fit of the mean observed R_n^2 appears to be attributable to the fact that different paths with high and low R_n^2 average out each other.

Therefore, in a second step, the same analysis – comparing the theoretical and observed net square displacement R_n^2 – was performed, but now by calculating the predicted R_n^2 for each path separately (taking the data of one path considered as a basis). Using this method, more paths were found to be appropriately described by a correlated random walk. Of 27 paths, 15 paths (including 5 paths from Prés de la Lienne) can be described with the correlated random walk model (56 %), while for 3 paths (including none from Prés de la Lienne) the R_n^2 increased faster than expected (11 %) and for 8 paths (including 2 paths from Prés de la Lienne) R_n^2 increased slower (30 %). One path displayed no clear trend. In Fig. 2.7, these three cases are shown by way of example on three paths. A path which can be described with the correlated random walk model according to the R_n^2 analysis can be seen in Fig. 2.7a. Here, the observed R_n^2 lies within the 95% confidence interval, and the corresponding path seems to be quite straight (as all paths where the observed R_n^2 equals that predicted). The path shown in Fig. 2.7b has a R_n^2 significantly higher than that calculated and also appears straight. In Fig. 2.7c, the observed path lies partly within the 95 % confidence interval, but for some steps significantly below the predicted R_n^2 . This reflects the shape of the path, where the butterfly changed direction completely and returned close to the starting point. This behaviour indicates a more systematic movement than a random walk.

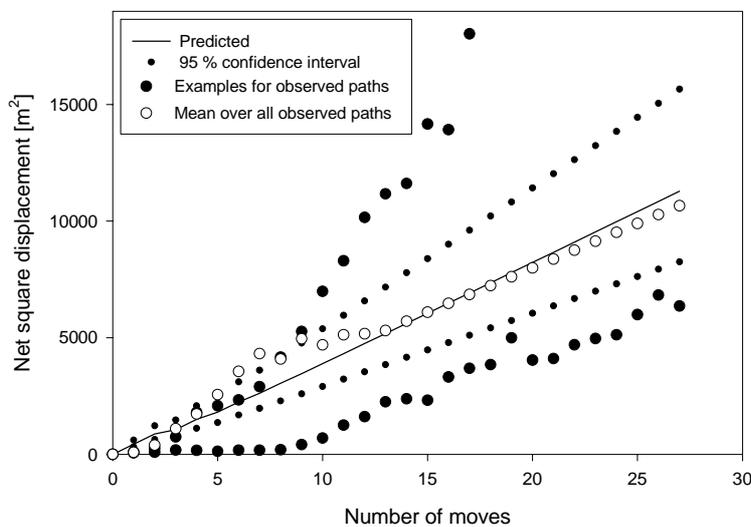


Figure 2.6 In order to test whether the paths can be described with a random walk model, the predicted and observed net square displacement (R_n^2) were compared (here shown for the data of Pisserotte). Predicted R_n^2 and 95 % confidence interval were obtained by simulations. White points represent the mean observed R_n^2 over all the paths of this site; black points represent two examples for the observed R_n^2 for single paths.

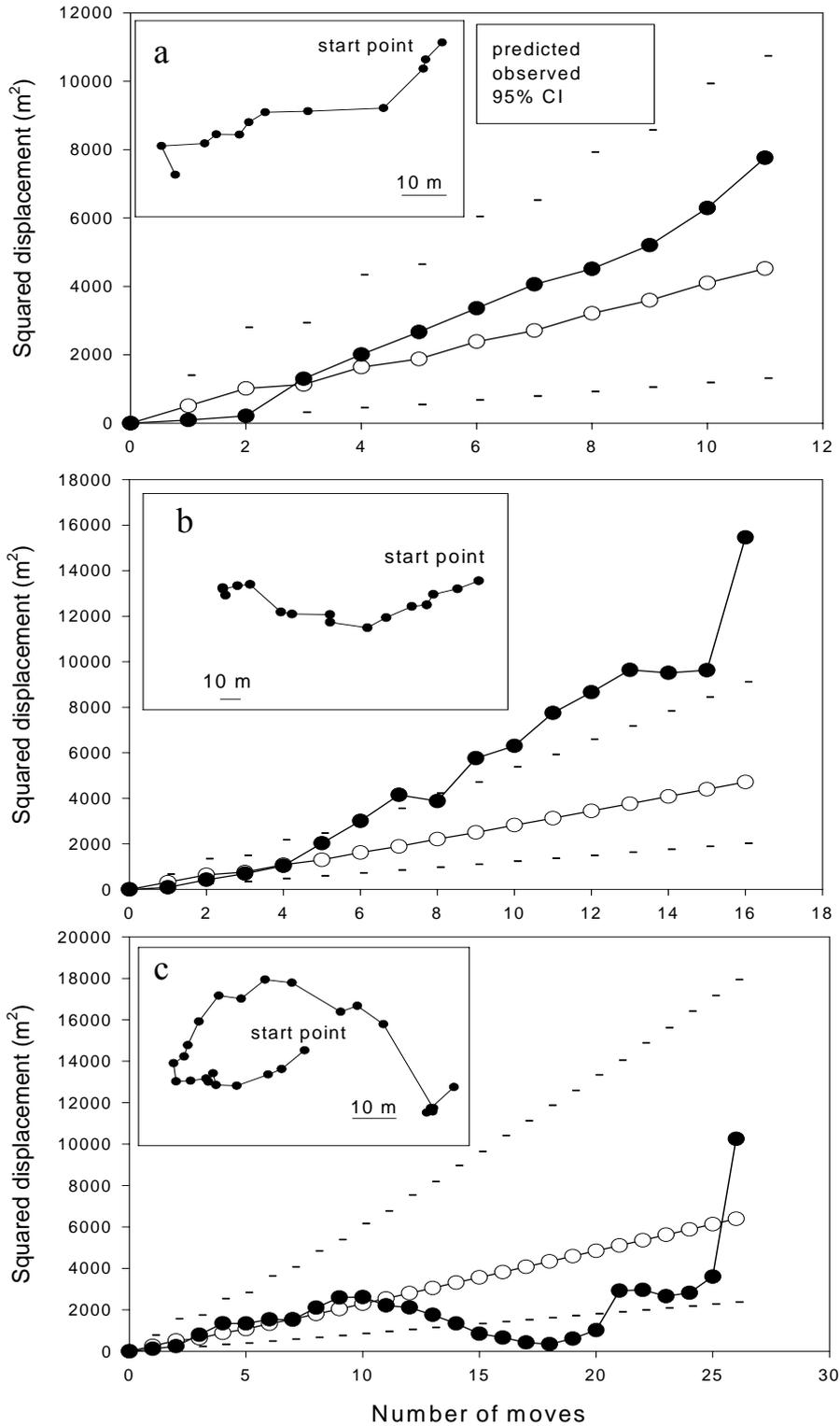


Figure 2.7 Examples of three paths with different results between theoretical (white dots) and observed (black dots) net squared displacement (R_n^2). 2a: Theoretical and observed R_n^2 coincide (observed for 15 paths out of 27). 2b: The observed R_n^2 lies above the theoretical one (observed for 3 paths out of 27). 2c: The observed R_n^2 lies below the theoretical one (observed for 8 paths out of 27).

Paths with a more systematic movement

A visual inspection of the paths shows that the paths with low R_n^2 are all bent and seem to have a tendency to turn in one direction more than in the other. We decided to test whether this tendency can be found from the means of turning angles and move lengths.

We did not find any preference to retain the orientation of one step in the next step ($\chi^2=0.931$, $P>0.05$).

By pooling the turning angles of all paths with low R_n^2 and testing for high-order autocorrelations (1 to 8 lags), we only found – similar to the data of all paths – a correlation at the first and second time lags, but not for higher lags. In contrast, when investigating the correlation for each path separately, high-order correlation that was even stronger than at the first lag was found – albeit for each path at a different lag. For example, correlation was found at the 4th lag of path 5, while in path 3 correlation was observed at lags 8 and 9 (for details see Table 2.1). These high autocorrelations at a certain lag suggest that the butterflies tend to turn in the same direction for several moves. Because the correlations were at different lags, they could not be found by amalgamating the turning angles of all the paths considered.

We also investigated whether the return rate of butterflies flying non-randomly differs from those flying randomly. Of the butterflies with the more systematic movement behaviour, 63 % arrived at the habitat patch – almost exactly the same proportion as was found for all butterflies released at 250 and 300 m (61 %; see above) .

Table 2.1 The correlation between angles at different lags for two paths with low R_n^2 (a correlation coefficient $r>0.1$ (or $r>-0.1$) is shown in bold type)

Lag	1	2	3	4	5	6	7	8	9	10
r of path 3 	0.105	0.028	0.087	-0.075	-0.078	-0.005	0.036	0.165	-0.184	-0.048
r of path 5 	0.319	0.026	0.059	0.247	0.030	-	-	-	-	-

4 Discussion

4.1 On the movement behaviour of *Proclossiana eunomia*

Perceptual abilities

Our results do not show any significant orientation towards the habitat for butterflies released at 50 m. From a 70–100 m release distance, animals were found to head towards the habitat right from the start, while for higher release distances no significant orientation was found. At the 50 m distance, the butterflies may have shown low motivation to aim for a habitat accurately (since from a short release distance deviations in the starting angles only result in small detours). For the 250 and 300 m release distance, the butterflies were probably no longer able to head for the patch. Furthermore, 100% of the butterflies released at 100 m returned to the habitat, while only 61% of the butterflies released at 250 m returned. From these arguments, it can be concluded that the apparent perceptual range of the butterflies released is at least 100 m. A similarly high perceptual range (over 70 m) was found for *Maniola jurtina* (Conradt *et al.* 2000), while for the Fender's Blue Butterfly *Icaricia icarioides fenderi* the distance from which butterflies react to the habitat edge seems to be much shorter (10–22 m (Schultz & Crone 2001)). The effect that butterflies released from very short distances showed no significant orientation towards the habitat patch was also found for *Maniola jurtina* (Conradt *et al.* 2000).

Since the concurrent performance of genetic studies prevented us from releasing individuals from one population at the other population's site, we cannot rule out the possibility that the release site was already familiar to the butterflies. However, there was a fragmentary boundary of trees between habitats and release sites. As such boundaries have been shown to be a barrier to emigration (Ries & Debinski 2001, Schtickzelle & Baguette 2003), it seems unlikely that the animals crossed the boundary to explore the hostile matrix.

The results of this study can also contribute to the understanding whether *P. eunomia* is a sedentary butterfly. Baguette & Nève (1994) and Petit *et al.* (2001) found a high level of movements between the patches of a structured population where the distance between habitat patches varied between 40–150 m; the maximum dispersal distance observed for *P. eunomia* is 4.6 km (Petit *et al.* 2001). This indicates that *P. eunomia* is a more dispersive butterfly than proposed in previous literature (Bink 1992). A perceptual range of 100 m may give an explanation for the high exchange rates: most movements between habitat patches in this population would be well within the perceptual range, which for small distances reduces the risk of moving.

Flight paths

Our analysis shows that most of the flight paths recorded for *P. eunomia* can be described with a correlated random walk model. However, 3 out of 27 paths showed a behaviour straighter than a correlated random walk, while 8 paths indicated a more systematic flight behaviour, where the butterflies exhibited a tendency to return to the release point. This more systematic movement behaviour is characterised by high-order correlations in turning angles. Since this correlation occurs at different lags for different paths, each path can only be comprehended individually.

Dispersal behaviour different from random has also been found by other authors. Conradt *et al.* (2000, 2001) observed systematic dispersal behaviour in two butterflies, *Maniola jurtina* and *Pyronia tithonus*. Mexican bean beetles released in a field with no host plants exhibited a spiralling movement pattern (Turchin 1998). Other studies have observed non-random movement for individuals searching for food or their nest (Hoffmann 1983, Müller & Wehner 1994). These investigations indicate that non-random movement behaviour is not an exception but can be found in a variety of species.

Furthermore, our results show that different individuals of one species can exhibit qualitatively different movement patterns. This corresponds with the results of other studies, which found variability in movement patterns in other species (Baars 1979, Morales & Ellner 2002, Angelibert & Giani 2003).

4.2 Consequences for analysing individual dispersal success, landscape connectivity and metapopulation dynamics

Findings such as a high perceptual range, the existence of non-random dispersal behaviour and the individual variability in movement patterns can influence our understanding of various ecological aspects of species in fragmented landscapes in general and *P. eunomia* in particular. This chiefly has implications for evolutionary questions, landscape ecology and metapopulation theory.

Firstly, the success of individuals in finding habitat patches (and ultimately their individual fitness) is likely to be influenced by these factors. It has already been found in simulation models that the perceptual range increases the search success (Zollner & Lima 1999b). While nearly straight correlated random walk was found to be especially advantageous in most landscape types (Zollner & Lima 1999b), Conradt *et al.* (2003) found a systematic search strategy to be more efficient in landscapes with a clumped distribution of habitat patches.

Secondly, both field studies and simulation studies have shown that the behaviour of animals can strongly influence the functional connectivity between habitat patches (Keitt *et al.* 1997, Pither & Taylor 1998, Heinz *et al.* 2003 submitted). This is especially relevant for behavioural aspects as perceptual range as well as type and variability of movement patterns. These three aspects should therefore be considered when dispersal functions are developed for further use in the context of connectivity. So far, these functions have usually been based on the assumption of (correlated) random walk (Turchin 1998).

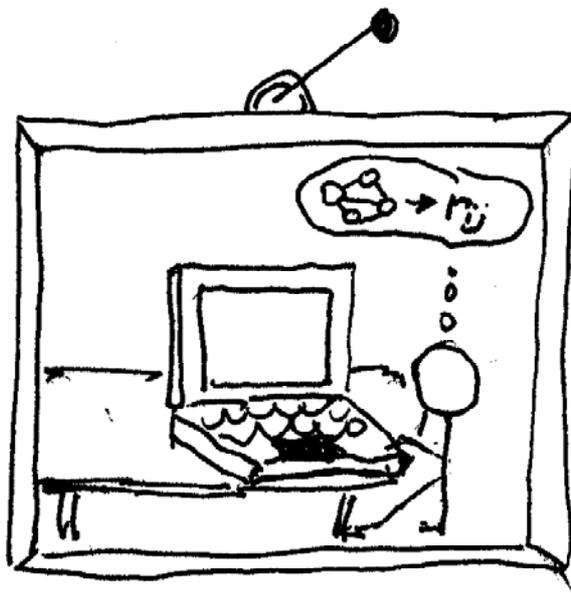
Thirdly, if the perceptual range and the movement behaviour alter search success and connectivity, via these factors they could also influence the whole dynamics and viability of spatially structured populations and metapopulations. The colonisation of empty habitat patches can be broken down into several processes: the emigration of individuals from an occupied patch, dispersal through a more or less inhospitable matrix, immigration into a new habitat patch, and establishment in this patch (Ims & Yoccoz 1997). Our results directly contribute to our understanding of how individuals move through the matrix; yet they also provide insights regarding the emigration in fragmented landscapes. Usually the emigration rates are related to the size and area of patches. Schtickzelle & Baguette (2003) showed that the emigration of *P. eunomia* additionally depends on the degree of fragmentation. The existence of a perceptual range of 100 m recorded in the present study probably gives an explanation. Habitat patches inside the perceptual range of a habitat patch under consideration can increase the willingness of individuals to leave and, hence, increase the emigration rate. This shows that emigration rates can only be correctly understood if the whole spatial configuration of the habitat network is considered and the perceptual range is taken as a spatial scale.

Part I demonstrated that the dispersal behaviour of individuals is often not random. To analyse the consequences of such non-random dispersal behaviour on metapopulation dynamics without spending tremendous simulation time on modelling each particular movement step, we need a modelling framework that subsumes the details of individual dispersal behaviour in a simple, but sufficiently explicit way. This will be the challenge of Part II.

Part II

Individual dispersal behaviour and patch
accessibility –

Developing a modelling framework



Dispersal behaviour in fragmented landscapes:

Deriving a practical formula for patch accessibility

1 Introduction

Many studies have shown that the ability of animals to move between habitat fragments is a key determinant of the viability of spatially structured populations and metapopulations (Levins 1970, Opdam 1990, Hanski *et al.* 1994, Hess 1996, Anderson & Danielson 1997, Frank & Wissel 1998, Thomas 2000, Johst *et al.* 2002). In this connection, one crucial factor is the probability r_{ij} of a certain patch j being reached by an emigrant from a certain patch i , referred to as patch accessibility.

To analyse the consequences of dispersal for population viability in mathematical models, the functional relationship between patch accessibility r_{ij} and landscape configuration needs to be subsumed in a simple way. The easiest approach is doubtless to take the distances between patches into account. In the literature, this is normally done by describing r_{ij} as a function of distance between start and target patch. It has been concluded that r_{ij} may decrease with increasing distance (Harrison *et al.* 1988). One of the simplest and most obvious approaches to describe this relationship is the exponential form, where r_{ij} declines exponentially with distance. This approach is used in a variety of models (Fahrig 1992, Hanski 1994, Adler & Nuernberger 1994, Hanski *et al.* 1996, Vos *et al.* 2001, Frank & Wissel 2002). Although Wolfenbarger (1949) proved this exponential dispersal function to be valid for a variety of small, passive organisms, it is debatable whether this approach is suitable to describe more complex situations, especially when the individuals' dispersal behaviour is taken into account. As many empirical studies have shown, animals' movement behaviour often cannot be described by a model of (correlated) random walk (Wiens *et al.* 1997, Conradt *et al.* 2000, Conradt *et al.* 2001) and some authors have stated that other functions describe the dependence of dispersal on distance better than the exponential approach (Hill *et al.* 1996, Baguette *et al.* 2000). Nevertheless, what kind of function is flexible enough to explain the distance dependence for different complex movement characteristics is not yet clear. Moreover, whether the effect of complex dispersal behaviour and landscape structure on patch accessibility can be described by a simple formula is an open question.

This paper addresses the problem of how to describe patch accessibility r_{ij} in a simple way. To tackle this problem we developed a simulation model to determine r_{ij} for varying landscape configurations and dispersal behaviours. Our model analyses show an important intrinsic effect of the interplay between landscape structure and dispersal behaviour on patch accessibility: the competition between patches for migrants.

Analysing landscapes of increasing complexity, we derive a formula to calculate r_{ij} . Although this formula is very simple, it is able to cover effects such as the competition for migrants. We show that this formula is applicable to a variety of spatial configurations and types of dispersal behaviour. We used simple movement patterns, such as the often used random walk (Doak *et al.* 1992, Ruckelshaus *et al.* 1997, With & King 1999) and the Archimedean spiral (Bell 1991, Dusenbery 1992, Zollner & Lima 1999b). We also used a more complex pattern observed in nature – the loop-like movement pattern observed for a variety of animals (Hoffmann 1983, Bell 1985, Müller & Wehner 1994, Durier & Rivault 1999), especially (in the context of dispersal) for *Maniola jurtina* and *Pyronia tithonus* (Conradt *et al.* 2000, Conradt *et al.* 2001). The essence of the model is condensed in this formula. This delivers insights into the consequences of dispersal in fragmented habitats for population dynamics and furthermore enables the potential and limits of the exponential approach to be analysed.

2 The model

In order to determine the probability r_{ij} of patch j being reached by an emigrant starting from patch i in any given landscape, we developed a spatially structured, individual-based model. Since we wanted to investigate the impacts of different landscape configurations (number and configuration of patches) and different movement patterns, both had to be variable in the model. The programming language used to build the model was C++.

2.1 Landscape

To determine the patch accessibility r_{ij} for any given landscape configuration, we used spatially continuous (rather than grid-based) landscapes with circular patches and a homogenous matrix. A specific number of patches was distributed randomly within a 100 x 100 area (scaled by virtual spatial units) by selecting x- and y-coordinates from a uniform distribution. The diameter of the habitat patches was set to 4 spatial units. If two patches overlapped, the location of the second patch was resampled. In contrast to most other existing models (Pulliam *et al.* 1992, Adler & Nuernberger 1994), we did not use any kind of border to restrict the landscape. The animals were allowed to run out of the patch-containing landscape

and to return as long as they were still alive. This seems biologically reasonable, because real landscapes do not necessarily have edges between patch-containing and empty matrices that are apparent to dispersing animals. Since in our case we need to be able to pinpoint an animal during its entire dispersal time, substituting one animal that runs out of the landscape by another animal coming in (as is done in models with periodic border conditions) would be pointless. Additionally, from an analytical viewpoint, omitting borders means the system is not made additionally complex by extra border effects.

Not only landscape aspects (distance between habitats, patch size) but also behavioural components (step-length, perceptual range, mean dispersal distance) are scaled by virtual spatial units. As long as the ratio between these features remains proportionate, they can be transformed for different animals and landscapes to any appropriate spatial scale.

2.2 Movement patterns

To investigate the probability of a certain patch being reached, the following movement patterns were applied: random walk with different degrees of correlation between the angles of consecutive steps, the Archimedean spiral and a loop-like movement pattern. The Archimedean spiral is a movement pattern where the individual circles outward from the start patch in a continuous curve. For the loop-like pattern found for *Maniola jurtina* and *Pyronia tithonus* (Conradt *et al.* 2000, Conradt *et al.* 2001), the individuals move away from the start point, describe a semi-circle and return to the starting point on a different path. The next loop is started in another direction, creating a petal-like path. The size of the loops increases with the number of loops, and so the radius searched increases.

In the model, all movement patterns are based on the elements of random walk. For simplicity's sake, the random walks are assumed to have a constant step length (half a spatial unit) with only the turning angles varying. The variation of the turning angles determines whether the direction of movement is uncorrelated between two consecutive steps (and therefore the movement is completely random) or correlated. These turning angles are drawn from a zero-mean Gaussian distribution. The variation of the turning angles (and therefore the degree of the correlation of the random walk) is determined by the standard deviation of this distribution. We model the standard deviation $std = (1-c)*2*\pi$, with c being the degree of correlation between consecutive movement directions. Thus for $c = 0$, the standard deviation of turning angles would be $2*\pi$ (360°) and therefore the random walk would be almost totally random. For $c = 1$, all turning angles would be 0° and the movement would be a straight line. We decided less extreme values would approximate biologically reasonable movements, and

so chose values for c of 0.00 for uncorrelated, 0.90 for fairly correlated and 0.99 for strongly correlated random walk (Fig. 3.1).

The two more complex movement patterns, spiral and loops, are generated by adding a few more rules to the random walk. Since these rules are very simple, it is conceivable that they reflect the actual movement behaviour of animals.

The spiral is created by a random walk in just one orientation (i.e. clockwise or anticlockwise) using the absolute valued of turning angles drawn from the Gaussian distribution. The orientation of the spiral is determined by the first randomly drawn step. For the typical spiral, the radius of the spiral increases as the number of steps grows. This increase in radius can be implemented by increasing the correlation degree of the random walk, which can be generated by decreasing the standard deviation of the Gaussian distribution utilised (see above). We used a power function for increasing c with the number of steps ($c_{step+1} = c_{step} + (0.01 * c_{step}^{1.3})$, with $c_{step(initial)} = 0.95$). Because the turning angles are taken randomly from the Gaussian distribution, this kind of spiral is subject to stochasticity. An example of the spiral-like movement pattern can be seen in Fig. 3.1b.

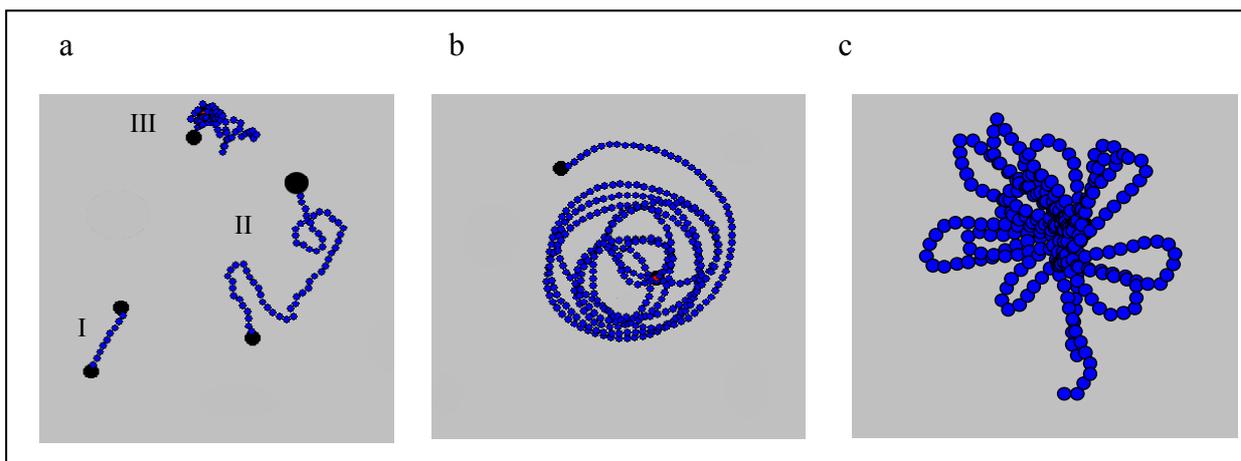


Figure 3.1 Different movement patterns: a) Random walk with three different degrees of correlation: strongly correlated (I), fairly correlated (II) and uncorrelated (III). b) Spiral c) Loop-like movement pattern. The diameter of the movement points reflects the perceptual range of the disperser.

The loops (Fig. 3.1c) are generated in three phases. In the first phase, the individuals move away from the starting-point in a random direction with a strongly correlated random walk ($c = 0.99$). The number of steps in this phase determines the length of the loop (we choose 4 steps for the initial loops). In the second phase, the animal starts to take all its steps in the same orientation (albeit with different turning angles), and so it describes an arched path ($c = 0.90$). In order to describe approximately a semi-circle, the number of steps in the second phase has to be adjusted to the correlation degree (in this case, we used 4 steps). The width of the loops is approximately determined by the number of steps in this phase. In the third phase the turning angle and the number of steps needed for the way back were calculated and the animal returns in a straight path to the starting patch. This behaviour reflects the orientation abilities of animals observed in nature. Some animals are known to be able to return straight to the starting-point by integrating their turning angles while moving. This behaviour is called path integration (dead reckoning) and has been observed for a number of animals (Wehner *et al.* 1996, Etienne *et al.* 1998, Durier & Rivault 1999, Menzel *et al.* 2001). For the next loop, the animal starts again in a random direction away from the starting-point, but not in the same quadrant of an imaginary circle around the starting-point as before. As observed in nature (Conradt *et al.* 2000), the size of the loops in the model increases with increasing number. This is done by increasing the number of steps in the first phase after each 4 loops about 2 more steps.

2.3 Parameters

Besides the movement rules there are two other parameters in the model that determine dispersal ability: mortality risk and perceptual range. We expressed mortality risk as the per-step probability of dying, as is done in various models (Pulliam *et al.* 1992, Zollner & Lima 1999b, Tischendorf 2001). This seems biologically reasonable since mortality is more likely to happen with increasing time spend in the hostile matrix. The mortality risk was varied between values of 0.001 and 0.01. Perceptual range describes the distance within which an animal can detect new patches and can therefore move towards them. It is commonly used in models (Cain 1985, Fahrig 1988, Armsworth *et al.* 2001) and has been well investigated in the field (Yeomans 1995, Zollner and Lima 1997, Zollner 2000, Conradt *et al.* 2000). In the model, we used values between 0 and 8 spatial units for the perceptual range. In Fig. 3.1, the perceptual abilities of the dispersing animals can be seen as the diameter of the circle symbolising the moving animal. Unless otherwise specified, a per-step mortality of 0.001 and a perceptual range with a radius of 2 spatial units are taken as standard model parameters.

2.4 Simulation

For one simulation run, 100 landscapes with a specific number of patches (2, 3 or 10) were produced. In each landscape, 1000 animals were released at patch i . After release, the individuals move through the landscape according to their movement rules (movement pattern and movement parameters) until they either find a patch or die. If a patch comes within the perceptual range of an individual (excluding the patch from which the individual emigrated), the individual moves straight to this patch and stays there. If there is more than one patch within the perceptual range, the individual moves randomly to one of these patches and stays there. The probability r_{ij} of patch j being reached is counted as the proportion of individuals arriving at this patch. Additionally, landscape features, such as the position of the patches and the corresponding distance d_{ij} between start patch i and target patch j (measured from centre to centre) are noted.

The results of the simulation model are analysed by using linear and non-linear regressions. All regressions are done using SigmaPlot which applies the Marquardt-Levensberg Algorithm for minimization of least squares. We also applied the Akaike Information Criterion (AIC, Motulsky and Christopoulos 2003) to compare functions with different number of fit parameters.

3 Results

In order to find the functional dependence of the patch accessibility r_{ij} on landscape configuration our twin aims are to identify the essential spatial characteristics of the landscape and to express the functional relationship between r_{ij} and these characteristics as simply as possible. Moreover, we are interested in understanding how the functional structure depends on the individuals' movement behaviour.

The simplest way of including landscape configuration is doubtless to take the distances between the patches into account. In the literature, this is usually done by describing r_{ij} in dependence on the distances between start and target patch. The commonest approach of this type uses an exponential fitting function given by:

$$R_{ij} = e^{-b*d_{ij}} \quad (3.1)$$

where d_{ij} is the distance between start patch i and target patch j , and $1/b$ is the mean distance an individual is able to cover. The notations r_{ij} and R_{ij} are needed to distinguish between simulated values (r_{ij}) and the fitting function (R_{ij}). However, since this approach is ad hoc, it is uncertain how well it predicts r_{ij} in the case that the individuals' movement behaviour is

taken into account. This question is especially relevant if the behaviour is more complex, as in the case of the loop-like behaviour observed in nature.

Therefore, in our initial experiment we investigate whether this exponential distance-based approach works to describe r_{ij} for the loop-like movement pattern taken as an example. In order to answer this question, we perform the above described simulation (2.4). We use landscapes with 10 patches and let the animals move in a loop-like movement pattern. To test the predictive power of the exponential approach, the resulting values of r_{ij} and d_{ij} are recorded for each of the 10 patches and each of the 100 landscapes. These r_{ij} - d_{ij} values are used as a basis for regression analysis, where the data are fitted to an exponential curve.

Fig. 3.2 shows the result of regression analysis, with each point representing one particular patch pair. As can be seen, the results exhibit high variation, and so r_{ij} can be neither predicted nor explained by the exponential function. This is not only caused by the shape of the exponential function, but mainly by the large variety of possible values of r_{ij} for a certain fixed distance d_{ij} . This large variation may be a result of statistical or systematic effects. Below we investigate the systematic effects. As the range of the r_{ij} values shows that distance d_{ij} is not the only determinant of r_{ij} , it is (at least for the loop-like movement pattern) not sufficient to consider merely the distance between start and target patch to describe r_{ij} . We hypothesise that the variation of r_{ij} is the result of the interactions with all the other patches. This means we have to consider the complete landscape configuration if we want to understand and predict r_{ij} .

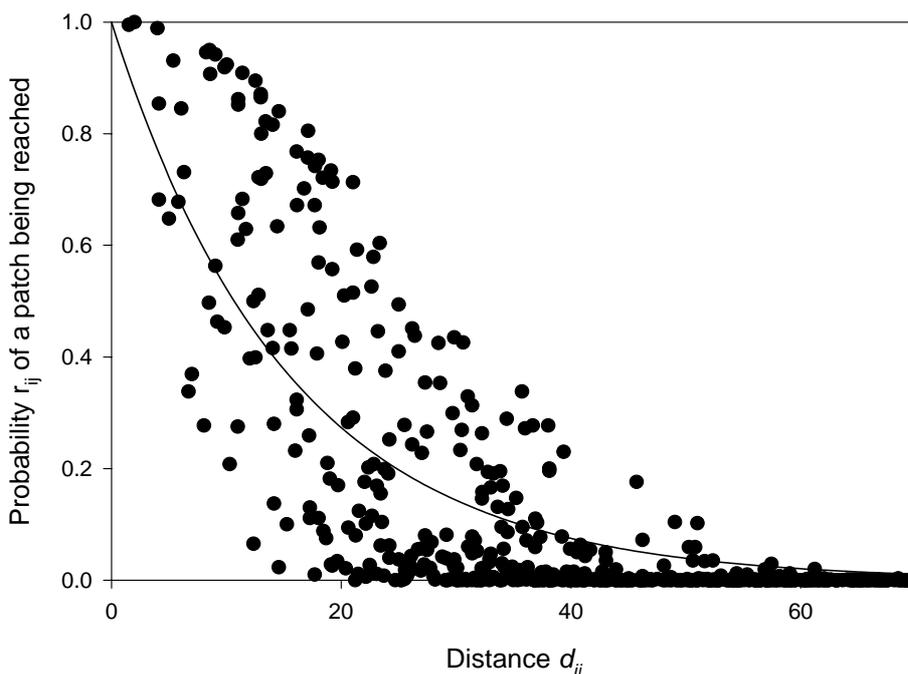


Figure 3.2 The probability r_{ij} of patch j being reached in landscapes with 10 patches as a function of distance d_{ij} between start patch and target patch for the loop-like movement behaviour. The dots represent the simulation results, the line a fitted exponential curve.

In order to examine the influence of landscape configuration systematically and to handle the complexity of the system, we use a hierarchical approach: In a first step, we focus on the simplest landscape (two-patch systems). By taking the results of this reference study as a basis, more complex landscapes (multi-patch systems) are investigated in a second step. In both steps, a set of the different movement patterns described is considered and investigated.

3.1 The patch accessibility r_{ij} in a two-patch system

Below, a landscape with only two patches is considered. Our aim is to find the simplest possible mathematical function that allows the functional relationship between the patch accessibility r_{ij} and the distance d_{ij} between start patch i and target patch j to be reproduced qualitatively correctly and quantitatively sufficiently.

To achieve this goal, the same experiment as before is performed, but now using landscapes with only two patches. The loop-like movement pattern is used as an initial case to search for a suitable function. Once an appropriate function type has been found, its predictive power is tested for a variety of model parameters of the complex loop-like pattern and later on for the other, more simple movement patterns, such as random walk with different degrees of correlation and Archimedean spirals.

The loop-like movement pattern

As can be seen in Fig. 3.3, the patch accessibility r_{ij} decreases with rising distance d_{ij} . In contrast to the results in Fig. 3.2, a clear functional relationship can be detected. However, comparison with the corresponding exponential fit (dashed line) reveals that the functional relationship is qualitatively different from the exponential one. For larger distances, the simulated r_{ij} values lie below the exponential curve, while for shorter distances they lie above it. It is especially noticeable that in the range of shorter distances the decrease is rather flat. For larger distances, however, an exponential decline can be observed. Therefore we are interested in finding the simplest possible fitting function R_{ij} that allows this type of functional behaviour (flat decrease in the short range, exponential decrease in the long range) to be described. An appropriate candidate is the so called sigmoidal function given by:

$$R_{ij} = 1 - e^{-a * e^{(-b * d_{ij})}} \quad (3.2)$$

where d_{ij} is the distance between start patch i and target patch j , and a and b are two fitting parameters. Comprising two parameters, this function has one parameter more than the exponential one. As can be easily checked (Appendix A1), it behaves approximately exponentially for larger distances.

The solid line in Fig. 3.3 indicates what happens if the sigmoidal function (3.2) is taken as a basis of a non-linear regression. There is a close correspondence between the data and the fitting curve for the range of both short and long distances. Moreover, the r^2 value is much better for the sigmoidal fit ($r^2 = 0.999$) than for the exponential fit ($r^2 = 0.877$). Applying the Akaike's Information Criterion (AIC), we found the sigmoidal function to be more likely to be correct ($\Delta AIC = -624$ with $\Delta AIC = AIC_{sig} - AIC_{exp}$, negative values indicating that the sigmoidal function more likely, positive values indicating that the exponential function is more likely). Even more important is the fact that the sigmoidal function gives a much better qualitative reflection of the simulated values than the exponential one. While the exponential function underestimates the patch accessibility for small distances and overestimates it for larger ones, the sigmoidal function gives a high-quality fit for the whole distance range.

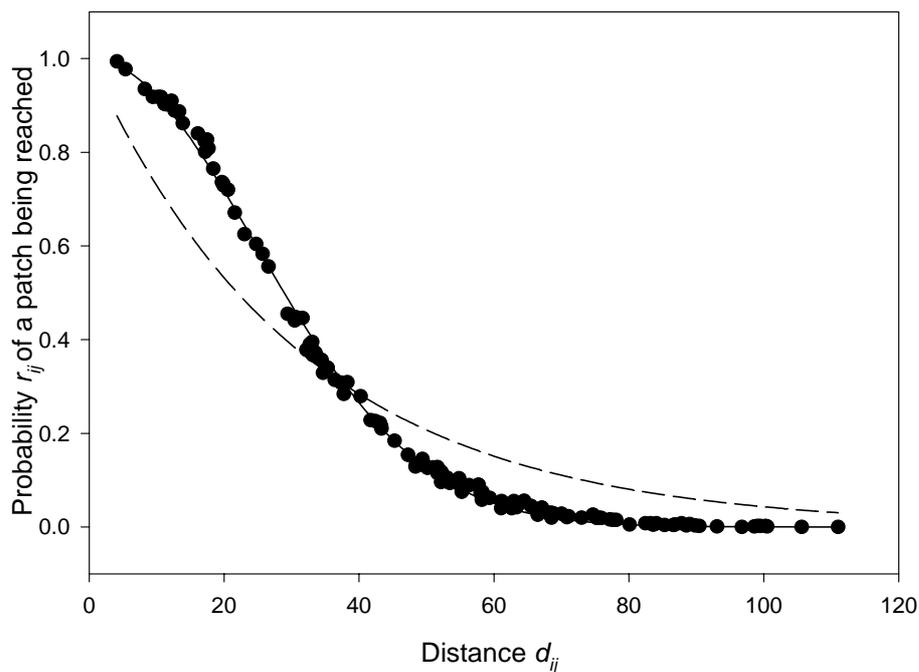


Figure 3.3 The probability r_{ij} of patch j being reached in a 2-patch system depending on the distance d_{ij} between start patch and target patch. The lines indicate two fitted functions, the sigmoidal function (3.2) (solid line; $r^2 = 0.999$) and the exponential function (3.1) (dashed line, $r^2 = 0.877$).

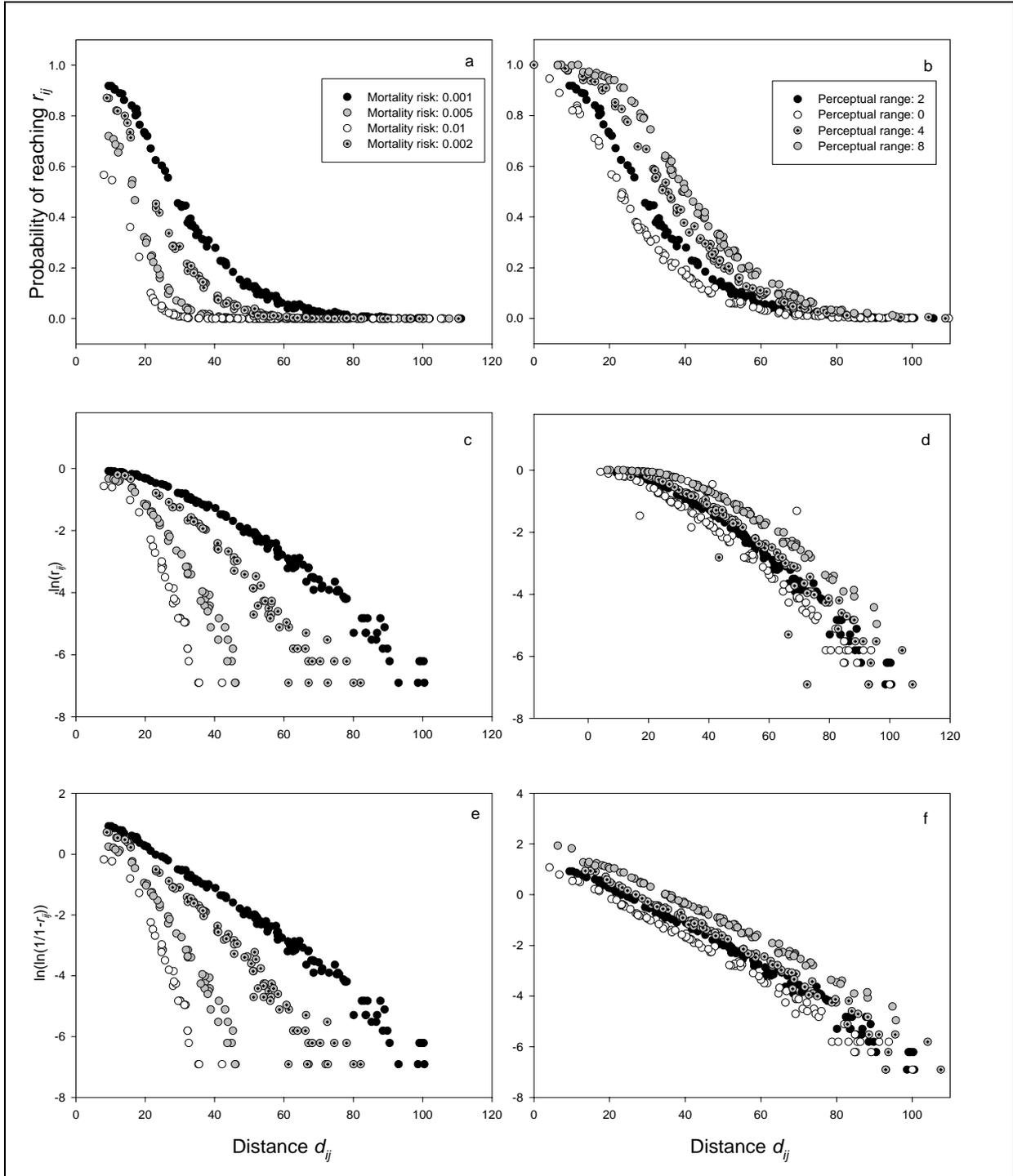


Figure 3.4 The probability r_{ij} of reaching a specific patch j depending on the distance d_{ij} between start and target patch for different mortality risks (left side) and different perceptual ranges (right side). The original r_{ij} - d_{ij} data show a rather sigmoidal shape (3.4a and 3.4b), the corresponding r^2 of the non-linear regression can be found in Table 3.1 (upper 7 values). To detect the fine structure of the curve, the log transformation was performed according to the exponential function (relation (3.1)) (3.4c and 3.4d) and the sigmoidal function (relation (3.2)) (3.4e and 3.4f). The linearity test for the correspondingly transformed values $\ln(r_{ij})$ and $\ln(\ln(1/(1-r_{ij})))$ indicate the original data r_{ij} to be sigmoidal rather than exponential.

Additionally to this non-linear regression, we performed a structural analysis of the functional relationship between r_{ij} and d_{ij} . If the r_{ij} values really show a mathematical dependence on the distance d_{ij} of this type (sigmoidal/exponential), then the correspondingly transformed values $\ln(1/1-r_{ij})$ for the sigmoidal (3.2) and $\ln(r_{ij})$ for the exponential (3.1) type must show a linear relationship with the distance d_{ij} .

The results of the non-linear transformation and the corresponding test for linearity performed for a variety of parameter combinations can be seen in Fig. 3.4. While the curve for the sigmoidal approach displays a strong linear dependence on the distance d_{ij} for all parameter combinations, the exponential approach leads to a rather bent curve. This curvature cannot be removed by adding one additional parameter to the exponential function (in this case the curve would undergo parallel displacement). Therefore the high-quality fit of the sigmoidal function is due not to its extra parameter, but rather its inner structure. This finding confirms that - as far as the loop-like movement behaviour is concerned - the sigmoidal function is found to be able to reproduce the functional relationship between r_{ij} and d_{ij} qualitatively correctly and quantitatively sufficiently.

Correlated random walks and Archimedean spiral

Below, the sigmoidal and the exponential function are compared regarding their predictive power for the more hypothetical movement patterns such as correlated random walks with different degrees of correlation and the Archimedean spiral.

The functional relationship between the patch accessibility r_{ij} and the distance d_{ij} for the movement patterns mentioned can be seen in Figure 3.5.

All the scenarios of the correlated random walk lead to a rather exponential shape, regardless of the degree of correlation. The corresponding non-linear regression analysis (Table 3.1), however, reveals a better adjustment of the sigmoidal function for strongly correlated random walk and fairly correlated random walk. For the uncorrelated random walk both functions show a good fit, with the exponential function fitting slightly better. If the Archimedean spiral is taken as movement pattern, the resulting r_{ij} - d_{ij} relationship shows a slightly flat decrease in the short range. The corresponding r^2 values reveal that both the sigmoidal and exponential function give rise to a high-quality fit. The better fit of the sigmoidal function is not surprising as this function has one parameter more than the exponential one. However, the AIC shows that the sigmoidal function is in most cases more likely to be correct, and furthermore this additional parameter allows the qualitative behaviour of the r_{ij} - d_{ij} relationship to be better reproduced.

Table 3.1 Results of the regression analyses for a two- and ten-patch system. ΔAIC is used as an indicator for which model (exponential or sigmoidal) is more likely to be correct taking the different number of fit parameters into account. Negative (positive) values indicate that the sigmoidal (exponential) function is more likely to be correct. The last column shows the results for a linear regression between simulated and calculated values in a 10-patch-system (calculated with $r_{ij}^{calc} = W_{ij}^{II} * R_{ij}$).

Parameters			2-patch-system			10-patch-system
Movement pattern	Mortality	Perceptual range	r^2 of	r^2 of	$\Delta AIC =$	r^2 of r_{ij}^{sim} vs. r_{ij}^{calc} $r_{ij}^{calc} = W_{ij}^{II} * R_{ij}$
			$R_{ij} = e^{-b*d_{ij}}$	$R_{ij} = 1 - e^{-a*e^{-b*d_{ij}}}$	$AIC_{sig} - AIC_{exp}$	
Loops	0.001	0	0.921	0.998	-368.2	0.958
	0.001	2	0.877	0.999	-624.1	0.979
	0.001	8	0.767	0.999	-507.1	0.963
	0.002	2	0.857	0.997	-378.4	0.955
	0.005	2	0.848	0.990	-254.8	0.949
Uncorrelated random walk (Correlation degree 0.00)	0.001	0	0.888	0.961	-102.4	0.830
	0.001	2	0.993	0.985	87.3	0.895
	0.001	8	0.941	0.941	3.1	0.897
	0.002	2	0.993	0.985	76.3	0.882
	0.005	2	0.980	0.980	2.3	0.913
Fairly correlated random walk (Correlation degree 0.90)	0.001	0	0.768	0.9523	-359.2	0.704
	0.001	2	0.307	0.974	-325.8	0.824
	0.001	8	0.781	0.880	-57.8	0.785
	0.002	2	0.393	0.935	-220.5	0.787
	0.005	2	0.576	0.970	-261.7	0.777
Correlated random walk (Correlation degree 0.99)	0.001	0	0.226	0.836	-152.8	0.648
	0.001	2	0.888	0.906	-28.6	0.740
	0.001	8	0.773	0.910	-89.7	0.808
	0.002	2	0.391	0.856	-141.2	0.604
	0.005	2	0.289	0.852	-154.5	0.652
Spirals	0.001	2	0.987	0.986	0.1	0.854

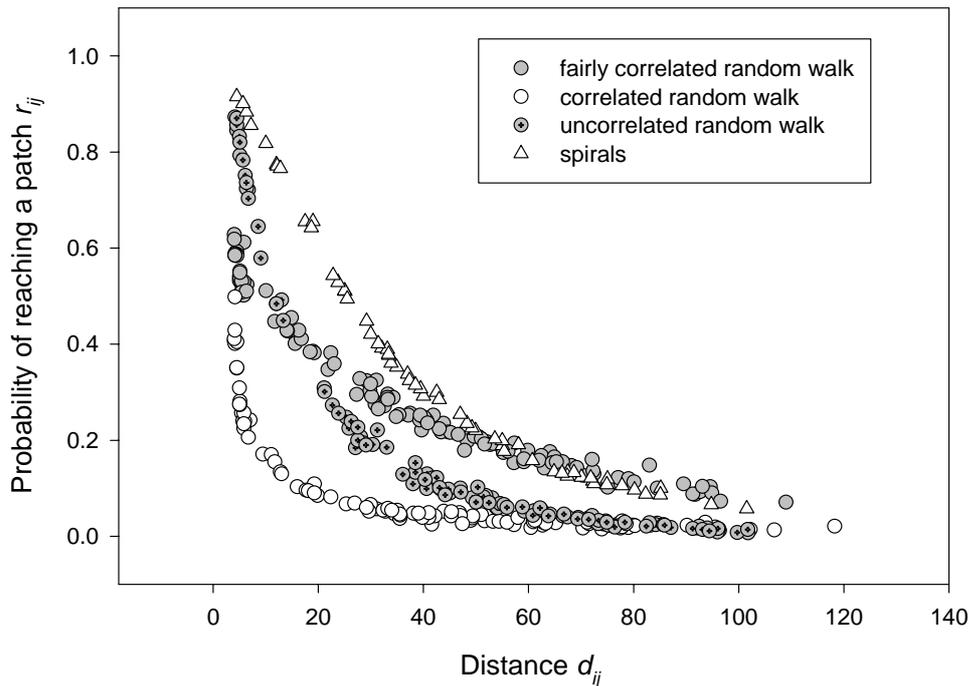


Figure 3.5 The probability r_{ij} of patch j being reached in a 2-patch system depending on the distance d_{ij} between start and target patch for different movement patterns. The r^2 of the regression analysis can be found in Table 3.1.

To summarise, we have seen that the sigmoidal function is able to reproduce the functional relationship between r_{ij} and d_{ij} for all movement patterns under consideration if the landscape only consists of two patches. The sigmoidal function is flexible to cover both, an exponential and a sigmoidal shape. This is not surprising, because the exponential function can be interpreted as a special case of the sigmoidal one, depending on the value of the parameter a : for $a \leq 1$ the sigmoidal function always behaves approximately exponentially (see the calculation in the Appendix B). For $a > 1$, however, the sigmoidal function displays the typical ‘flattening’ in the short distance range, which cannot be described by an exponential approach. This ‘flattening’ reflects an important ecological effect, namely an above-average presence in the range of short distances, as derived from movement patterns such as the loops (returning to the start patch) or the spirals (initial focus on the short range). This ‘flattening’ points out the limits of the exponential function as this function cannot reflect this shape.

There may also be other functions which allow the typical shape of the r_{ij} - d_{ij} curves and the ecological phenomena mentioned to be reflected. In the present paper, the sigmoidal function is used for further analysis because of its appropriateness and structural simplicity.

3.2 The patch accessibility r_{ij} in a multi-patch system

As we have shown (Fig. 3.2), the probability r_{ij} of a certain patch being reached by an emigrant starting at patch i depends not only on the distance d_{ij} between start patch i and target patch j if a landscape with more than two patches is considered. We hypothesised that the variety found in the r_{ij} values for a given distance d_{ij} results from an interaction of the start patch with all other patches in the landscape. Therefore, our aim in this section is to obtain a better understanding of this interaction and to find the simplest way of describing it formally.

To attain this goal, we perform a similar model experiment as in Section 3.1, but now with 3 (or 10) patches in each of the 100 randomly produced landscapes. As before, we start with the loop-like movement pattern and the standard parameter set mentioned (mortality risk = 0.001, perceptual range = 2 spatial units). The resulting r_{ij} - d_{ij} curves are taken as the starting-point for further investigation. In a first step, we analyse the predictive power of the sigmoidal fitting approach that was found to be suitable for predicting r_{ij} in a two-patch system.

Figs. 3.6a and 3.6b show the resulting plot of the r_{ij} - d_{ij} curves. As in the 10-patch system discussed above (Fig. 3.2), high variety is seen in the r_{ij} values for a given distance d_{ij} . The solid lines in both figures correspond to the sigmoidal fitting function (3.2) derived from the two-patch system with the same movement behaviour taken as a basis. It can be seen that none of the r_{ij} values exceeds the sigmoidal curve. This means that the sigmoidal function (3.2) provides an upper limit for the simulated r_{ij} values in both the 3-patch and the 10-patch system. The same effect can be seen in Figs. 3.6c and 3.6d, where the simulated r_{ij} values are plotted against the correspondingly calculated values $r_{ij}^{calc} = R_{ij}$ determined by the sigmoidal function (3.2): all the simulated values are on or below the identity curve (full line), indicating that they are smaller than or equal to the calculated ones. While the values are quite close to the identity curve in the 3-patch system ($r^2=0.903$), they are evenly scattered over the whole ‘lower triangle’ in the 10-patch system ($r^2=0.273$).

These model results show that the interaction between start patch i and all other patches in the landscape first of all leads to a reduction of the probability r_{ij} of the target patch j being reached. The more patches a landscape contains, the stronger this reduction will be. This effect can be ecologically explained: We assumed in our model that an individual will stay at the first patch it successfully reaches. Staying at this patch naturally prevents this individual from reaching any other patch. As a result of this interception effect, the patches effectively ‘compete’ for migrants (following the terminology by Hanski (1994)). This finding also explains why the sigmoidal function provides an upper limit for the actual values of the probability r_{ij} of a certain patch being reached bearing in mind that the sigmoidal function

describes the patch accessibility of the target patch in a system with two patches, i.e. without any competing patch. Therefore the sigmoidal function R_{ij} can also be interpreted as the potential patch accessibility of patch j in a competition-free space.

In the next step, we are seeking ways of modifying the formula (3.2) for the calculated patch accessibility r_{ij}^{calc} such that the reduction effect caused by competition between patches for migrants is taken into account. The idea is to amend the existing formula ($r_{ij}^{calc} = R_{ij}$) with an appropriate correction term W_{ij} and to test the predictive power of the modified formula ($r_{ij}^{calc} = W_{ij} * R_{ij}$) for a multi-patch system.

An appropriate candidate for W_{ij} can be obtained by the following reflections. The ability of a certain patch k to intercept a migrant from patch i is strongly related to the potential patch accessibility R_{ik} of this patch. Thus, the probability of a migrant actually reaching patch j and not being intercepted by another patch has to be weighted according to the potential accessibility R_{ij} of patch j in relation to the potential accessibility R_{ik} of all competing patches k . A possible correction term is:

$$W_{ij}^I = \frac{R_{ij}}{\sum_{k \neq i} R_{ik}} \quad (3.3)$$

As can be seen, this correction term has the structure of a weighting factor where the sum of all W_{ij} equals 1. By taking this correction term $W_{ij} = W_{ij}^I$ as a basis, we obtain the following formula:

$$r_{ij}^{calc} = W_{ij} * R_{ij} \quad (3.4)$$

In order to test the predictive power of formula (3.4), the calculated r_{ij}^{calc} values are plotted against the simulated r_{ij} values. The results for the 3-patch and the 10-patch systems are shown in Figs. 3.6e and 3.6f. Both show much stronger correspondence between the simulated and the calculated values than in Figs. 3.6c and 3.6d, where the original formula (3.2) instead of the modified one (3.4) was used. Fig. 3.6e also reveals that in the case of 3 patches, in addition to a high r^2 value (0.971), there is also good concordance between the regression curve (broken line) and the identity curve (solid line). A slightly different picture occurs in the case of 10 patches (see Figs. 3.6f), where the r^2 value is lower (0.804). Much more critical is the fact that the regression curve (dashed line) is markedly above the identity curve (solid line). This indicates that the modified formula (3.4) underestimates the simulated r_{ij} values in this system, i.e. it overestimates the reduction effect caused by competition. This underestimation can also be seen in the 3-patch system (Fig. 3.6e), but only in the range of higher r_{ij} values.

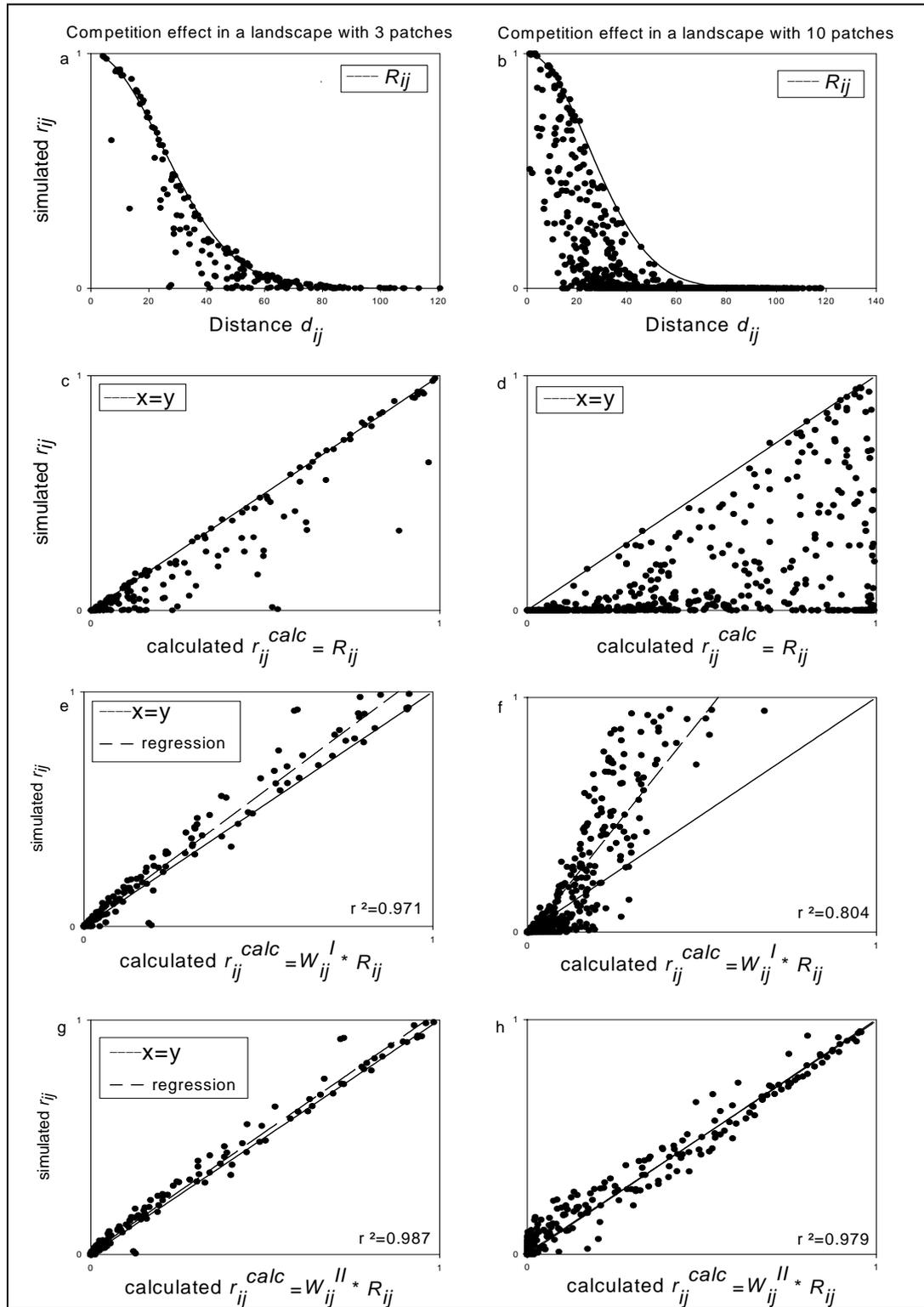


Figure 3.6 The probability r_{ij} of patch j being reached in a 3-patch system (left side) and in a 10-patch system (right side, 100 simulated landscapes at each case). 3.6a and 3.6b: r_{ij} depending on d_{ij} ; the solid line indicates the functional relationship R_{ij} between r_{ij} and d_{ij} in a two-patch system. 3.6c - 3.6h: Simulated vs. calculated values (calculated with different relations). The solid line indicates the identity curve $x=y$, the dashed line represents the linear regression. 3.6c and 3.6d: R_{ij} vs. simulated r_{ij} . 3.6e and 3.6f: r_{ij}^{calc} calculated under consideration of the weighting factor W_{ij}^I vs. simulated r_{ij} . 3.6g and 3.6h: r_{ij}^{calc} under consideration of the weighting factor W_{ij}^{II} vs. simulated r_{ij} . In Figure 3.6h, broken and solid lines are almost identical.

This effect of underestimating the patch accessibility by using W_{ij}^I can be explained by the fact that all patches are considered with their potential accessibility determining the overall competition effect. This assumption is not realistic because in systems with many patches, a distant patch is less likely to be reached because migrants are intercepted by other patches. Therefore this patch cannot effectively intercept individuals and so cannot provide competition with other patches. Thus, the weighting factor used overestimates the competitive power of distant patches and underestimates the effective patch accessibility of the target patch. To overcome this problem, we corrected the weighting factor as follows:

$$W_{ij}^{\text{II}} = \frac{R_{ij}^{(N-1)}}{\sum_{k \neq i} R_{ik}^{(N-1)}} \quad (3.5)$$

where N is the number of patches in the landscape. This weighting factor is expressed in terms of the potential patch accessibility, but raised to the power of the number of competing patches ($N-1$). This approach ensures that the interception effect of more distant patches decrease with the number of patches ($R_{ij}^{(N-1)} \approx 0$).

In order to test the predictive power of the modified formula, the corresponding r_{ij}^{calc} values are plotted against the simulated r_{ij} values. The result for both the 3-patch and the 10-patch systems is shown in Figs. 3.6g and 3.6h. In both figures, in addition to a clear linear relationship between calculated and simulated values ($r^2 = 0.987$ for the 3-patch system and $r^2 = 0.979$ for the 10-patch system), the regression line almost coincides with the identity curve in each case. These findings give rise to the hope that the modified formula will allow the functional relationship between the patch accessibility and the landscape configuration to be appropriately described.

The predictive power of the modified r_{ij}^{calc} is also tested for the loop-like movement pattern with other model parameters (Fig. 3.7 and Table 3.1). As in Figs. 3.6g and 3.6h, there is strong correspondence between simulated and calculated r_{ij} values.

Finally, the predictive power of r_{ij}^{calc} is assessed for the other movement patterns. Fig. 3.8 shows the results for the correlated random walks with different degrees of correlation and the Archimedean spiral with standard parameters (see Table 3.1 for the results of all model parameters tested). As can be seen, again there is good correspondence between simulated and calculated values. The r^2 values range from 0.895 for the uncorrelated random walk, through 0.854 (spiral), 0.824 (fairly correlated random walk), to 0.740 for correlated random walk. It is noticeable that the straighter the movement behaviour, the worse the predictive power of r_{ij}^{calc} . This can be explained by the fact that even in the two-patch system the sigmoidal

function fits worse for straighter movement patterns. Additionally, for straight movements, a patch between the source and the target patch competes more than a patch at the same distance from the source patch but to the opposite direction. As the weighting factor should be structurally simple, it does not account for this specific fact.

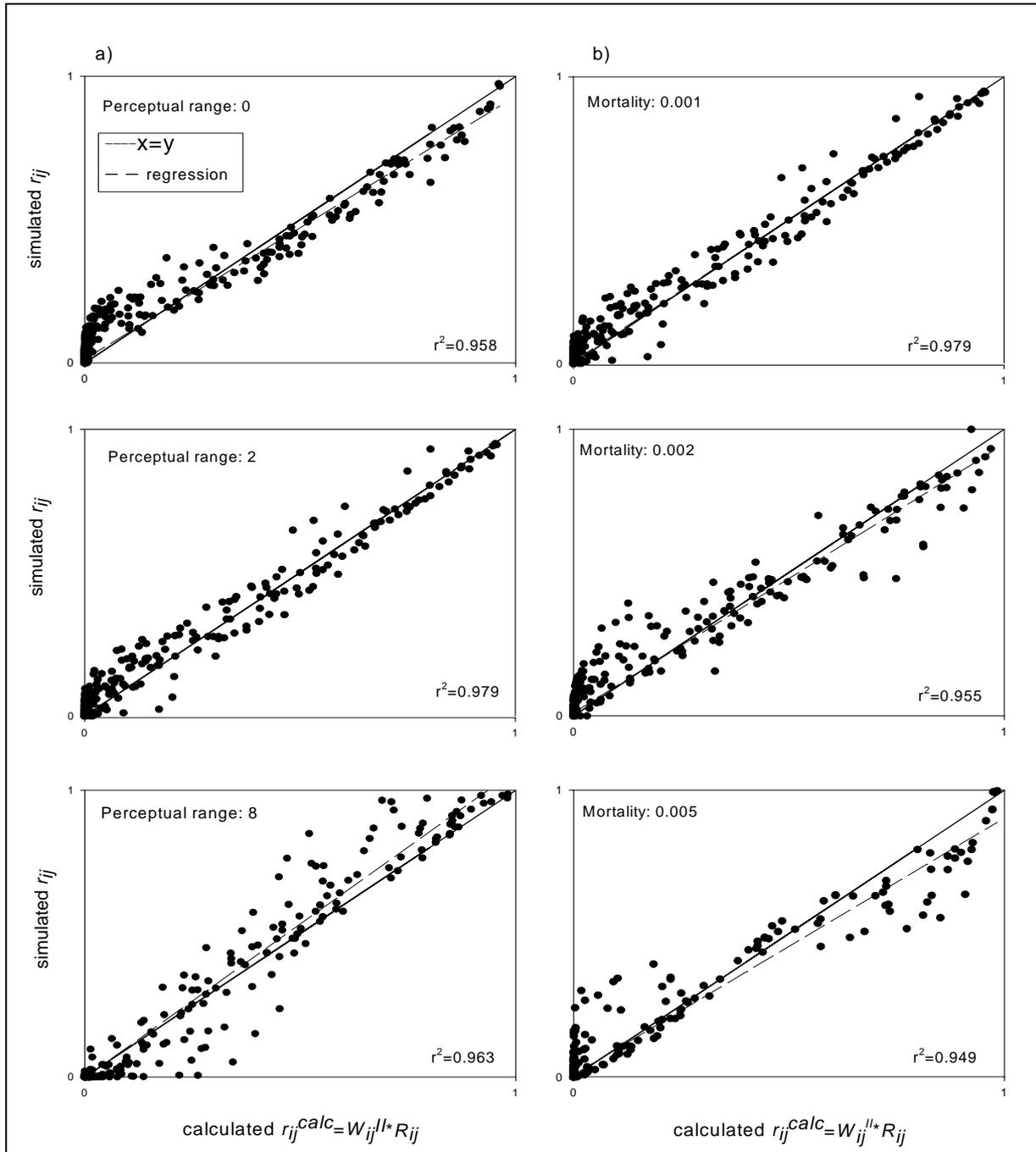


Figure 3.7 Simulated versus calculated r_{ij} in landscapes with 10 patches and different movement parameters of the loop-like behaviour.

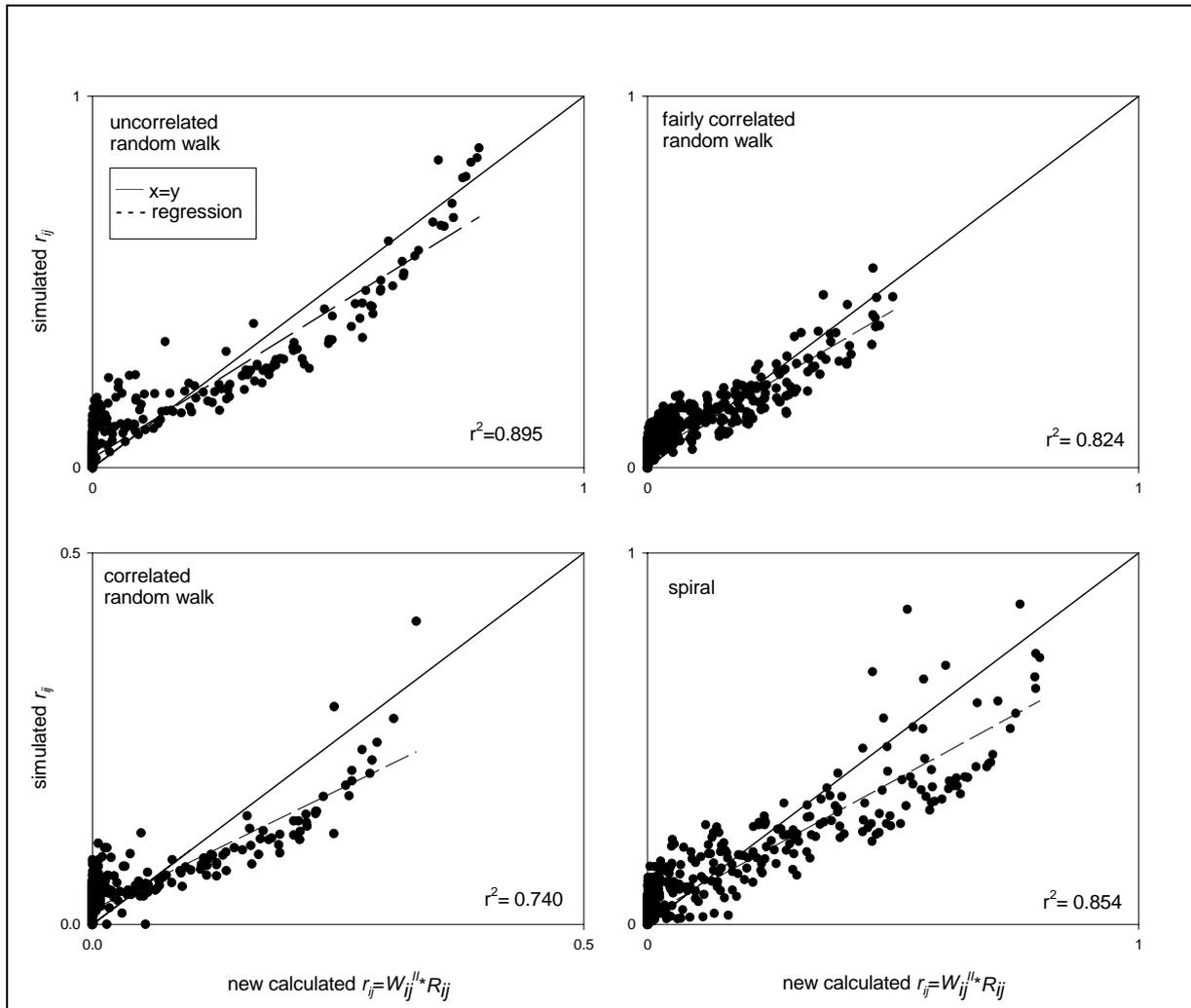


Figure 3.8 Simulated versus calculated r_{ij} in landscapes with 10 patches and different movement patterns.

4 Discussion

4.1 A formula for the patch accessibility r_{ij}

One major result of this paper is the identification of the functional relationship between the probability r_{ij} of a certain patch j being reached by an emigrant from a certain patch i and the landscape configuration. Moreover, we have found a simple formula r_{ij}^{calc} that allows this relationship to be reproduced qualitatively correctly and quantitatively sufficiently. This formula is given by

$$r_{ij}^{calc} = \frac{R_{ij}^{N-1}}{\sum_{k(\neq i)} R_{ik}^{N-1}} \cdot R_{ij} \quad \text{where} \quad R_{ij} = 1 - e^{-a \cdot e^{(-b \cdot d_{ij})}} \quad (3.6)$$

The predictive power of this formula has been successfully tested for a wide range of randomly generated landscapes. We have shown that the formula works for all the well-known simple movement patterns (uncorrelated random walk, correlated random walk, Archimedean spirals) as well as for the more realistic and complex loop-like pattern. Since the investigated movement patterns are qualitatively so different from each other and cover a wide range of biologically reasonable situations, it can be supposed that the formula will work for most movement patterns. But our study also clarifies the formula's limits: the predictive power of the formula has been found to be extremely high as long as movement patterns are concerned where the individual trails cover a large part of the nearby area of the start patch (as is the case for usual random walks, the spirals or loops). The predictive power decreases slightly if the movement becomes straight as in the case of the correlated random walk. This is mainly due to the fact that for this movement pattern the sigmoidal function does not fit as well as for the other movement patterns. In such cases, the predictive power of the formula could be enhanced by using the weighting factor with another function for the potential patch accessibility instead of the sigmoidal one. Additionally, the formula was investigated only for the case that individuals stay on the first patch they discover. Assuming that individuals can visit multiple patches before staying at one, the strength of the competition effect may change. We also should note that the model analysis is based on the assumption that a homogeneous matrix is considered or the individuals do not respond to matrix heterogeneity. Many theoretical and empirical studies indicate that the movement and distribution of individuals is influenced by the structure of the landscape (Crist *et al.* 1992, Wiens *et al.* 1993, Gustafson & Gardner 1996, Wiens *et al.* 1997, With *et al.* 1997, McIntry & Wiens 1999, Ricketts 2001, Goodwin & Fahrig 2002, Tischendorf *et al.* 2003). Furthermore, the patches are assumed to be circular and equal-sized, although patch size and shape could influence the immigration

rate (Bender *et al.* 2002). In the case of heterogeneous matrix or heterogeneously sized patches, changes in search success and therefore in the functional structure found here could be expected .

The functional structure of the derived formula (3.6) reveals that the probability r_{ij} of a certain patch being reached mainly consists of two components: the potential patch accessibility R_{ij} of patch j and a correction term describing the competition effect caused by interception of migrants.

As relation (3.2) indicates, the potential patch accessibility R_{ij} can be described by a simple sigmoidal function of the distance d_{ij} between start patch i and target patch j and two parameters a and b . We have seen that whenever $a \leq 1$, the sigmoidal function behaves approximately exponentially. This means that the widely used exponential approach can be interpreted as a special case of the presented sigmoidal one and is therefore justified to a certain extent. The sigmoidal function, however, is much more flexible. This function is able to cover an exponential decline, but additionally it allows the reproduction of the flat decrease for small distances describing an above-average presence in the short-distance range, as has been found in many field studies (Endler 1977, Brakefield 1982).

The functional structure of the correction term in relation (3.6) provides a better understanding of the relevance of competition effects in the context of species' dispersal. Regardless of the actual movement behaviour of the individuals, the mentioned competition effect inevitably and inherently results as a consequence of the interception of migrants. In the context of dispersal kernels, however, competition effects have so far been considered rarely and cursorily (e.g. Frank & Wissel 1998, Hanski *et al.* 2000, Frank & Wissel 2002). This drawback is overcome by formula (3.6). The correction term presented summarises all the relevant effects of competition between the individual patches for the migrants from patch i , produced by the simulation model. Even so, the term is structurally simple (a weight) and completely expressed in terms of the potential patch accessibility between pairs of patches. The probability r_{ij} of a certain patch being reached can therefore be completely described by the distances between the patches. However, we can also see that it is not sufficient to only take the distance d_{ij} between start patch i and target patch j into account. Correct conclusions can only be drawn if the whole spatial configuration, i.e. the distances d_{ik} between start patch i and all other patches k , are taken into consideration. This is certainly the most important result of this paper. Consequently, we conclude that each approach which only refers to the distance between start patch and target patch (as in the case of the usual exponential approach) is

doomed to fail in more complex landscapes because it neglects interaction with the other patches. Furthermore, we see that there are only two parameters a and b needed to fit the whole formula. These parameters summarise all the relevant details investigated of the movement behaviour. Therefore they allow the relationship between the accessibility of the patches and the landscape configuration to be described in a species-specific manner.

Although the formula reflects the rather complex interplay between species behaviour and landscape configuration, is it still structurally simple.

In most metapopulation models, the competition effect is ignored. A few studies account for the competition effect, but the expressions used to describe competition are extremely different to each other (Hanski & Thomas 1994, Hanski *et al.* 2000, Frank & Wissel 1998). This may be due to the fact that these studies assume a certain ad hoc approach to model competition, but do not explain the underlying mechanisms. We highlight here one of these approaches that is structurally very similar to the patch accessibility function derived here (relation (3.6)). Hanski & Thomas (1994) use the following expression for describing patch accessibility:

$$r_{ij} = \frac{\exp(-\alpha d_{ij})}{\sum_{k \neq i} \exp(-\alpha d_{ik})} * \exp(-\mu d_{ij})$$

with two parameters α and μ summarizing effects of dispersal behaviour and landscape structure (e.g. number of patches N) on patch accessibility. The strength of formula (3.6) is that a and b are independent of the patch configuration. Hence, the effects of behaviour and spatial structure can be separately analysed, to the benefit of a better understanding.

4.2 The practical value of the presented formula

First of all, the formula presented here provides a tool for modelling. It can be used as a dispersal function for further analysis. Until now, the exponential approach has been used in most models (Fahrig 1992, Hanski 1994, Adler & Nuernberger 1994, Hanski *et al.* 1996, Vos *et al.* 2001, Frank & Wissel 2002). The formula propounded here was found to be much more realistic than the exponential function and can therefore be used instead since, although simple, it provides a more realistic approach. The most important advantage of the formula presented over the exponential one is that it allows the inherent competition effect between the patches to be taken into account in a very simple way.

Furthermore, the formula provides as well a tool for understanding. In this study, the formula was a useful tool for understanding that the distances between patches (start patch and all other patches in the landscape) are sufficient to explain the dependence of patch accessibility

on landscape configuration. It also helped to understand that competition between patches is an inherent and essential effect in the context of patch accessibility.

Last but not least, the formula provides a tool for prediction. By taking the formula and the parameters a and b as a basis, the probability of a certain patch being reached can be assessed without having to run any simulations. The formula contains the whole essence of the simulation model, summarising the complex effects of interaction between landscape and movement behaviour concerning the probability of a certain patch being reached. Therefore the formula is able to give the same answer as the model itself.

4.3 Some general remarks on the hierarchical approach put forward

The functional structure of the patch accessibility r_{ij} could only be revealed because we used a hierarchical approach where we increased the spatial complexity step by step (2-, 3- and 10-patch systems).

Before using the hierarchical approach, we started our investigation by analysing the plot of r_{ij} - d_{ij} data for a 10-patch system and by taking the hypothesis of having an exponential relationship as a basis (see Fig. 3.2). Viewed via this exponential approach, no pattern was identified. The general impression was that of an unstructured cloud of data points. As a result of going back to a 2-patch system, we obtained an insight into the functional structure of the potential patch accessibility R_{ij} of a certain target patch j . A clear functional relationship between the potential patch accessibility R_{ij} and the distance d_{ij} between start and target patch was detected and the sigmoidal function was found to describe it appropriately. By increasing the number of patches and taking the potential patch accessibility (i.e. the sigmoidal function R_{ij} from the 2-patch system) as a reference, we obtained a better understanding of the effect of the interaction between the target patch and all the other patches. By analysing exactly the same data set for the 10-patch system as before, but now from the angle of the sigmoidal approach (see Fig. 3.6b), a clear pattern emerged: all the r_{ij} values were found to lie below the values for the potential patch accessibility R_{ij} . This finding was the starting-point for the identification of the competition effect caused by the interception of migrants. It provided some idea of possible correction terms (W_{ij}^I and W_{ij}^{II}). To summarise, the hierarchical approach presented here resulted in a whole series of bottom-up model experiments each providing additional insights into the functional structure of the patch accessibility r_{ij} .

4.4 Some prospects

In this study we developed a formula with the two parameters a and b of the sigmoidal function summarising all the relevant effects of individual movement behaviour. One prospect for further research would be to try to understand the biological meaning of these two function parameters, as will be done in a forthcoming paper. One aspect of investigating this biological significance is to examine the effect of a change of these two parameters on the functional dependence (as was partly done for the function parameter a). A second aspect is to investigate the way in which the movement characteristics influence the function parameters. This knowledge would enable our formula to be interpreted purely in the terms of movement characteristics and distances.

On this basis it would be also feasible to categorise movement patterns and their function parameters. With regard to the probability of a certain patch being reached, movement patterns with similar a and b values react similarly to changes in landscape configuration. Therefore it could be possible to determine groups of organisms with similar reactions to landscape changes.

To obtain an initial understanding of the structure of the patch accessibility, it was studied here in a relatively simple landscape, with a homogeneous matrix and equal-sized patches. Another aim for further research would be to extend the formula presented here to more complex situations, e.g. a landscape with heterogeneously sized patches or a heterogeneous matrix.

The formula could be used to study the consequences of the interaction between movement behaviour and landscape configuration described here at a metapopulation level in order to acquire further knowledge for decision support.

5 Appendices

Appendix A1: The sigmoidal function behaves exponentially for larger distances

There is some analytical evidence that the sigmoidal function (3.2) is able to reproduce the qualitative behaviour of the functional relationship between r_{ij} and d_{ij} (i.e. the exponential decrease in the long range). For large values of d_{ij} , the exponential term $e^{(-b*d_{ij})}$ is close to zero. It is well known that for small values of x , $1 - e^{(-x)} = x$. Consequently, for large values of d_{ij} we obtain:

$$R_{ij} \approx a * e^{-b*d_{ij}} , \tag{A.1}$$

Relation (A.1) reveals that the sigmoidal function (3.2) behaves exponentially for larger distances d_{ij} as required.

Appendix A2: Identifying the parameter value for an approximately exponential decline of the sigmoidal function

At the turning point x_{tp} of the sigmoidal function, the curve starts to decline exponentially. In the following, we therefore determine the turning point x_{tp} by analytical means and reveal the conditions under which $x_{tp} \leq 0$. This condition ensures that the range of all relevant distance values ($d_{ij} \geq 0$) completely lies in the area of exponential decline.

Mathematically, the turning point x_{tp} is defined to be the x value for which the second $f''(x)$ derivative becomes zero. Therefore, we start by determining the second derivative of the sigmoidal function (3.2).

For simplicity's sake, we rewrite the function as $f(x) = 1 - e^{-g(x)}$ where $g(x) = a * e^{-bx}$

This simplified function is taken as a basis to obtain the second derivative $f''(x)$ of $f'(x)$ by subsequently applying the chain rule.

$$f''(x) = e^{-g(x)} * (-g'(x)^2 + g''(x))$$

As we can see, $f''(x)$ becomes zero if the right part $-g'(x)^2 + g''(x)$ becomes zero (since $e^{-g(x)} > 0$). Therefore, the turning point x_{tp} has to meet the following condition

$$g'(x)^2 = g''(x)$$

The first and the second derivative of $g(x) = a * e^{-bx}$ are given by

$$g'(x) = -a * b * e^{-bx} \quad \text{and, hence,} \quad g'(x)^2 = (a * b)^2 * e^{-2*b*x}$$

$$g''(x) = a * b^2 * e^{-b*x}, \quad \text{so the condition is}$$

$$(a * b)^2 * e^{-2*b*x} = a * b^2 * e^{-b*x}$$

This is exactly the case if $a * e^{-b*x} = 1$, i.e. $x_{tp} = \frac{\ln a}{b}$

This relation shows that the condition for an approximate exponentiality $x_{tp} \leq 0$ is given if

$$\frac{\ln a}{b} \leq 0. \quad \text{This is only the case if } \ln a \leq 0, \quad \text{i.e. } a \leq 1 \quad (\text{since } b \text{ is assumed to be positive}).$$

Therefore, the function declines approximately exponentially for all distances if $a \leq 1$.

Integrating individual movement behaviour into dispersal functions

1 Introduction

In order to understand the role of dispersal, its consequences for population dynamics need to be analysed in mathematical models. If dispersal is to be integrated into more complex studies (e.g. analyses of landscape connectivity or population viability) as simply as possible, dispersal functions are needed so that the probability of a certain patch being reached by an emigrant (referred to as patch accessibility) can be calculated (Fahrig 1992, Adler & Nuernberger 1994, Hanski 1994, Hanski *et al.* 1996, Vos *et al.* 2001, Frank & Wissel 2002). Ideally, such a dispersal function should explicitly consider the landscape configuration as well as the animals' movement behaviour while summarising all the details in a simple manner.

The literature contains various approaches for finding a dispersal function with the attributes required (Hanski 1994, Adler & Nuernberger 1994, Hill *et al.* 1996). These approaches are very simple: the corresponding dispersal functions contain only one or two parameters which summarise all the effects of movement behaviour. Because of the highly aggregated nature of these parameters, it is difficult to assess the effect of a particular behavioural aspect. Taking the dispersal function of Heinz *et al.* (submitted) as an example, we show how the movement behaviour can be integrated by means of an individual-based simulation model. This function was found to have a high predictive power for a variety of movement patterns. The landscape configuration is explicitly subsumed by this dispersal function, while the movement behaviour is described by two function parameters a and b summarising all the relevant aspects of movement.

In this study, we investigate the effect of movement behaviour on the previously found function for the accessibility of patches. Therefore, we analyse the relationship between the aggregated parameters a and b of the dispersal function and all the relevant movement details. As a result, we find fitting functions for the functional relationship between the parameters of the dispersal function investigated and the movement details. In addition to trying to describe this relationship statistically, we also attempt to give an ecological interpretation of it. We do this by way of example for the relevant movement details of a complex movement pattern

observed in nature – the loop-like movement pattern observed for a variety of animals (Hoffmann 1983, Bell 1985, Müller & Wehner 1994, Durier & Rivault 1999, Conradt *et al.* 2000, Conradt *et al.* 2001). The approach presented of integrating movement behaviour into dispersal functions is more general and can be applied to other movement behaviours as well. Combining the dispersal function previously found and the functional relationship between the function parameters and the movement details revealed in the present study gives a better understanding of the role of movement behaviour, including implications for how the movement behaviour of animals can be taken into account in the management of endangered species. It provides a framework for investigating the impacts of dispersal behaviour on metapopulation viability.

2 Methods

2.1 The dispersal function

We investigate the effect of movement behaviour on the dispersal function derived in Chapter 3, relation (6.3). This dispersal function is given by the following formula for the probability r_{ij} of a certain target patch j being reached by an emigrant from a certain start patch i :

$$r_{ij} = W_{ij} \cdot R(d_{ij}) \quad (4.1)$$

$$\text{where } W_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}} \quad (4.2)$$

$$\text{and } R(d) = 1 - e^{-a \cdot e^{(-b \cdot d)}} \quad (4.3)$$

As mentioned in Chapter 3, the function $R(d)$ (relation(4.3)) gives the potential accessibility of a patch in a landscape with two patches (start and target patch) only by considering the distance d between them. In this study, $R(d)$ is referred to as the potential accessibility function. It only contains two parameters, a and b , which summarise all the relevant details of movement behaviour. In a landscape with more than two patches the patches compete for emigrants, as an emigrant intercepted by one patch cannot reach another patch (assuming that movement stops when a non-source patch is reached). This competition is described by the weighting factor W_{ij} (relation(4.2)). This weighting factor is completely expressed in terms of the potential accessibility function $R(d)$, the distances d_{ik} between the start patch i and all the other patches k , and a power given by the number N of patches in the landscape. The overall dispersal function (relation(4.1)) is therefore completely expressed in terms of the potential

accessibility function. Consequently, there are only two function parameters a and b specifying the whole dispersal function.

To analyse the effect of movement on the potential accessibility function $R(d)$ (relation(4.3)) several methods complementing one another were used. First of all, to obtain a better understanding of the effect of the two function parameters a and b we used Mathematica to study their impact on the curve shape. In a second step, movement characteristics were taken into account and their effect on the function was analysed in several respects. To obtain the R - d curves for different movement characteristics, we used the individual-based simulation model described in Chapter 3. The simulation runs are slightly different to those described in Chapter 3 and are therefore described in the following.

2.2 The model

In order to determine the potential accessibility function $R(d)$ for different movement parameters, we used the spatial, individual-based simulation model described in Chapter 3 (Section 2). It allows both patch configuration and individual movement through the landscape to be taken into account.

Simulation

For each simulation run, 100 landscapes (100 x 100 spatial units) with two patches at different distances from each other are randomly produced. Note that in a two-patch system the potential accessibility R coincides with the accessibility r because of the lack of competing patches. In each landscape, 1000 animals are released at the start patch. After release, the individuals move through the landscape with the loop-like movement behaviour. If the target patch comes within the perceptual range of an individual, the individual moves straight to this patch and stays there. The probability r of the target patch being reached (and hence the potential accessibility R) is counted as the proportion of individuals arriving at this patch. The corresponding distance d between the two patches was noted.

Parameters

We varied three parameters in the model which determine dispersal ability: mortality risk, perceptual range and loop length. We expressed mortality risk as the per-step probability of dying, varying it between values of 0.001 and 0.01. Perceptual range describes the distance within which an animal can detect new patches and can therefore move straight towards them.

In the model, we used values between 0 and 10 spatial units for the perceptual range. The loop length determines radius and intensity of the search. It is given by the number per steps of the initial loops (the 4 first loops) and the increase in step number of each of the next subsequent quartets of loops. This increase in step number is modelled by adding after each 4 loops half of the steps of the initial loop length to the steps determining the last loops (i.e. if we have an initial loop length of 4 steps, we increase it after the 4 first loops about 2 steps to 6 steps, after the next 4 loops to 8 steps, than to 10 steps and so on). We utilised 4 different loop lengths: small, intermediate, large and very large. This suits a step number of 4 initial steps plus an increase of 2 steps for the 4 subsequent loops respectively (small), 8 initial steps plus an increase of 4 steps (intermediate), 16 initial plus an increase of 8 steps (large), and 32 initial steps plus an increase of 16 steps each (very large).

3 Results

The aim of our study is to investigate the effect of movement characteristics relevant for the loop-like behaviour (mortality risk, perceptual range, loop size) on the relationship between the potential accessibility R and the distance d between two patches. As we know from a previous study (Heinz *et al.* submitted), this relationship can be described by the following function referred to as the potential accessibility function (see also relation (4.3))

$$R(d) = 1 - e^{-a \cdot e^{(-b \cdot d)}} \quad (4.4)$$

where a and b are two parameters. These two function parameters a and b summarise all the details of movement behaviour relevant for the potential accessibility and completely determine the qualitative and quantitative behaviour of function (4.4). Therefore it seems reasonable to analyse the relationship between the two function parameters and the movement characteristics. However, this is not uncritical because the summarising character of a and b also harbours a disadvantage: the two parameters are too highly aggregated to allow a direct ecological interpretation. Therefore, we perform a pre-analysis to look for appropriate ecologically interpretable measures which allow – as a and b themselves – the shape of the potential accessibility function $R(d)$ to be characterised and which can be expressed in terms of a and b . These measures help clarify the relationship between the accessibility-function and movement characteristics, and permit an ecological understanding of this relationship.

3.1 Pre-analysis: characterising the shape of the potential accessibility function $R(d)$

To obtain a basic grasp of the behaviour of the potential accessibility function $R(d)$, we start by varying the parameters a and b and analysing their effect on the resulting shape of the R - d

curves. For enabling a more systematic, quantitative analysis of all these effects, we look for appropriate measures which (a) characterise the shape of the curves, (b) can be expressed in terms of the parameters a and b , and (c) can be ecologically interpreted.

The resulting R - d curves for different a and b values are shown in Fig. 4.1. To obtain a maximum understanding of the formal relationship, we extend the range of distances into the ecologically meaningless area of negative values.

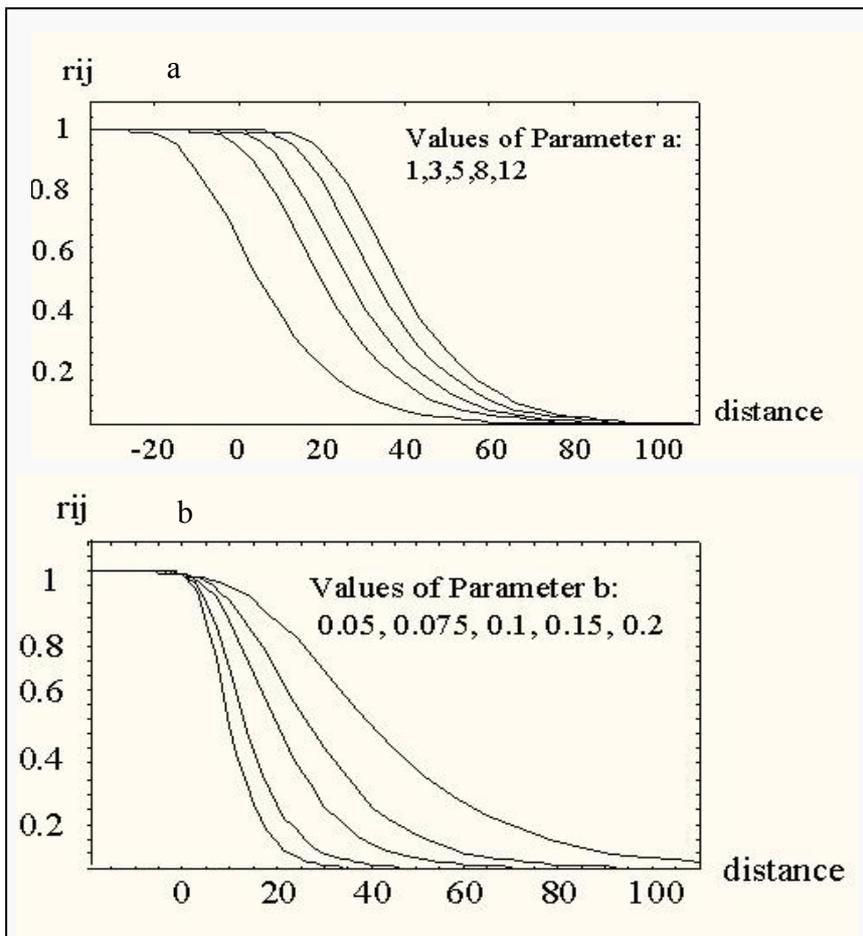


Figure 4.1 The impact of the function parameters a and b on the potential accessibility function $R(d)$. Fig. 4.1a: The parameter a is varied (a increases from the left to the right curve) while the parameter b is constant ($b = 0.075$). Fig. 4.1b: The parameter b is varied (b increases from the left to the right curve) while the parameter a is constant ($a = 5.84$).

In Fig. 4.1a, the parameter a is varied, while the parameter b is fixed. Each curve displays a typical sigmoidal behaviour, i.e. there is a plateau where the R -values are close to 1. Changing the parameter a seems to shift curves to shift along the d -axis. This is a reflection of the fact that:

$$R(d) = 1 - e^{(-a * e^{-bd})} \equiv 1 - e^{-b(d - \frac{\ln a}{b})} \quad (4.5)$$

(since $a = e^{\ln a}$). Relation (4.5) shows that, for one given value of parameter b , all sigmoidal functions emerge from each other by a shift about the distance $\frac{\ln a}{b}$. As can be seen in

Appendix A1, the distance $\frac{\ln a}{b}$ coincides with the value of the so-called turning point d_{TP} , i.e. the distance at which the shape of sigmoidal function $R(d)$ changes from concave to convex decline. In the range of distances d below the turning point d_{TP} where the decline is concave, the migrant's search for a patch is found to be above-average effective. Above d_{TP} , however, the curves rapidly convexly decline to 0. This allows us to ecologically interpret

$$d_{TP} = \frac{\ln a}{b} \quad (4.6)$$

as an “index of effective search” which can take both positive and negative values, depending on the values of the parameters a and b . Negative values (i.e. $d_{TP} < 0$) indicate missing effectiveness and an exclusively convex decline of R with distance d , while positive values (i.e. $d_{TP} > 0$) indicate both existence and scale of effective search.

Varying parameter b results in a totally different effect (Fig. 4.1b). All curves coincide in their points of interception $R(d=0)$ with the R -axis, but differ in the turning points d_{TP} and the rapidness of the decline of $R(d)$ with distance d . This motivates to investigate the scale of decline d_{decl} , i.e. the distance over which the R - d curve declines to 0 measured from the turning point $d_{TP} = \frac{\ln a}{b}$. An appropriate measure for the scale of decline is given by

$$d_{decl} = 1.12 \cdot \frac{1}{b}, \quad (4.7)$$

as the calculation in Appendix A2 indicates.

To summarise, we found two measures characterising the shape of the R - d curves: the index of effective search d_{TP} and the scale of decline d_{decl} . Both measures are expressed in terms of the parameters a and b . They allow the effect of movement details on the potential accessibility R to be ecologically interpreted.

3.2 The effect of the movement characteristics

Now we investigate the effect of movement characteristics relevant for the loop-like behaviour (perceptual range, mortality risk, loop length) on the potential accessibility function $R(d)$ (relation(4.3)). This is done by changing sequentially each of the movement details of the loop-like behaviour and assessing the effect on the shape of the corresponding R - d curves directly, as well as on the function parameters a and b and the two measures characterising the curve shape, d_{TP} and d_{decl} . This enables us to obtain a statistical description of the functional relationship between the function parameters a and b and the details of movement, as well as an ecological interpretation of the effect of movement details. Analysis is done using the individual-based model. The results are illustrated in Figs. 4.2—4.4.

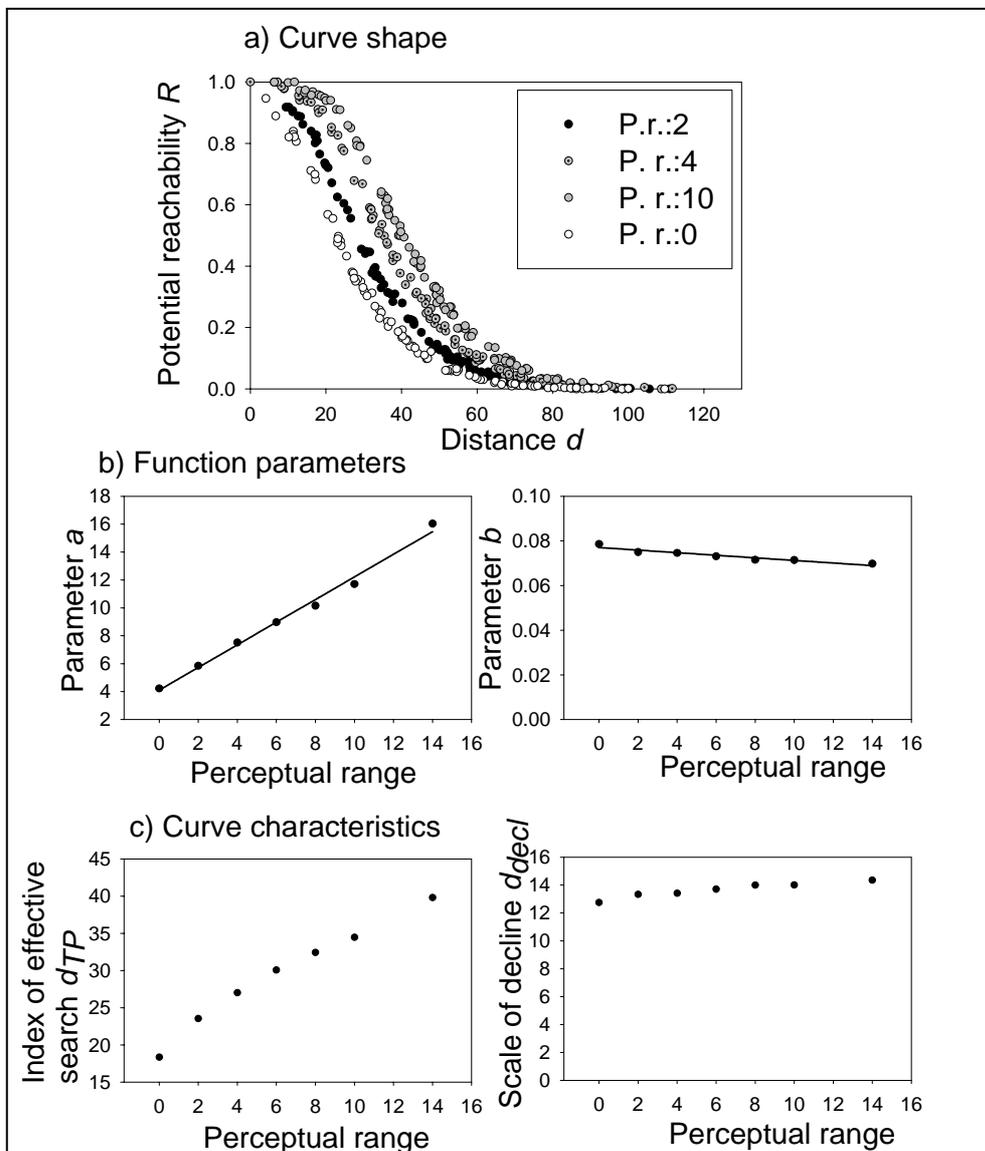


Figure 4.2 The effect of perceptual range on the potential accessibility function $R(d)$: a) The effect on the curve shape, b) the effect on the function parameters a and b and c) the effect on the curve characteristics d_{TP} and d_{decl} .

The effect of perceptual range

Fig. 4.2a shows the effect of perceptual range on the potential accessibility function, Fig. 4.2b the effect on the function parameters a and b , and Fig. 4.2c the effect on the two curve characteristics d_{TP} and d_{decl} . It can be seen that both function parameters exhibit a clear functional dependence on the perceptual range. For both a and b , a linear function fits with a high r^2 (Table 4.1). While a markedly increases with rising perceptual range, the parameter b decreases slightly (in the third decimal place). Corresponding to the effect on parameters a and b , an increase in the perceptual range leads to an increase in the index of effective search d_{TP} (depending on both parameters), while the scale of decline d_{decl} (depending on parameter b only) seems to be robust to a change in the perceptual range. This shows that an increase in the perceptual range leads mainly to an increase in the effectiveness of the search for small distances. These findings are confirmed by the shape of the function, where mainly the sigmoidal plateau of the curve is extended with increasing perceptual range.

The effect of mortality risk

The function parameter a decreases with increasing mortality while parameter b increases (Fig. 4.3b). The functional relationship between the function parameter a and the mortality risk can be described by an exponential decay. For function parameter b , a hyperbola fits the resulting curve very well (Table 4.1). Since both parameters act in the same direction regarding the index of effective search d_{TP} , it is not surprising that d_{TP} becomes very small for a high mortality risk (Fig. 4.3c). The values for the scale of decline d_{decl} which are only influenced by function parameter b decrease. Therefore, the two curve characteristics d_{TP} and d_{decl} indicate both a reduction in search effectiveness and the faster decline of potential accessibility with distance. Both result in reduced search success. All these effects are reflected by the shape of the $R-d$ curves (Fig. 4.3a).

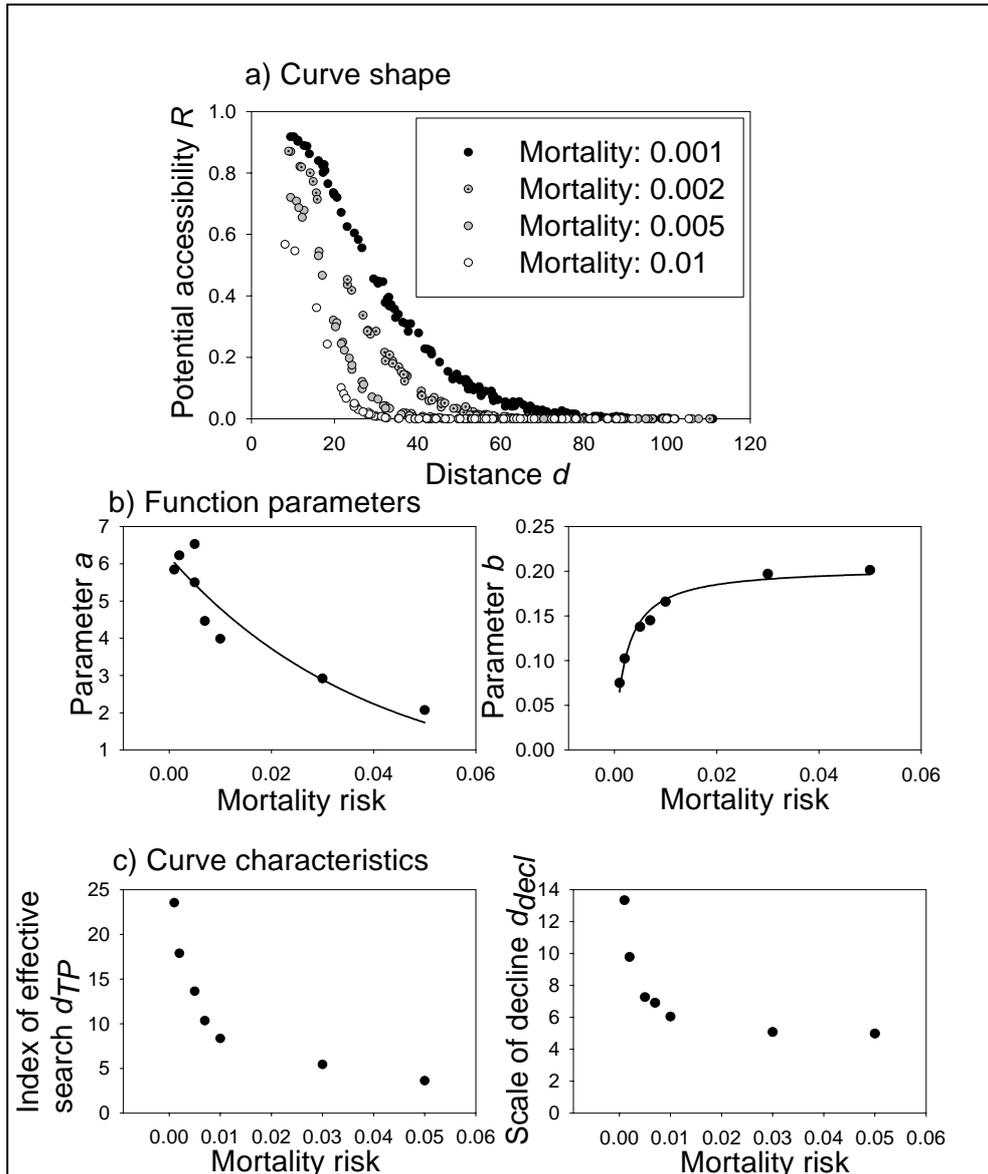


Figure 4.3 The effect of mortality risk on the potential accessibility function $R(d)$: a) The effect on the curve shape, b) the effect on the function parameters a and b and c) the effect on the curve characteristics d_{TP} and d_{decl} .

The effect of loop length

Both function parameters, a and b , decrease as the loop length increases (Fig. 4.4b). As with perceptual range and mortality, the function parameters exhibit a clear functional dependence on loop length. The resulting curves of both parameters can be fitted with a rational function (Table 4.1). Since both parameters decrease, they act in different directions on the potential accessibility R , which is reflected by the curve characteristics d_{TP} and d_{decl} (Fig. 4.4b). With increasing loop length, the index of effective search decreases, while the scale of decline d_{decl} increases. Therefore, the search success becomes lower for small distances but higher for

large ones. This is confirmed by the curve shape (Fig. 4.4a). Small loops express a larger plateau for small distances, but decline faster for large ones.

The fitting functions found here can be included in the potential accessibility function $R(d)$ (relation(4.4)). Taking loop length (i.e. the length of the initial loops) l as an example, we obtain the function:

$$R_l(d) = 1 - e^{(-1/(0.075 + 0.024 * l))} * e^{(-1/(9.56 + 1.025 * l)) * d}$$

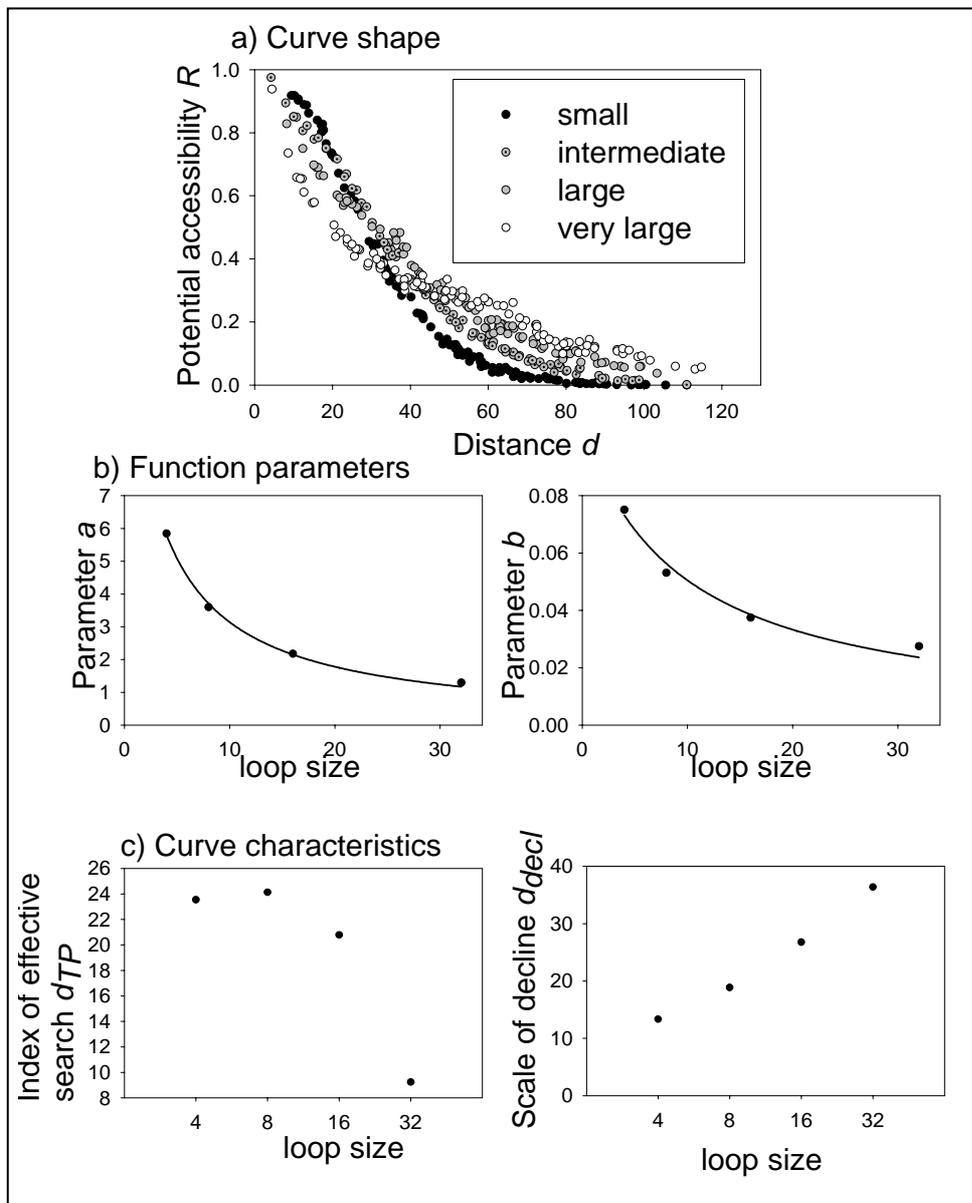


Figure 4.4 The effect of loop length on the potential accessibility function $R(d)$: a) The effect on the curve shape, b) the effect on the function parameters a and b and c) the effect on the curve characteristics d_{TP} and d_{decl} .

Table 4.1 The functional relationship between the movement details (perceptual range, mortality and loop length) and the function parameters a and b can be described with simple fitting functions.

Movement detail	Fitting function	Parameter of the fitting function
Perceptual range (pr)	$a = \alpha + \beta * pr$	$\alpha = 4.097$ $\beta = 0.8115$ $r^2 = 0.991$
	$b = \alpha + \beta * pr$	$\alpha = 0.07702$ $\beta = 0.0005782$ $r^2 = 0.907$
Mortality (m)	$a = \alpha * e^{-\beta^n}$	$\alpha = 6.188$ $\beta = 25.41$ $r^2 = 0.857$
	$b = \alpha m / (\beta + m)$	$\alpha = 0.2048$ $\beta = 0.002154$ $r^2 = 0.973$
Loop length (l)	$a = 1 / (\alpha + \beta * l)$	$\alpha = 0.07478$ $\beta = 0.02437$ $r^2 = 0.998$
	$b = 1 / (\alpha + \beta * l)$	$\alpha = 9.564$ $\beta = 1.025$ $r^2 = 0.977$

4 Discussion

Our study provides a thorough insight into the effect of movement characteristics on patch accessibility. Our main aims were to establish the functional relationship between the function parameters a and b and the details of movement, and to give an ecological interpretation of these effects. We achieved these goals by using an individual-based simulation model.

We have shown that there are clear functional relationships between the function parameters of the potential accessibility function $R(d)$ and the movement details investigated. We found

very simple fitting functions (for an overview see Table 4.1) to describe these functional relationships. These fitting functions were found by univariate analysis for each movement parameter. Therefore, it is not possible to give one single $R(d)$ -function for a combination of all three parameters. But these fitting functions could help to roughly indicate the range of parameter values possible for one movement behaviour. Estimating the right parameters may often be a problem when working with dispersal functions. The fact that different movement characteristics have different effects on the function parameters a and b makes it difficult to estimate the function parameters. This can be overcome by the results presented, which indicate that there is a clear functional relationship between the function parameters and the movement characteristics. Once this functional relationship is known, it is at least possible to perform sensitivity analyses around the range of potential parameter values for a single aspect of movement behaviour.

We found two measures characterising the shape of the potential accessibility function $R(d)$: the index of effective search d_{TP} and the scale of decline d_{decl} , which allow the effect of the movement details on the dispersal success to be ecologically interpreted. These measures can be expressed in terms of the function parameters a and b . These two measures make the effect of the different movement details on $R(d)$ better understandable, allowing rules of thumb about these effects to be drafted. The increasing perceptual range positively affects d_{TP} strongly, but only has a slight effect on d_{decl} . An increase in the mortality risk leads to a decrease in both characteristics, while increasing the loop length depresses d_{TP} but leads to an increase in d_{decl} . Every effect can be completely described with the two measures.

In this study, we only investigated the case of the loop-like behaviour observed in nature. Therefore, the functional relationship between the function parameters and the movement details derived in this paper cannot be directly used for other movement behaviours. However, the general approach, as well as the two measures index of effective search d_{TP} and scale of decline d_{decl} , can be used for other movement behaviours, too, as relation (4.3) was found to be appropriate for a variety of movement behaviours.

It could be also feasible to categorise movement patterns and their function parameters on this basis. Regarding the dispersal function finally resulting (relation (4.1)), movement patterns with similar a and b values and therefore similar $R-d$ curves react similarly to changes in landscape configuration. Therefore it could be possible to determine groups of organisms with similar reactions to landscape changes.

5 Appendices

A1. Calculation of the turning point d_{TP}

The turning point d_{TP} of the sigmoidal function $R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$ is defined to be the d -value where the function changes from a concave to a convex shape. This point is given by the null of the second derivation of $R(d)$, i.e. is determined by the solution of equation $R''(d) = 0$. The second derivation $R''(d)$ is given by

$$R''(d) = -a \cdot b \cdot e^{-(a \cdot e^{-b \cdot d} + b \cdot d)} \cdot b \cdot (a \cdot e^{-b \cdot d} - 1).$$

This shows that the condition $R''(d) = 0$ is only met if the third part of expression $R''(d)$ becomes 0, i.e. $a \cdot e^{-b \cdot d} - 1 = 0$. By solving this equation, we obtain $d_{TP} = \frac{\ln a}{b}$.

A2. Calculating the scale of decline d_{decl}

Starting point of the following calculation is the finding that each sigmoidal function $R(d) = 1 - e^{-a \cdot e^{-b \cdot d}}$ shows a convex decline to zero in the range of distances d above the turning point $d_{TP} = \frac{\ln a}{b}$. This motivates a scale of decline d_{decl} defined to be the distance measured from the turning point d_{TP} upwards over which $R(d)$ goes to 0. By adopting the idea that the

scale of an exponential decline is given by $\frac{1}{\lambda} = \left(\int_0^{\infty} x \cdot e^{-\lambda \cdot x} dx \right) / \left(\int_0^{\infty} e^{-\lambda \cdot x} dx \right)$, we define d_{decl} by

$$d_{decl} = \frac{\int_{d_{TP}}^{\infty} (x - d_{TP}) \cdot R(x) dx}{\int_{d_{TP}}^{\infty} R(x) dx}.$$

By taking into consideration that $R(x) = 1 - \exp(-a \cdot e^{-b \cdot x}) = 1 - \exp(-e^{-b(x - \frac{\ln a}{b})})$ (see relation (5) in the text) and that $d_{TP} = \frac{\ln a}{b}$, we get the following expression for d_{decl} :

$$d_{decl} = \frac{\int_{\frac{\ln a}{b}}^{\infty} (x - \frac{\ln a}{b}) \cdot (1 - \exp(-e^{-b(x - \frac{\ln a}{b})})) dx}{\int_{\frac{\ln a}{b}}^{\infty} (1 - \exp(-e^{-b(x - \frac{\ln a}{b})})) dx} = \frac{\int_0^{\infty} x \cdot (1 - \exp(-e^{-bx})) dx}{\int_0^{\infty} (1 - \exp(-e^{-bx})) dx}$$

Substituting the term $b \cdot x$ by the variable $z = b \cdot x$ leads to

$$d_{decl} = \frac{\int_0^{\infty} z \cdot (1 - e^{-e^{-z}}) dz}{\int_0^{\infty} (1 - e^{-e^{-z}}) dz} \cdot \frac{1}{b}.$$

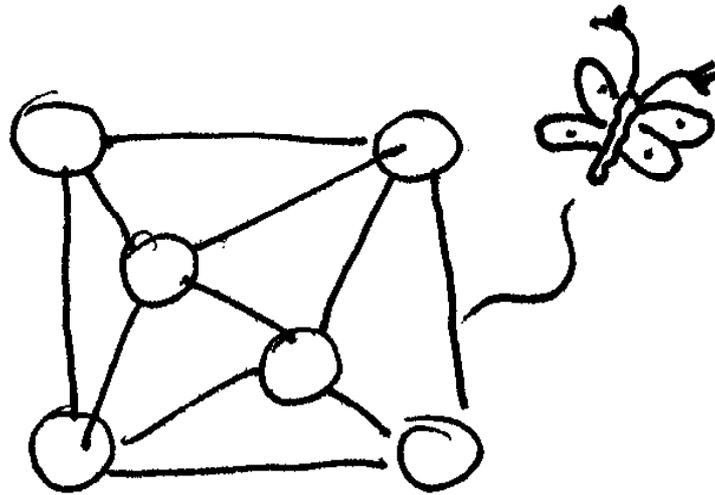
This relation shows that the scale of decline d_{decl} is independent of parameter a and proportional to $1/b$, where the factor of proportionality is given by the ratio of two integrals, namely $\int_0^{\infty} z \cdot (1 - e^{-e^{-z}}) dz / \int_0^{\infty} (1 - e^{-e^{-z}}) dz$. We used *Mathematica* 3.0 (Wolfram 1996) for numerically determining the ratio between the integrals and obtained 1.12 as result. Consequently,

$$d_{decl} = 1.12 \cdot \frac{1}{b}.$$

In Part II, we developed and analysed a simple formula for the patch accessibility that is able to cover a wide range of different movement patterns. The formula can now be used to investigate the effect of individual dispersal behaviour on metapopulation viability. This is done in Part III.

Part III

On the metapopulations' level



On the viability of metapopulations: individual dispersal behaviour matters

1 Introduction

Assessing fragmented landscapes regarding their ability of maintaining viable metapopulations is a very difficult aim (Hanski & Ovaskainen 2000, Etienne & Heesterbeek 2001, Frank & Wissel 2002). Metapopulation models are a useful tool to address this task (review by Verboom *et al.* 1993, Hanski 1999). Certainly, models cannot give exact quantitative predictions, but by comparing different landscapes, they can give qualitative assessments of which landscape configuration would be most effective (sustainable). Such an analysis can give ranking orders of landscapes that can be used as aids for decision support in landscape planning and conservation practice (Lindenmayer & Possingham 1996, Drechsler 2000, Possingham *et al.* 2000).

In order to avoid too much model complexity, the processes that determine metapopulation viability are often modelled in a simple way. Animals' dispersal between habitat fragments is mostly taken into account by using a simple (exponential) dispersal function that assumes the underlying process of dispersal to be random movement (Fahrig 1992, Hanski 1994, Adler & Nuernberger 1994, Vos *et al.* 2001, Frank & Wissel 2002). Species-specific dispersal behaviour, for example, the orientation of animals along landscape structures (Haddad 1999, Merriam 1991), the ability to move straight to another patch due to a large perceptual range (Zollner & Lima 1997, Zollner & Lima 1999), or the systematic search for patches with a specific movement pattern (Conradt *et al.* 2000, Conradt *et al.* 2001), can therefore only very roughly be considered. Such specific dispersal behaviours will affect exchange rates between patches. Therefore, it will undoubtedly influence the viability of a metapopulation considered. If we want to compare different landscapes regarding their effect on metapopulation viability, it is not yet clear, whether and how such specific dispersal behaviour affects the predictions of landscapes' ranking order. Is it possible that a landscape is assessed as the more effective one of two landscapes assuming one underlying dispersal behaviour, but is assessed as the less effective one assuming another underlying dispersal behaviour?

The present paper addresses these questions by comparing metapopulation viability in different landscape configurations, where different underlying dispersal behaviours are taken into account. This is done by using META-X, a software for metapopulation viability analysis

(Frank *et al.* 2002). Metapopulation viability is measured in terms of the mean lifetime T_m and landscape ranks are determined by comparing the T_m -values for the different landscape configurations considered. To incorporate dispersal behaviour in META-X, we use a submodel for the colonisation rates which utilises the formula for the accessibility of patches (Chapter 3) and allows different movement patterns to be considered. We focus on random walk with various degrees of correlation, as well as on the loop-like movement pattern found for a variety of animals (Hoffmann 1983, Müller & Wehner 1994, Durier & Rivault 1999, Conradt *et al.* 2000, Conradt *et al.* 2001). We analyse whether and under what circumstances the dispersal behaviour influences ranking orders of landscapes. We discuss implications for metapopulation modelling, planning and conservation.

2 Methods

Throughout the paper, the mean lifetime T_m subsuming all details of viability of an established metapopulation was used as a quantifier for metapopulation viability. To obtain the values for T_m of metapopulations in a given landscape for a given movement behaviour, we used META-X (Frank *et al.* 2002), a software for metapopulation viability analysis.

2.1 META-X

The META-X model (Frank *et al.* 2002) is identical with the spatially realistic stochastic levins-type model of Frank & Wissel (1998). Technically speaking, the META-X model is a time-continuous Markov chain model for finite metapopulations.

The metapopulation consists of N patches. Each patch is either occupied or empty. The state of the whole metapopulation is given by the state of the individual patches. The patches state's can be changed by local extinction of on occupied patch or recolonization of an empty patch. Therefore, the dynamics of the metapopulation are determined by three parameters: the local extinction rate of a patch e_i , the correlation degree of extinction c_{ij} between subpopulations and the colonisation rate b_{ij} from patch j to patch i .

META-X offers two possibilities to include spatial structure and species ecology into the main model parameters: either by using the submodels provided or by reading in corresponding data files, which allow the use of external submodels.

2.2 Specification of the main model parameters

2.2.1 Extinction rate and correlation degree of extinction

In order not to overload the study with too many details, we decided to ignore the correlated extinction between patches ($c_{ij} = 0$) and to assume patches to be identical having an equal rate of local extinctions for all patches ($e_i = e = 0.1$). All parameters that were needed to run the model can be found in Table 5.1.

2.2.2 Colonisation rate

The colonisation rate b_{ij} with which patch i colonises patch j can be described as a product of three factors: (i) the mean number of emigrants E_i leaving the occupied patch i per year, (ii) the probability that an emigrant starting from patch i reaches patch j , called patch accessibility r_{ij} , and (iii) the number of emigrants I_j needed on patch j to establish a new subpopulation.

The movement behaviour acts on the patch accessibility r_{ij} . The submodel for the colonisation rates provided by META-X assumes a simple exponential dependence for the patch accessibility on interpatch distance. Such an exponential dependence was found in Chapter 3 to be unable to cover the functional relationship between patch accessibility and distance for all movement patterns. Furthermore, if we assume that individuals stay at the first patch they reach, patches “compete” for migrants. Competition between patches for migrants is considered only very simplistically in the submodel provided by META-X, as emigrants are equally distributed to all connected patches not accounting for the fact that emigrants may be more attracted by a closer patch than by a distant one. Therefore, we decided to use our own submodel for covering more explicitly the effect of different movement patterns considered.

We calculated the colonisation rates in the following way:

$$b_{ij} = E_i * r_{ij} * \frac{0.5}{I_j} \quad (5.1)$$

where E_i is the mean number of migrants leaving the occupied patch i to other patches and I_j is the number of immigrants needed on patch j to establish a new subpopulation with a 50 % probability of success.

We assumed patches to be identical and therefore kept the emigration rate E_i and the number of immigrants needed I_j equal for all patches. Therefore, relation (5.1) could be simplified to

$b_{ij} = E * r_{ij} * \frac{0.5}{I}$. The values used for E and I can be found in Table 5.1.

Table 5.1 The parameters needed to calculate local extinction, correlated extinction, colonisation rates and the patch accessibility included in the colonisation rates

Process	Parameter determining the process	
Local Extinction	Rate of Extinction	0.1
Correlated Extinction	Mean Correlation length	0
Colonisation rates	E_i	10
	I_j	3
Parameter a and b for patch accessibility of different movement patterns	Parameter a ->Loops	5.840
	Parameter b ->Loops	0.075
	Parameter a ->uncorrelated random walk	2.149
	Parameter b ->uncorrelated random walk	0.076
	Parameter a -> fairly correlated random walk	0.796
	Parameter b -> fairly correlated random walk	0.025
	Parameter a ->correlated random walk	0.580
	Parameter b -> correlated random walk	0.091

2.2.2.1 A formula for calculating patch accessibility for different movement patterns

For calculating the for the probability r_{ij} of reaching a certain target patch j from a certain start patch i (patch accessibility), we used according to Chapter 3 the following formula:

$$r_{ij} = W_{ij} \cdot R(d_{ij}) \quad (5.2)$$

$$\text{where } W_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k(\neq i)} R(d_{ik})^{N-1}} \quad (5.3)$$

$$\text{and } R(d) = 1 - e^{-a \cdot e^{-b \cdot d}} \quad (5.4)$$

The function $R(d)$ (relation (5.4)) gives the potential patch accessibility in a landscape with two patches (start and target patch) only by considering the distance d between them. It only contains two parameters, a and b , which summarise all the relevant details of dispersal behaviour. In a landscape with more than two patches the patches compete for emigrants as an emigrant intercepted by one patch cannot reach another patch (assuming that migrants stay on the first patch they reach). This competition is described by the weighting factor W_{ij}

(relation (5.3)). This weighting factor is completely expressed in terms of the potential patch accessibility $R(d)$ and a power given by the number N of patches in the landscape. This weighting factor accounts for the fact that the competition strengths of patches depends on the relation of the potential accessibility of patch j to the potential accessibilities of all patches k in the landscape. The overall dispersal function (relation (5.2)) is completely expressed in terms of the potential patch accessibility. Consequently, there are only two function parameters a and b specifying the whole formula.

The resulting patch accessibility of this formula was compared with the results of a simulation model, where the patch accessibility for different movement patterns in varying landscape configurations was simulated (Chapter 3). This comparison showed a high predictive power of the formula presented for each movement pattern and landscape simulated. The simulation furthermore enables us to determine the parameters a and b for the different dispersal behaviours (Chapter 4). Therefore, we could use the formula instead of using the simulation model, keeping so the model simple, but allowing a realistic approximation to real movement patterns.

2.2.2.2 The movement patterns

The movement patterns investigated were loops, uncorrelated random walk, fairly correlated random walk, strongly correlated random walk. While random walk is a rather simple movement pattern, the loop-behaviour is a very complex pattern, found in nature for a variety of animals (Hoffmann 1983, Bell 1985, Müller & Wehner 1994, Durier & Rivault 1999, Conradt *et al.* 2000, Conradt *et al.* 2001). For this loop-like pattern the individuals move away from the start point, returning to it on a different path. The next loop is started in another direction, creating a petal-like path. The size of the loops increases with the number of loops, and so the radius searched increases. The parameters a and b of the formula subsuming all the relevant details of those movement patterns can be found in Table 5.1.

2.3 Simulations

In the two first experiments (Sections 3.1 and 3.2), we used randomly generated landscapes. For this, x- and y-coordinates of patches were randomly taken from 100 uniformly distributed values. In the third experiment, landscapes were generated in a systematic way (for the description see Section 3.3).

From the resulting patch positions, we calculated inter patch distances (measured between patch centres). With these distances, the patch accessibilities r_{ij} and the corresponding

colonisation rates were calculated for the movement patterns considered (loops, uncorrelated random walk, fairly correlated random walk, strongly correlated random walk). All these calculations were done in C++. The resulting matrix of colonisation rates was read in META-X and the mean lifetime T_m was obtained.

The time horizon of META-X is limited to 10 000 years. This horizon is sufficient for using META-X in the context of conservation. Since we are interested in gaining understanding, we need an unlimited time horizon. For simulations where the resulting mean lifetime exceeds the limit given by META-X, we used the original model forming the basis of META-X (Frank & Wissel 1998). This original model was programmed in Mathematica[®] (Wolfram 1996).

3 Results

3.1 Does behaviour matter?

The aim of the present study is to understand the influence of the individual dispersal behaviour on the viability of metapopulations with respect to both (a) the absolute values of the mean lifetime T_m for a particular landscape and (b) the relative ranking orders between the T_m -values in varieties of alternative landscapes.

In order to get an initial impression about these questions, we generate 10 random landscape configurations with 9 patches each as examples (Fig. 5.1). In Figure 5.2, the resulting mean lifetime T_m is plotted for every landscape and every movement pattern. The absolute values of T_m for a particular landscape differ between the different movement patterns. This quantitative effect of behavior is not surprising. By comparing the T_m -values for the different landscapes between each other, we see that also the landscape ranks differ between the movement patterns. A landscape where this can drastically be seen is Landscape 9. Assuming ‘Loops’ and ‘Fairly correlated walk’ as underlying movement patterns, this landscape is one with the lowest T_m -value and hence the lowest rank. But considering ‘Uncorrelated’ or ‘Strongly correlated random walk’, Landscape 9 has the highest T_m -value of all landscapes and the highest rank. Another drastic example for different landscape ranks is Landscape 4. While this landscape has a low rank for ‘Loops’, ‘Fairly correlated’ and ‘Uncorrelated random walk’, it has a comparatively high rank for ‘Strongly correlated random walk’.

The fewest differences in landscape ranks between movement patterns can be found when we compare ‘Loops’ and ‘Fairly correlated random walk’. But even here landscape ranks changes considerably. If we consider ‘Loops’ as underlying movement behaviour, T_m -value and rank of Landscape 2 are lower than for Landscapes 3, 5 and 7, while for ‘Fairly correlated random

walk', the opposite is true. Note that the differences between landscapes in the absolute T_m -values are not as high as in the more drastic examples. Still, the ranking orders are changing. Although these results are merely based on few examples, they bring an important problem to light: They indicate that the individual dispersal behaviour can markedly influence not only the absolute T_m -value for a particular landscape but also relative results on T_m for varieties of different landscapes. The latter result has serious implications for theory and conservation (see the Discussion) since relative results as ranking orders or trends are important aids for decision making. Therefore, there is a strong need to fully understand the effect of behaviour on the ranking orders between different landscapes.

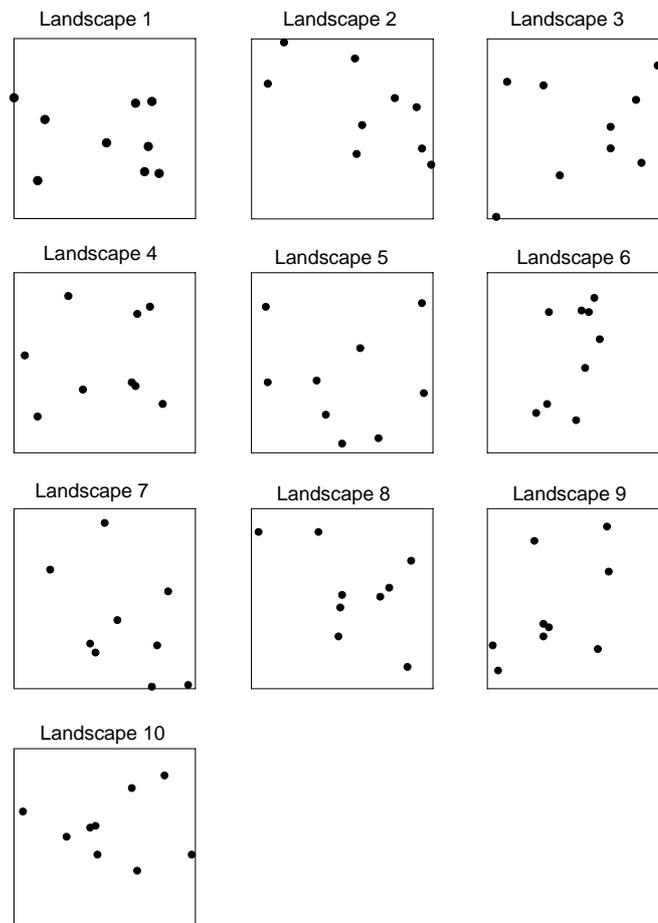


Figure 5.1 The 10 randomly generated landscapes that were used for the analysis

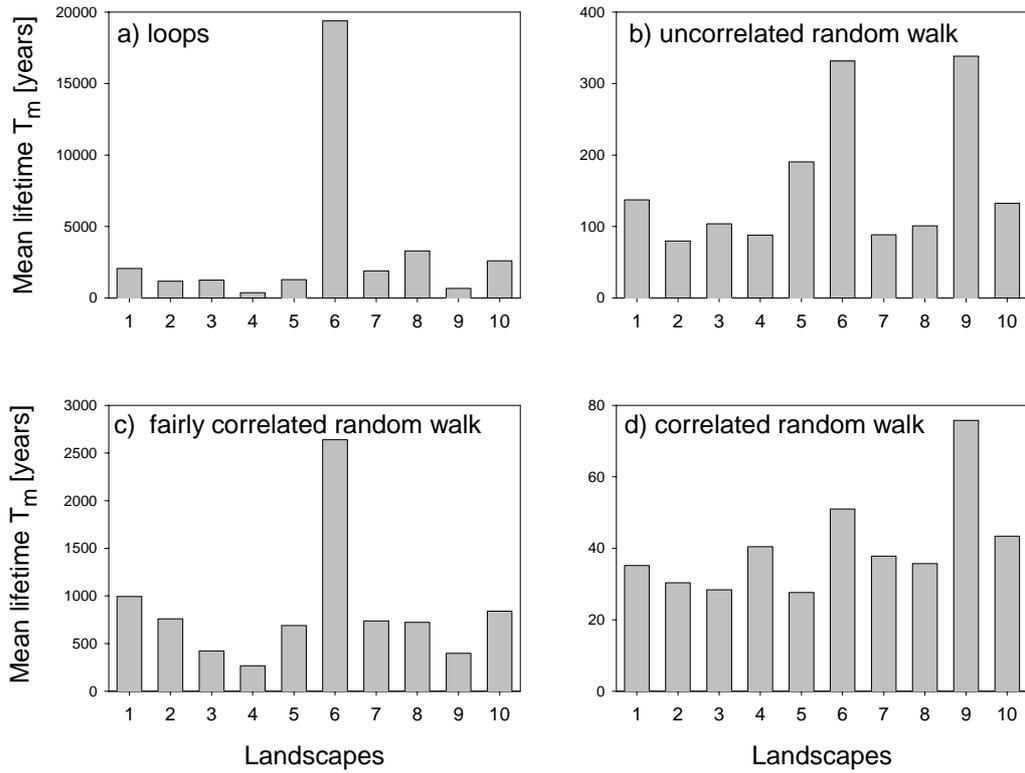


Figure 5.2 The mean metapopulation lifetime T_m for metapopulations in 10 different randomly generated landscape configurations calculated assuming different underlying individual dispersal behaviours: a) loop-like behaviour, b) uncorrelated random walk, c) fairly correlated random walk, d) correlated random walk

3.2 Why behaviour matters

In the following, we want derive a hypothesis concerning why individual dispersal behaviour changes landscape ranks. With our settings ($e_i = e, b_{ij} = \frac{0.5 \cdot E}{T \cdot e} \cdot r_{ij}$), T_m is exclusively influenced by landscape structure and individual behaviour via patch accessibility r_{ij} . Relation (5.2) reveals that r_{ij} consists of two components: the potential patch accessibility $R(d_{ij})$ (relation (5.4)) and the weighting factor W_{ij} (relation (5.3)) accounting for the competition between patches for migrants (see Section 2.2.2.1). Both components can be responsible for the change in the landscape rank.

To test whether the competition between patches causes a change in landscape ranks, we repeat the same experiment as before using the 10 landscapes of the first experiment (Fig. 5.1), but modifying formula (5.2) for the patch accessibility in such a way that the competition between patches is ignored, i.e. $r_{ij} = R(d_{ij})$, as is done in many metapopulation

models (Fahrig 1992, Adler & Nuernberger 1994, Vos *et al.* 2001). We therefore calculate the patch accessibility r_{ij} by using the potential accessibility function $R(d)$ (relation (5.4)).

The resulting mean lifetimes T_m of all landscape configurations and movement patterns for the competition-free case are shown in Fig. 5.3. As before, the absolute T_m -values for a particular landscape are affected by a change in the movement patterns. The ranking orders in the T_m -values between the different landscapes, however, are the same for all underlying dispersal behaviours. Without competition, there seems to be no effect of dispersal behaviour on the landscape ranks. This gives rise to the hypothesis that the competition effect is responsible for the change in the ranking orders.

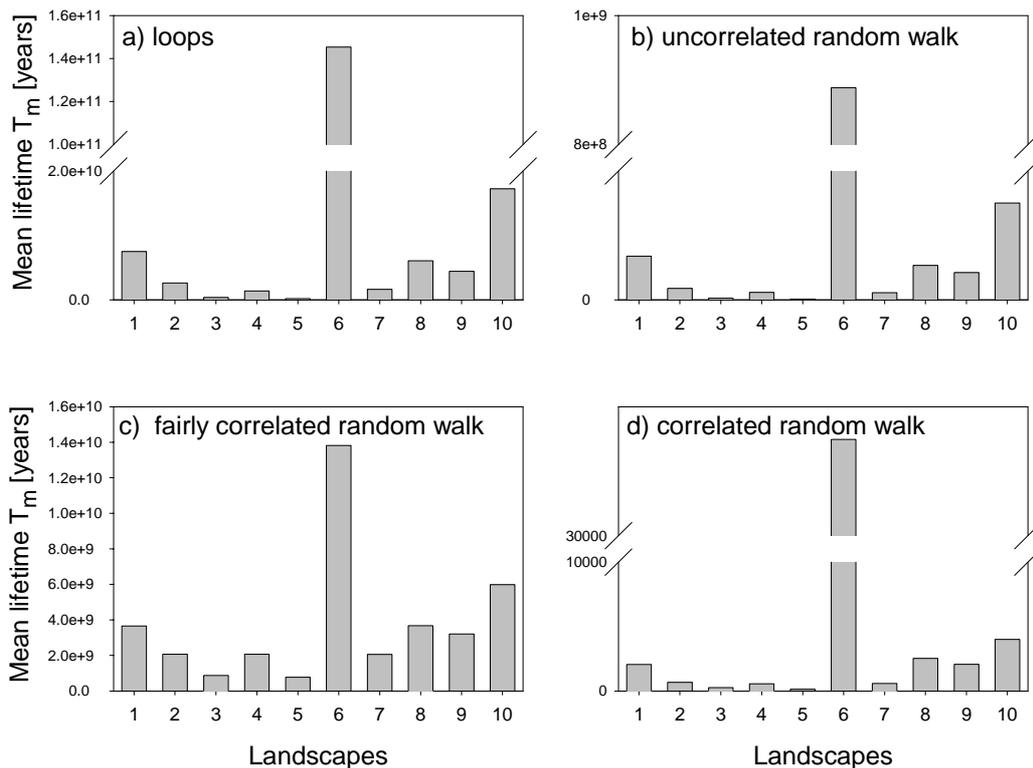


Figure 5.3 The mean metapopulation lifetime T_m for metapopulations in 10 different randomly generated landscape configurations calculated with relation (5.3) only, ignoring the competition between patches. Different underlying individual dispersal behaviours were assumed: a) loop-like behaviour, b) uncorrelated random walk, c) fairly correlated random walk, d) correlated random walk

3.3 Gaining understanding: how competition acts

Now, we are interested in gaining a mechanistic understanding of the effect of landscape structure and individual behaviour on metapopulation viability and the role of the competition effect in this context. Hence, it is no longer sufficient to comparatively analyze randomly generated landscapes. These landscapes differ in too many factors that produce complexity.

We therefore perform a more systematic experiment with a hypothetical landscape consisting of five patches. We change the position of merely one patch (Figs. 5.4a) by gradually moving Patch 1 towards Patch 2. The corresponding patch accessibilities r_{ij} are calculated in two different ways: (i) without competition between patches using relation (5.4) (see Section 3.2) and (ii) with competition using relation (5.2) (see Section 3.1).

Additionally, we analyze the functional structure of a previously published approximation formula T_m^a for the mean lifetime T_m (Frank & Wissel 2002) which gives insight into the relationship between T_m and all the model parameters. This formula has been found to have a high predictive power for a wide range of landscape configurations. By inserting our settings ($e_i = e, b_{ij} = \frac{0.5 \cdot E}{I \cdot e} \cdot r_{ij}$) into T_m^a , we obtain

$$T_m \approx T_m^a = \frac{1}{e} \cdot \sum_{i=1}^N \sum_{k=i}^N \frac{1}{k} \cdot \frac{(N-i)!}{(N-k)!} \cdot \frac{1}{(N-1)^{k-i}} \cdot x^{k-i} \quad (5.5)$$

with

$$x = \prod_{i=1}^N \max \left(\sqrt{2}, \frac{0.5 \cdot E}{I \cdot e} \cdot \sqrt{\left\{ \frac{1}{2} \left[\left(\sum_{j(\neq i)} r_{ij} \right)^{-2} + \left(\sum_{j(\neq i)} r_{ji} \right)^{-2} \right] \right\}^{-1}} \right)^{1/N} \quad (5.6)$$

Relation (5.5) reveals that T_m can be approximated by a polynomial of a certain term x that characteristically depends on the patch accessibilities r_{ij} . It is evident that merely the total

outgoing accessibilities $r_{out,i} = \sum_{j(\neq i)} r_{ij}$ and the total incoming accessibilities $r_{in,i} = \sum_{j(\neq i)} r_{ji}$ of the individual patches i as well as the corresponding harmonic mean of

these two quantities $H(r_{out,i}, r_{in,i}) = \sqrt{\left(\frac{1}{2} (r_{out,i}^{-2} + r_{in,i}^{-2}) \right)^{-1}}$ are decisive for the value of T_m .

This reflects the well-known effect that the effective colonization ability of the subpopulations (given by x) depends on the ability to colonise patches and the chance of becoming recolonized after extinction.

In Figs. 5.4b and 5.4c, the resulting mean lifetime T_m of the simulation experiment is plotted against the distance d_{12} . Since the T_m -values drastically differ for the same landscape but

different movement patterns (we found 50 000 years ('Loops') and 250 years ('Strongly correlated random walk') in the initial landscape), we normalised T_m , i.e. we measured T_m in percentage of the maximum T_m -value found in the variety of landscapes considered for a given movement pattern.

In case without competition (Fig. 5.4b), T_m increases with decreasing distance d_{12} between Patches 1 and 2, regardless of the movement behaviour. Therefore, the ranking orders of landscapes are the same for all the movement patterns considered. This effect can be explained as follows: Shifting Patch 1 towards Patch 2 mainly results in a decrease of the distance $d_{12} = d_{21}$ between Patches 1 and 2, while all the other distances d_{ij} remain almost unchanged. Since in the case without competition $r_{ij} = R(d_{ij})$, the accessibilities $r_{12} = r_{21} = R(d_{12})$ increase, while all the other accessibilities r_{ij} remain almost constant. In consequence, the total incoming and outgoing accessibilities $r_{in,i}$ and $r_{out,i}$ for Patches 1 and 2 and the harmonic mean $H(r_{in,i}, r_{out,i})$ between them increase, while the terms $r_{in,j}$, $r_{out,j}$ and $H(r_{in,j}, r_{out,j})$ for all the other patches j remain constant. The functional structure of the T_m -formula (5.5) reveals that these findings result in a positive effect on T_m .

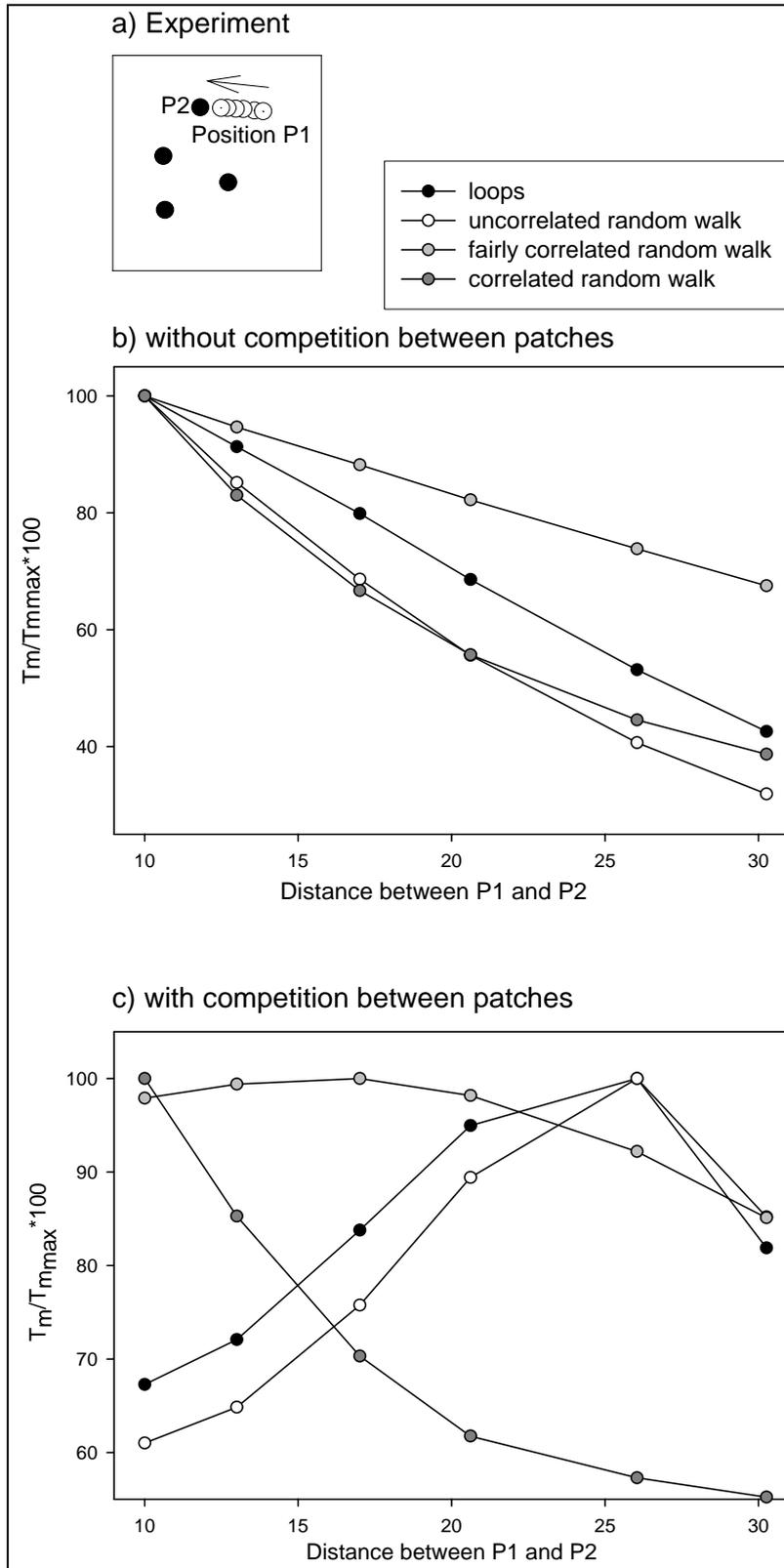


Figure 5.4 a) An experiment to investigate the effect of the interaction between movement behaviour and landscape systematically: the position of one patch is changed in the way that Patch 1 is moved closer to Patch 2 while the position of all other patches was kept constant. b) and c) The resulting mean lifetime T_m (to allow a better comparison between movement patterns, T_m is measured in percentage of the maximum T_m -value found for a given movement pattern in the variety of landscapes of one experiment) for different landscape configurations and movement patterns, calculated b) without considering the competition between patches and c) by considering competition between patches.

A totally different picture occurs in the case where competition between patches is included (Fig. 5.4c). For each movement pattern, there is some optimum distance d_{12} at which T_m is highest. This optimum distance differs between the dispersal behaviours considered. The existence of different optima results in different ranking orders for different movement patterns. While the decrease in distance d_{12} may result in an increase of T_m for one movement pattern (for example for ‘Strongly correlated random walk’), it may already result in a decrease for another movement pattern (for example ‘Loops’).

What are the mechanisms leading to the behaviour-dependent optimum? An optimum always indicates some trade-off. Such a trade-off can actually be read-off from the functional structure of the formulas for T_m (relations (5.5; 5.6)) and r_{ij} (relation (5.2)) in the case of competition:

(a) As we know from relation (5.2), the accessibilities r_{12} and r_{21} between the Patches 1 and 2 are given by

$$r_{12} = \frac{R(d_{12})^{N-1}}{\underbrace{R(d_{12})^{N-1} + \sum_{k \neq (1,2)} R(d_{1k})^{N-1}}_{W_{12}}} \cdot R(d_{12}) \quad \text{and} \quad r_{21} = \frac{R(d_{21})^{N-1}}{\underbrace{R(d_{21})^{N-1} + \sum_{k \neq (1,2)} R(d_{2k})^{N-1}}_{W_{21}}} \cdot R(d_{21}). \quad (7)$$

Since there is a decrease in $d_{12} = d_{21}$, while all other d_{ij} ’s remains constant, the potential accessibilities $R(d_{12}) = R(d_{21})$ and the weighting factors W_{12} and W_{21} increase. This results in an increase of the overall values r_{12} and r_{21} .

(b) The accessibilities r_{1j} and r_{2j} for emigrants from Patches 1 and 2 to all other patches j are given by

$$r_{1j} = \frac{R(d_{1j})^{N-1}}{\underbrace{R(d_{12})^{N-1} + \sum_{k \neq (1,2)} R(d_{1k})^{N-1}}_{W_{1j}}} \cdot R(d_{1j}) \quad \text{and} \quad r_{2j} = \frac{R(d_{2j})^{N-1}}{\underbrace{R(d_{21})^{N-1} + \sum_{k \neq (1,2)} R(d_{2k})^{N-1}}_{W_{2j}}} \cdot R(d_{2j}). \quad (8)$$

Here, the potential accessibilities $R(d_{1j})$ and $R(d_{2j})$ remain almost unchanged. The weighting factors W_{1j} and W_{2j} , however, decrease because of the increasing terms $R(d_{12}) = R(d_{21})$ in the denominators. This reflects the fact that any improvement of the exchange between Patches 1 and 2 goes to the disadvantage of the exchange to all other patches. In consequence, the overall values r_{1j} and r_{2j} decline.

(c) The accessibilities r_{ij} between all other patches i and j remain almost unchanged.

The findings on the pair-wise accessibilities r_{ij} result in the following total incoming and total outgoing accessibilities $r_{in,i} = \sum_{j(\neq i)} r_{ji}$ and $r_{out,i} = \sum_{j(\neq i)} r_{ij}$ for all the patches i : For the two Patches 1 and 2, both $r_{in,i}$ and $r_{out,i}$ increase (because of the increase in r_{12} and r_{21}) and so does the harmonic mean $H(r_{in,i}, r_{out,i})$ between them. For all other patches $j(\neq 1,2)$, the total incoming accessibilities $r_{in,j}$ decrease (because of the decrease in r_{1j} and r_{2j}), while the outgoing accessibilities $r_{out,j}$ remain almost unchanged (because of the almost constant r_{jk} 's). Hence, the corresponding harmonic means $H(r_{in,j}, r_{out,j})$ for the patches j decrease.

Since relations (5.5; 5.6) reveals that T_m depends on the product of all the (2 increasing and $(N-2)$ decreasing) harmonic means $H(r_{in,i}, r_{out,i})$ of the individual patches, we conclude that the change in the position of Patch 1 actually results in a trade-off effect on T_m .

The optimum distance d_{12} , where advantage and disadvantage of the change in the position of Patch 1 compensate each other, depends on two things: the strength of the increase in r_{12} and r_{21} as the only source of advantage and the strength of the decrease in r_{1j} and r_{2j} as the only source of disadvantage. All these changes are related to the change in $R(d_{12})$. Therefore, the optimum distance depends on the shapes of the R vs. d curves. As is illustrated in Fig. 5.5, these shapes and so the optimum distance depend on the movement pattern. This is the reason why different movement behaviours result in different optimum distances and, hence, in different landscape ranks.

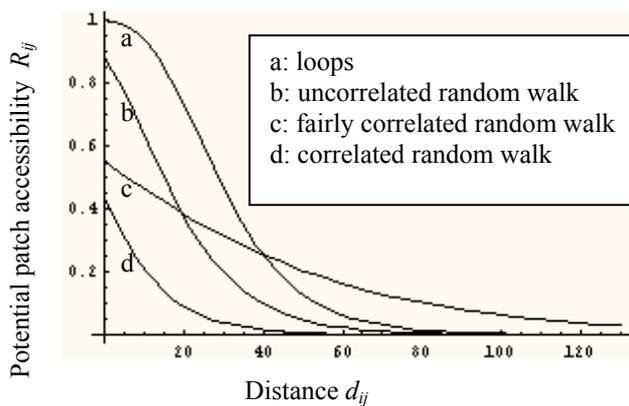


Figure 5.5 The relationship between the potential patch accessibility R_{ij} and the distance d_{ij} .

4 Discussion

Behaviour matters

We found that the dispersal behaviour of the individual does not only have a quantitative effect on the viability of a metapopulation, but also a qualitative effect: It influences ranking orders among alternative landscapes regarding the mean lifetime T_m of the corresponding metapopulations. The competition between patches for migrants was found to be an important factor driving the shift in landscape ranks. Our analysis of the consequences of a systematic change in a hypothetical 5-patch landscape revealed the mechanism how competition acts on the landscape ranks: If the distance between two patches is decreased while the rest of the landscape is kept constant, a trade-off between advantage (improved potential patch accessibility) and disadvantage (increased strength of competition) of this decrease in one inter-patch distance results. Whether the advantage compensates the disadvantage in a given landscape was found to depend on the shape of the potential accessibility function $R(d)$ and hence on the dispersal behaviour. These results have serious implications for metapopulation modelling, planning and management:

Our study shows that it is very important to incorporate dispersal behaviour in metapopulation models in an appropriate way. In most existing metapopulation models, dispersal behaviour is only cursorily taken into account by using an exponential function assuming the underlying process of dispersal to be random movement (Fahrig 1992, Hanski 1994, Adler & Nuernberger 1994, Vos *et al.* 2001, Frank & Wissel 2002). As our results indicate, this bears the risk of getting a bias in landscape ranking orders. Therefore, the dispersal behaviour has to be considered explicitly enough to allow an as good as possible landscape ranking. This reflects the opinion of many other authors calling for better integration of behavioural aspects into the analyses of ecological landscapes (Lima & Zollner 1996, Roitberg & Mangel 1997, Morales & Ellner 2002). On the other side, models need to be simple enough to be understandable and comprehensible (Gillman & Hails 1997). To model the movement behaviour explicitly is very time consuming and may complicate the model considerably, therefore models are usually working with formulas. As is shown in this study, not all formulas are able to reflect the differences in movement behaviour with an appropriate resolution. As we have seen, landscape ranks determined by a formula without competition between patches differ from those determined by formula with competition. Therefore, dispersal functions which do not incorporate competition will lead to (quantitatively and qualitatively) different results. The formula used here is an example for a formula that is structurally simple, but allows the effect of a variety of (hypothetical and realistic) movement

patterns to be described. For this formula, the dependence of the function parameters on the behaviour was already investigated (Chapter 4). This shows that it is possible to keep the dispersal behaviour in metapopulation models simple enough to be understandable, but explicit enough to be reliable.

Our results indicate the need of taking the movement behaviour in the context of landscape planning and metapopulation management into account, otherwise there is a high risk of counter-productive recommendations. This finding seems to provide the impression that it is impossible to derive any transferable statements on the effect of landscape changes on metapopulation viability which are generally valid for all species. But as we have seen, all the behavioural effects on relative results and ranking orders among the T_m -values of alternative landscapes are summarized in the shape of the potential accessibility function $R(d)$ (relation (5.4)) which is completely determined by the two function parameters a and b . These two parameters give rise to a categorization of species in the sense that movement patterns which result in the same values a and b lead to the same ranking orders and, hence, to common recommendations for landscape management. This corresponds with the results of other studies that it is needed and possible to derive ecologically differentiated, but still simple rules of thumb which are valid whole ecological classes of species (Verboom *et al.* 1993, Weaver *et al.* 1996, Frank & Wissel 1998, Frank 2004).

On the potential of approximation formulas

The present study demonstrates the potential of using formulas for particular model parameters (here: patch accessibility r_{ij}) or target quantities (here: mean lifetime T_m). The formula for the patch accessibility r_{ij} (relation (5.2)) revealed that r_{ij} is the product of the potential accessibility R_{ij} and a competition term W_{ij} . In consequence, the competition term could be switched on and off and the hypothesis that competition for migrants is responsible for the ranking effect could be tested. This would have been impossible by using the underlying individual-based simulation model. The formula for the mean lifetime T_m (relation (5.5)) provided structural insight into the functional relationship between T_m and the r_{ij} 's. It revealed that merely the total incoming ($r_{in,i} = \sum_{j(\neq i)} r_{ji}$) and outgoing ($r_{out,i} = \sum_{j(\neq i)} r_{ij}$) accessibilities of the individual patches are decisive for T_m . By inserting formula (5.2) for r_{ij} and systematically analyzing the functional dependence of $r_{in,i}$ ($r_{out,i}$) on all the inter-patch distances d_{ij} , a trade-off effect of decreasing the distance between two patches on T_m could be shown and the role of the movement behaviour could be explained. All these aspects were

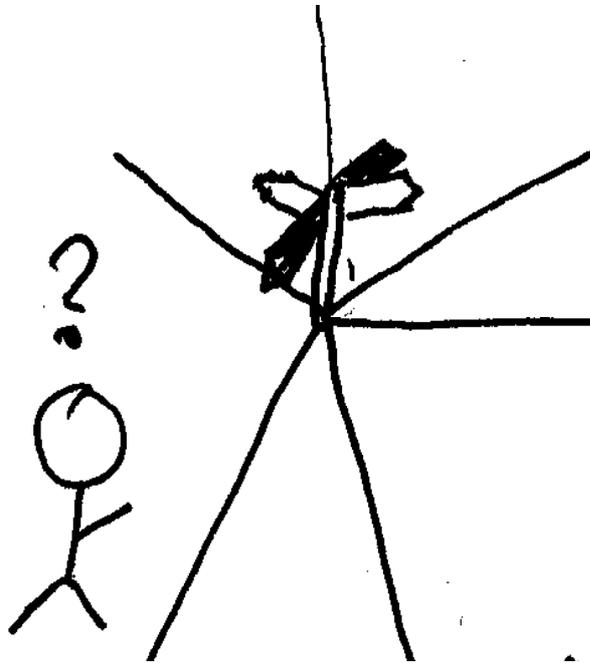
decisive for fully understanding the behavioural effects on the landscape ranks. This shows that the practical value of such formulas is much more than just “allowing predictions without having to run any simulation”; gaining insight into the functional structure is even more important. This indicates that it is worth to look for approximation formulas for measures of (meta-)population persistence (Hanski & Ovaskainen 2000, Frank & Wissel 2002, Ovaskainen & Hanski 2004, Frank submitted) and justifies the approach of deriving patch accessibility functions from individual-based simulation models.

Prospects for further research

To understand the effect of dispersal behaviour on landscape ranks, we started with most simple systematic landscapes, with 5 equally sized patches only. Real landscapes are more complex. They usually differ not only in one aspect from each other, but in a variety of aspects. These aspects may impact the shift in landscape ranks in the same or in the opposite direction, being complementary or contrary to each other. Furthermore, it is not yet clear how heterogeneous patch sizes would influence effect of dispersal behaviour on the ranking orders of landscapes. Heterogeneously sized patches may strengthen or soften the effects found in this study. Here, there is more research needed to make a systematic assessment possible.

Where to go from here:

Possible directions and first results



Where to go from here: Possible directions and first results

A thesis is never finished. There are a lot of subjects that I would have liked to work (more) on. Some challenges for future work are already mentioned in the respective parts. In the following, I would like to discuss some prospective ideas which have already been subject to further investigations. Therefore, I will not only present ideas here, but also some first results. These results are only the first step on investigating these ideas, since the themes presented here are too broad and too important to be covered completely within this chapter of the thesis.

1 Including landscape heterogeneity into the formula for patch accessibility

The patch accessibility formula derived in Chapter 3 was found to have a high predictive power for a variety of movement patterns and landscape configurations. Simulations were done in a binary landscape, with habitat and non-habitat only, and equal sized patches. Landscape heterogeneity was considered in the simulation model only in that way that we used different landscape configurations. Therefore, it is an open question whether the formula is able to predict patch accessibility in landscapes with further heterogeneity as well. Heterogeneity in landscapes can be due to heterogeneously sized patches or due to heterogeneous matrix structures, such as different matrix quality (Roland *et al.* 2000, Jonsen *et al.* 2001, Ricketts 2001, Vandermeer & Carvajal 2001) or landscape elements acting as corridors, barriers or directing components (Merriam 1991, Neve *et al.* 1996, Gustafson & Gardner 1996, Haddad & Baum 1999, Ries & Debinski 2001, Berggren *et al.* 2001, Pe'er *et al.* submitted b). In this section, several attempts to investigate the formulas applicability in heterogeneous landscapes – done by colleagues (Eckhardt *et al.* unpublished data, Pe'er *et al.* submitted) or by myself - are discussed.

1.1 Heterogeneously sized patches

Patch size is likely to have an important impact on patch accessibility as large patches should have a higher probability of being reached than small patches (Hill *et al.* 1996, Kuussaari *et al.* 1996).

To investigate the effect of patch size, we perform the simulation described in Chapter 3, Section 2.4, releasing animals at patch i and counting the proportion of individuals arriving at patch j . We use landscapes with 10 heterogeneously sized circular patches. The patch size is generated randomly and varies between a radius of 1 and 5, covering so an area between 3.14 units^2 for the smallest and 78.54 units^2 for the largest patch. As in Chapter 3, the resulting simulated values for the patch accessibility were plotted against the calculated values that were computed with relation (3.6).

Fig. 6.1a shows the results of this analysis. There is a strong correspondence between simulated and calculated values ($r^2 = 0.94$), but compared to the equal-sized case, there is a wider spread of values. Therefore, in landscapes with patch-size heterogeneity, formula (3.6) for the patch accessibility has a significantly lower predictive power.

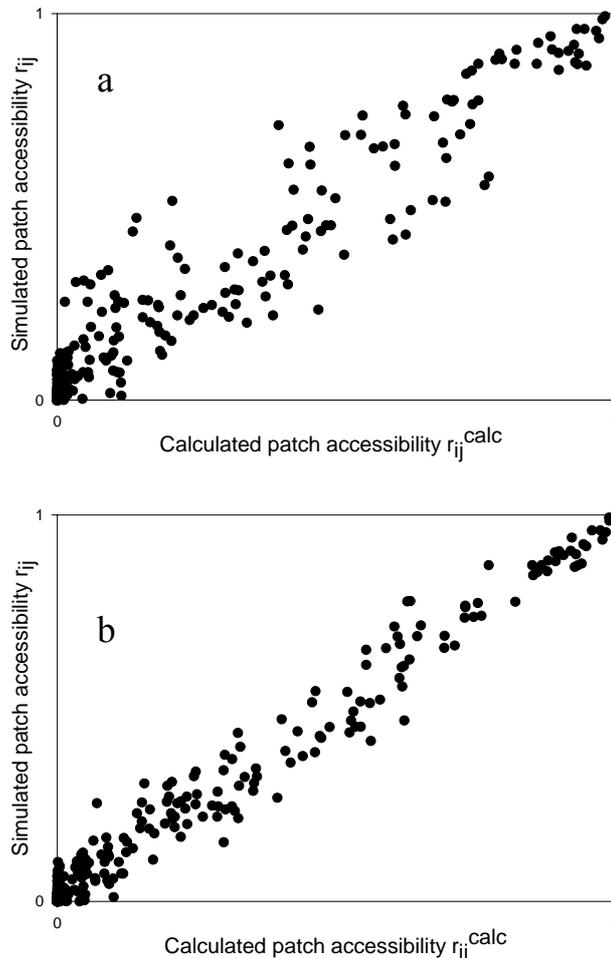


Figure 6.1 Simulated vs. calculated patch accessibility r_{ij} in landscapes with heterogeneously sized patches. a: The patch accessibility r_{ij}^{calc} is calculated by using the original formula $r_{ij}(d)$. b: The patch accessibility r_{ij}^{calc} is calculated by using the formula $r_{ij}(d^{new})$, with d^{new} being the distance between patches calculated in the following way: $d_{ij}^{new} = d_{ij} - rad_i - rad_j$ with rad being the radius of a patch.

How can patch size be included in the formula for patch accessibility in a simple way? In the formula, the distance between patches is measured from patch centre to centre. Thinking of a very large patch, it may be already a problem that – measuring the distance from centre to centre – this distance exceeds the “real” distance from one patch edge to the other by far. In landscapes with heterogeneous sized patches, the deviance between real and calculated distance varies between the different sized patch combinations and therefore leads to a bias when calculating the competition effect.

Therefore, the easiest approach to consider heterogeneous sized patches would be to take only the distance between the edges of patches into account:

$$d^{new} = d - rad_i - rad_j \quad (6.1)$$

with rad being the radius of patches. The new calculated distances can be inserted in relation (3.6).

In Fig. 6.1b, the simulated values are plotted against the resulting calculated ones. Here, the values are less scattered and the regression analyses show a stronger correspondence ($r^2 = 0.98$) with a predictive power as good as in the homogeneous case. Therefore, for the patch accessibility it seems sufficient to consider patch size by correcting the distance between patches. This may be valid as long as one thinks of circular patches. For irregular shaped patches another approach may be needed. This could be one aim of prospective research.

Why is it not needed to correct for the radius in landscapes with homogeneous sized patches? As long as all patches are equal sized, the deviance between real and calculated distance is the same for all distances. Therefore, this deviance can be covered by the fitting parameter a of the formula as can be seen in the following transformation:

$$1 - e^{-a * e^{-b(d-rad)}} = 1 - e^{-a * (e^{-b*d} * e^{-b*rad})} = 1 - e^{-(a * e^{-b*rad}) * e^{-b*d}} = 1 - e^{-a' * e^{-b*d}} \quad (6.2)$$

with rad being the radius of patches. As can be seen in relation (6.2), the deviance between the distance from centre to centre and the distance from edge to edge can be completely expressed in terms of the fitting parameter a' .

1.2 Heterogeneous matrix: the effect of barriers

Landscape elements can act as barriers which can not or hardly be crossed by animals (Ries & Debinski 2001). Examples for such landscape elements are matrix types unsuitable for movement (such as dense forest that cannot be crossed by butterflies or open fields avoided by forest species), roads or rivers. Such barriers may result in an altered patch accessibility as

they block the access to some patches and deflect the animals path in the direction of other patches.

During an internship with my supervision, Winnie Eckhardt investigated the effect of barriers on patch accessibility (Eckhardt *et al.* unpublished data). For our analysis, the same simulation as described in Chapter 3, Section 2.4 is performed, but with landscapes containing a barrier. An impermeable barrier with either 34 or 64 units lengths and 4 units width is placed in the middle of each (100x100 units) landscape. This fixed position of the barrier is used to enable a systematic analysis of the barriers effects and to avoid edge effects. Individuals are released from the start patch and move through the landscape with the loop-like dispersal behaviour. If they encounter a barrier, they change their next intended step by an angle of 10 degree in order to avoid the barrier. If they still encounter the barrier, they change this step again by 10 degrees, continuing like this until they can make this step without hitting the barrier. The following step is again according to the loop-like movement behaviour, but if animals encounter the barrier again, the procedure starts from the beginning. Therefore, it happens sometimes that the animals' path is deflected along the barrier (for an example of the movement behaviour see Fig. 6.2). As in Chapter 3, the movement is subject to stochasticity, so that the individuals' paths are varying. As above, the patch accessibility is determined by counting the proportion of animals arrived at patch j . The resulting simulated values for the patch accessibility were plotted against the values calculated with relation (3.6) using the parameters a and b fitted for the movement pattern considered in a homogeneous matrix. The effect of the barrier on patch accessibility can be seen in the derivation between calculated and simulated values.

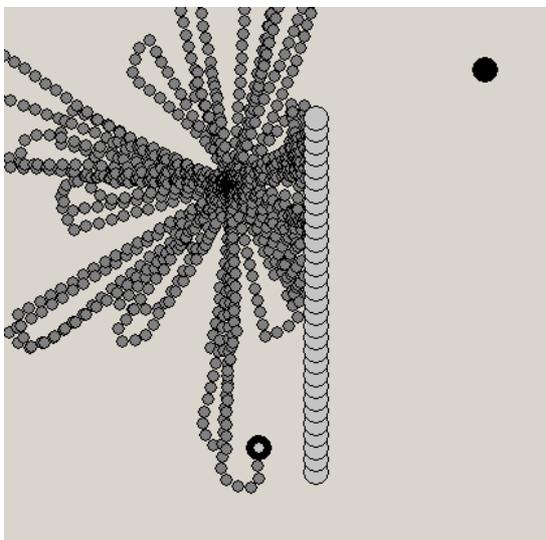


Figure 6.2 The loop-like movement behaviour in a landscape with the barrier.

The effect of a barrier in the middle of a 10-patch-landscape

In a first experiment, 10 patches are distributed randomly in each landscape and a barrier with 64 units is used. The position of all target patches are categorised as either on the same side of the barrier as the start patch or on the opposite side of the barrier. This categorisation is not only determined by the barrier itself but also by its imaginary prolongation. The resulting patch accessibility values are plotted against the calculated ones (calculated with relation (3.6) and the parameters derived from the homogeneous landscape) marked regarding the position of start and target patch in relation to the barrier. In Fig. 6.3, it can be seen that most of the values are on the identity line ($r^2 = 0.93$) with only a few being close to zero, showing only a slight effect of the barrier. By comparing the results of the regression analyses for values divided regarding the patch position in relation to the barrier, it can be seen that those patch combinations with start and target patch being on the same side of the barrier (black dots) are less effected by the barrier ($r^2 = 0.96$) than those combinations with start and target patch being on opposite sides (white dots, $r^2 = 0.27$). From those patch combinations with start and target patch being on the same side of the barrier some patch accessibility values are above as well as below the identity line, indicating that some patch combinations benefit from the barrier while others lose. From those patch combinations being on opposite sides, derivations from the identity line are mainly below the line, indicating that the barrier reduces the patch accessibility of patches being on the opposite side of it. This can be due to the barrier blocking the animals' path. This effect is strongest for those patches which are close to the start patch, but not reachable due to the barrier. Due to the fact that the barrier blocks the access to patches on its other side, some patches situated on the same side can benefit from the barrier as they have less competition of other patches.

One may have expected a stronger effect of such a long barrier in the middle of the landscape. However, patches on opposite sides of a barrier are often far away from each other, having so only a low potential patch accessibility. Patches on the same side are often less distant to each other, having therefore on average a higher potential patch accessibility. This trend is intensified by the competition effect. Therefore, the patch accessibility of most patches being on opposite sides is already low without barrier so that the barriers blocking has for most cases no impact.

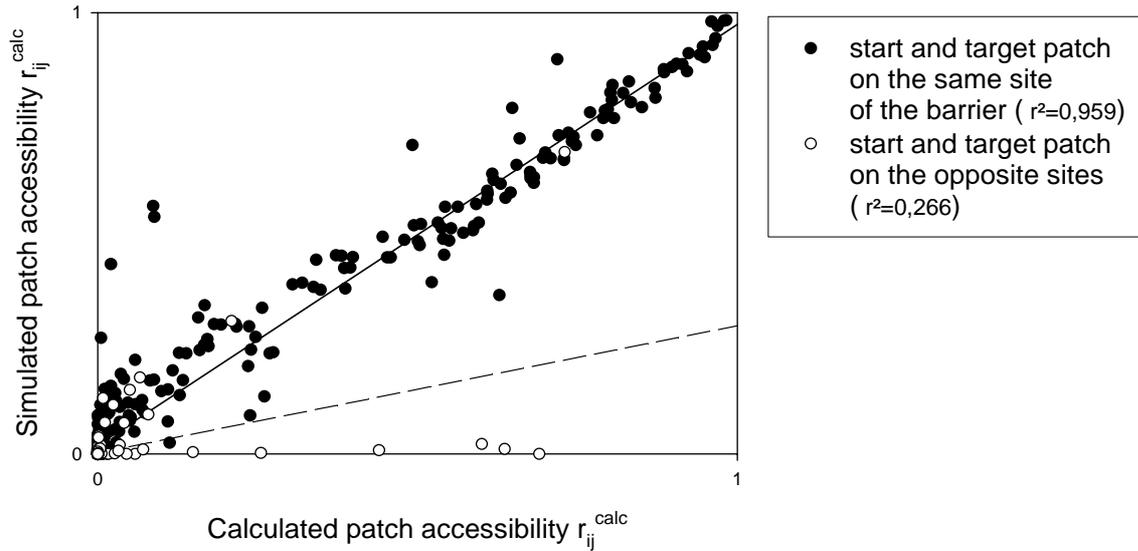


Figure 6.3 The effect of a 64-units-barrier in the middle of the landscape on the simulated patch accessibility r_{ij} . The linear regression shows a good correspondence between simulated and calculated values for those patch combinations being on the same side of the barrier (black dots, $r^2=0.96$), but a weak correlation between simulated and calculated values for patch combinations being on opposite sides (white dots, $r^2=0.27$).

In the first experiment, we gained some understanding about the impact of a barrier. It is still an open question how the effects of barriers can be covered by the formula for the patch accessibility. In order to gain more insight into the barriers impact on the formula, a hierarchical approach, as in Chapter 3, is used. The potential patch accessibility subsumes all relevant movement details, and barriers alter the movement of individuals. We assume that the barrier acts primarily on the potential patch accessibility and that the competition effect only intensifies existing effects. Therefore, we focus first on a two-patch-system, using it as a reference situation for the multi-patch-system.

The effect of a barrier in a two-patch-landscape

In the second experiment, a landscape with only two-patches is considered. A start patch is fixed on one side of the 34-units-barrier (Fig. 6.4a), while the target patch is placed randomly in each landscape. The patch accessibility of the target patch and the distance are noted and plotted against each other.

The resulting r_{ij} - d_{ij} -curves can be seen in Fig. 6.4b. As a reference, the potential patch accessibility function $R(d)$ of a two-patch-landscape without barrier is shown (line). The r_{ij} - d_{ij} -values of the simulations with barrier (black and white dots) are either on this line or below it. It looks like values are shaping two curves, one close to the line and one below.

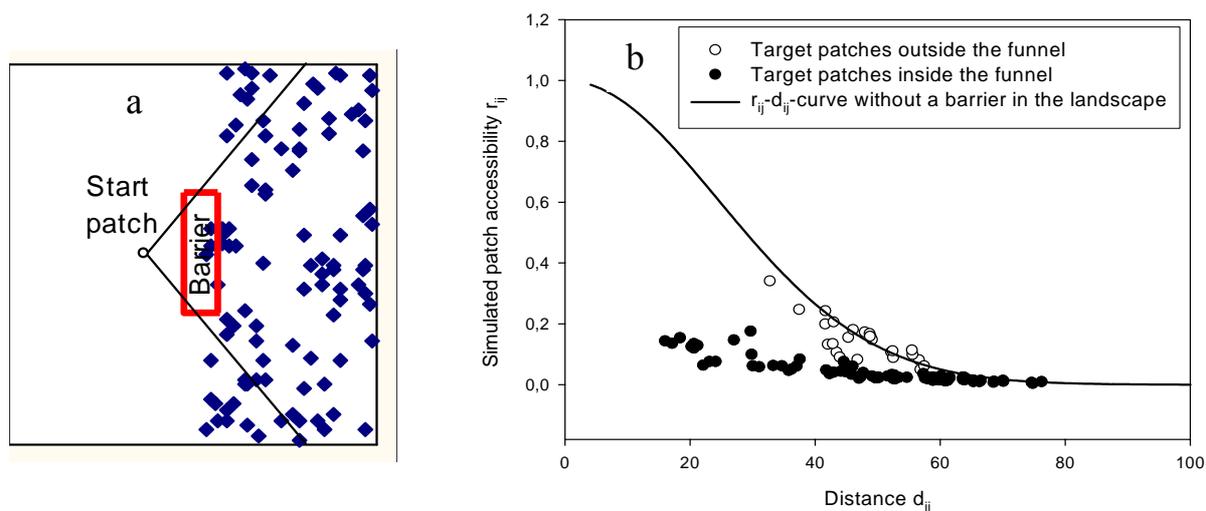


Figure 6.4 The effect of a barrier in the middle of the landscape with two habitat patches on opposite sides of the barrier. a) A scheme of the landscape with the funnel indicating which patches are counted as shadowed by the barrier. b) The simulated patch accessibility depending on the distance; r_{ij} - d_{ij} -relationships are shown for patch combinations with the target patch being either inside or outside the funnel (black and white dots), and for a landscape without a barrier (line).

These two curves can be assigned to two different patch positions: We put a funnel in the landscape (Fig. 6.4a), derived by drawing a line from the start patch to the edges of the barrier and by elongating this line through the landscape. For a fixed position of the barrier the position of the start patch determines the shape of r_{ij} the funnel. By this funnel patches can be divided into two categories, namely patches which are shadowed by the barrier and patches which are outside the barriers shadow. With this method, the two curves in Fig. 6.4b can be explained. The flat curve (black dots) consists of the patches in the shadow of the barrier, while the other curve similar to the one without barrier (white dots) consists of the less effected patches outside the funnel. This analysis shows that the barrier effects mainly patches inside the funnel. Therefore, it is more important whether patches are in the shadow of the barrier rather than on which side of the barrier they are.

How to include the effect of barriers into the formula for patch accessibility?

One possibility to include the barrier effect into the formula would be to calculate the potential patch accessibility $R(d)$ by using two different parameter sets. While patches outside the funnel (regardless of which side of the barrier they are) can be fitted by the $R(d)$ -function with the standard parameters of the movement pattern (black dots), a fitting of patches inside the funnel $R(d)^{bar}$ (white dots) results in other parameter values, namely $a = 0.5755$,

$b = 0.0595$. The two resulting functions for the potential patch accessibility can be inserted in relation (3.6), using for each patch outside the funnel $R(d)$ and for each patch inside the funnel $R(d)^{bar}$.

To test whether this approach is able to predict the patch accessibility in a landscape with barrier, we perform a simulation in a 10-patch-landscape. The start patch is fixed in order to calculate the funnel easily, while all other patches are distributed randomly.

In Fig. 6.5, the resulting simulated vs. calculated plots can be seen for two different positions of the start patch (Position 1: start patch in the middle of the barrier (Fig. 6.5a and 6.5c), Position 2: start patch close to the end of the barrier (Fig. 6.5b and 6.5d), see also drawing in the left upper corner). In Fig. 6.5a and 6.5b, the patch accessibility is calculated by using the original $R(d)$ function only with the parameters fitted for the movement pattern without barrier. As in Fig. 6.3, values are scattered (Position 1: $r^2 = 0.85$, Position 2: $r^2 = 0.92$). In Fig. 6.5c and 6.5d, the patch accessibility is calculated by using the two different $R(d)$ -functions, $R(d)$ for patches outside the funnel and $R(d)^{bar}$ for patches inside the funnel. Using the two functions, values are less scattered and the regression analysis reveals a strong correspondence between simulated and calculated values (Position 1: $r^2 = 0.98$, Position 2: $r^2 = 0.97$). Therefore, the formula is able to consider landscape heterogeneity due to barriers by using two different parameter sets for the potential patch accessibility function. However, this is only possible, because a barrier allows to classify patch positions into two categories, namely shadowed and not shadowed by the barrier. Landscape heterogeneity that acts more gradually allows no separation of matrix types and is therefore not covered by this approach.

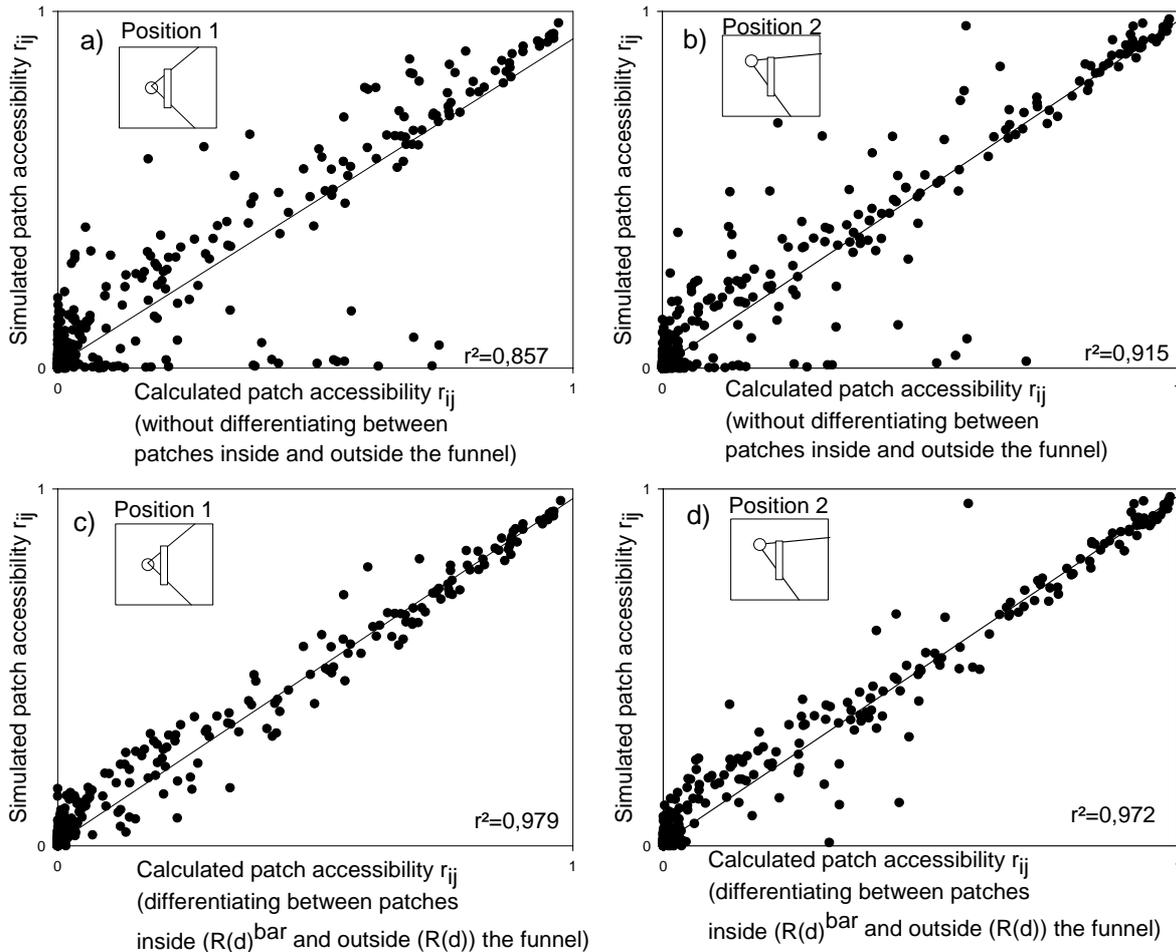


Figure 6.5 How can the patch accessibility be calculated in a landscape with a barrier? The start patch is either positioned in the middle of the barrier (Position 1, Fig. 6.5a and 6.5c) or positioned at the end of the barrier (Position 2, Fig. 6.5b and 6.5d).

6.5a and 6.5b) The patch accessibility is calculated by the original formula using the same potential accessibility $R(d)$ for target patches which are shadowed by the barrier (inside the funnel) and for target patches which are outside the funnel.

6.5c and 6.5d) The patch accessibility is calculated by using different potential accessibilities depending on whether the target patch is shadowed by the barrier ($R(d)^{bar}$) or not ($R(d)$).

1.3 Heterogeneous matrix: the effect of gradually changing topography

Another source of matrix heterogeneity is a gradually change of landscape topography as given by the relief of a landscape. A prominent example for a species reaction to topography are hilltopping butterflies (Shields 1967). Hilltopping is a mate-searching strategy in which males and virgin or multiple-mating females seek a topographic summit to meet and mate there. Having left the reproduction habitat (patches of host plants), males and virgin females ascend to summits and congregate there. After mating, females disperse from the summits in

search of patches of host-plants. This behaviour drives animals out of habitat patches and therefore facilitates and directs a dispersal-like movement.

Pe'er *et al.* (submitted a) used the formula for patch accessibility (Chapter 3) to analyse the effect of topography on summit accessibility, i.e. the ascendance of males and virgin females to summits. This study was done in cooperation with Guy Pe'er from the Ben Gurion University, Israel. The model was developed by Guy Pe'er, the application of the formula on the model results was done by myself and the analyses of the overall results were discussed together during Guy Pe'er's stay at the UFZ-Centre for Environmental Research.

This study differs in some aspects from the investigations done in this thesis so far. Instead of focusing on the probability that emigrants reach a specific patch, we focus on the probability that individuals reach a specific summit to find mating partners there. Furthermore, the simulation model developed for investigating the effect of topography differs considerably from the model used for deriving the formula (Chapter 3). Therefore, the following study reveals not only whether the formula is able to predict patch (resp. summit) accessibility when animals' movement is influenced by topography. It also can be seen as a test whether and how the formula can be applied in situations completely different to the original one.

To analyse the effect of topography, Pe'er *et al.* (submitted a) developed an individual- and gridbased simulation model, where landscapes with heterogeneous elevation could be considered. Since this model differs in some aspects from the one presented in Chapter 3, it is explained in the following a little bit more thoroughly.

A model for hilltopping butterflies

The model consists of two components: a landscape generator for creating virtual, topographically heterogeneous, patchy landscapes on a grid basis, and an individual-based model for simulating the movements of hilltopping butterflies in these landscapes. The model is based on simplified behavioural rules obtained from field observations in the hilltopping butterfly *Melitaea trivia* (Pe'er *et al.* in press).

Landscape – We assume that landscape heterogeneity solely results from topography. We use landscapes of 200 x 200 unit cell size, including six summits. We place summits with an elevation of 10000 units randomly. The elevation of each cell is calculated based on its distance to the closest summit. We use a Gaussian function to create 'bell-shaped' hills. Since this leads to even hills without small regional summits or valleys, we provide the possibility to add additional landscape variation in elevation. This additional landscape variability in elevation is added to each cell independently as a random value with a normal distribution

around 0. The magnitude of variability lv is determined by the standard deviation as a percentage of summit elevation (e.g. a standard deviation of 4% summit height) and varies as parameter for different experiments. To reduce edge effects, we restrict the location of summits and release points to the middle 100 x 100 cells. Since this middle area is always higher than the outer surrounding, animals which respond to topography cannot be lost to the edges.

Movement rules – As a basic movement without considering topography, individuals move through the landscape by choosing randomly one of the eight neighbouring cells at each step. Hilltopping behaviour in topographically heterogeneous landscapes is simulated by probability: at each step, a butterfly can move upward towards the neighbouring cell with the steepest slope with a probability of q , or move randomly with a probability of $1-q$. The probability q varies regarding the butterflies response to elevation. In simulation runs with individuals showing no response to topography, q is set to 0 (random movement), in simulations with individuals showing a very strong response to topography, q is set to 0.6 (highly directed by topography). In each simulation run, all butterflies have the same level of response to topography. Individuals can recognise a summit (the peak) from each of the 8 neighbouring cells. Upon spotting one butterflies move towards it and stay there.

Simulation run - In each simulation run, 500 butterflies were released at a random ‘release point’ and move through the landscape according the movement rules described above until they die or reach a summit. Each butterfly has a maximum life span of 10,000 steps, its probability of dying in each step being 0.001. For every parameter value, we repeat the simulation runs 200 times, simulating therefore 200 different landscape configurations and release points. This experiment was done for different parameter values of q and different levels of landscape variability. Summit accessibility was noted as proportion of individuals arriving at a summit and the distances between release point and all summits were recorded.

How does animals’ response to topography influences summit accessibility?

To analyse the effect of the animals’ response to topography q on the formula for patch accessibility, we varied the parameter q in a first experiment using values of $q = 0$ (no response to topography), $q = 0.1$ (slight response to topography), $q = 0.3$ (strong response to topography) and $q = 0.6$ (very strong response to topography). The resulting simulated values for the summit accessibility were plotted against the values predicted by relation (3.6). Since the movement behaviour is considerably influenced by the response to topography, for each value of the parameter q , the formula’s parameters a and b were fitted first at the

corresponding “two-patch” (in this case one-releasepoint-one-summit)-landscape (compare Chapter 3, Section 3.1).

In Fig. 6.6a, the resulting plot for the case that individuals show no response to topography ($q = 0$) can be seen. In this case, the formula is able to predict the simulated values qualitatively and quantitatively sufficient ($r^2 = 0.89$). This is not surprising, since animals move randomly and therefore the formula should be able to predict the summit accessibility. Compared with the result of the regression analysis for uncorrelated random walk of the original model ($r^2 = 0.99$, Chapter 3), the results of the regression analysis indicate here, however, a quite bad predictive power. This is probably due to the fact that the model used for this investigation runs on a grid and therefore measured distances (from point to point) diverge from really moved distances (from cell to cell).

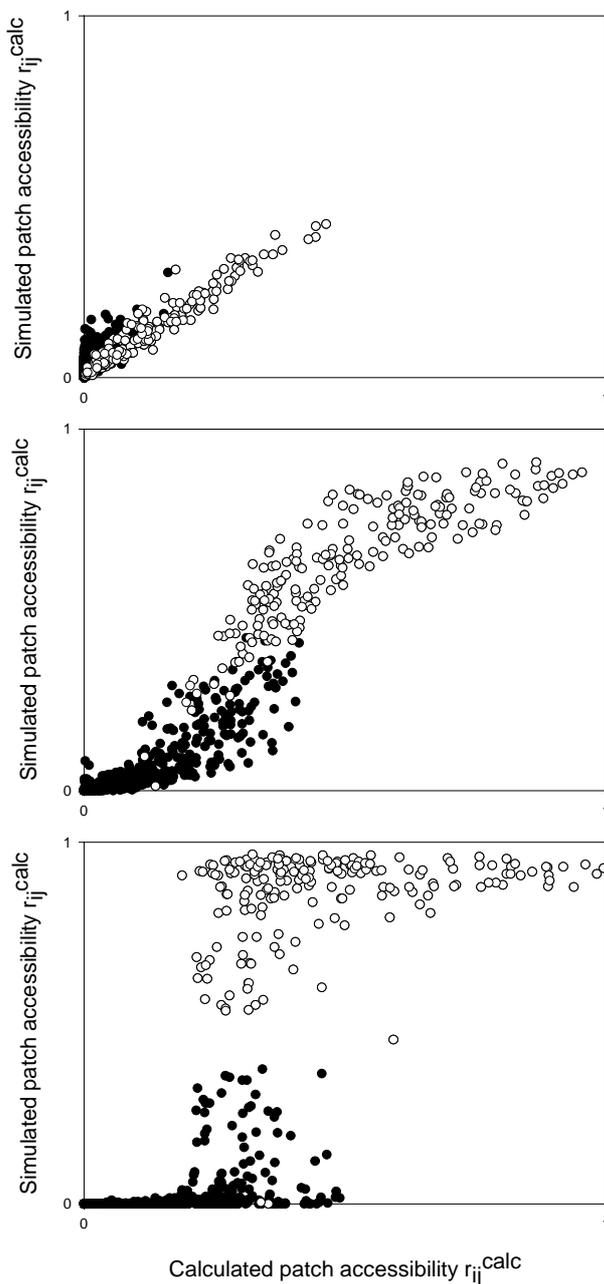


Figure 6.6 The effect of animals’ response to topography on patch accessibility. Simulated vs. calculated patch accessibility when different degrees of response are assumed: (a) no response to topography ($q=0$), (b) weak response to topography ($q=0.1$), (c) strong response to topography ($q=0.3$). White dots represent values belonging to summit closest to the release point of one landscape, black dots represent all other summits in one landscape.

In Fig. 6.6b, values are plotted for the case that individuals show a slight response to topography ($q = 0.1$). Here, we find a rather sigmoidal than linear relationship between simulated and calculated values although the predictive power of the formula is quite high ($r^2 = 0.91$). The sigmoidal effect becomes strongly intensified when a strong or even a very strong response to topography is assumed ($q = 0.3$, Fig. 6.6c and $q = 0.6$, Fig. 6.7a). In this case, there is not at all a linear relationship, rather a step function with two ranges of almost constant values: one with very high accessibility values ($r_{ij} \approx 1$) and one with very low accessibility values ($r_{ij} \approx 0$). Between the areas with either very high or very low patch accessibility values, there is a certain overlap region, where we find for one given calculated patch accessibility very low as well as very high values for the simulated patch accessibility. Such an overlap can not be covered by any function. The corresponding regression analysis shows that the predictive power of the formula is low ($r^2 = 0.56$ for $q = 0.3$ and $r^2 = 0.37$ for $q = 0.6$). Therefore, the formula is not able to predict the summit accessibility when animals exhibit a strong response to topography.

Although we are not able to provide a formula that can cover all the effect of topography, we can explain this effect and give a first clue how the accessibility can be predicted nevertheless. In Fig. 6.6, values are marked regarding the summit they belong to: white dots indicate that the accessibility value belongs to the summit with the shortest distance to the release point, while black dots indicate that the reached summit is one of the summits which are further away from the release point. It can be seen that almost all accessibility values belonging to the closest summit exhibit an extremely high accessibility (for most cases $r_{ij} = 1$), higher than predicted by the formula. In contrast, all accessibility values belonging to summits which are further away show a much lower accessibility than predicted ($r_{ij} = 0$). This can be explained by the fact that a strong response to topography leads to a highly directed movement where animals follow the slope towards the summit. Such a directed movement completely changes the way competition acts between summits. Almost all animals are moving to the closest summit, while almost none arrive at another summit. Therefore, for a strong response to topography, we do not need a formula for predicting summit accessibility, but can estimate the accessibility by the following simple rule:

$$r_{ij} \approx \begin{cases} 1 & \text{for the closest summit} \\ 0 & \text{for all other summits} \end{cases}$$

Back to random movement: how landscape variability effects summit accessibility

In the second experiment, we want to investigate how an additional variability of landscape elevation effects the summit accessibility. In each cell, an additional elevation is added, randomly drawn from a distribution determined by the level of additional landscape variability lv (see above). We used three different levels of lv , namely 0%, 4% and 10% landscape variability and we assumed a strong response to topography ($q = 0.6$). The resulting simulated values for the summit accessibility were plotted against the values calculated with relation (3.6). For calculating the accessibility, we estimated the formulas parameter a and b again from the one-releasepoint-one summit-landscape.

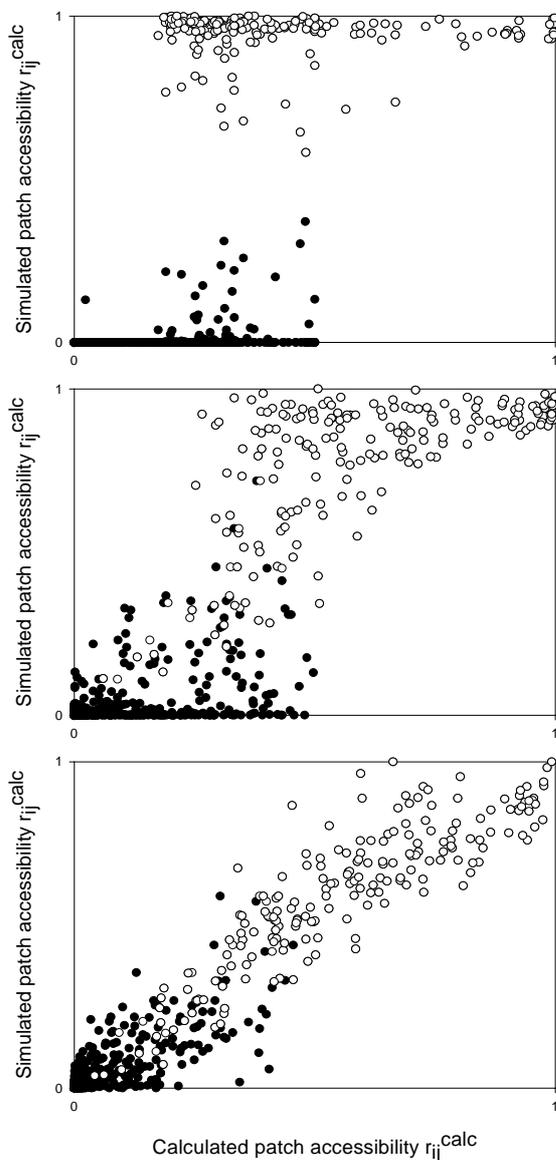


Figure 6.7 The effect of topography in landscapes with different levels of variability in landscape elevation: (a) no landscape variability ($lv = 0\%$), (b) a intermediate level of landscape variability ($lv = 4\%$), (c) high level of landscape variability ($lv = 10\%$). White dots represent values belonging the summit closest to the release point of one landscape, black dots represent all other summits in one landscape. In all simulations, we used a strong animals' response to topography ($q = 0.6$).

In Fig 6.7, the results for the three different levels of landscape variability lv can be seen. Without additional landscape variability ($lv = 0\%$), the plot results in a step function familiar from Fig. 6.6 ($r^2 = 0.37$). By adding a slight landscape variability ($lv = 4\%$), the relationship between simulated and calculated values becomes sigmoidal and the predictive power of the formula better ($r^2 = 0.80$). For a high level of landscape variability ($lv = 10\%$), we regain a linear relationship and the predictive power is high ($r^2 = 0.94$). This shows that the formula can predict the summit accessibility even for animals with strong response to topography as long as the movement occurs in a landscape with a high level of landscape variability. In such a landscape, the movement is less directed despite topography. Therefore, the competition between summits acts as it is described by the formula and the formula can predict the accessibility.

The overall study shows that the formula which has been originally developed for predicting the accessibility of patches in landscapes with homogeneous matrix can be widened to a certain extent to topographically heterogeneous landscape. As long as animals' response to topography is low or landscape variability is high, the formula can be used to predict the accessibility of patches (resp. summits). However, the formula cannot be used for predicting highly directed movements as they result from a strong response to topography in a landscape without additional landscape variability. But even in situations where the formula cannot be used for predicting, it can be taken as a reference situation to gain understanding on how certain landscape elements change patch (resp. summit) accessibility. In the study presented here, the formula helped to understand how topography influences the summit accessibility and how this summit accessibility can be predicted when a strong response to topography is considered.

1.4 Summary

We exemplarily included landscape heterogeneity in three different ways: (i) by heterogeneously sized patches, (ii) by barriers and (iii) by animals' response to a gradually changing topography. Our results showed that all the three different ways of including landscape heterogeneity effect the accessibility of patches. Consequently, this reduces the predictive power of the original formula for patch accessibility derived for landscapes where heterogeneity only occurs due to patch configuration (relation (3.6)). For most cases, however, we regained a better predictive power of the formula by discovering ways of including the respective landscape heterogeneity in our calculations. We showed that the effect of heterogeneously sized patches can be widely covered by the formula by simply

correcting for the distances between patches. The effect of a barrier in the landscape can be included in the formula by fitting and using two different potential patch accessibilities depending on the position of start patch, target patch and the barrier (Eckhardt *et al.* unpublished data). We found no way to change the formula in that respect that it can cover every effect of landscape topography (Pe'er *et al.* submitted a). Nevertheless, we were able to determine the range of parameter values for which the formula is still valid. In the range of parameter values where the formula cannot be used as tool for prediction, it still can be applied as a reference for the homogeneous case. By comparing the formula's results with the results of the simulation model, the effect of topography could be filtered. Therewith, we understood how patch accessibility can be roughly predicted in the parameter range where the formula cannot be used. We therefore showed that the formula is a useful tool for analysing the three situations of landscape heterogeneity simulated here: The formula can be either used in a modified way to predict patch accessibility or it can be at least applied for gaining a better understanding of the situation investigated.

In the investigations presented in this chapter, we examined only some specific situations of landscape heterogeneity. We still do not know how other elements of landscape heterogeneity (for example corridors (Merriam 1991, Gustafson & Gardner 1996, Haddad & Baum 1999, Berggren *et al.* 2002) change patch accessibility. Furthermore, it is an open question how patch accessibility reacts when we combine several elements of landscape heterogeneity. And lastly, in the approaches presented here, we could just provide solutions that are valid for the specific case of landscape heterogeneity investigated. In order to use the formula on a variety of heterogeneous landscapes without bothering about the source of it, we need to find ways how landscape heterogeneity can be included in the formula for patch accessibility in a more general way. These three questions are important subjects to further research.

2 How can the formula be compared with MRR-data?

So far, we compared the patch accessibility resulting from the formula with the simulation results. Doing so, we found that the formula predicted the simulated patch accessibility values with high congruence. In discussions with field ecologists, the question arose whether and how the formula's results can be compared with data from the field, namely Mark-Release-Recapture (MRR) –data widely collected for butterflies (Dowdeswell *et al.* 1949, Brakefield 1982, Wahlberg *et al.* 2002). MRR-data are collected by catching individuals in the field, marking and releasing them to recapture them again in the next time step. With this method,

ecologists can determine how far individuals move between time steps (intervals of recapture).

In order to compare such MRR-data with the results of the formula derived here, the field data have to fulfil some requirements. As these requirements can be rarely found in MRR-data, I will not perform this comparison within this thesis. Nevertheless, I would like to explain what has to be taken into account by collecting MRR-data in order to make them comparable with the formula. Furthermore, I will give some ideas, how such a comparison can be made, what the difficulties are and how they can be solved.

What kind of MRR-data are needed?

For every MRR-study, it is important that population size and observer capacity are related to each other. If the population is too small, we will not get enough data for our analysis. On the other hand, if the population size is too large, we will catch each time new individuals, but we will not recapture already marked individuals. It is also important for every MRR-study that depending on the individuals' dispersal range, the dimensions of the landscape, especially the distances between habitat patches, are in the range needed for the question.

To be able to compare MRR-data with the formula's results, two aspects are especially important when performing a MRR-study: (i) For a first comparison it would be best to have MRR-data from an as homogeneous as possible landscape, i.e. a landscape without barriers or directing elements in the matrix and with rather homogeneous patch sizes. (ii) One problem is that animals may visit many habitat patches before being recaptured. Therefore, it would be important to observe the patches in equal intervals in order to keep the rate of continued migration constant.

MRR-data collected under these circumstances can be used for a comparison with the formula. In the following, I will give first ideas how such a comparison can be made.

Comparing MRR-data with the formula: some problems

MRR-data declare how many of the individuals found at day one in patch i have been recaptured at day two in patch j . In contrast to the results of the formula and the simulation which give the probability that an emigrant starting at patch i reaches patch j , we have here some unknown factors:

(i) How many of the individuals found at day one in patch i did leave this patch (emigration rate)?

(ii) How many of the emigrated individuals did directly go to patch j , how many did go via patch k to patch j ? Or via patch j to patch k or back to patch i (rate of continued migration)? Since we cannot choose discretionary small time step, the risk that we miss movements is always present.

(iii) How many of the individuals arriving at patch j can be recaptured by the ecologist (catching rate)?

When we now compare MRR-data with the formulas results, we have to consider that our field data bear all these unknown factors, i.e. the emigration rate, the rate of continued migration and the catching rate. To make them comparable, we have to know more about the effect of these factors.

I exemplarily show for the catching rate how we can learn more about this factor. I perform a small simulation study with a virtual ecologist to demonstrate how the catching rate influences the resulting data set.

A virtual ecologist catching butterflies

Field ecologists doing MRR-studies on butterflies can never assume that they catch all individuals of the study area. Therefore, they miss some of the butterflies' movements between patches. How does this gap in data changes our result when we want to compare field data with modelling results? To tackle this question, I sent a virtual ecologist into the model developed and used in Chapter 3.

As in Chapter 3, individuals started at a patch i in a randomly generated landscape and moved through it with the loop-like movement pattern. The proportion of emigrants starting at patch i and arriving at patch j were counted. In contrast to the original simulation model, butterflies in this analysis could start again from the former target patch j to search for a new target patch. I assumed that emigrating, searching and finding of a new habitat patch happens in one time step, the emigration from this new habitat patch (and again the searching and finding) happens in the next time step. Once per time step, the virtual ecologist walks through the habitat patches and notes all the butterflies he catches. The probability that he catches a specific butterfly depends on the catching rate that can be varied in the model. I choose values of 90 % (high catching rate), 50 % (intermediate) and 20 % (low catching rate). If the ecologist catches a butterfly during one time step, he considers the current patch of the butterfly as the butterflies start patch for the next time step. If a butterfly is not caught by the ecologist at one time step, the patch where it was caught last is taken by the ecologist as the butterfly's start patch at the next time step. This procedure obviously bears the risk of getting

a bias in data. However, if all data where the actual start patch is exactly known were omitted data sets would become very small. Therefore, this procedure of assuming the patch where the butterfly was found last as start patch is usually practised. On the basis of the ecologist's observations the patch accessibility values were calculated and compared with the simulated patch accessibility values based on all data.

The simulation is done for one landscape with 10 patches, releasing in the beginning 1000 individuals per patch.

In Fig. 6.8, the simulated patch accessibility assessed by the ecologist (white dots) with different catching rates and the simulated patch accessibility determined by the complete knowledge of movements are plotted against the distance (Fig. 8a, 8c, 8e) and against the patch accessibility calculated by relation (3.6) (Fig. 8b, 8d, 8f). Data are presented as mean over all time steps.

By comparing the ecologists patch accessibility with the complete patch accessibility, we can see the following:

For small and intermediate distances (respective high and intermediate calculated accessibility values), the patch accessibility determined by the ecologist is lower than the patch accessibility determined on the basis of all movements. This effect strongly increases with decreasing catching rate. Both data sets, the complete data as well as the ecologist's data increase linearly with increasing calculated patch accessibility, but with a flatter slope. Therefore, the differences between the ecologist's results and the real results increase with increasing calculated patch accessibility.

For large distances (and therefore small calculated accessibility values), a few data points of the ecologist exceed the real patch accessibility data (this can be especially well seen at the simulated values vs. distance plots). This may be due to the fact that the ecologist missed the patches which were visited by the butterfly in between the seen start patch and the seen target patch. However, this effect is difficult to determine, because also some of the real simulated patch accessibility values fitted less good to the calculated patch accessibility data than in former figures. This can be explained as follows: At the beginning of the simulation 1000 individuals were released per start patch. After some time steps, the distribution of individuals changes completely depending of the accessibility of a patch: patches with a high accessibility may have more than 1000 emigrating individuals, while patches with low accessibility may have only a few starting individuals. Furthermore, some individuals die between time steps. Therefore, the statistic becomes worse after some time steps, since the sample size decreases.

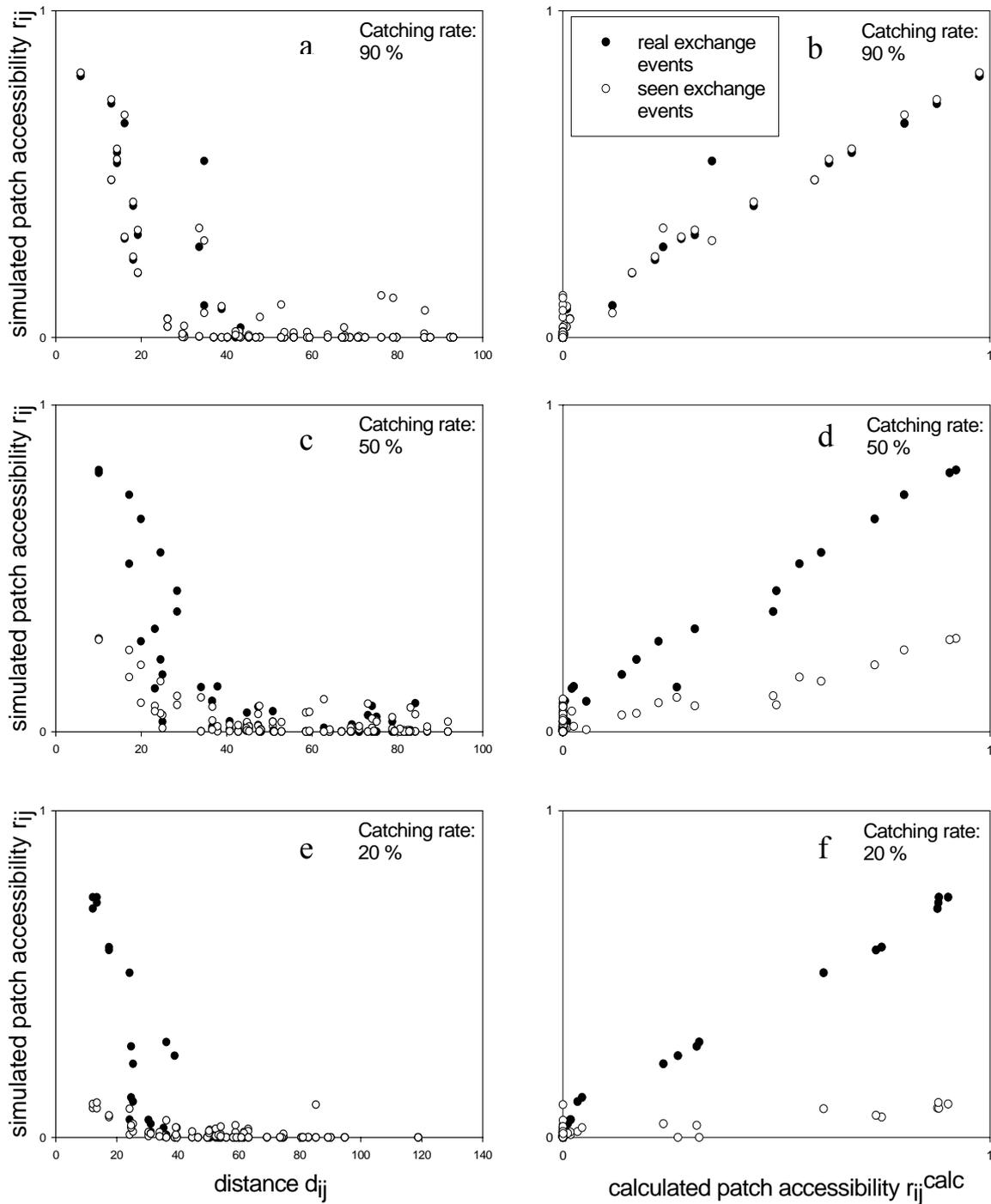


Figure 6.8 The simulated patch accessibility versus the distance (Fig. 6.8a, 6.8c, 6.8e) and versus the calculated patch accessibility (Fig. 6.8b, 6.8d, 6.8f). Black dots indicate that all exchange events between patches can be seen. White dots indicate that the ecologist caught only some of the individuals according to the catching rate (90 % (Fig. 6.8a and 6.8b), 50 % (Fig. 6.8c and 6.8d) and 20 % (Fig. 6.8e and 6.8f)) and therefore saw not all exchange events between patches.

We have seen how the catching rate influences the resulting patch accessibility data. Since the most important effect of the catching rate can be clearly identified, we should be able to identify these effects in the MRR-data as well. By means of the analysis, we can also estimate the strengths of the error due to catching rate. For the case that the catching rate can be estimated from field observations (for example Hanski *et al.* 2000) this intention would be even more feasible.

This analysis gives also a first idea how the catching rate can be included into the formula in order to compare it with field data. Since the analysis showed that there is still a linear relationship between calculated patch accessibility and the patch accessibility found by the ecologist, we can include the catching rate by multiplying a simple prefactor with the original formula (relation (3.6)):

$$r_{ij}^{MRR} = c * r_{ij} \quad (6.3)$$

with c being the catching rate.

With this additional parameter for the catching rate, the formula could be fitted to field data. Note, that we assumed one catching rate to be valid for the whole landscape. One could also assume that the catching rate depends on the patch (that, for example, the vegetation of one patch is more open and therefore the rate of catching higher than in another patch). Then the parameter c has to be replaced by a parameter c_j .

This analysis is only a first rough idea of how the formula can be related to appropriate field data. Further work is now needed to transfer theory into praxis.

3 Dispersal behaviour and the metapopulation's patch incidence

In the model used in Chapter 5, we assessed metapopulation viability of landscapes by determining the mean metapopulation lifetime T_m . In the field, metapopulation viability is often determined by using the incidence pattern of patches (Hanski 1994). The patch incidence gives the probability of a patch being occupied by a subpopulation. It is an indicator of the role a patch plays within the landscape: most important to metapopulation persistence are those patches with a high incidence. The patch incidence also indicates the importance of a certain connectivity pattern (Frank *et al.* 2002).

We have seen in Chapter 5 that the mean metapopulation lifetime T_m of a landscape depends strongly on the movement pattern of dispersing animals. We did not investigate whether the movement pattern also effects the incidence of patches. Does the patch incidence pattern change if we assume different underlying movement patterns? And do patch incidence and

the mean metapopulation lifetime react in the same way, allowing to conclude from the reaction of one to the reaction of the other? I address this question here exemplarily on two of the landscapes used in Chapter 5.

We obtain the patch incidence by the analysis described in Chapter 5 (Section 2), inserting colonisation rates according to movement pattern and landscape in META-X (Frank *et al.* 2002) and running the simulation. I used the same four movement patterns as in Chapter 5, (loops, uncorrelated random walk, fairly correlated random walk and correlated random walk) and the same 10 randomly generated landscapes. The incidence of patches is calculated by META-X by dividing the number of years a patch is occupied by the total number of years for which the patch is observed.

By the way of an example, I pick up here two of the 10 landscapes which demonstrate two extremes in the way their patch incidence pattern and T_m react to different movement pattern, namely Landscape 9 (Chapter 5, Section 3.1) and Landscape 6 (Chapter 5, Section 3.1). In Fig. 6.9, we can see the incidence pattern of these landscapes assuming different underlying movement patterns.

The patch incidence pattern of Landscape 9 is the same for different underlying movement patterns, only the magnitude of values changes. Nevertheless, as we have seen in Chapter 5 (Figure xy), this landscape shows an extreme shift regarding its landscape ranks: While Landscape 9 is one of the landscapes with the highest mean metapopulation lifetime T_m if we assume uncorrelated and correlated random walk, it has one of the lowest T_m if loops or fairly correlated random walk are taken as underlying movement pattern. Landscape 6, in contrast, shows a strong shift in the patch incidence pattern for different dispersal behaviours. For example, Patch 6 of this landscape has a relatively low incidence for correlated random walk, but a high incidence for all other movement patterns. As another example, Patch 2 has a higher incidence than Patch 1 and Patch 3 if the loops are taken as dispersal behaviour, but a lower incidence as those patches for all other movements. Unlike the incidence pattern, the landscape rank of Landscape 6 regarding T_m changes only slightly (Chapter 5, Figure xy).

These examples show that the landscape ranking regarding T_m can stay constant, while the patch incidence patterns exhibit large shifts for different movement patterns, or reverse. Therefore, it is impossible to draw conclusions from the reaction of the patch incidence to the reaction of the mean metapopulation lifetime or the other way around.

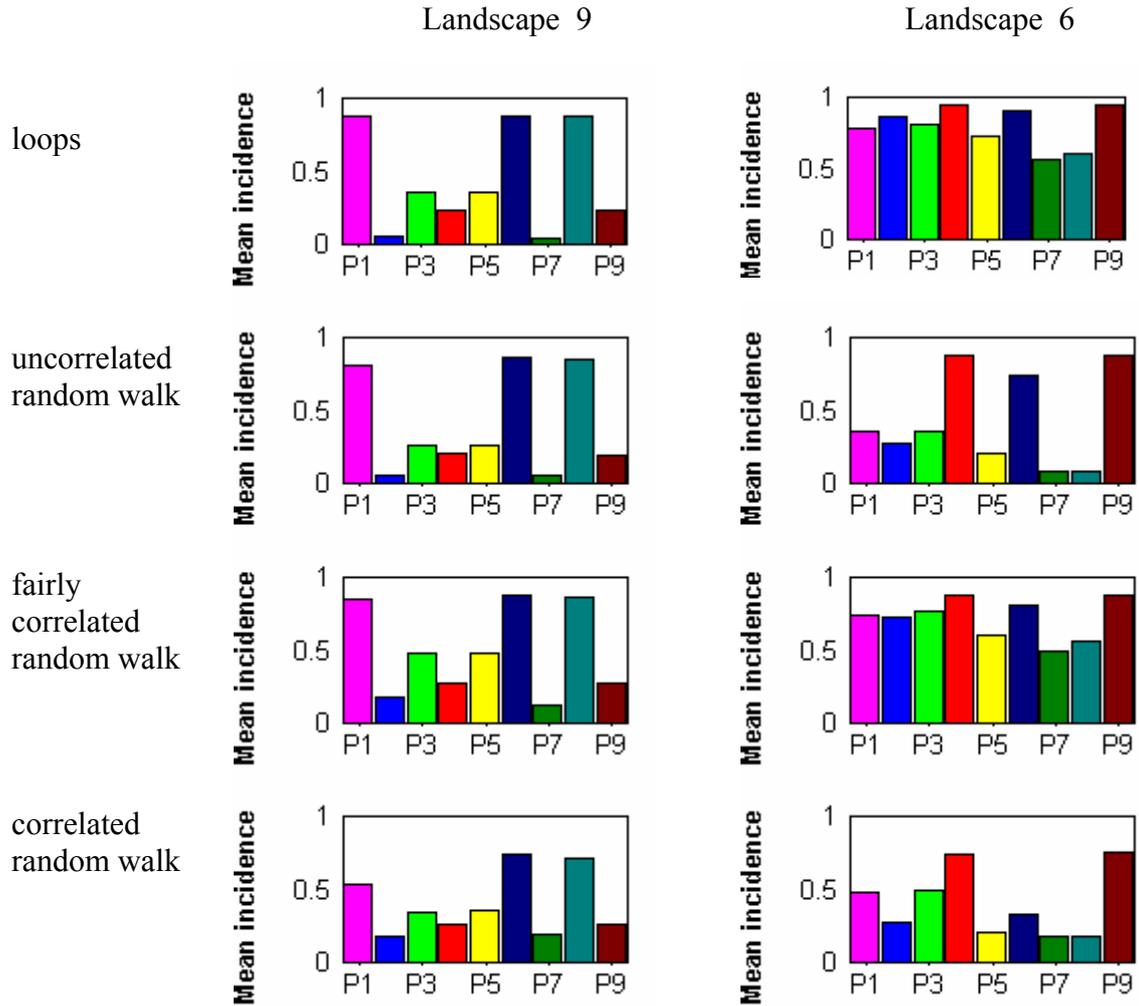
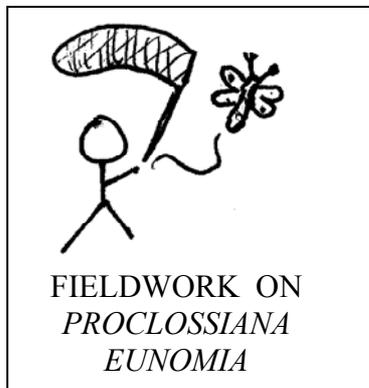


Figure 6.9 The patch incidence pattern of landscape 9 and landscape 6 (for landscape configuration see chapter 5, Figure xy) for different dispersal behaviours: while the incidence pattern of landscape 9 does not change between the movement patterns, that of landscape 6 varies noticeable.

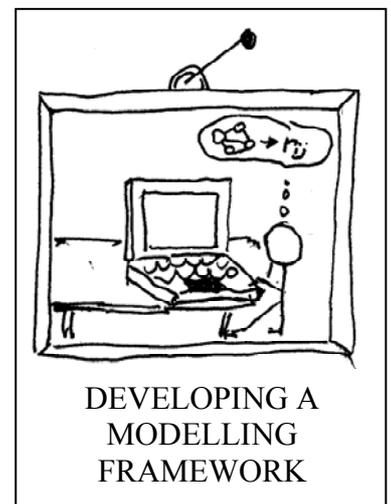
T_m and the patch incidence pattern are both used as measure for metapopulation persistence. While we already roughly understood how T_m reacts to different landscapes and dispersal behaviours (Chapter 5), the reaction of the incidence is not yet clear. Here, further investigations are needed to understand the reaction of the patch incidence for different movement patterns. This could also help in finding some connection between the reaction of T_m and the reaction of the patch incidence in order to be able to conclude from one to the other.

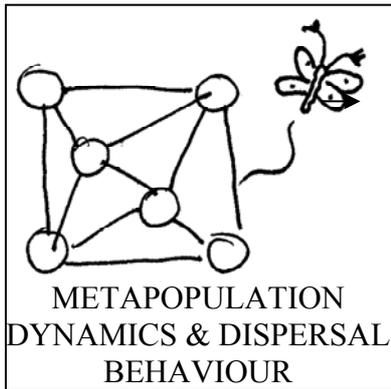
Overview over the central results



- To get an impression about individual movement behaviour, we performed a field experiment on the movement of the bog fritillary butterfly *Proclossiana eunomia*.
- Butterflies were found to orient towards a habitat patch from at least 100 m away.
- Most of the paths of the individual butterflies display a dispersal pattern different from random walk
- Different individuals of the same species can exhibit different movement patterns.

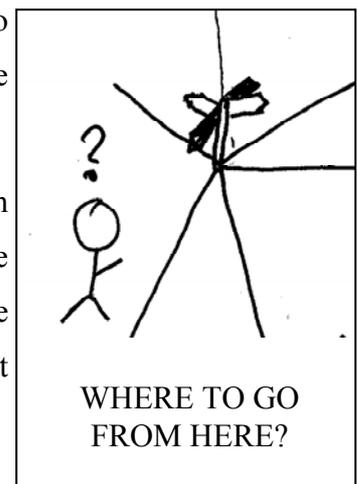
- To investigate the effect of dispersal in fragmented landscapes on patch accessibility (the probability of a certain patch being reached by individuals starting at another patch), we developed an individual based simulation model for simulating different landscape configurations and dispersal behaviours.
- Our model analyses show that competition between patches for migrants is an intrinsic consequence of dispersal in multi-patch landscapes and has an important effect on patch accessibility.
- As a key result of this thesis, we derived a formula for the patch accessibility. This formula is structurally simple, but covers important effects such as the competition between patches for migrants. It was found to predict the patch accessibility for a variety of movement patterns. The formula can be integrated in other models and used for further analyses.
- We found fitting functions for the functional relationships between the parameters of the formula and several details of the movement behaviour. We derived measures for an ecological interpretation of these relationships.





- We incorporated the formula for patch accessibility in a stochastic metapopulation model to analyse the effect of dispersal behaviour on metapopulation viability.
- We found that ranking orders among landscapes regarding the viability of the hosted metapopulation change when different dispersal behaviours are assumed. This has implications for metapopulation theory, modelling and management.
- The competition between patches for migrants is an important factor driving the shift in landscape ranks.
- When analysing the effect of the landscape structure on metapopulation viability, the individuals' dispersal behaviour has to be incorporated in an adequate way.
- The parameters of the patch accessibility formula can be used for a classification of dispersal behaviours which result in the same landscape ranks.

- We analysed the applicability of the formula for the patch accessibility to situations with additional sources of landscape heterogeneity.
- We found correction terms with which the formula can be applied to landscapes with heterogeneously sized patches or barriers in the landscape matrix.
- Given topographical heterogeneity, the formula was found to work in the case of weak individuals' response to topography or moderate landscape noise. In all other cases, the formula loses its predictive power, but still codes important information on the resulting movement patterns.
- We give first ideas how the formula can be compared with field data.
- By comparing incidence pattern and mean lifetime of metapopulations, different sensitivities to the dispersal behaviour were found. This indicates that incidence patterns are of limited use as measure for (stochastic) metapopulation persistence.



References

- Adler FR & Nuernberger B (1994) Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45: 41-75.
- Anderson GS & Danielson BJ (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.
- Angelibert S & Giani N (2003) Dispersal characteristics of three odonate species in a patchy habitat. *Ecography* 26: 13-20.
- Armsworth PR, James MK & Bode L (2001) When to press on or turn back: Dispersal strategies for reef fish larvae. *American Naturalist* 157: 434-450.
- Baars MA (1979) Patterns of Movement of Radioactive Carabid Beetles. *Oecologia* 44: 125-140.
- Baguette M & Nève G (1994) Adult movements between populations in the specialist butterfly *Proclissiana eunomia* (Lepidoptera, Nymphalidae). *Ecological Entomology* 19: 1-5.
- Baguette M, Convie I & Nève G (1996) Male density affects female spatial behaviour in the butterfly *Proclissiana eunomia*. *Acta Oecologica* 17: 225-232.
- Baguette M, Vansteenwegen C, Convi I & Nève G (1998) Sex-biased density-dependent migration in a metapopulation of the butterfly *Proclissiana eunomia*. *Acta Oecologica* 19: 17-24.
- Baguette M, Petit S & Queva F (2000) Population spatial structure and migration of three butterfly species within the same habitat network: consequences for conservation. *Journal of Applied Ecology* 37: 100-108.
- Baguette M, Mennechez G, Petit S & Schtickzelle N (2003) Effect of fragmentation on dispersal in the butterfly *Proclissiana eunomia*. *Comptes Rendus Biologies* 326: S200-S209.
- Batschelet E (1981) Circular statistics in biology. Academic Press, New York.

- Begon M., Harper JL & Townsend CR (1990) Ecology: individuals, populations and communities. Blackwell Scientific Publ., London.
- Bell WJ (1985) Source of information controlling motor pattern in arthropod local search orientation. *Journal of Insect Physiology* 31: 837-847.
- Bell WJ (1991) Searching behaviour. Chapman & Hall, London.
- Bender DJ, Tischendorf L & Fahrig L (2002) Using patch isolation metrics to predict animal movement in binary landscapes. *Landscape Ecology* 18:17-39.
- Berggren A, Carlson A & Kindvall O (2001) The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets *Metrioptera roeseli*. *Journal of Animal Ecology* 70: 663-670.
- Berggren A, Birath B & Kindvall O (2002) Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). *Conservation Biology* 16: 1562-1569.
- Bink FA (1992) Ecologische Atlas van de Dagvlinders van Noordwest-Europa. Schuyt, Haarlem.
- Brakefield PM (1982) Ecological studies on the butterfly *Maniola jurtina* in Britain. I. Adult behaviour, microdistribution and dispersal. *Journal of Animal Ecology* 51: 713-726.
- Cain ML (1985) Random search by herbivorous insects: a simulation model. *Ecology* 66: 876-888.
- Burgess RL & Sharpe DM (1981) Forest island dynamics in man-dominated landscapes. New York, Springer.
- Conradt L, Bodsworth EJ, Roper TJ & Thomas CD (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 TJ & Thomas CD (2001) Dispersal behaviour of individuals in metapopulations of two British butterflies. *Oikos* 95: 416-424.
- Conradt L, Zollner PA, Roper TJ, Frank K & Thomas CD (2003) Foray search: an effective systematic dispersal strategy in fragmented landscapes. *American Naturalist* 161 (6): 905-915.

- Crist TO, Guertin DS, Wiens JA & Milne BT (1992) Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Funct. Ecol.* 6: 536-544.
- Den Boer PJ (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18: 165-194.
- Den Boer PJ (1970) On the significance of dispersal power for populations of carabid-beetles (*Coleoptera, Carabidae*). *Oecologia* 4: 1-28.
- Doak DF, Marino PC & Kareiva PM (1992) Spatial scale mediates in influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* 41: 315-336.
- Dover JW (1996) Factors affecting the distribution of satyrid butterflies on arable farmland. *Journal of Applied Ecology* 33: 723-734.
- Dowdeswell WH, Fisher RA & Ford EB (1949) The Quantitative Study of Populations in the Lepidoptera. *Heredity* 3: 67-84.
- Drechsler M & Wissel C (1997) Separability of local and regional dynamics in metapopulations. *Theor. Popul. Biol.* 51: 9-21.
- Drechsler M (2000) A model-based decision aid for species protection under uncertainty. *Biological Conservation* 94: 23-30.
- Durier V & Rivault C (1999) Path integration in cockroach larvae, *Blattella germanica* (L.) (insect: Dictyoptera): Direction and distance estimation. *Animal Learning & Behaviour* 27: 108-118.
- Dusenbery DB (1989) Ranging strategies. *Journal of Theoretical Biology* 136: 309-316.
- Dusenbery DB (1992) Sensory ecology: how organisms acquire and respond to information. W. H. Freeman, New York.
- Ebert G (1991) Die Schmetterlinge Baden-Württembergs. Verlag Eugen Ulmer, Stuttgart.
- Eckhardt W, Frank K & Heinz SK (work in progress) The effect of barriers on the formula for the patch accessibility.
- Efron B & Tibshirani R (1993) An Introduction to the Bootstrap. Chapman & Hall, London.

- Endler JA (1977) Geographic variation, speciation and clines. Princeton University Press, Princeton, N.J.
- Etienne AS, Maurer R, Berlie J, Reverdin B, Rowe T, Georgakopoulos J & Seguinot V (1998) Navigation through vector addition. *Nature* 396: 161-164.
- Etienne RS & Hesterbeck JAP (2001) On optimal size and number of reserves for metapopulation persistence. *Journal of Theoretical Biology* 203: 33-50.
- Fahrig L (1988) A general model of population in patchy habitats. *Applied Mathematics and Computation* 27: 53-66.
- Fahrig L (1992) Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* 41: 300-314.
- Fisher NI (1993) Statistical analysis of circular data. CUP, 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.
- Frank K, Lorek H, Koester F, Sonnenschein M, Wissel C & Grimm V (2002) META-X: Software for Metapopulation Viability Analysis. Springer, Berlin, Heidelberg, New York.
- Frank K (2004) Ecologically differentiated rules of thumb for habitat network design: lessons from a formula. *Biodiversity and Conservation* 13: 189-206.
- Frank K (submitted to American Naturalist) Extinction thresholds in metapopulations: lessons about the effect of stochasticity.
- Gillman M & Hails R (1997) An introduction to ecological modelling: putting practice into theory. Blackwell Science, Oxford.
- Gilpin M & Hanski I (1991) Metapopulation dynamics: empirical and theoretical investigations. London, Academic Press.
- Goodwin BJ & Fahrig L (2002) Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*. *Canadian Journal of Zoology* 80: 24-35.

- Gustafson EJ & Gardner RH (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77: 94-107.
- Haddad NM (1999) Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications* 9: 612-622.
- Haddad NM & Baum KA (1999) An experimental test of corridor effects on butterfly densities. *Ecological Applications* 9: 623-633.
- Hanski I (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151-162.
- Hanski I & Thomas CD (1994) Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation* 68: 167-180.
- Hanski I, Kuussaari M & Nieminen M (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* 75: 747-762.
- Hanski I, Moilanen A, Pakkala T & Kuussaari M (1996) The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Conservation Biology* 10: 578-590.
- Hanski IA & Gilpin ME (1997) *Metapopulation biology: ecology, genetics, and evolution*. San Diego, London, Academic Press.
- Hanski I, Alho J & Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* 81: 239-251.
- Hanski I & Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. *Nature* 404: 755-758.
- Harrison S, Murphy DD & Ehrlich PR (1988) Distribution of the Bay Checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *American Naturalist* 132: 360-382.
- Harrison S (1989) Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. *Ecology* 70: 1236-1243.
- Harrison S & Quinn JF (1989) Correlated environments and the persistence of metapopulations. *Oikos* 56: 1-6.

- Heinz SK, Conradt L, Wissel C & Frank K (in press) Dispersal behaviour in fragmented landscapes: Deriving a practical formula for the patch accessibility. *Landscape Ecology*.
- Hess GR (1996) Linking extinction to connectivity and habitat destruction in metapopulation models. *American Naturalist* 148: 226-236.
- Hill JK, Thomas CD & Lewis OT (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. *Behavioural Ecology and Sociobiology* 13: 93-106.
- Huffaker CB (1958) Experimental studies of predation: Dispersal factors and predator-prey oscillation. *Hilgardia* 27: 343-383.
- Ims RA & Yoccoz NG (1997) Studying transfer processes in metapopulations: emigration, migration and colonization. –In: Hanski IA and Gilpin ME (eds), *Metapopulation biology: ecology, genetics, and evolution*, San Diego, London, Academic Press, p. 247-266.
- Johst K, Brandl R & Eber S (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos* 98: 263-270.
- Jonsen ID, Bouchier RS & Roland J (2001) The influence of matrix habitat on *Aphthona* flea beetle immigration to leafy spurge patches. *Oecologia* 127: 287-294.
- Kareiva PM & Shigesada N (1983) Analyzing insect movement as a correlated random walk. *Oecologia* 56: 234-238.
- Keitt TH, Urban DL & Milne BT (1997) Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1: 4.
- King AW & With KA (2002) Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling* 147: 23-39.
- 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.
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.*, 15: 237-240.

Levins R (1970) Extinction. –In: Gerstenhaber M (ed), Some mathematical questions in biology, American Mathematical Society, Providence, Rhode Island, p 75-107.

Lima SL & Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11: 131-135.

Lindenmayer DW & Possingham HP (1996) Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using Population Viability Analysis. *Conservation Biology* 10: 1-18.

Matter SF & Roland J (2002) An experimental examination of the effect of habitat quality on the dispersal and local abundance of *Parnassius smintheus*. *Ecological Entomology* 27: 308-316.

Menzel R, Geiger K, Chittka L, Joerges J, Kunze J & Muller U (2001) The knowledge base of bee navigation. *Journal of Experimental Biology* 199: 141-146.

Merriam G (1988) Landscape dynamics in farmland. *Trends in Ecology & Evolution* 3:16-20.

Merriam G (1991) Corridors and connectivity: animal populations in heterogeneous environments. - In: Saunders DA & Hobbs RJ (eds.), Nature conservation 2: the role of corridors. Surrey Beatty & Sons, pp. 133-142.

McIntyre NE & Wiens JA (1999) Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecol.* 14: 437-447.

Morales JM & Ellner SP (2002) Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology* 83: 2240-2247.

Motulsky H & Christopoulos, A (2003) Fitting Models to Biological Data using Linear and Nonlinear Regression, GraphPad Software Inc., San Diego, CA

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

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

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

- Odendaal FJ, Turchin P & Stermitz FR (1989) Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). *Oecologia* 78: 283-288.
- Okubo A (1980) Diffusion and ecological problems: mathematical models. Springer-Verlag, Berlin, Heidelberg, New York.
- Opdam P (1990) Dispersal in fragmented populations: the key to survival. – In: Bunce RGH and Howard DC (eds), Species dispersal in agricultural habitats, Belhaven Press, London; New York, p 3-17.
- Ovaskainen O & Hanski I (2004) Metapopulation dynamics in highly fragmented landscapes. – In: Hanski I & Gaggiotti O (eds), Ecology, Genetics, and Evolution in Metapopulations, Academic Press (in press).
- Possingham HP, Ball IR, Andelman S (2000) Mathematical models for reserve design. - In: Ferson S, Burgman M (eds.) Quantitative Methods for Conservation Biology, pp. 291-306 Springer-Verlag, New York
- Quinn JF & Hastings A (1987) Extinction in subdivided habitats. *Conservation Biology* 1: 198-208.
- Pe'er G, Saltz D, Thulke H & Motro U (submitted to Animal Behaviour) Response mechanisms to topography in a hilltopping butterfly and implications for modelling non-random dispersal.
- Pe'er G, Heinz SK & Frank K (submitted) Movements in heterogeneous landscapes: analyzing the effect of topography.
- Petit S, Moilanen A, Hanski I & Baguette M (2001) Metapopulation dynamics of the bog fritillary butterfly: movements between habitat patches. *Oikos* 92: 491-500.
- Pither J & Taylor PD (1998) An experimental assessment of landscape connectivity. *Oikos* 83: 166-174.
- Pretscher P (1998) Rote Liste der Großschmetterlinge (Macrolepidoptera). – In: M. Binot, R. Bless, P. Boye, H. Gruttke & P. Pretscher (eds), Rote Liste gefährdeter Tiere Deutschlands. - Schriftenreihe für Naturschutz und Landschaftspflege, Heft 55, pp. 87-111.

- Pulliam HR, Dunning JB & Liu J (1992) Population dynamics in complex landscapes: a case study. *Ecological Applications* 2: 165-177.
- Ricketts TH (2001) The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist* 158: 87-99.
- Ries L & Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *Journal of Animal Ecology* 70: 840-852.
- Roitberg BD & Mangel M (1997) Individuals on the landscape: behavior can mitigate landscape differences among habitats. *Oikos* 80: 234-240.
- Roland J, Keyghobadi N & Fownes S (2000) Alpine Parnassius butterfly dispersal: Effects of landscape and population size. *Ecology* 81: 1642-1653.
- Ruckelshaus M, Hartway C & Kareiva P (1997) Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology* 11: 1298-1306.
- Schstickzelle N & Baguette M (2003) Behavioral responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationship in fragmented landscape. *Journal of Animal Ecology* 72: 533-545.
- Schstickzelle, N & Baguette M (in press) Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. *Oikos*.
- Schultz CB & Crone EE (2001) Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82: 1879-1892.
- Settele J, Feldmann R & Reinhardt R (2000) Die Tagfalter Deutschlands. Verlag Eugen Ulmer, Stuttgart.
- Shields O (1967) Hilltopping: An ecological study of summit congregation behavior of butterflies on a southern California hill. *The Journal of research on the Lepidoptera* 6: 69-178.
- Stelter C, Reich M, Grimm V & Wissel C (1997) Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryodemus tuberculata*. *J. Anim. Ecol.* 66: 508-518.
- Taylor PD, Fahrig L, Henein K & Merriam G (1993) Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.

- Tischendorf L, Bender DJ & Fahrig L (2003) Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology* 18:41-50.
- Thomas CD (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London B* 267: 139-145.
- Tischendorf L (2001) Can landscape indices predict ecological processes consistently? *Landscape Ecology* 16: 235-254.
- Turchin P (1998) Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland.
- Vandermeer J & Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. *American Naturalist* 158: 211-220.
- Verboom J, Metz JAJ & Meelis E (1993) Metapopulation models for impact assessment of fragmentation. - In: Vos CC & Opdam P (eds.), *Landscape ecology of a stressed environment*. Chapman & Hall, pp. 172-192.
- Vos CC, Verboom J, Opdam PFM & Ter Braak CJF (2001) Toward ecologically scaled landscape indices. *American Naturalist* 157: 24-41.
- Wahlberg N, Klemetti T, Selonen V & Hanski I (2002) Metapopulation structure and movements in five species of checkerspot butterflies. *Oecologia* 130: 33-43.
- Weaver JL, Paquet PC & Ruggiero LF (1996) Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10: 964-976.
- Wehner R, Michel B & Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. *The Journal of Experimental Biology* 199: 129-140.
- Wiens JA, Stenseth NCV & Ims RA (1993) Ecological mechanisms and landscape ecology. *Oikos* 66: 369-380.
- Wiens JA, Schooley RL & Weeks RD (1997) Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78: 257-264.
- Wiens JA (1997) Metapopulation Dynamics and Landscape Ecology. -In: Hanski IA and Gilpin ME (eds), *Metapopulation biology: ecology, genetics, and evolution*, San Diego, London, Academic Press, p. 43-60.

- Wilcove DS, McLellan CH & Dobson AP (1986) Habitat fragmentation in the temperate zone. –In: M. E. Soule (ed), Conservation biology : the science of scarcity and diversity. Sinauer, Sunderland, Mass, pp. 237-256.
- With KA, Gardner RH & Turner MG (1997) Landscape connectivity and population distribution in heterogeneous environments. *Oikos* 78: 151-169.
- With KA & King AW (1999) Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. *Landscape Ecology* 14: 73-82.
- Wright S (1940) Breeding structure of populations in relation to speciation. *American Naturalist* 74: 232-248.
- Wolfenbarger DO (1949) Dispersion of small organisms. *American Midland Naturalist* 35: 1-152.
- Wolfram S (1991) Mathematica: a system for doing mathematics by computer. Addison-Wesley, New York.
- Yeomans SR (1995) Water-finding in adult turtles: random search or oriented behaviour? *Animal Behaviour* 49: 977-987.
- Zar JH (1999) Biostatistical Analysis. Prentice Hall, Upper Saddle River.
- Zollner PA & Lima SL (1997) Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80: 51-60.
- Zollner PA & Lima SL (1999a) Illumination and the perception of remote habitat patches by white-footed mice. *Animal Behaviour* 58: 489-500.
- Zollner PA & Lima SL (1999b) Search strategies for landscape-level interpatch movement. *Ecology* 80: 1019-1030.
- Zollner PA (2000) Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* 15: 523-533.

Zusammenfassung

Die Überlebensfähigkeit von Populationen in fragmentierten Landschaften hängt maßgeblich von der Fähigkeit der Individuen ab, sich zwischen Habitatfragmenten bewegen zu können. Teilhabitate, in denen eine Population ausgestorben ist, können durch die Ausbreitung von Individuen wieder besiedelt werden. Dadurch kann eine Art regional überleben, obwohl die einzelnen Teilpopulationen einem hohen Aussterberisiko ausgesetzt sind. Das Konzept, dass verschiedene, vom Aussterben bedrohte Teilpopulationen durch gegenseitige Wiederbesiedlung eine überlebensfähige Gesamtpopulation bilden, nennt man Metapopulationskonzept.

Für die Überlebensfähigkeit einer Metapopulation ist es nicht nur wichtig, dass ein migrierendes Individuum irgendein neues Habitat erreicht, sondern auch welches Habitat es erreicht. Um es aus der Habitat-Perspektive zu formulieren: es ist entscheidend, mit welcher Wahrscheinlichkeit ein bestimmtes Habitat j von einem Emigranten erreicht wird, der von einem anderen Habitat i startet (Erreichbarkeit eines Habitates). Ob ein Individuum ein bestimmtes Habitat erreicht, hängt von der Landschaftsstruktur und dem Ausbreitungsverhalten des Individuums ab. Letzteres ist besonders wichtig bei Tieren, die sich aktiv durch die Matrix, den Raum zwischen den Habitaten, bewegen können. Den Weg, den ein Tier durch die Matrix nimmt, kann von einer Reihe von Faktoren abhängen: von Landschaftselementen, welche die Wanderung der Tiere durch die Landschaft erleichtern (Korridore) oder aufhalten (Barrieren), von der Wahrnehmung des Tieres, die es ihm ermöglicht, sich gezielt in Richtung des Habitates zu bewegen (Wahrnehmungshorizont), oder auch von einer dem Tier eigenen Suchstrategie, mit der es die Umgebung systematisch nach Habitaten absucht. Ein solches aktives Ausbreitungsverhalten kann die Erreichbarkeit der Habitate und damit die Überlebensfähigkeit der Metapopulation deutlich beeinflussen.

Diese Arbeit beschäftigt sich damit, wie sich das Ausbreitungsverhalten von Individuen auf die Überlebensfähigkeit von Metapopulationen auswirkt. Ein großes Problem dabei besteht darin, wie man diesen Effekt auf einfache Weise analysieren kann. Um die Konsequenzen von Ausbreitung auf die Überlebensfähigkeit einer Metapopulation bestimmen zu können, werden häufig Modelle verwendet. Damit solche Modelle verständlich bleiben, werden die Prozesse, welche die Metapopulation beeinflussen, möglichst einfach dargestellt. Ausbreitung wird in der Regel als zufällige, diffusionartige Bewegung angenommen. Systematische Suchstrategien oder die Existenz eines Wahrnehmungshorizontes werden nicht oder nur grob

berücksichtigt. Deshalb wird in dieser Arbeit mit Hilfe eines Simulationsmodells ein Modellerrahmen entwickelt, mit dem das individuelle Ausbreitungsverhalten detailliert genug, aber doch strukturell einfach in Modellen dargestellt werden kann. Dieser Modellerrahmen wird dann in ein existierendes Metapopulationsmodell eingesetzt, um zu analysieren, wie das Ausbreitungsverhalten auf die Überlebensfähigkeit der Metapopulation wirkt. Der Entwicklung des Modellerrahmens ist eine Freilanduntersuchung vorangestellt, die anhand einer Fallstudie zeigt, wie sich Tiere in der Matrix bewegen.

Die Arbeit besteht aus 3 Teilen, die unabhängig voneinander lesbar sind. Im ersten Teil wird untersucht, wie sich Tiere in der Matrix bewegen. Der Randring-Perlmutterfalter, *Proclossiana eunomia*, wird als Beispiel herangezogen, um nicht nur zu zeigen, wie sich dieser Schmetterling ausbreitet, sondern auch, wie man das Ausbreitungsverhalten von Individuen messen und analysieren kann. Dafür wurden Individuen in der Matrix freigelassen und ihr Weg auf der Suche nach einem Habitat festgehalten. Zwei Fragen standen hierbei im Vordergrund: (i) Wie groß ist die Distanz, von der aus *P. eunomia* Habitate entdecken kann? (ii) Bewegt sich *P. eunomia* zufällig in der Matrix oder benutzt der Schmetterling eine systematische Suchstrategie? Die zweite Frage wurde analysiert, in dem das beobachtete Verhalten mit einem Modell für "correlated random walk" (korreliertem Zufallslauf) verglichen wurde. Die Ergebnisse zeigen, dass *P. eunomia* sich in der Matrix aus einer Distanz von mindestens 100 m in Richtung des Habitates orientieren konnte. Einige Pfade der Individuen konnten mit dem "correlated random walk"-Modell beschrieben werden, während die meisten nicht damit beschrieben werden können. Das zeigt, dass sich verschiedene Individuen einer Art unterschiedlich ausbreiten können. Da Wahrnehmungshorizont und Ausbreitungsstrategie die Erreichbarkeit von Habitaten und damit die Überlebensfähigkeit von Metapopulation beeinflussen können, ist es wichtig, dass man das Ausbreitungsverhalten auch für andere Arten näher untersucht und in Metapopulationsmodellen detaillierter berücksichtigt.

Der zweite Teil handelt davon, wie der Effekt von individuellem Ausbreitungsverhalten in Metapopulationsmodellen analysiert werden kann. Im ersten Kapitel des Teils wird die Frage behandelt, ob und wie die Wechselwirkung von individuellem Ausbreitungsverhalten und Landschaftsstruktur auf die Erreichbarkeit von Habitaten in eine einfache Formel gefasst werden kann. Um den Effekt dieser beiden Faktoren auf die Erreichbarkeit untersuchen zu können, wurde ein Simulationsmodell entwickelt. Die Modellanalyse zeigte, dass es einen

wichtig intrinsischen Effekt der Wechselwirkung zwischen Ausbreitungsverhalten und Landschaftsstruktur auf die Erreichbarkeit gibt: wenn Migranten im ersten Habitat bleiben, das sie erreichen, konkurrieren die Habitate effektiv um Migranten. Außerdem gelang es uns, eine Formel für die Erreichbarkeit zu entwickeln. Diese Formel ist sehr einfach, kann aber dennoch die wichtigen Effekte aus dem Wechselspiel zwischen Ausbreitungsverhalten und Landschaftsstruktur, wie die Konkurrenz um Migranten, abdecken. Dies geschieht dadurch, dass sie nicht nur die Distanzen zwischen Starthabitat und Zielhabitat mit einbezieht, sondern auch die Distanzen zwischen dem Starthabitat und allen anderen Habitaten in der Landschaft. Die Formel zeigt eine hohe Vorhersagekraft für verschiedene Bewegungsmuster (Random walk mit verschiedenen Korrelationsgraden, Archimedische Spiralen, Schleifen) in jeder Landschaft mit homogener Matrix. Die Formel kann für verschiedene Zwecke genutzt werden: als Denkhilfe, um strukturelle Einsichten in die Konsequenzen des Ausbreitungsverhaltens zu bekommen, als Ausbreitungsfunktion in Metapopulationsmodellen zu weiterführenden Analysen und als Werkzeug zur Vorhersage von Austauschraten zwischen Habitaten im Naturschutz.

Im zweiten Kapitel des zweiten Teils wird der Effekt von verschiedenen Bewegungsparametern auf die Formel untersucht. Das Verhältnis zwischen den aggregierten Parametern der Formel und den relevanten Details des Ausbreitungsverhaltens wird analysiert. Mit Hilfe des individuenbasierten Simulationsmodells wurden Fitfunktionen für den funktionellen Zusammenhang zwischen den Formelparametern und verschiedenen Details des Ausbreitungsverhaltens entwickelt. Zusätzlich wird eine ökologische Interpretation dieses Zusammenhangs gegeben. Die Untersuchung beschäftigte sich beispielhaft mit dem schleifenförmigen Ausbreitungsverhalten, das in der Natur an einigen Schmetterlingen beobachtet wurde. Der Ansatz, wie man Ausbreitungsverhalten in Ausbreitungsfunktionen integrieren kann ist jedoch generell und kann für eine große Bandbreite an Bewegungsmustern verwendet werden. Mit Hilfe solcher Untersuchungen kann der Bereich, in dem sich die Parameter einer Ausbreitungsfunktion für eine Art bewegen, besser abgeschätzt werden.

Im dritten Teil wird die im zweiten Teil entwickelte Formel genutzt, um die Auswirkungen von Verhalten auf die Überlebensfähigkeit von Metapopulation zu untersuchen. Mit Hilfe von Metapopulationsmodellen können wir beurteilen, in welchem Maße eine Landschaft eine überlebensfähige Metapopulation tragen kann. Das Ausbreitungsverhalten von Tieren wird in solchen Modellen meist als zufällig angenommen. Ein artspezifisches systematisches

Ausbreitungsverhalten wird oft nicht berücksichtigt, obwohl es möglich ist, dass solch ein systematisches Ausbreitungsverhalten die Überlebensfähigkeit einer Metapopulation deutlich ändert. Wir untersuchten, ob das Ausbreitungsverhalten die Beurteilung von Landschaften dahingehend beeinflusst, dass es die Rangfolgen, nach denen Landschaften bezüglich ihrer Fähigkeit eine lebensfähige Metapopulation zu tragen geordnet sind, verändert. Um die Überlebensfähigkeit von Metapopulationen in verschiedenen Landschaften für verschiedene Suchstrategien ermitteln und vergleichen zu können, nutzten wir META-X, eine bereits bestehende Software zur Metapopulationsanalyse. Um verschiedene Bewegungsmuster in META-X einzufügen, wurde ein Submodell benutzt, das die in Part II entwickelte Formel nutzt. Indem für jedes Bewegungsmuster die resultierende Mittlere Lebensdauer für verschiedene Landschaften verglichen wurde, erhielten wir für jedes Bewegungsmuster Landschaftsrangfolgen. Die Ergebnisse zeigen, dass sich diese Rangfolgen stark zwischen den einzelnen Bewegungsmustern unterscheiden. Diese Verschiebung zwischen den Rangfolgen ist vor allem durch die Konkurrenz zwischen den Habitaten um Migranten bedingt. An systematisch angelegten Landschaften mit wenigen Habitaten konnten wir sehen, welche Mechanismen wirken. Die Studie zeigt, dass das Verhalten seinen deutlichen Einfluß auf die Landschaftsrangfolgen hat. Deshalb sollte es in Metapopulationmodellen zur Landschaftsbewertung detailliert genug berücksichtigt werden, um diesen Effekt widerspiegeln zu können.

Die Doktorarbeit endet mit einem Kapitel, das nicht nur mögliche Wege für weitere Forschungsarbeit darstellt, sondern auch erste Schritte auf diesen Wegen geht. Es werden erste weiterführende Ergebnisse dargestellt. Da die vorgestellten Themen jedoch zu komplex sind, um eingehend innerhalb der Doktorarbeit behandelt zu werden, ist hier weitere Forschung nötig.

In diesem Kapitel werden verschiedene Möglichkeiten dargestellt, wie zusätzliche Landschaftsheterogenität mit der in Part II entwickelten Formel untersucht werden kann. Der Effekt von heterogenen Habitatgrößen und von heterogenen Matrixstrukturen wie Barrieren und eine sich graduell verändernde Topographie auf die Erreichbarkeit von Habitaten wird untersucht.

Außerdem wird diskutiert, wie die Formel für die Erreichbarkeit mit Felddaten verglichen werden kann. Im letzten Absatz des Kapitels wird in Frage gestellt, ob das Besetzungsmuster von Habitaten ein guter Indikator für Veränderungen in den Landschaftsrangordnungen ist.

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