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Research article

Dispersal behaviour in fragmented landscapes: Deriving a practical formula for patch accessibility

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Abstract

Dispersal has been shown to be a key determinant of spatially structured populations. One crucial aspect is predicting patch accessibility: the probability r_{ij} of a certain patch *j* being reached by individuals starting at another patch *i*. Patch accessibility r_{ij} depends on both the landscape structure and the individuals' dispersal behaviour. To investigate the effects of these factors on r_{ij}, we developed a simulation model focusing on animal dispersal. Our 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. This formula is very simple because it just takes distances into account: not only the distance between start patch and target patch, but also between the start patch and all the other patches in the landscape. Despite its simplicity, the formula 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 (random walk with various degrees of correlation, Archimedean spirals and loops) in any given landscape. The formula can be interpreted as a generic function for patch accessibility for further population dynamics analyses. It also delivers insights into the consequences of dispersal in fragmented landscapes.

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 and Danielson 1997; Frank and Wissel 1998; Thomas 2000; Johst et al. 2002). One crucial factor is the probability r_{ij} of a certain patch *j* being reached by an emigrant from a certain patch *i*, i.e., the connectivity between the two patches. Since the term connectivity is used in a variety of ways and often to describe a property of the landscape (Tischendorf and Fahrig 2000, 2001; Moilanen and Hanski 2001), we refer to r_{ij} as patch accessibility.

The consequences of dispersal for population viability are often analysed using mathematical models (Verboom et al. 1993; Hanski and Gilpin 1997; Frank and Wissel 2002). In order not to complicate these models, the functional relationship between patch accessibility r_{ij} and landscape configuration needs to be subsumed in a simple way. The easiest approach is 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 (Gustafson and Parker 1994; McCarigal and Marks 1995; Hanski et al. 1996; Hansson 1998; Hokit et al. 1999). 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 and Nuernberger 1994; Hanski et al. 1996; Vos et al. 2001; Frank and 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. 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). The function needs to be flexible enough to explain the distance dependence for different complex movement characteristics. Moreover, whether the effect of dispersal behaviour and landscape structure on patch accessibility can at all 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. Assuming that the migrants stay at the first patch they reach, our model analyses show an important effect resulting from 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} which considers not only the distance between start and target patch, but also between the start patch and all the other patches in the landscape. Despite its simplicity, the formula is able to cover effects such as the competition between patches 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 (correlated) random walk (Doak et al. 1992; Ruckelshaus et al. 1997; With and King 1999) and the Archimedean spiral (Bell 1991; Dusenbery 1992; Zollner and Lima 1999). 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 and Wehner 1994; Durier and Rivault 1999), especially, in the context of dispersal, for the butterfly species *Maniola jurtina* and *Pyronia tithonus* (Conradt et al. 2000, 2001). The essence of the model is condensed in this formula, delivering insights into the consequences of dispersal in fragmented habitats for population dynamics.

The model

Landscape

To determine the patch accessibility r_{ij} for any given landscape configuration, we used randomly generated spatially continuous (rather than grid-based) landscapes with circular patches and a homogenous matrix. A specific number of patches were distributed randomly within a 100×100 area (scaled by virtual spatial units) by selecting x- and y-coordinates from a uniform distribution. In the case of equally sized patches, the diameter of the habitat patches was set to 4 spatial units; where patch size was heterogeneous, the diameter was randomly taken from a uniform distribution between 2 and 10 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 and 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.

Movement patterns

We developed a spatially structured, individual-based model. To cover a wide range of dispersal behaviours, the following movement patterns were applied: random walk with different degrees of correlation between the angles of consecutive steps, the

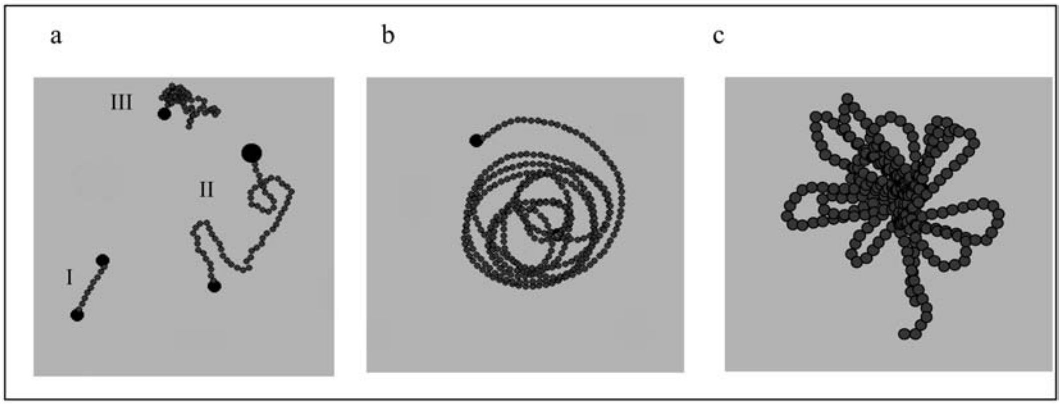

Figure 1. Examples for different movement patterns: a) Random walk with three different degrees of correlation: strongly correlated (I, c = 0.99), fairly correlated (II, c = 0.9) and uncorrelated (III, c = 0). b) Spiral c) Loop-like movement pattern.

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, 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. Such behaviour has been described in a variety of animals (Hoffmann 1983; Bell 1985; Mü;ller and Wehner 1994; Durier and Rivault 1999; Conradt et al. 2000, 2001) and was found to be very efficient in detecting habitat patches (Conradt et al. 2003).

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 (one 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 completely random) or correlated. These turning angles are drawn from a zero-mean Gaussian distribution following the approach of Kareiva and Shigesada (1983). 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 $std = (1\text{-}c)*2*\pi$, 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 (if a standard deviate greater than $2*\pi$ is chosen during the simulation, it is wrapped around to the other side). 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 (Figure 1a). Note that a degree of correlation as high as 0.9 still produces paths that have a considerably random-looking phenomenology.

The two more complex movement patterns, spiral and loops, are generated by adding a few more rules to the random walk. The spiral is created by a random walk in just one orientation (i.e., clockwise or anticlockwise) using the absolute values of the turning angles drawn from the Gaussian distribution. The orientation of the whole 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 ($c_{step+1} = c_{step} + (m^* c_{step})$, with $m = 0.01$, $n = 1.3$ and $c_{step(initial)} = 0.95$). 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 Figure 1b.

The loops (Figure 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).

Table 1. Summary of all model parameters.

	Default values	Variation
Landscape		
Patch containing area	100 × 100 units	–
Patch size (radius)	2 units	Heterogeneous sized patches (1-5 units)
Movement		
Step lengths	1 unit	–
Perceptual range	2 units	0-8 units
Mortality	0.001	0.001-0.005
Description of movement behaviour		
Random walk, correlation degree c	Uncorrelated random walk: c = 0.00 Fairly correlated random walk c = 0.90 Strongly correlated random walk c = 0.99	
Loops	3 phases: – random walk (c = 0.99) – all steps in one orientation (c = 0.9) – return to the habitat patch	
Spiral	All steps in one orientation, initial correlation degree c = 0.95, increasing correlation degree with step number	

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. For this phase we used a less strongly correlated random walk ($c = 0.90$). 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). In the third phase 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 the right turning angle 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 and 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 (quadrants are defined by fixed axes). 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.

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 and Lima 1999, Tischendorf 2001). We did not assume a maximum lifespan. 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 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 units for the perceptual range, covering therewith an area between no and high perceptual abilities (4 times a patch diameter). A similar relationship has be found in a field study, where the perceptual range of the bog fritillary butterfly *P. eumonia* was found to be at least 100 m, while some habitat patches in the study area are not larger than 20 × 20 m (Heinz 2004). Table 1 gives an overview of all model parameters, default values (which are used unless otherwise specified) and ranges of variation used in the study.

Simulation

For one simulation run, 100 landscapes with a specific number of patches (2, 3 or 10) were produced. In each landscape, 1000 individuals were released at a randomly determined start 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 by a single migrant 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.

Results

The main goal of our study is to find the functional dependence of the probability r_{ij} of patch j being reached by an emigrant starting from patch i (referred to as patch accessibility) on landscape configuration. Therefore 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 to take the distances between the patches into account. The most common approach of this type uses an exponential function given by:

$$r_{ij}^{calc} = e^{-b^* d_{ij}} \tag{1}$$

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. However, since this approach is *ad hoc*, it is uncertain how well it predicts the actual r_{ij} values 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.

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 a landscape with 10 patches. To keep this example simple, we assumed equal-sized patches. The resulting values of r_{ij} and d_{ij} are used as a basis for regression analysis, where the data are fitted to an exponential curve.

Figure 2 shows the result of regression analysis, with each point representing one particular patch pair. The results exhibit high variation, and so r_{ij} can be neither predicted nor explained by the exponential function. This is caused not only 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 indicates that distance d_{ij} is not the only determinant of 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 are to understand and predict r_{ij}.

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

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

We begin with a landscape with only two patches. Our aim is to find the simplest possible mathematical function that allows the functional relationship between patch accessibility r_{ij} and distance d_{ij} between the two patches 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

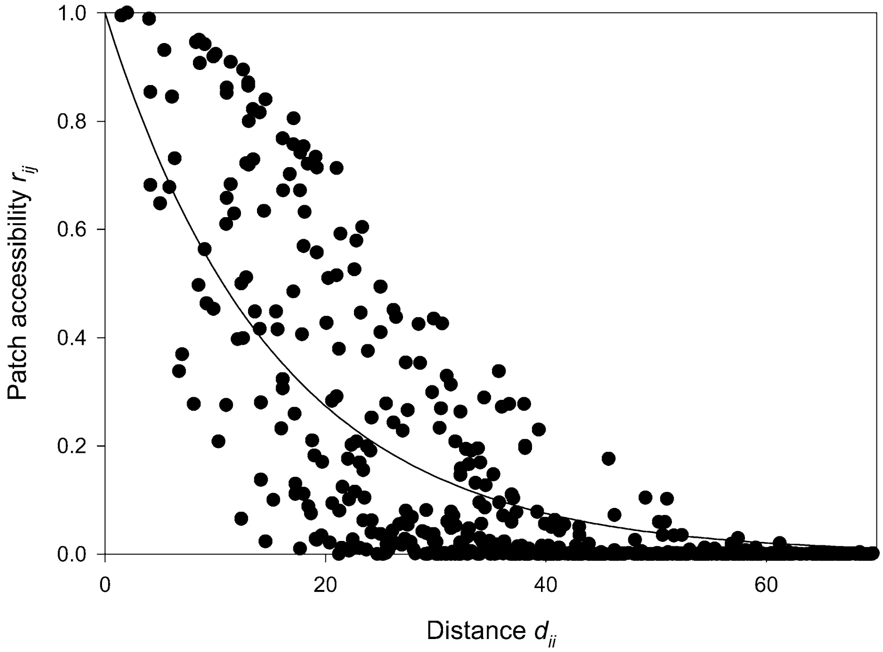

Figure 2. The probability r_{ij} of patch *j* being reached in landscapes with 10 patches as a function of distance d_{ij} between start patch and target patch for the loop-like movement behaviour patterns (mortality 0.001, perceptual range 2). The dots represent the simulation results, the line a fitted exponential curve.

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

The patch accessibility r_{ij} decreases with rising distance d_{ij}(Figure 3). In contrast to the results in Figure 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 $r_{ij} = R_{ij}$ (R_{ij} indicating the patch accessibility in a two-patch landscape) 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 sigmoidal function given by:

$$R_{ij} = 1 - e^{-a*e^{(-b*d_{ij})}} \qquad (2)$$

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

The solid line in Figure 3 indicates what happens if the sigmoidal function (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). We also applied the Akaike's Information Criterion (AIC, Motulsky and Christopoulos (2003)) to compare the goodness of fit of both functions. The AIC gives a measure of which model can be considered to be the best by taking the maximum log likelihood of a model as well as the number of free parameters into account (Sakamoto et al. 1986). We found the sigmoidal function to be the better model ($\Delta AIC = -624$ with $\Delta AIC = AIC_{sig}\text{-}AIC_{exp}$, where negative values indicate that the sigmoidal function is a better model than the exponential function, while positive values indicate the opposite).

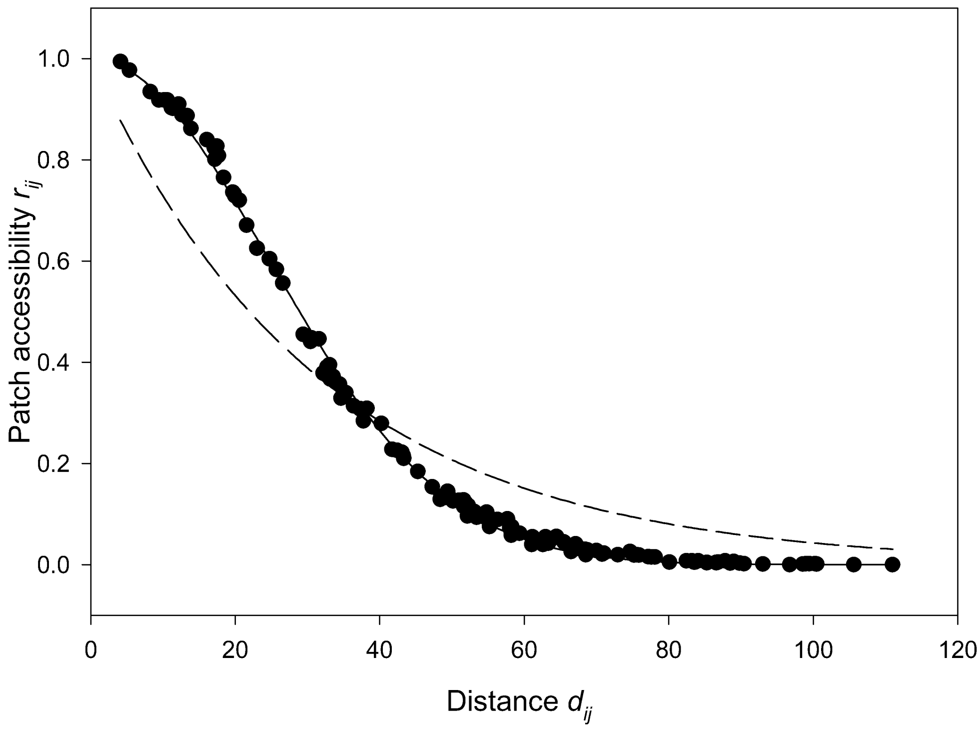

Figure 3. The probability r_{ij} of patch j being reached in a 2-patch system depending on the distance d_{ij} between start patch and target patch for the loop-like movement behaviour (mortality 0.001, perceptual range 2). The lines indicate two fitted functions, the sigmoidal function (2) (solid line; r^2 = 0.999) and the exponential function (1) (dashed line, r^2 = 0.877).

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.

All the scenarios of the correlated random walk lead to a rather exponential shape of the functional relationship between the patch accessibility r_{ij} and the distance d_{ij}, regardless of the degree of correlation (Figure 4). The corresponding non-linear regressions and AIC analyses (Table 2), however, reveal a better fit 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.

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 (equal-sized) patches. The flexibility of the sigmoidal function allows it to cover both an exponential and a sigmoidal shape characterised by the typical ‘flattening’ in the short distance range. 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.

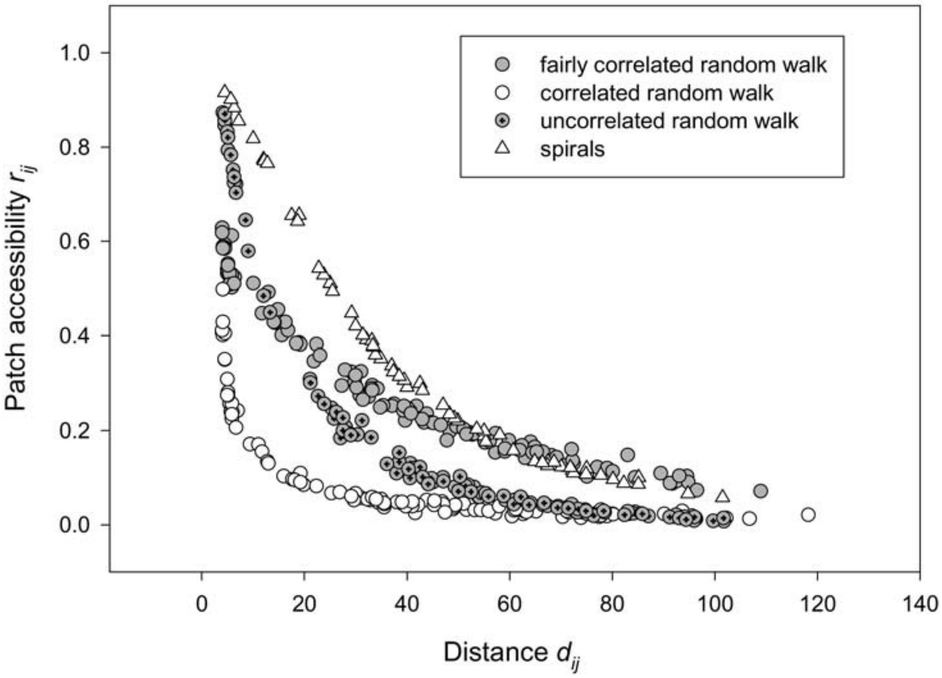

Figure 4. The probability r_{ij} of patch *j* being reached in a 2-patch system depending on the distance d_{ij} between start and target patch for different movement patterns (mortality 0.001, perceptual range 2). The r^2 of the regression analysis can be found in Table 2.

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

As we have shown (Figure 2), the patch accessibility r_{ij} 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 and to get an impression of the role of the number of patches, we perform a similar model experiment as in the previous section, but now with either 3 or 10 patches in each of the 100 random landscapes. As before, we start with the loop-like movement pattern. In a first step, we take the resulting r_{ij}-d_{ij} plots as a basis and analyse the predictive power of the sigmoidal fitting approach that was found to be suitable for predicting r_{ij} in a two-patch system.

Figure 5a and Figure 5b show the resulting r_{ij}-d_{ij} curves. As in the 10-patch system discussed above (Figure 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 (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 (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 Figure 5c and Figure 5d, where the simulated r_{ij} values are plotted against the correspondingly calculated values $r_{ij}^{calc} = R_{ij}$ determined by the sigmoidal function (2): all the simulated values are very close to or below the identity curve (solid 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 sigmoidal function (2) alone is not able to predict the patch accessibility r_{ij} in a multi-patch system, despite its high predictive power in the two-patch system. There is a significant reduction in the r_{ij}-values primarily caused by interaction between start patch *i* and all other patches in the landscape. The more patches a landscape contains, the stronger this reduction will

Table 2. 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 (calculated with $r_{ij}^{calc} = W_{ij} * R_{ij}$).

Parameters			2-patch-system			10-patch-system
Movement pattern	Mortality	Perceptual range	r^1 of $R_{ij} = e^{b^* d_{ij}}$	r^1 of $R_{ij} = 1e^{a^* e^{(b^* d_{ij})}}$	ΔAIC = $AIC_{sig} - AIC_{exp}$	r^1 of r_{ij}^{sim} vs. r_{ij}^{calc} $rij^{calc} = W_{ij} * R_{ij}$
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 0.90)	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

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 prevents this individual from reaching any other patch. As a result, 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 r_{ij} – values: the value R_{ij} resulting from the sigmoidal function describes the patch accessibility in a two-patch system, without any competing patch. Therefore the sigmoidal function R_{ij} can also be interpreted as the potential patch accessibility of patch j in the absence of competition between patches for migrants.

In order to calculate the patch accessibility r_{ij} in such a way that the reduction effect caused by competition between patches for migrants is taken into account, we need a correction term W_{ij}. 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:

$$W_{ij}^{\mathrm{I}} = \frac{R_{ij}}{\sum_{k \neq i} R_{ik}} \quad (3)$$

This correction term has the structure of a weighting factor, i.e., 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:

$$r_{ij}^{calc} = W_{ij} * R_{ij} \quad (4)$$

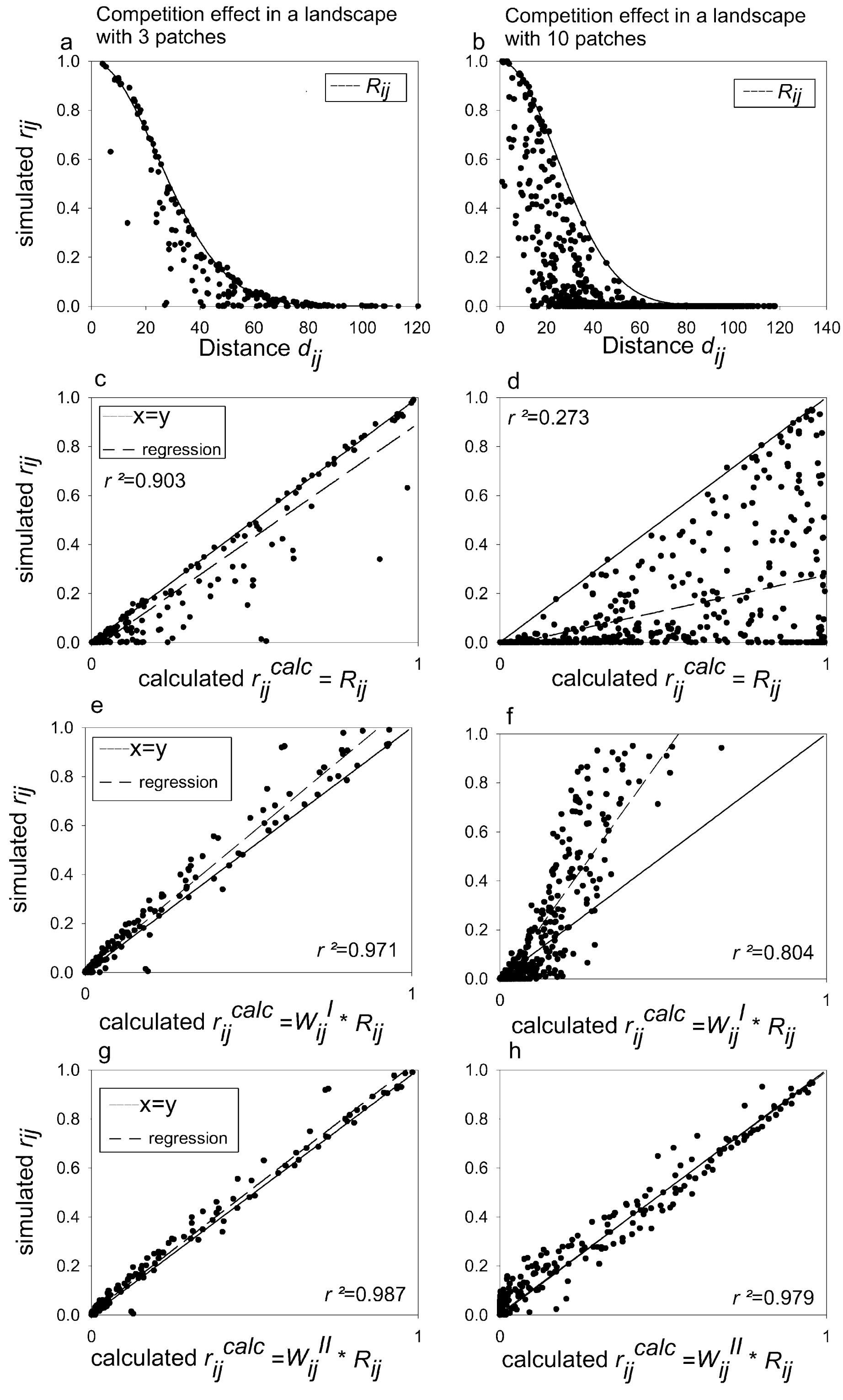

Figure 5. The probability r_{ij} of patch j being reached in a 3-patch system (left side) and in a 10-patch system (right side, 100 simulated landscapes at each case) for the loop-like movement behaviour patterns (mortality 0.001, perceptual range 2). 5a and 5b: r_{ij} depending on d_{ij}; the solid line indicates the functional relationship R_{ij} between r_{ij} and d_{ij} in a two-patch system. 5c-5h: Simulated vs. calculated values (calculated with different relations). The solid line indicates the identity curve $x = y$, the dashed line represents the linear regression. 5c and 5d: R_{ij} vs. simulated r_{ij}. 5e and 5f: r_{ij}^{calc} calculated under consideration of the weighting factor W_{ij}^{I} vs. simulated r_{ij}. 5g and 5h: r_{ij}^{calc} under consideration of the weighting factor W_{ij}^{II} vs. simulated r_{ij}. In Figure 5h, broken and solid lines are almost identical.

In order to test the predictive power of formula (4), the calculated patch accessibility values (r_{ij}^{calc}) are plotted against the simulated ones (r_{ij}). The results for both the 3-patch and the 10-patch systems (Figure 5e, Figure 5f) show much stronger correspondence between the simulated and the calculated values than the results determined without the weighting factor (Figure 5c, Figure 5d). In the case of 3 patches (Figure 5e), 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 different picture occurs in the case of 10 patches (Figure 5f), where the r^2 value is lower (0.804) and the regression curve (dashed line) is markedly above the identity curve (solid line). This indicates that the modified formula (4) underestimates the simulated r_{ij} values in this system, i.e., it overestimates the reduction effect caused by competition.

The underestimation of the patch accessibility by W_{ij}^{I} can be explained by the fact the weighting factor overestimates the competitive power of distant patches (which often cannot compete at all, because individuals are intercepted by other patches) and underestimates the effective patch accessibility of the target patch. To overcome this problem, we corrected the weighting factor as follows:

$$W_{ij}^{\mathrm{II}} = \frac{R_{ij}^{(N-1)}}{\sum_{k \neq i} R_{ik}^{(N-1)}} \qquad (5)$$

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 ($R_{ij} \approx 0$).

Figure 5g and Figure 5h show the result of the comparison between r_{ij}^{calc} and r_{ij} for the modified weighting factor (5). 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. When testing the predictive power of the modified formula (relations 4 and 5) for the loop-like movement pattern with other model parameters we found a good correspondence between all simulated and calculated values (Table 2).

The predictive power of r_{ij}^{calc} is also assessed for the other movement patterns. Figure 6 shows the results for the correlated random walks with different degrees of correlation and the Archimedean spiral with standard parameters (see Table 2 for the results of all model parameters tested). 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.

Heterogeneous patch size

Patch size is likely to have an important impact on patch accessibility (Hill et al. 1996; Kuussaari et al. 1996). So far, however, we assumed equal-sized patches. As a final step in this study, we abandon the assumption of patch size homogeneity. We perform the simulation described in the previous section, but using 10 heterogeneously sized circular patches. Patch size is generated randomly and varies between a radius of 1 and 5 units, covering so an area between 3.14 units^2 for the smallest and 78.54 units^2 for the largest patch. The resulting simulated patch accessibility values (r_{ij}) for the loop-like behaviour as an example were plotted against the calculated values (r_{ij}^{calc}) calculated with relations (4) and (5).

There is a strong correspondence between simulated and calculated values (Figure 7a, r^2 = 0.941), but compared to equal-sized case, there is a wider spread of values. Therefore, in landscapes with patch-size heterogeneity, the formula for the patch accessibility (relations 4 and 5) has a significantly lower predictive power.

How can patch size be included in the formula for patch accessibility in a simple way? So far, the distance between patches is measured from patch centre to centre. In the context of reaching a patch, it seems more natural to measure distance from edge to edge. Therefore, with a (circular) start patch i of area A_i and

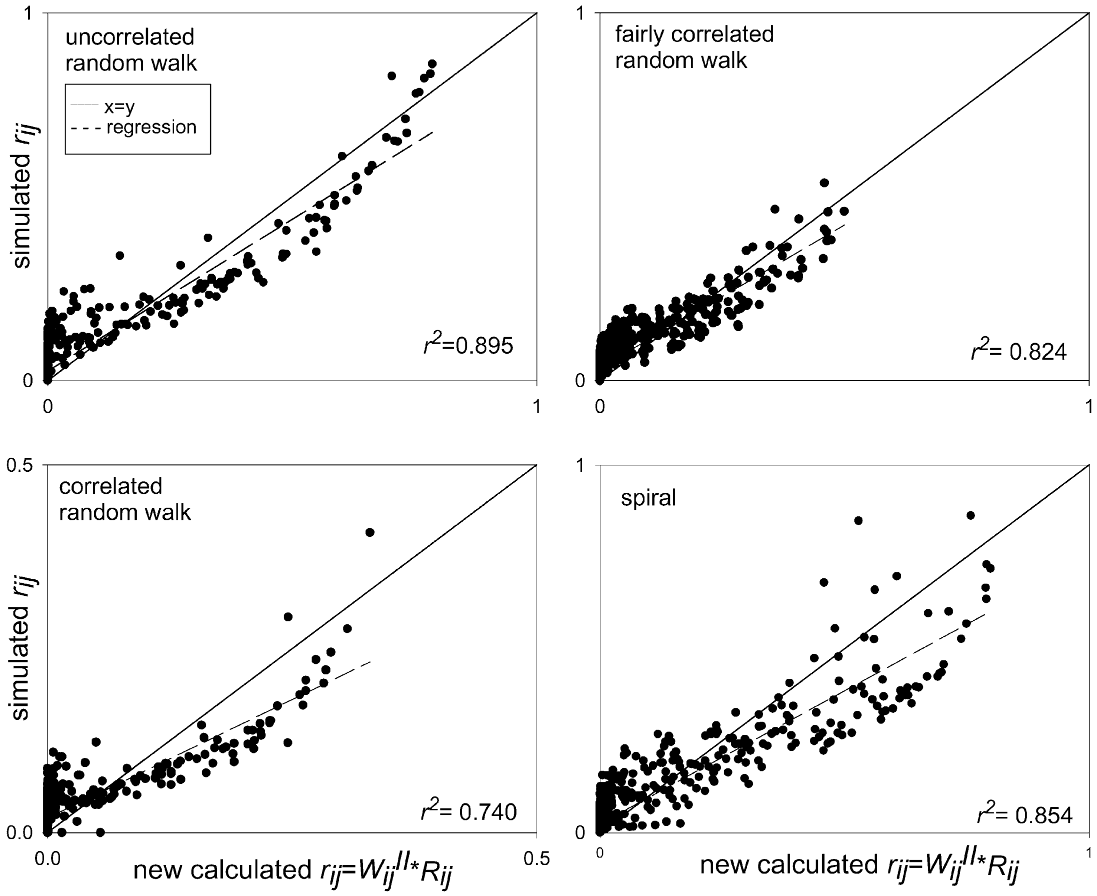

Figure 6. Simulated versus calculated r_{ij} in landscapes with 10 patches and for different movement patterns (mortality 0.001, perceptual range 2).

a (circular) target patch j of area A_j, the former value for the distance d_{ij}^{old} between these to patches has to be corrected by subtracting the corresponding radii. By taking into consideration that the radius of a circle of area A is given by $\sqrt{A/\pi}$, we obtain the following rule for correcting the distances:

$$d_{ij}^{new} = d_{ij}^{old} \sqrt{Ai/\pi} - \sqrt{Aj/\pi} \qquad (6)$$

We inserted these corrected values for the distance d_{ij} between the patches in relations (2), and plotted the simulated values (r_{ij}) against the resulting calculated ones (r_{ij}^{calc}). The values are less scattered (Figure 7b) and the regression analyses show a stronger correspondence (r^2 = 0.980) with the predictive power of the calculated values being as good as in the equal-sized case. This corresponds with the results by Baveco and Goedhart (unpublished) who found similar effects for the case of (correlated) random walk. Therefore, for calculating the patch accessibility in the case of heterogeneous patch size, it seems to be sufficient to correct the distance between patches.

We should note that all the results on the patch accessibility r_{ij} in the case of equal-sized patches presented were based on centre-to-centre measurement of distance. The validity of these results, however, is not affected by moving to edge-to-edge measurement since the two distances d_{ij}^{new} and d_{ij}^{old} only differ in a constant value, $2\sqrt{A/\pi}$ (relation (6)), in this case. The properties of exponential functions ensure that $ae^{-bd_{ij}^{old}} = (ae^{-2b\sqrt{A/\pi}})e^{-bd_{ij}^{new}} = a'e^{-b_{ij}^{new}}$. This indicates that changing the measurement of distance just means appropriately modifying the value of parameter a in the sigmoidal function fitting the potential patch accessibility R_{ij}.

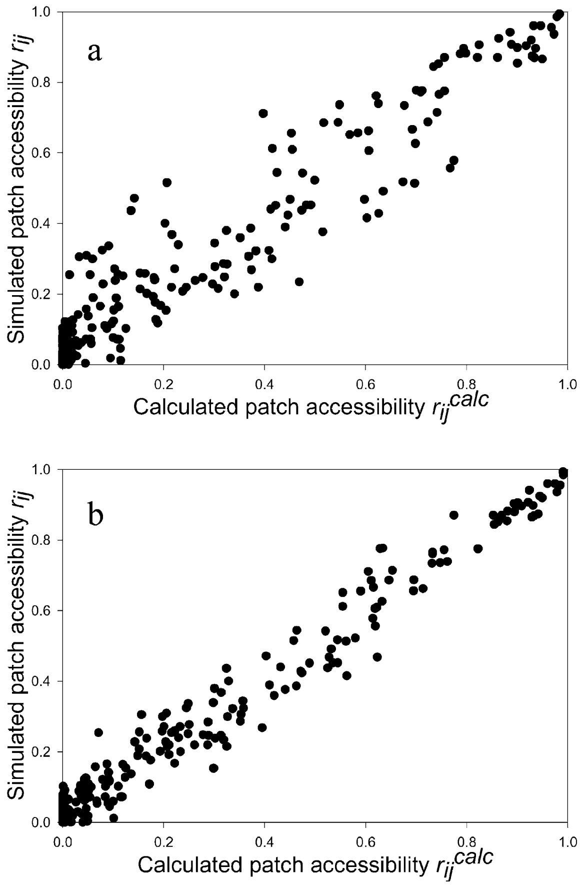

Figure 7. Simulated vs. calculated patch accessibility r_{ij} in landscapes with patch size heterogeneity. 7a: The patch accessibility r_{ij}^{calc} is calculated by using the original formula (2, 4, 5). 7b: The patch accessibility r_{ij}^{calc} is calculated by using the formula (2, 4, 5) but with the distance d_{ij} calculated from edge to edge.

Discussion

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. We derived a simple formula r_{ij}^{calc} that allows this relationship to be reproduced qualitatively correctly and quantitatively sufficiently in landscapes with homogeneous matrix and circular patches. This formula is given by

$$r_{ij}^{calc} = \frac{R_{ij}^{N-1}}{\sum\limits_{k \neq i} R_{ik}^{N-1}} \cdot R_{ij} \qquad (7)$$

where

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

where d_{ik} is the distance between patch i and patch k measured from edge-to-edge. This formula consists of two components: the potential patch accessibility R_{ij} described by a sigmoidal function and a weighting factor determined by all the R_{ik} values. Formula (7) is completely expressed in terms of distances d_{ij} and two fitting parameters a and b summarising via the shape of the $r_{ij} - d_{ij}$ curves all the relevant effects of the movement behaviour. But note that it is necessary to take not only the distance d_{ij} from start patch i to target patch j as done using relation (2) only (Figure 5d, $r^2 = 0.273$). 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 (Figure 5h, $r^2 = 0.979$).

The predictive power of this formula has been successfully tested for a wide range of randomly generated landscapes with homogeneous matrix and different numbers of circular patches. The formula has been found to work for all the movement patterns (uncorrelated random walk, correlated random walk, Archimedean spirals, loops) considered. Since these movement patterns qualitatively differ from each other and cover a wide range of biologically reasonable situations, it can be supposed that the formula works for most movement patterns. The current study is based mainly on the set of standard parameter values and the selected parameter variations listed in Table 1. A high predictive power of formula (7), however, was also found in a more detailed analysis where the movement parameters were systematically varied and their effects on a and b were analyzed (Heinz et al. unpublished).

Our study also clarifies the formula's limits: a high predictive power of formula (7) was found for movement patterns 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 slightly decreases 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 did not provide as good a fit for the potential patch accessibility R_{ij} as for the other movement patterns. In such cases, the predictive power of the formula could be enhanced by using a weighting factor with another function for the potential patch accessibility R_{ij} instead of the sigmoidal one.

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 and Gardner 1996; Wiens et al. 1997; With et al. 1997; McIntyre and Wiens 1999; Ricketts 2001; Goodwin and Fahrig 2002; Tischendorf et al. 2003). Furthermore, we assumed circular patches, although patch shape is likely to have an important impact on patch accessibility (Bender et al. 2003). In the case of heterogeneous matrix or heterogeneously shaped patches, changes in search success and therefore in the functional structure found here could be expected.

The formula (7) presented for the patch accessibility r_{ij}, mainly differs in three aspects from the exponential formula (1). (a) A sigmoidal (instead of an exponential) function is used for describing the potential patch accessibility R_{ij}. Sigmoidal functions are able to cover exponential-like declines, but also sigmoidal ('flattened') shapes reflecting an above-average preference for the short-distance range, as has been found in several field studies (Endler 1977; Brakefield 1982). (b) Distance is measured from edge-to-edge instead from centre-to-centre. (c) There is a weighting factor in relation (7) that depends on the distances d_{ik} between start patch i and all other patches k, and that reflects the intrinsic effect of the competition between the patches for migrants. Such an element is completely missing in the exponential approach. Note that the competition effect mentioned inherently results from our assumption that the migrants stay at the first patch they reach. If we were to assume that individuals could visit multiple patches before staying at one, the strength of the competition effect and hence the structure of the weighting factor may change.

The practical value of the presented formula

First, the formula provides a tool for prediction. Taking patch configuration (position, size) and the parameters a and b as a basis, the resulting patch accessibility can be predicted without having to run any simulations. The formula contains the essence of the simulation model and gives rise to the same conclusions regarding patch accessibility as the model itself. Second, the formula provides as well a tool for understanding the key factors of patch accessibility. The formula revealed that two effects are decisive: the potential patch accessibility and the competition effect. Both effects can be analyzed in terms of their dependence on patch configuration, patch size and movement behaviour, but also regarding their relative importance or their combined effects. Third, the formula provides a tool for modelling. The patch accessibility can be used to calculate the immigration rates in metapopulation models. Assuming that $y{\cdot}A_i$ migrants start from patch i, the immigration rate c_{ij} from patch i to patch j is $c_{ij} = y \cdot_{Ai} \cdot r_{ij}$. Until now, the exponential approach has been used in most models to calculate r_{ij} resulting in $c_{ij} = y \cdot_{Ai} \cdot e^{bd_{ij}}$(Fahrig 1992; Hanski 1994; Adler and Nuernberger 1994; Hanski et al. 1996; Vos et al. 2001; Frank and Wissel 2002). Formula (7) was found to be more realistic than the exponential function and can therefore be used instead. This leads to

$$c_{ij} = y \cdot A_i \cdot \frac{R_{ij}^{N-1}}{\sum_{k \neq i} R_{ik}^{N-1}} \cdot R_{ij} \tag{8}$$

By using this relation, important aspects of patch configuration (position, size) and individual dispersal behaviour (summarized in a and b, see relation (7)) can be incorporated in metapopulation analyses in a simple way. The major advantage of relation (8) is that the intrinsic effect of competition between patches for migrants is covered. In most metapopulation models, the competition effect is ignored. In the few studies that account for the competition effect, the expressions used to describe competition vary widely (Hanski and Thomas 1994; Frank and Wissel 1998; Hanski et al. 2000; Frank 2004). Hanski and Thomas (1994), for instance, suggested a structurally similar submodel for the immigration rate: $c_{ij} = yA_j e^{-\mu d_{ij}} \big/ \sum_{k \neq i} e^{-\mu d_{ik}} e^{-\alpha d_{ij}}$ with two parameters α and μ. Their approach is based on fitting all the patch accessibility values r_{ij} of a given landscape and determining α and μ by Maximum Likelihood techniques. This has the advantage that, as long as the given landscape is concerned, the resulting c_{ij}-function may even have a higher predictive power than formula (8) derived from 100 randomly determined landscapes. One consequence of this approach is that α and μ summarize the effects of both the dispersal behaviour and aspects of the spatial structure (e.g., the number of patches N) of the specific landscape considered. However, it is often useful to analyze the effects of behaviour and landscape structure separately, to the benefit of a better understanding. Such a task is better supported by formula (8) because its parameters a and b (see relation 7 for details) are independent of the patch configuration.

Both, formula (7) for the patch accessibility r_{ij} and formula (8) for the immigration rate c_{ij} can be interpreted as landscape indices. There are numerous landscape indices that take landscape characteristics such as patch configuration, size or shape into account (e.g., Franklin and Forman 1987; O'Neill et al. 1988; Turner et al. 1989; Ripple et al. 1991; McGarial and Marks 1995; Schumaker 1996; Gustafson 1998; Bender et al. 2003). Landscape indices, however, are often neutral, and do not count for the species' specific perception of the landscape. The indices presented here are ecologically scaled (Vos et al. 2001) and allow landscape evaluation through the eyes of a species (Verboom et al. 1991; Hanski 1994; Hanski and Thomas 1994; Wiegand et al. 1999; Hanski and Ovaskainen 2000; Frank and Wissel 2002). A further advantage of these indices is that they are not *ad hoc* but proven to be realistic by comparing its outcome with the outcome of an individual-based, spatially realistic simulation model. Moreover, they can be directly ecologically interpreted and used in further analyses.

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