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Corridors as Conduits for Small Animals: Attainable Distances Depending on Movement Pattern, Boundary Reaction and Corridor Width
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Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width

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Corridors are supposed to facilitate and conduct moving individuals between habitat remnants within an otherwise inhospitable landscape. Despite the scientific interest in corridors, their function as conduits is open to question. In this paper we present hypothetical answers to this question based on simulations of individual movements through corridors. Our generic modeling approach is individual-based and spatially explicit. The model is designed to simulate conceivable movements of small animals through line corridors with clear boundaries such as hedgerows. The parameters of the individual movements correspond with empirical data of tracking studies. We define the transition probability as the likelihood that moving individuals attain a distant target area within a certain period of time. We determine the transition probability based on distance frequency distributions. Our results show how the transition probability depends on the degree of movement autocorrelation, the returning angle at boundaries and the corridor width. In general, the transition probability is essentially determined by the degree of movement autocorrelation. The relative importance of both the returning angle at boundaries and the corridor width on the transition probability increases with higher degrees of movement autocorrelation. With increasing corridor width the transition probability increases asymptotically towards an upper level depending on movement velocity and time. Consequently, the corridor width has to be regarded as the main easily modified aspect for controlling transition probabilities. We use our findings to discuss the issue of an optimum corridor width. We take up the important effects of movement canalization within corridors and the way corridors influence both mortality en route and movement velocity. We compare the consequences of these effects on transition probabilities to situations without corridors in order to evaluate corridors in a more unbiased fashion.

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Almost all natural landscapes are usually fragmented for each species because resources are scattered across the landscape. Most species are adapted to this natural kind of fragmentation which also enables the coexistence of various species within a landscape. However, human impact on a landscape scale results in the reduction of natural habitats and simultaneously leads to the isolation of habitat remnants due to partitioning of the landscape with barriers (e.g. arterial roads or agricultural areas). This kind of fragmentation restricts native species to the smaller habitat remnants and additionally impedes the movement of these species between them (e.g. Mader 1984, Merriam et al. 1989, Fahrig et al. 1995, Vermeulen 1995). Consequently, the size of native

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populations and also their survival probabilities decrease. To analyze and evaluate the survival probabilities of species in fragmented landscapes, island biogeographic theory (McArthur and Wilson 1967) has been applied, while metapopulation theory (Hanski 1989) and landscape ecology (Forman and Godron 1986) have among others been developed (see Dawson 1994). This theoretical work demonstrates that the survival probability for species in fragmented landscapes depends on recolonization after local extinctions. Recolonization depends on the exchange of individuals between habitat remnants which has to be accomplished by individual movements across heterogeneous, more or less hospitable landscapes. Therefore all these theoretical approaches are based on individual movements whose study "deserves a key position within all disciplines of ecology" (Ims 1995).

Because movements are restricted in cultural landscapes as mentioned above, the idea of corridors arose as a way of overcoming this restriction. Corridors are thought to conduct species across an inhospitable landscape toward isolated habitat remnants. Corridors have been of scientific interest for about 30 yr and have also been created in landscapes on different scales. For example small strips of vegetation known as hedgerows or fencerows form extensive networks in agricultural landscapes especially in western Europe. Many experimental findings (e.g. Lorenz and Barrett 1990, Merriam and Lanoue 1990, Soulé and Gilpin 1991, LaPolla and Barrett 1993, Lindenmayer and Nix 1993, Bennett et al. 1994, Demers et al. 1995, Vermeulen 1995, Andreassen et al. 1996) and discussions (e.g. Forman 1983, Noss 1987, Simberloff and Cox 1987, Harrison 1992, Hobbs 1992, Bonner 1994, Dawson 1994) have been published. We do not want to repeat this extensive discussion, but we would like to draw the reader's attention to Saunders and Hobbs (1991) and a very critical and constructive review by Dawson (1994). Despite this effort, the function of corridors as conduits remains at issue.

The purpose of this paper is to adopt some crucial aspects often emphasized in former publications. We present a generic simulation model which is adapted to small-scale or line corridors such as hedgerows with clear boundaries. Such corridors can serve small animals as extended habitats by catering not only to their daily needs but also their seasonal movements. We address the question of the extent to which such corridors are capable of connecting otherwise isolated habitat remnants. To answer this, it is crucial to get an idea of the distances achievable by moving individuals through corridors. We use our simulation model to systematically ascertain the impact of three separate factors (movement autocorrelation, returning angle at the boundary and corridor width) on these attainable distances. In particular we are interested in the relative importance of these three factors. Based on our simulations we will discuss the issue of an optimum corridor width. Furthermore, we assess the value of corridors by referring to the destination function of corridors by which individuals are steered along a line towards a target site or region within a landscape. Here we compare our results with simulations in a homogeneous reference situation where individuals could move without spatial restrictions in all directions.

With this work we are responding to the appeal expressed in Dawson (1994: 65) and in Friend (1991: 405) to use the power of simulation models to overcome the present theoretical problems concerning corridors as conduits. Although the model is based on hypothetical assumptions concerning movement description and boundary reaction, our approach is closely related to empirical work, i.e. our model parameters are very compatible with data of tracking studies and can directly be obtained in field experiments. Hints for the design of field experiments and clues for crucial information required for more specific models can therefore be derived from the results of our generic simulation model.

Model

Our model is based on a special methodology we developed for generally modeling individual movements in heterogeneous landscapes. We refer to the complete description in Tischendorf (1995, unpubl.).

The corridor model is designed as illustrated in Fig. 1. The whole area is covered with two different patch types, hospitable habitat surrounded by inhospitable habitat. A border between them acts as a barrier for moving individuals. The hospitable habitat is shaped as a rectangular strip divided into three patches: habitat, starting area and corridor. Boundaries between these patches of equal type are permeable. During simulation we only change the width of the habitat strip. The length of the corridor exceeds the attainable distances of the moving individuals in order to preclude errors due to possible reactions at the right end.

We use a neutral unit of distance measurement for landscape and movement step lengths called *lu*. This measurement defines the relationship between the movement step length and the size of the patches of the landscape.

Individuals are modeled in an object-oriented way, i.e. individuals are defined in terms of objects (see e.g. Silvert 1993). Each individual has a pair of coordinates among other state variables. Because individual positions are points and not areas, movement patterns can be defined vector-based using frequency distributions for step sizes and angles. The movement pattern is described by two parameters, step length and step angle (see Kareiva and Shigesada 1983). Step length is randomly drawn from a negative exponential distribution with a mean of 1 *lu*. The angle between two consecutive steps of movement determines the degree of autocorrelation and is also taken randomly from a stochastic distribution. Based on the biologically plausible assumption that each individual exhibits a movement pattern between two extremes – random walk and directed movement – we model three different movement patterns by using symmetrical distributions for the step angle with the following characteristics:

1. random walk (RW); uniform distribution between $-\pi$ and $+\pi$
2. correlated walk (CW); normal distribution; mean 0; $SD = \pi/6$ (0.5236)
3. directed walk (DW); normal distribution; mean = 0; $SD = \pi/30$ (0.105)

In addition, boundary reactions have to be defined. A boundary encounter is detected if an individual has crossed the boundary. After such boundary crossing, the individual is put back to the previous position from which the next position is calculated by adding special step angles to the angle of the previous movement step (see Fig. 1b–d). Because of this setting back, individuals will return before they really encounter the border line. The attainable distance to the border line varies within the range of the modeled movement step length. We regard this implementation as biologically meaningful because each organism might perceive a boundary with an individual detection distance and react in advance. We distinguish between three different boundary reactions. Firstly, we model a reflection (Fig. 1b). Secondly, an angle of +90° or −90° is added to the previous step angle so that the next position lies inside the original patch (Fig. 1c). Thirdly, we add 180° to the step angle (Fig. 1d), so that the individual returns in the opposite direction. We do not determine the transition probability by counting individuals, at the right end of the corridor. Instead, starting from the initial positions of the individuals, we calculate distance frequency distributions. Note that individuals may return due to boundary reactions or stochastic properties of the movement pattern and therefore can move in both directions, to the right into the corridor (positive) and to the left into the habitat (negative). We only count individuals which covered 'positive' distances because they determine the transition along the corridor. We use the distance frequency distributions to calculate a transition probability which is defined as the likelihood that an individual covers a certain (positive) distance, and therefore attains a defined target area, within simulation time.

Simulations are run with 500 individuals moving independently of each other for 100 time steps. Initially, individuals are uniformly distributed inside the starting area. Their initial direction or starting angle is set to zero (see Fig. 1). Each simulation is carried out with uniform boundary reactions.

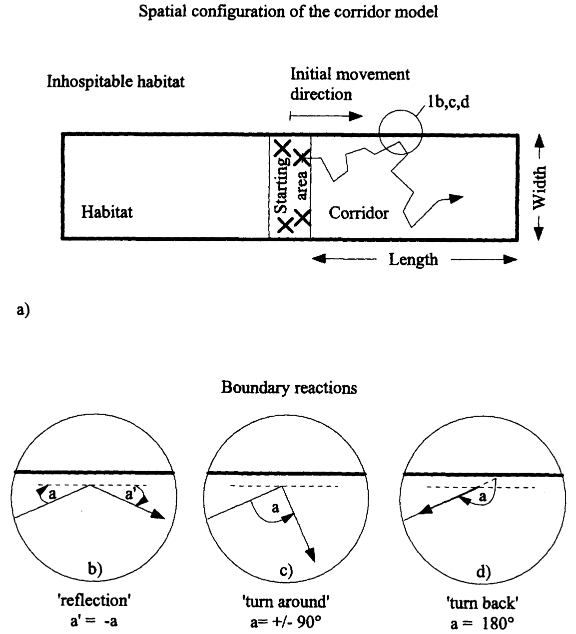

Fig. 1. (a) Spatial configuration of the corridor model. Initially, 500 individuals are uniformly distributed within the starting area moving independent of each other forced by three different stochastic movement patterns. (b, c, d) Individuals return at the boundary to the inhospitable habitat with three different angles whereas simulations are run with uniform returning angles.

Results

Movements without a corridor – reference case

Initially we simulate our three defined movement patterns under homogeneous conditions. We place the 500 individuals in a central area from which they accomplish 100 movement steps without any spatial restriction in all directions. We determine relative distance frequency distributions for each movement pattern (Fig. 2a–c). These distributions provide information about how many individuals achieve a certain distant area within the given period of time. This reflects the displacement potential of the movement pattern which has also been of interest in terms of a mathematical analysis of the mean or mean squared displacement by Kareiva and Shigesada (1983) and McCulloch and Cain (1989). As one can see in Fig. 2, simulated distance frequency distributions provide much more information than their mean value alone, especially in cases where some individuals displace over essentially larger distances than the average and the distribution becomes very asymmetrical.

We calculate the inverse distribution functions of the distance frequency distributions (Fig. 2d–f), which ex-

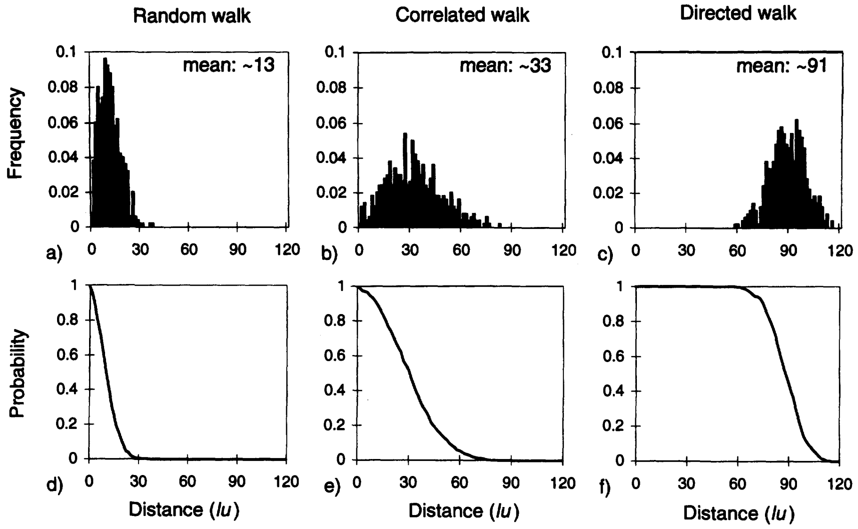

Fig. 2. Reference case. (a–c) Distance frequency distributions of the three movement patterns under homogeneous conditions. (d–f) Inverse distribution functions or probabilities for individuals to cover a distance within simulation time.

press the probability that an individual covers a certain distance within the given period of time. We will use the curves of Fig. 2d–f as references for our further results. However, these reference cases are only valid with respect to the distances attainable by moving individuals. Because corridors canalize movements in one direction, the transition probability includes a spatial aspect, the achieving of a defined target area. We will take up this important aspect below.

Movement pattern and boundary reaction

We carry out simulations as explained above. We simulate all the movement patterns combined with each boundary reaction separately in corridors 2 *lu* and 20 *lu* wide. We calculate transition probabilities for the corridor (positive direction) based on the computed distance frequency distributions. The results are shown in Fig. 3a–i.

At first we observe that almost all the results show common features. Except for the 2 *lu* wide corridor in Fig. 3b the transition probabilities along the corridor completely lie below the reference curves. Although the transition probability is not really comparable with the displacement under homogeneous conditions (as mentioned above), this representation makes clear how strongly the movement velocities are reduced by the different boundary reactions and corridor widths. In general, the displacement potential of almost all movement patterns is reduced, but with different strengths for different subsets of the individuals. We will focus on the special case displayed in Fig. 3b. Here the transition probability exceeds partly the covered distances under homogeneous conditions. That means a portion of individuals is able to cover larger distances within a corridor than without any spatial restriction. In this special case stochasticity of the CW is partly outweighed by the deterministic reflection at the boundary which speeds up the overall movement resulting in larger displacements within the same period of time.

Another common feature of the results is that the transition probability at length ‘0’ is reduced by 0.5, due to the fact that individuals return inside the corridor and walk in both directions. In our model they leave the corridor toward the ‘habitat’. The amount of this reduction can be interpreted as a returning probability within the corridor. This returning probability increases with decreasing movement autocorrelation with one remarkable exception in Fig. 3g. The returning probability for the RW combined with ‘Turn back’ is very low. We did not expect such strong influence of this boundary reaction on the movement directness of RW. So we are also astonished at the opposite effect for ‘Reflection’ and RW as shown in Fig. 3a. These results were confirmed by additional simulations we carried out in corridors 3–5 *lu* wide.

The comparison of the diagrams in Fig. 3 shows two systematic differences. Firstly, the transition probability is predominantly determined by the movement pattern and decreases clearly with decreasing movement autocorrelation. Secondly, as the degree of movement autocorrelation increases, both the type and the quantity (varied by the corridor width) of boundary reactions more strongly affect the transition probability. From these results we can conclude that both the way individuals move and their returning behavior at boundaries determine the transition probability along corridors. While more correlated movement patterns result in comparatively higher transition probabilities, the relative importance of both the type of boundary reaction and the corridor width for the transition probability increases.

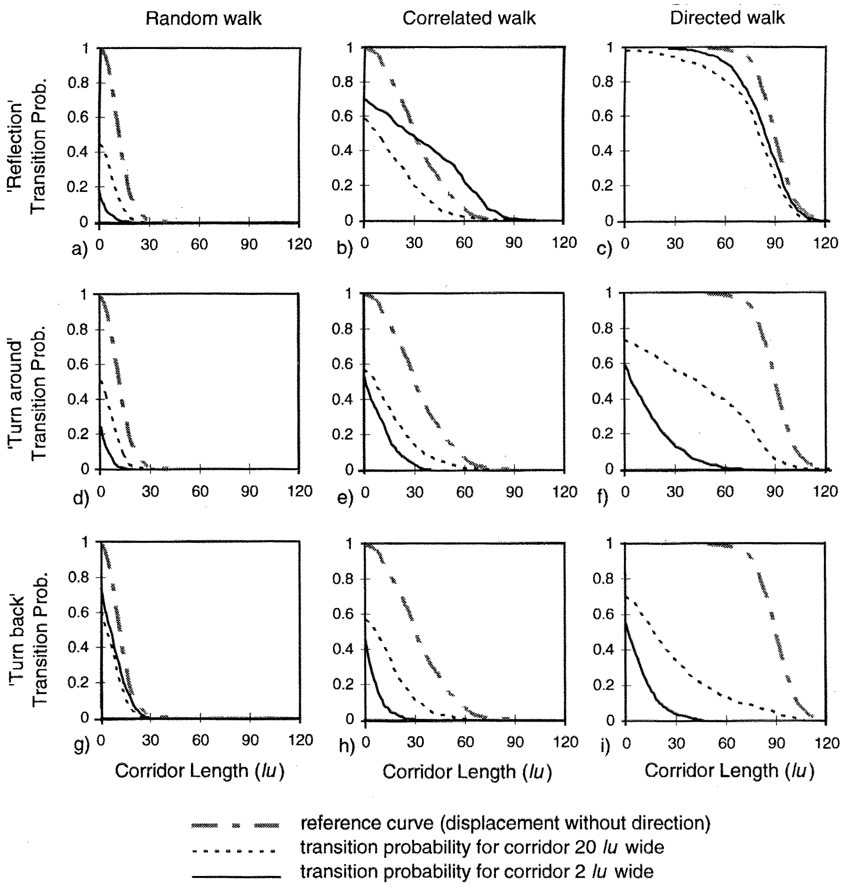

Fig. 3. Transition probabilities determined from distance frequency distributions for all simulated movement patterns combined with all boundary reactions through two corridors with different widths (2 *lu* and 20 *lu*). The comparison of the transition probabilities with the reference curves shows that the movement velocity or the displacement probability are reduced differently within corridors. Except for (b), where the transition probability partly exceeds the reference curve. In this special case the stochasticity of the movement pattern itself is outweighed by the deterministic 'Reflection'.

Corridor width

We determine the effect of corridor width on the transition probability by examining the mechanism responsible for the asymptotic increase of the transition probability with increasing corridor width as also found by Soulé and Gilpin (1991).

The transition probability depends on the small scale velocity (movement step length within a time step), the degree of autocorrelation of subsequent movement steps, and the influence of landscape structure dependent behaviors such as boundary reactions. The last of these plays a crucial part in explaining corridor width, which determines the number of boundary reactions. This quantitative boundary impact is determined by the frequency of boundary encounters for which we introduced a measure, the relative boundary pressure (BP). BP is calculated by dividing the total number of all boundary encounters by the product of the number of time steps and the number of individuals. Hence, BP gives the mean frequency of boundary encounters per movement and time step. We have found by another model (Tischendorf et al. unpubl.) that BP and the perimeter:area ratio (P/A) of a patch are linearly correlated independent of movement patterns and patches size and shape (Fig. 4a). Hence, P/A clearly determines BP and therefore the number of boundary reactions. Fig. 4b shows how P/A is related to the width of thin and elongated strips such as corridors. As one can see, P/A decreases asymptotically with increasing width. Consequently BP decreases approximately in the same way (Fig. 4c) because of the linear relationship between BP and P/A. Based on this finding we explain why the transition probability increases asymptotically with increasing corridor width.

Unlike Soulé and Gilpin (1991), we did not examine mortality near or at boundaries. We have concentrated on what individuals might do if encountering a boundary that acts as a barrier and have investigated the situation where individuals are diverted at boundaries. Such returning boundary behavior is linked to a more or less sharp change in the movement direction. In most cases the autocorrelation of the movement pattern decreases. Less autocorrelated movement patterns result in smaller displacements and hence in smaller transition probabilities. Consequently as corridor width decreases, the transition probability is increasingly reduced except for CW and DM combined with 'Reflection' (Fig. 3b, c) and RW combined with 'Turn back' (Fig. 3g). It is not possible to state a uniform relationship for this reduction, for the transition probability is not reduced uniformly along the corridor length (see also Fig. 3). However, it is significant that generally the increase of the transition probability with decreasing corridor width follows a curve that is approximately inversely related to that of Fig. 4c and therefore shows an asymptotic shape (Fig. 5). The saturation level of the transition probability depends on the distance and the movement velocity of the individuals. This upper level therefore corresponds to the reference curves as shown in Fig. 2d–f. That means the upper level to which the transition probability rises decreases with larger distances within a fixed period of time.

Our finding as well as that of Soulé and Gilpin (1991) contradicts the hypothesis of an optimum corridor width, at least for the assumptions we made for our model. The maximum width corresponds to the optimum because the transition probability shows no peak at a medium width. This issue is taken up in the discussion.

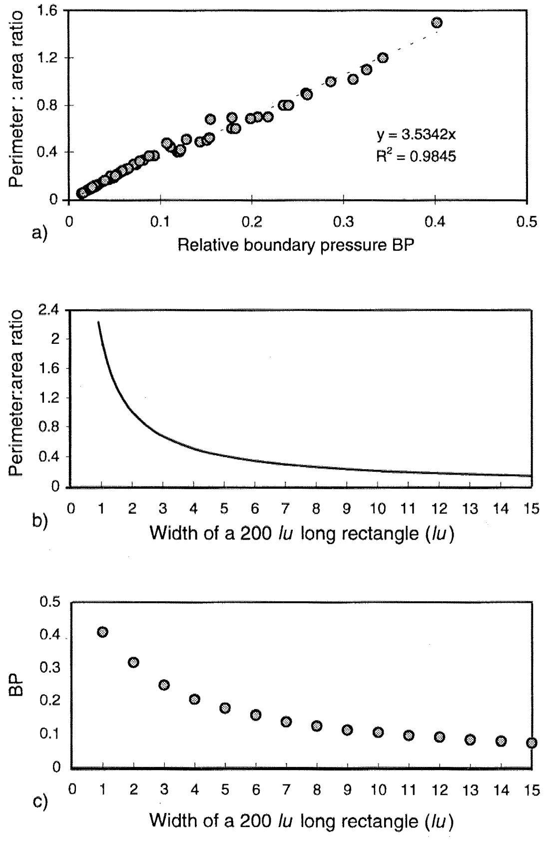

Fig. 4. (a) The relative boundary pressure (BP) is linearly correlated with the perimeter:area ratio (P/A) of patches (see text). This relationship only depends on the mean movement velocity but not on patch size and shape. (b) The P/A decreases asymptotically with increasing corridor width. (c) The relationship between BP and the width of corridors is determined by the relationships of (a) and (b).

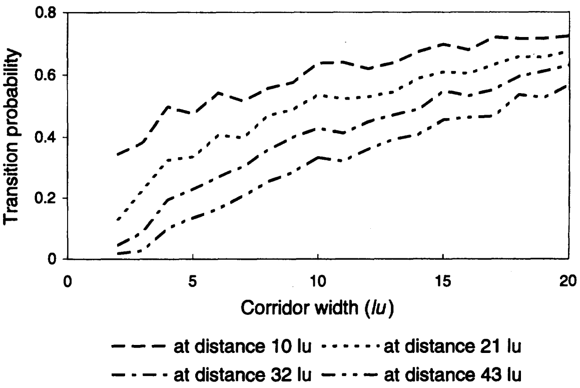

Fig. 5. These curves correspond with the simulations 'DW' combined with 'Turn around' (see Fig. 2e) and show exemplary that the transition probability increases asymptotically towards an upper level. This asymptotic increase is basically determined by the relationships between P/A and BP (see Fig. 4). The maximum attainable transition probability depends on movement velocity and decreases with increasing distance for a fixed period of time.

The significance of movement canalization

In this section we refer to the 'destination function' of corridors as conduits to steer individuals along a line toward a defined target area. Because of this spatial aspect, the transition probability is a spatio-temporal and a very local measure. We defined it above as the probability that an individual attains a distant target area within simulation time. From this point of view, corridors increase the probabilities for moving individuals finding isolated habitat remnants. We examine the effect of movement canalization and highlight its significance for the general evaluation of corridors.

The canalization of individual movements has different consequences. With respect to our modeling assumptions, the movement velocity slows down depending on the boundary impact of corridors. While the displacement probability is reduced, corridors focus moving individuals toward a target area within the landscape. Consequently, the probability of meeting specific landscape locations becomes essentially higher compared with the lack of canalization. We want to explain this by assuming that individuals are not restricted in their movement direction and are not capable of finding their way over large distances. Starting from a central point, individuals would distribute themselves within a circle after a certain period of time. The transition probability for a certain target area within this circle would correspond to the portion of individuals found on that target area depending on both the size of the target area and its distance to the starting point. If we assume that individuals distribute uniformly within a small ring of a circle after moving a certain period of time, the portion of individuals on a target area can roughly be compared with a simple geometric ratio. We will use the geometric ratio between a rectangular target area located at a ring of a circle and the area of this ring (Fig. 6a) to get a quantitative idea how this portion reduces with increasing distance between the starting place and the target area. Fig. 6b shows this ratio for an arbitrary configuration. Because the portion of individuals on this target area further depends on the displacement probability of the individuals, this curve has to be multiplied with some of the reference curves which would reduce it further. Although this comparison is very approximate, it becomes clear that the transition probability without any movement canalization would lie far beneath transition probabilities promoted with corridors. This effect has to be taken into account if corridors are evaluated, in particular for specialists which movements are more likely canalized by corridors.

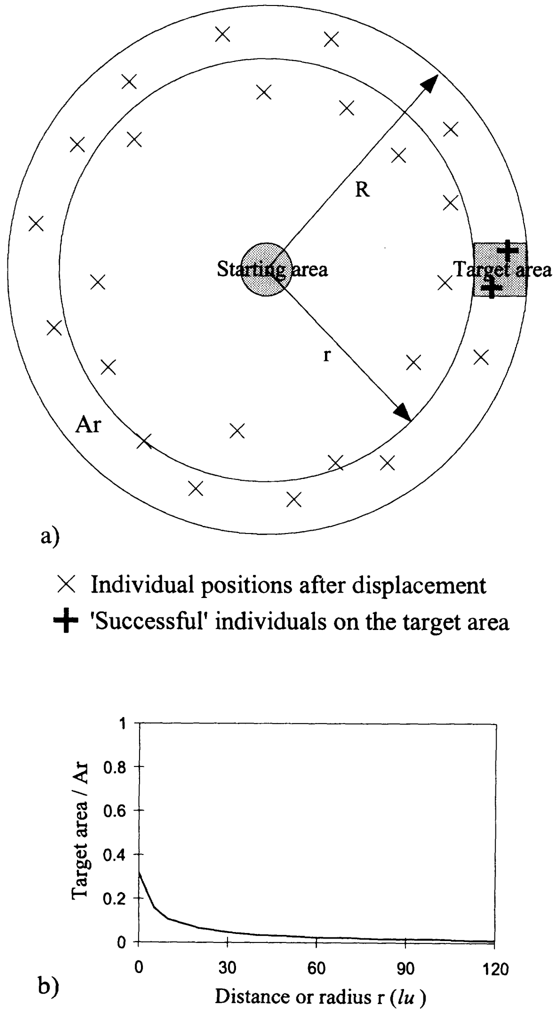

Fig. 6. (a) If individuals move without any canalization they would distribute uniformly within a ring of a circle after a certain time. Based on this assumption the subset found on a distant target area can be compared with a simple geometric ratio between the target area and the area of a ring of a circle, Ar. (b) The geometric ratio for a square 100 lu^2 target area and $R = r + 10$ lu is calculated with the formula: $[100\ lu^2/(\pi \cdot (R^2 - r^2))]$. This ratio lies far beneath most of the transition probabilities of Fig. 3.

Discussion

Our first result (Fig. 2) confirms that the degree of movement autocorrelation of a species strongly determines its displacement capability under homogeneous conditions (e.g. Marsh and Jones 1988, Cain 1991). As the degree of movement autocorrelation increases, the achievable distances enlarge and at the same time more individuals attain shorter distances. We want to emphasize that the shape of the frequency distributions of covered distances differs for various movement patterns (see Fig. 2a–c). The entire distribution provides more information than the mean value alone, in particular when some individuals cover larger distances. Hence, the mean displacement as calculated by Kareiva and Shigesada (1983) is incomplete when describing the displacement capability of a specific movement pattern. Therefore evaluating the whole spectrum of covered distances, as is possible using an individual-based simulation approach, is a step forward.

As we have found, the relative importance of the returning behavior at boundaries increases simultaneously with the degree of movement autocorrelation. While the number of boundary encounters determined by the corridor width is fundamentally decisive for the transition probability, knowledge of the concrete behavior at boundaries only seems to be important for species moving in a straight line. Because it is difficult to measure or to observe what individuals really do at boundaries, this is an important hint for field experiments. The detailed observation of this specific behavior is only important when individuals move fairly randomly.

Our findings about the asymptotic increase of the transition probability with increasing corridor width agree with the model of Soulé and Gilpin (1991) but contradicts experimental results indicating an optimum width as for example by Andreassen et al. (1996). The modeling results are based on the assumptions that individuals return at boundaries or, as in the Soulé and Gilpin model, are more likely to die near boundaries. These assumptions share a common feature. Each boundary encounter reduces the transition probability. Therefore the asymptotic increase of the transition probability is strongly determined by the number of boundary encounters and the way it changes with increasing corridor width (Fig. 4c). An optimum width would correspond with a peak of the transition probability. Because the two existing models do not exhibit such behavior, but experimental results indicate an optimum width, we have to consider the assumptions concerning boundary behaviors. It might be that more complex behavioral patterns within corridors influence the transition probability. We want to give one possible explanation here. Some species might use boundaries as a form of guidance. That would imply a more correlated movement pattern along boundaries with a reduced probability of returning to the middle of the corridor. As a result, more boundary encounters would speed up individual movements and promote the transition probability. Consequently, smaller corridors would increase the transition probability. An opposite effect could be induced by psychological inhibition levels which could prevent species from using small corridors as hypothesized by Andreassen et al. (1996). Both effects together could induce a maximum transition probability for an optimum corridor width.

We want to discuss two additional aspects important for the evaluation of corridors. As we have shown above, the value of corridors can be estimated by comparing the transition probability as a local measure with situations without corridors. In addition to the important effect of movement canalization, corridors can reduce the so called mortality on the journey by providing for the daily needs of moving individuals. It is likely that mortality increases with time and distance covered if individuals have to move across inhospitable territory. This would particularly decimate the small proportion of individuals managing large distances. Because corridors contribute to lower and more balanced mortality probabilities, the transition probability would increase relative to situations without corridors. Another effect could reduce at least the maximum attainable distances. It is known and documented for some species (e.g. Baars 1979, Mauremooto et al. 1995, Vermeulen 1995) that movement patterns vary among different types of vegetation. Individuals often move faster and in a more correlated fashion on inhospitable terrain than on habitat-like areas. Hence, some individuals can cover larger distances within shorter periods of time on open areas. In contrast to this conditional acceleration, individual movements through habitat-like corridors are slowed down due to daily activities and often induced by a relatively high space resistance within hedgerows. From this angle movements through corridors appear "slow but sure" in contrast to "fast but risky" moves across open or inhospitable areas. It remains difficult to evaluate which strategy is more successful for the task of recolonizing local habitat remnants important for metapopulations.

It is noteworthy that the evaluation of the corridor length depends on time. If corridors do not provide a habitat for reproduction or hibernation, time becomes strongly decisive, for unless individuals cross a corridor during one activity period, it will act as a cul-de-sac. The estimation of a maximum corridor length therefore also depends on the temporal behavioral pattern of the target species. Most hedgerows are probably much too long rather than too narrow, at least for invertebrates such as carabids (as we found in Tischendorf 1995).

Finally, we want to stress that the results of the presented model are a first step toward an urgently needed understanding of the complex interactions between individual movements and landscapes. Hence, our results have to be interpreted within the context of the modeling assumptions. Various changes toward more complex models are imaginable such as the incorporation of landscape dynamics, dynamic interactions between movements and the landscape and more complex movement descriptions. However, such complexity should be developed step by step and, whenever possible, closely linked with empirical studies. Our approach lacks this direct link but provides insights in generic relationships and sensitivities which may not be detectable using a very complex model adapted to a certain species within a very concrete corridor situation. Even though our model is a generic one, the model parameters are the same as the data of empirical tracking studies. This permits the interpretation of empirical studies within the frame of this model.

Conclusion

We simulated individual movements through narrow, rectangular corridors. Our hypothetical model corresponds with small scale or line corridors such as hedgerows with clear boundaries acting as barriers for moving small animals. We estimated the transition probability depending on the degree of movement autocorrelation, the returning angle at boundaries and the corridor width. We found that individuals expressing a higher degree of movement autocorrelation are capable of covering essentially larger distances under homogeneous conditions but also within corridors. The returning behavior at boundaries is only significant for the transition probability for species moving in a straight line. The corridor width influences the transition probability for all modeled scenarios in a remarkable fashion, because it fundamentally determines the frequency of boundary encounters. Therefore corridor width generally has to be regarded as the significant structural feature of corridors which can be most easily modified to control transition probabilities.

We take our results as hypothetical references against which concrete studies can and should be evaluated. This can easily be done, because our model parameters can directly be obtained in field experiments which focus on movements of single individuals using for example telemetry.

However, corridors should not only be evaluated by a certain transition probability for a given species. Corridors such as hedgerows often serve as additional habitat areas across vast regions without habitats. Besides, hedgerows provide permanent vegetation in contrast to arable land which loses vegetation after harvesting. Additionally, they provide many other important abiotic features in agricultural landscapes such as various microclimates and the reduction of soil erosion by wind. Therefore they should generally be established and maintained.

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