Integrating individual movement behaviour into dispersal functions

Simone K. Heinz, Christian Wissel, Larissa Conradt, Karin Frank

Abstract

Dispersal functions are an important tool for integrating dispersal into complex models of population and metapopulation dynamics. Most approaches in the literature are very simple, with the dispersal functions containing only one or two parameters which summarise all the effects of movement behaviour as for example different movement patterns or different perceptual abilities. The summarising nature of these parameters makes assessing the effect of one particular behavioural aspect difficult. We present a way of integrating movement behavioural parameters into a particular dispersal function in a simple way. Using a spatial individual-based simulation model for simulating different movement behaviours, we derive fitting functions for the functional relationship between the parameters of the dispersal function and several details of movement behaviour. This is done for three different movement patterns (loops, Archimedean spirals, random walk). Additionally, we provide measures which characterise the shape of the dispersal function and are interpretable in terms of landscape connectivity. This allows an ecological interpretation of the relationships found.

1. Introduction

Dispersal of animals is a spatial process that influences structure, dynamics and stability properties of ecological systems (Levins, 1970; Opdam, 1990; Hanski et al., 1994; Hess, 1996; Anderson and Danielson, 1997; Frank and Wissel, 1998; Thomas, 2000; Heinz et al., 2006). It is a result of the interplay between landscape structure and animals' dispersal behaviour. To get a mechanistic understanding of the effect of dispersal on ecological systems, one set of quantities is of particular importance: the probability \( r_{ij} \) of a certain patch \( j \) being reached by a disperser starting from a certain patch \( i \) (referred to as “patch accessibility”). Patch accessibility quantifies the primary effect of dispersal (transport from \( i \) to \( j \)) that basically determines all further effects. Analyses of the effect of dispersal on ecological systems can than be split in two steps: (i) analysis of the effect of dispersal on patch accessibilities and (ii) analysis of the effect of patch accessibilities on structure and dynamics of the ecological system considered.

Dispersal functions aim to approximate the functional relationship between (empirically determined or simulated) patch accessibilities \( r_{ij} \) and landscape structure by means of simple equations (Fahrig, 1992; Adler and Nuernberger, 1994; Hanski, 1994; Hanski et al., 1996; Vos et al., 2001; Frank and Wissel, 2002). In fragmented landscapes, landscape structure is usually characterised by distances \( \{d_{k}\} \) between patches. This leads to dispersal functions of the following type: \( r_{ij} \approx f_{\mu,\nu,...}(\{d_{k}\}) \), where \( f_{\mu,\nu,...}(\ldots) \) is a function with parameters \( \{\mu, \nu, \ldots\} \) determining its shape. The values of \( \{\mu, \nu, \ldots\} \) can be determined by statistical methods such as non-linear regression or maximum likelihood techniques. Dispersal functions are explicitly expressed in terms of landscape characteristics. However, as dispersal always depends on both landscape structure and animals’ movement behaviour, shape and parameters \( \{\mu, \nu, \ldots\} \) of dispersal functions summarise all behavioural effects that are relevant for the patch accessibility (King and With, 2002).
A major advantage of working with dispersal functions is that they provide insight into the influence of the landscape structure on patch accessibility and allow predictions of consequences of landscape changes. However, movement behaviour of animals is merely implicitly included via the parameters \{\mu, v\ldots\} summarising all behavioural effects. This hampers efforts to understand the effects of single aspects of movement behaviour on patch accessibility.

In a previous publication, we used an individual-based simulation model for deriving a generic dispersal function that can be used for a variety of movement behaviours and landscapes (Heinz et al., 2005). In this paper, we take the derived dispersal function as an example for presenting a way of explicitly integrating aspects of movement behaviour into dispersal functions. We take the individual-based simulation model of Heinz et al. (2005) as a basis, analyse the functional relationship between the parameters of the dispersal function and several movement details, and provide appropriate fitting functions for these relationships. This is done for three different movement patterns: two systematic ones, namely loop-like movement and Archimedean spirals, as well as the random walk. By inserting the fitting functions for the parameters in the original dispersal function, we obtain a dispersal function that is explicitly expressed in terms of the movement detail of interest. Furthermore, we provide measures which characterise the shape of the dispersal function and which are interpretable in terms of landscape connectivity. The result is a framework for the investigation of movement behavioural aspects and their effect on landscape connectivity and (meta)population dynamics.

2. Theoretical background

As dispersal functions are merely approximate, several dispersal functions exist. The most prominent example is \( r_{ij} \approx \exp(-zd_{ij}) \), a negative exponential function of the distance \( d_{ij} \) between start and target patch, where \( 1/\alpha \) denotes the mean distance a disperser is able to move. Such an exponential relationship has empirically been found for many small organisms (Wolfenbarger, 1949) and it is used in most metapopulation models (e.g. Fahrig, 1992; Hanski, 1994; Adler and Nuernberger, 1994; Hanski et al., 1996; Turchin, 1998; Vos et al., 2001; Frank and Wissel, 1998, 2002). 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), especially if individuals move in a systematic way or stay at the first patch they recognise. In the latter case, the patches start to ‘compete’ for migrants as they attract individuals and prevent them from moving to other patches. As a result, patch accessibility \( r_{ij} \) does not only depend on the distance \( d_{ij} \) between start and target patch, but also on the distances \( d_{ik} \) between start patch and all other patches \( k \). This is taken into account in a dispersal function derived by Heinz et al. (2005):

\[
    r_{ij} = W_{ij} R(d_{ij}),
\]

where

\[
    W_{ij} = \frac{R(d_{ij})^{N-1}}{\sum_{k \neq j} R(d_{ik})^{N-1}}
\]

and

\[
    R(d) = 1 - e^{-a e^{-\beta d}}.
\]

The function \( R(d) \) (Eq. (3)) gives the potential patch accessibility in a landscape with two patches (start and target patch) only by considering the distance \( d \) between them. Its shape is determined by the individual movement pattern. For the range of movement patterns considered, negative exponential and sigmoidal shapes were found to be typical. The double-exponential structure of function \( R(d) \) is flexible enough to include both exponential and sigmoidal shapes while it is at the same time structurally simple (Heinz et al., 2005). In comparison with an exponential function (using linear regression and AIC), \( R(d) \) was found to be the better model (Heinz et al., 2005).

In a landscape with more than two patches, emigrants intercepted by one patch cannot reach another one (assuming that the migrants stay on the first patch they reach (Hein et al., 2004; Heinz et al., 2005)). This induces a “competition” between patches for emigrants. This competition is described by the weighting factor \( W_{ij} \) (Eq. (2)). The patches \( j \) are weighted according to a power of their potential accessibilities \( R(d_{ij})^{N-1} \). The higher their potential accessibility, the higher is their competition strength. The power \( N-1 \) is introduced in order to reflect the fact that the competition strength of a relatively distant patch decreases with increasing number of patches \( N \), as the likelihood of being reached decreases and so the chance to compete.

The overall patch accessibility formula (Eq. (1)) is completely expressed in terms of the distances \( d_{ik} \) from the start-patch \( i \) to all other patches \( k \) and two function parameters, \( a \) and \( b \), which subsume all the relevant effects of individuals’ movement behaviour.

Heinz et al. (2005) showed that dispersal function (1)–(3) has a high predictive power for a wide range of randomly generated patchy landscapes with homogeneous matrix and various numbers of circular patches and for different movement patterns (e.g. random walks with different degrees of correlation, Archimedean spirals, loop-like movement behaviour).

3. Methods

To investigate the integration of movement behaviour into the dispersal function, we used the following individual-based movement model for simulating different movement behaviours. Since the effects of \( a \) and \( b \) are summarised in the potential accessibility function \( R(d) \)
which gives the potential patch accessibility in a landscape with two patches (start and target patch), we concentrate on landscapes with two patches. From our model, we obtained $R(d)$ curves for different movement characteristics. By fitting Eq. (3) to those $R(d)$ curves using SigmaPlot which applies the Marquardt–Levensberg Algorithm for minimisation of least squares, we derived the parameters $a$ and $b$ of the formula.

### 3.1. The model

To determine the potential accessibility function $R(d)$ for different movement details, we developed a spatial, individual-based movement model (implemented in C+ +).

For each simulation run, 100 landscapes with two circular equal-sized patches at different distances from each other are produced. The two patches were distributed randomly within a $100 \times 100$ 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. Patch size influences patch accessibility (Hill et al., 1996; Kuussaari et al., 1996). Heinz et al. (2005) showed that in landscapes with heterogeneous patch sizes, parameter changes of less than 2* were observed in nature (Hoffmann, 1983; Bell, 1985; Müller and Wehner, 1994; Durier and Rivault, 1999; Conradt et al., 2000, 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. Additionally, we investigated two other movement patterns: the Archimedean spiral as another systematic movement pattern which has been frequently used in search strategy models (Bell, 1991; Dusenbery, 1992; Zollner and Lima, 1999) and (uncorrelated) random walk (see Table 1 for an example of all movement patterns).

In our model, all movement patterns are based on the elements of the random walk. For simplicity, the random walk is 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 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 $std = (1-c)*2*\pi$, 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).

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### 3.1.1. Movement behaviour

To investigate the effect of different movement patterns, we intensively analysed a loop-like movement pattern observed in nature (Hoffmann, 1983; Bell, 1985; Müller and Wehner, 1994; Durier and Rivault, 1999; Conradt et al., 2000, 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. Additionally, we investigated two other movement patterns: the Archimedean spiral as another systematic movement pattern which has been frequently used in search strategy models (Bell, 1991; Dusenbery, 1992; Zollner and Lima, 1999) and (uncorrelated) random walk (see Table 1 for an example of all movement patterns).

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<table>
<thead>
<tr>
<th>Movement Details</th>
<th>Loops</th>
<th>Spirals</th>
<th>Uncorrelated random walk</th>
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<tbody>
<tr>
<td>Perceptual range</td>
<td>$a = z + b*pr$</td>
<td>$a = z + b*pr$</td>
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<td>$b = z + b*pr$</td>
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<td></td>
<td>$r^2 = 0.99$</td>
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<tr>
<td>Mortality</td>
<td>$a = z* e^{-b**}$</td>
<td>$a = z* e^{-b**}$</td>
<td>$a = z* e^{-b**}$</td>
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<tr>
<td></td>
<td>$b = zm/(b + m)$</td>
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<td>$r^2 = 0.86$</td>
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<td>Loop length</td>
<td>$a = 1/(z + b*hl)$</td>
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<td>$b = 1/(z + b*hl)$</td>
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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 ($c_{\text{step}+1} = c_{\text{step}} + (m \ast c_{\text{step}})$, with $m = 0.01$, $n = 1.3$ and $c_{\text{step}(\text{initial})} = 0.95$). Because the turning angles are taken randomly from the Gaussian distribution, this kind of spiral is subject to stochasticity.

The loops 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. 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 (path integration (dead reckoning); Wehner et al., 1996; Durier and Rivault, 1999). 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. Using those patterns as a basis, various movement parameters were altered.

### 3.1.2. Parameters

There are three parameters in the model that are important determinants of movement behaviour: mortality risk ($m$), perceptual range ($p$) and loop-size ($l$). 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). The mortality risk was varied between values of 0.001 and 0.05. These values were chosen to cover a range of mortality from relative safety to great risk. We ignored additional sources of mortality such as the risk of starvation during the movement as it would have been difficult to keep apart effects of mortality risk and starvation and in order to prevent an overloading of the study with too many details. Perceptual range describes the distance within which an animal can detect new patches and can therefore move straight towards them. It is commonly used in dispersal models (Cain, 1985; Fährig, 1988) and has been well investigated in the field (Yeomans, 1995; Zollner and Lima, 1997; Zollner, 2000; Conradt et al., 2000; Heinz, 2004). In our model, we used values between 0 and 12 spatial units for the perceptual range, covering an area between no and extremely high perceptual abilities (6 times a patch diameter). In a field study, 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 were not larger than $20 \times 20 m$ (Heinz, 2004). The loop size determines radius and intensity of the loop-like search. It is given by the number of 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 every 4 loops half of the steps of the initial loop size to the steps determining the last loops (i.e. if we have an initial loop size of 4 steps, we increase it after the 4 first loops by 2 steps to 6 steps, after the next 4 loops to 8 steps, than to 10 steps and so on). Loops size was found to differ between individuals (Conradt et al., 2000) and we were interested in seeing how loop size influences patch accessibility. We utilised 4 different loop sizes: 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). Unless otherwise specified, a per-step mortality of 0.001, a perceptual range with a radius of 2 spatial units and a small loop size are taken as standard model parameters.

The movement parameters varied in the model are parameters most relevant for dispersal of smaller organisms as insects (e.g. Cain, 1985) or small mammals (e.g. Zollner, 2000). A large proportion of dispersal literature is concentrating on these groups. Larger mammals often apply more complex movement rules as for example an active choice of dispersal habitat dependent on dispersal habitat quality (Kramer-Schadt et al., 2004). Since we cannot vary all possible movement parameters for all organisms, we concentrate here on the most general ones, namely mortality and perceptual range. In addition, we use the loop-size as an example for a more specific movement detail to show that also more complex movement details can be considered.

### 3.2. Preliminary analysis: reparameterising the potential accessibility function $R(d)$

Since the two parameters $a$ and $b$ are first of all ‘technical quantities’ (fitted parameters), they do not permit straightforward ecological interpretation. This is a drawback given the wish to support a mechanistic understanding of how
patch accessibility in a given patchy landscape will change with changing movement behaviour. As we know from a previous study (Heinz et al., 2005), all the effects of the movement behaviour on the patch accessibility are summarised in the shape of the \( R(d) \)-function. Therefore, we perform a pre-analysis to look for appropriate measures that are: (a) characteristic of the shape of \( R(d) \); (b) directly interpretable from the point of view of patch accessibility; and (c) expressed in terms of the parameters \( a \) and \( b \). The latter condition ensures that the fitting functions for \( a \) and \( b \) can be used for relating the characteristics of the shape to the movement details of interest.

In order to find measures which characterise the shape of the potential accessibility function \( R(d) \), we re-write \( R(d) \) as follows:

\[
R(d) = 1 - e^{-a} e^{-bd} = 1 - e^{-b(d-a/b)}. \tag{4}
\]

This formulation reveals that the function \( R(d) \) and its shape are determined by two quantities: \( a/b \) and \( b \). Both, Fig. 1a and the calculation in Appendix A, indicate that the quantity \( d_T = a/b \) coincides with the so-called turning point of the function \( R(d) \), i.e. the distance where the \( R(d) \)-curve changes from concave to convex shape. Since \( R(d) \geq R(d_{TP}) = 1 - e^{-1} \approx 0.63 \) for all \( d \leq d_T \), we interpret \( d_T \) as an “index of effective search”. This index can take both positive and negative values, depending on the values of the parameters \( a \) and \( b \). Negative values (i.e. \( d_T < 0 \)) indicate missing effectiveness in search and an exclusively convex decline of \( R \) with distance \( d \), while positive values (i.e. \( d_T > 0 \)) indicate both existence and scale of effective search.

Fig. 1b indicates that quantity \( b \) determines the rate with which the potential accessibility \( R(d) \) declines if \( d \) increases beyond \( d_T \). Therefore, we refer to \( b \) as “rate of decline”. The two quantities \( d_T \) and \( b \) are expressed in terms of \( a \) and \( b \) as required. While the parameters \( a \) and \( b \) are easier to handle for parameterising dispersal functions, the two quantities give ecological interpretable insight into the nature of the response of the landscape connectivity to alterations in a certain movement detail (decrease/increase in the scale of effective search, decrease/increase in the rate of decline).

4. Results

4.1. The effect of the movement details for the loop-like movement pattern

Now we investigate the effect of movement characteristics relevant for the loop-like behaviour (perceptual range, mortality risk, loop size) on the potential accessibility function \( R(d) \) (Eq. (4)). We do this by sequentially changing each movement detail of the loop-like behaviour, assessing the effect on the shape of the corresponding \( R(d) \) curves as well as on the parameters \( a \) and \( b \), and describing the functional relationships between \( a \) and \( b \) and the movement details by appropriate fitting functions. Moreover, we analyse the effect of the movement details on the two measures characterising the curve shape: the index of effective search \( d_T \) and the rate of decline \( b \). Based on this, we draw some conclusions regarding the implications of the movement details for landscape connectivity. The results are shown in Fig. 2.

4.1.1. The effect of perceptual range

Both 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 1). While \( a \) markedly increases with rising perceptual range, 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 \( d_T \). This shows that an increase in the perceptual range leads mainly to an extension of the range of effective search, while the rate of decline is not affected. These findings are confirmed by the shape of the function, where mainly the sigmoidal plateau of the curve is extended with increasing perceptual range.

4.1.2. The effect of mortality risk

The parameter \( a \) decreases with increasing mortality risk, while parameter \( b \) increases. The functional relationship between function parameter \( a \) and mortality risk can be described by an exponential decay. For function parameter \( b \), a hyperbola fits the resulting curve very well (Table 1).

Fig. 1. The impact of the index of effective search \( d_T \) and the rate of decline of \( b \) on the potential accessibility function \( R(d) \): (a) \( d_T \) is varied while \( b \) is constant and (b) \( b \) is varied while \( d_T \) is constant.
Since both parameters act in the same direction regarding the index of effective search $d_T$, it is not surprising that $d_T$ becomes very small for a high mortality risk. Therefore, the two measures of the curve shape $d_T$ and $b$ indicate both a reduction in search effectiveness and the faster decline of potential accessibility with distance. Both findings are an effect of the reduced time available for the patch search. All these effects are reflected by the shape of the $R(d)$ curves.

### 4.1.3. The effect of loop size

Both parameters, $a$ and $b$, decrease as the loop size increases. As with perceptual range and mortality, the parameters exhibit a clear functional dependence on loop size. The resulting curves of both parameters can be fitted with a rational function (Table 1). Since both parameters decrease, they act in different directions on the potential accessibility $R$, which is reflected by the curve characteristics $d_T$ and $b$. With increasing loop size, the index of effective search $d_T$ decreases, while $b$ increases. Therefore, the search success becomes lower for small distances but higher for large ones. This is confirmed by the curve shape. Small loops express a larger plateau for small distances, but decline faster for large ones.
4.2. The effect of the movement details for Archimedean spirals and the random walk

For the loop-like movement pattern both parameters were found to have a clear functional relationship to the movement details investigated. In the following, we investigate whether the same is true for (uncorrelated) random walk and the Archimedean spirals, and we investigated the nature of the functional relationships (Fig. 3 and Table 1). A change in perceptual range leads to similar functional relationships for Archimedean spirals and the random walk as for loops. For both movement patterns parameter $a$ increases linearly. Parameter $b$ decreases slightly for spirals, but shows no clear trend for the random walk. In both cases, values of $b$ remain nearly unchanged. In correspondence to the loops, the index of effective search $d_F$ increases for both movement patterns (no figure shown). As for the loops, increasing mortality leads to a hyperbolic increase of parameter $b$ for both spirals and the random walk. Parameter $a$ shows no clear trend for both movement patterns; for the spirals, its values remain nearly unchanged. The index of effective search $d_F$ shows no clear trend for the random walk and decreases for spirals in the same way as for the loops (no figure shown).

To summarise, our model results reveal that, under all movement patterns, there are clear functional relationships between the parameters $a$ and $b$, respectively, and the movement details considered. Appropriate fitting functions can be given in all cases. The shape of the fitting functions even seems to be independent of the type of movement pattern considered. This indicates that the fitting functions for $a$ and $b$ listed in Table 1 can actually be used for integrating movement details in the potential accessibility function $R(d)$. Taking the loop-like movement pattern and the movement detail “loop size $l$” as an example, we obtain the function (for $p = 2$, $m = 0.001$):

$$R(d) = 1 - e^{(-1/0.073 + 0.024)} e^{(-1/0.56 + 0.025)d}$$  \hfill (7)

5. Discussion

The aim of our study was to integrate movement behaviour into the dispersal function by Heinz et al. (2005). We achieved this goal by using an individual-based simulation model.

We have shown that there are clear functional relationships between the parameters of the potential accessibility function $R(d)$ and the movement details investigated. We found very simple fitting functions (for an overview see Table 1) to describe these functional relationships. Since the relationships between the parameters and the movement details are qualitatively similar for all movement patterns, most of the fitting functions are valid for all three movement patterns as well. But note that the presented fitting functions only allow the effect of one particular movement detail to be described (because they have been determined by univariate analysis of each movement detail). Therefore, it is not possible to give one single $R(d)$-function for a combination of all three parameters.

We found two measures characterising the shape of the potential accessibility function $R(d)$: the index of effective search $d_F$ and the rate of decline $b$, which allow the effect of the movement details on the landscape connectivity to be ecologically interpreted. These measures can be expressed in terms of the parameters $a$ and $b$. The two measures $d_F$ and $b$ make the effect of the different movement details on $R(d)$ more understandable, allowing rules of thumb about these effects to be drafted. The increasing perceptual range positively affects $d_F$ strongly, but only has a slight effect on $b$. An increase in the mortality risk leads to a decrease in both characteristics, while increasing the loop size depresses $d_F$ but leads to a decrease in $b$. Every effect can be completely described with the two measures.
Parameterisation may often be a problem when working with dispersal functions. The fact that different movement details have different effects on the parameters $a$ and $b$ makes it difficult to estimate the two parameters. This can be overcome by the results presented, which indicate that there is a clear functional relationship between the parameters and the movement detail of interest. Once this functional relationship is known, it is at least possible to perform sensitivity analyses over the reasonable range of values for the movement detail or to integrate the effect of the movement detail in more complex models in a simple way.

In this study, we only investigated three different movement patterns, two movement patterns which are applicable for most animals (mortality and perceptual range) and a more specific movement detail (loop-size). While we could show that the functional relationship between parameters and movement details are similar for these movement patterns, we cannot know how they will look like for other movement patterns. We just investigated an assortment of possible movement details. There surely will be other movement details capable of influencing the parameters of the dispersal function. The general approach, however, as well as the two measures scale of effective search $d_{ef}$ and rate of decline $b$, can be used for investigating the effect of other movement behaviours and details, as Eq. (3) was found to be appropriate for a variety of movement behaviours.

Since the effect of the movement behaviour is summarised in the potential accessibility function $R(d)$ that gives patch accessibility in a two-patch system, we only analysed landscapes with two patches. Once the shape of $R(d)$ is determined, the results can be integrated in more complex landscapes by using the weighting factor. Our results of the effect of movement behaviour on the dispersal function are valid in two-patch as well as in more complex landscapes.

Models need to be simple enough to be understandable and comprehensible (Gillman and Hails, 1997), but at the same time a better integration of behavioural aspects into ecological analyses is needed (Lima and Zollner, 1996; Roitberg and Mangel, 1997; Vos et al., 2001, Morales and Ellner, 2002; Heinz et al., 2006; Heinz and Strand, 2006). Modelling movement behaviour explicitly may complicate models considerably, which is why (meta)population models usually work with formulas. It is essential to be able to integrate species-specific movement behaviour into such formulas in a simple way. Our study aims to bridge between individual- and behavioural-based approaches and modelling theory.

On the basis of our study, it could be feasible to categorise movement patterns and their function parameters. Regarding the overall dispersal function (Eq. (1)), movement patterns with similar $a$ and $b$ values and therefore similar $R(d)$ curves result in similar responses of patch accessibility to changes in landscape configuration. Therefore it could be possible to determine groups of organisms with similar reactions to landscape changes.

### Appendix A. A calculation of the turning point

The turning point $d_{TP}$ of the sigmoidal function $R(d) = 1 - e^{-a - e^{-bd}}$ 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

$$R''(d) = -ab e^{-(a - e^{bd})} [a e^{-bd} - 1].$$

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

### References


