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A simulation experiment on the potential of hedgerows as movement corridors for forest carabids

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Abstract

Understanding the response of organisms to heterogeneous, mosaic-like landscapes is of key importance for landscape ecology, especially for predicting the consequences of the impacts of landscape patterns on the spatial distribution of species. It is of current interest whether simulation models can carry out the necessary transformation between field data and larger spatial and temporal scales. We present a model which simulates the small scale movements of forest carabids, adjusted to a typical representative, *Abax parallelepipedus*, through hedgerows of different widths and lengths. The modelled individual's responses to the heterogeneous landscape differ because movement patterns, survival times and boundary reactions differ among the different patch types. We evaluate the transition probability through hedgerows as the proportion of the individuals attaining a patch at the end of a hedgerow. Our results predict maximum immigration distances of about 100 m into hedgerows for forest carabids during one season which corresponds with empirical findings based on trapping studies. This result is a promising example that the effect of landscape-dependent movements can be estimated using suitable simulation models and that transformation between the different scales inherent in the empirical methods, tracing and trapping is possible.

Keywords: Simulation model; Movements; Corridors; Hedgerows; *Abax parallelepipedus*

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1. Introduction

Hedgerows are linear strips of vegetation within arable landscapes. They induce many important abiotic properties, such as windbreaks and different microclimates, but also provide valuable biotic qualities such as habitats, refuges or stepping

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stones for small mammals, birds and invertebrates. In addition, hedgerows are supposed to promote the exchange of species between otherwise isolated habitat remnants. With this function they might act as line corridors (Forman, 1983) for moving organisms such as small mammals and invertebrates, for which the vegetation communities and width of hedgerows are most important (Sustek, 1992).

Because of their small spatial dimensions, the influence of hedgerows on species occurrences can be studied comparatively easily. This has mostly been done by trapping to analyse the spatial distribution and density of various species (Mader, 1984; Henderson et al., 1985; Krohne and Miner, 1985; Hansson, 1987; Hingst, 1991; Bennett, 1992; Kromp and Steinberger, 1992; Mommertz, 1993; Bennett et al., 1994; Burel and Baudry, 1994; Hill, 1995; Mauremooto et al., 1995; Vermeulen, 1995; Irmler et al., 1996; Pfiffner and Luka, 1996). These investigations show that an organism was present at a defined position within a certain period of time. This method can be used to ascertain whether species use hedgerows for their dispersion, how extensively hedgerows are used, and how far species immigrate into them (Hill, 1995; Irmler et al., 1996). Although the occurrence of an organism in a trap is the result of its movement across the specific landscape structure, the actual movement behaviour of the organism cannot be observed by trapping.

How the movement behaviour of organisms is affected by specific landscape structures (Ims, 1995), e.g. hedgerows within arable landscapes, is of crucial importance for landscape ecology and other theoretical concepts dealing with population dynamics in fragmented landscapes, such as metapopulation theory (Hanski, 1989) and island biogeography (McArthur and Wilson, 1967). The capability of hedgerows as corridors for different species could be estimated more fundamentally on the basis of insights into the results of boundary dynamics, movement velocities or the form of guidance of border lines and their respective importance. In addition, the understanding of movements along hedgerows could support a general theoretical basis for corridors as conduits urgently called for by Saunders and Hobbs (1991), Dawson (1994) and others.

In this paper our principal aim is to understand the relationship between the modelled movement behaviour of forest ground beetles and their capability of passing hedgerows of different widths and lengths. We simulate individual behaviour dependent on a two-dimensional heterogeneous landscape model consisting of different patch types. With this model we intend to create a realistic reconstruction of how forest carabids might move through hedgerows and to explain the results of trapping experiments with respect to immigration into hedgerows. The model is also a tool to estimate the significance of the parameters for the measured transition probability and to pinpoint areas where more exact data are needed. *A. parallelepipedus* was chosen for modelling because comprehensive knowledge for this species exists and extensive trapping studies within hedgerows have been carried out by the authors. However, the entire data set for this simulation experiment could not be derived by these empirical studies. Therefore in addition we used published movement data of comparable species.

2. Modelling approach

We use a specific methodology for our simulation experiment which is designed to model individual movements within heterogeneous landscapes (Tischendorf, 1995, 1997). The essence of our approach is to separate the modelling of landscape and individuals. Landscapes are modelled using an efficient spatial data structure (irregular grid) designed to represent structural features (line features as boundaries) at a high resolution within a large extent (for scale sector see Wiens (1989), Fig. 1), as appropriate for the species or questions of interest. This has so far not been possible with regular grids for technical reasons. In the context of this paper we use this irregular grid to model a hedgerow as a simple rectangular strip embedded in a landscape with different patch types.

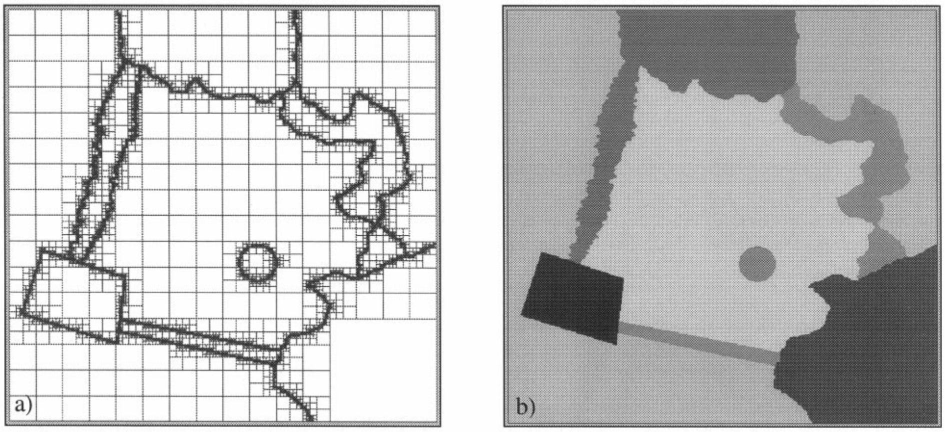


Fig. 1. (a) Landscape modelling based on a special spatial data structure, an irregular grid. It forms the basis for efficient heterogeneous landscape models expressing structural features (boundary shapes) on a wide range of spatial scales; (b) the combination of different sized cells to clusters provides flexible patch and boundary shapes (compare with Tischendorf (1997)).

Individuals are modelled in an object-oriented manner, i.e. individuals are defined in terms of objects (Silvert, 1993). Each individual has a pair of coordinates among other state variables. The pair of coordinates makes individuals both spatially explicit themselves and spatially independent of landscape model units (cells). Our approach has clear advantages for movement modelling. Because individual positions are points and not areas, we are able to define the relationship between two consecutive movement steps in a vector-based manner with two frequency distributions for step sizes and angles. Furthermore, movement steps become completely independent of the cell sizes, a prerequisite for modelling individual movements on every scale of interest.

After their separate definition, the landscape model and the individual-based population model are combined. This is done by projecting individual coordinate pairs onto the area of the landscape model at each time step. Individuals are then allocated to the given patch attributes which are used as parameters for the behavioural rules. In this way we can model patch-dependent individual behaviours or different boundary reactions, as well as many other influences that differ among landscape elements.

3. The model

3.1. Landscape model

The landscape model is structured as outlined in Fig. 2. The whole area is divided into four patches, source, hedgerow, sink and surrounding, whereas the last one summarises three different patch types: cornfield, carrot and fallow, which in turn are used separately for different scenarios. Each patch type induces a different behaviour of the modelled individuals (see below). The patches are separated by boundaries of three different types. They can act as barriers, as permeable borders or they can be completely open for moving individuals. In Fig. 2 the different boundary types are marked by differently shaped arrows.

Initially all individuals are uniformly distributed within the source from which they start to move. During simulation the individuals move through the hedgerow and some of them could attain the sink depending on the width and the length of the hedgerow as well as the patch type of surrounding. The sink can be associated with a modelled pitfall trap, i.e. individuals cannot leave it. By contrast, some of the individuals leave the hedgerow during transition because of the permeability of the boundary to the surrounding.

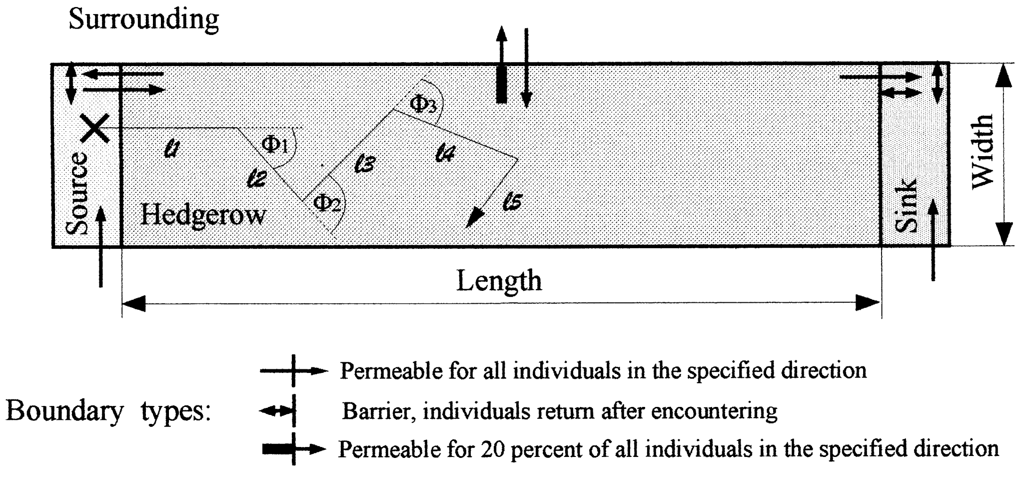


Fig. 2. Spatial configuration of the landscape model. Initially, 1000 individuals are uniformly distributed within the source patch with an initial direction towards sink. Individuals move independently of each other driven by a vector-based, stochastic movement pattern with step lengths l_t and step angles Φ_t (t, time step) drawn from probability distributions (Table 1). In cases where individuals perceive the boundary as a border they return into the hedgerow by adding an angle of $\pi/2$ or $-\pi/2$ to the previous step angle.

We carry out three changes on the landscape model expressing different scenarios. We change the width and the length of the hedgerow as well as the patch type of the surrounding. Our initial simulations are executed with cornfield. Afterwards we change it to the type carrot and fallow to investigate the impact of the landscape context (or composition) on the transition probability since these different patch types influence mortality and movement pattern (Table 1).

3.2. Model for *Abax parallelepipedus*

A. parallelepipedus is a stenotopic, zoophagous species which is predominantly found in beech forests on dry soils (Thiele, 1977). As a forest beetle its dispersal possibilities strongly depend on a dense canopy cover. Hingst (1991) detected a centre of concentration of *A. parallelepipedus* within oak–beech rampart hedgerows in arable lands. We assume that hedgerows represent the only opportunity for *A. parallelepipedus* to spread across otherwise arable landscapes. Tannigel (1991) found intensive interactions between forest and hedgerows for *A. parallelepipedus*, but strongly reduced movements into adjacent grasslands. Irmler et al. (1996) found that silvicolous carabids seldom immigrate into hedgerows further than about 100 m. No significant differences in the movement characteristics between sexes or age-classes for comparable carabids are known (Wallin and Eckbom, 1988) and are therefore not applied in our model.

Timing: we observed a period of peak movement activity for *A. parallelepipedus* between June and August. Furthermore *A. parallelepipedus* preferably moves at dusk and on average 4 h a day (Thiele, 1977). We simulate the real time of movement activity only. We consider 90 days with 4 h a day as the simulation time. Because our simulation follows discrete time steps, we have to identify a time unit. The modelled movement steps should be smaller than the structural features of the landscape, i.e. the width of the hedgerow. Hence the velocity of the real movement is a crucial measure. We use 5 min as a time unit which leads to a mean step length between about 0.2 and 0.4 m. The overall simulation time results in $90 \times 4 \times 12 = 4320$ time steps.

Movement pattern: our approach permits vector-based movement modelling (Fig. 2). This way of quantifying a continuous movement path was introduced by Kareiva and Shigesada (1983) for the mathematical analysis of the mean displace-

Table 1
Parameter values for movement pattern and mortality on the different patch types

Patch type	Mortality (proportion of individuals/time steps) [days]	Movement velocity mean step length (m)[a]	Movement autocorrelation (step angle)
Hedgerow	0.1/4320 [90]	0.17	RW-DW
Source	0.1/4320 [90]	0.17	RW-DW
Sink	0.1/4320 [90]	0.17	RW-DW
Cornfield	0.1/480 [10]	0.16	DW
Carrot	0.1/96 [2]	0.16	DW
Fallow	1.0/96 [2]	0.4	DW

RW, random walk (uniform probability distribution $(-\pi, \pi)$); DM, directed walk (normal probability distribution, mean: 0, standard deviation: $\pi/20$); RW-DM means an alternating movement pattern between these two types changing after 200 time steps (about 4 days).

[a] The step lengths are drawn from an exponential distribution with the corresponding mean value.

ment of a series of consecutive movement steps. The detection of moving individuals in space and time (telemetry or otherwise traced individuals, Wallin and Eckbom, 1988; Johnson et al., 1992a; Riecken and Ries, 1992) can also provide these types of movement parameters. As already mentioned above no quantified movement data for *A. parallelepipedus* were available. To fill this gap we use published data from studies carried out on comparable species, *Pterostichus melanarius* (Baars, 1979) and *Pterostichus versicolor* (Wallin and Eckbom, 1988). Based on personal observations and similar physiological characteristics of the chosen species we assume that *A. parallelepipedus* moves similarly. While Baars (1979) detected radioactively marked individuals daily, Wallin and Eckbom (1988) traced the movements with a portable radar system at night within the period of highest activity at a time interval of 15 min. Both field experiments provide data about the covered distances per time and the degree of the movements' autocorrelation. We adapt these data to our chosen time unit (see above). That means we use smaller step lengths and step angles. We obtain frequency distributions comparable with the original, experimental results after simulating the rescaled movement pattern over the corresponding time. In addition, we adapt the velocity of the modelled movements to the increased space resistance within hedgerows. As a result of a higher vegetation density carabids move slower resulting in smaller step length per time unit.

Furthermore the traced carabids show an alternating movement pattern between periods in which small distances were covered, i.e. random walk, and periods in which the movement activity was much higher, i.e. directed walk (Baars, 1979). This was mainly the case on habitat-like ground. When individuals moved across unfavourable terrain, they moved faster and in a more correlated fashion (Johnson et al., 1992a; Mauremooto et al., 1995; Vermeulen, 1995, p. 92). Additionally the vegetation structure and its lower density accelerate the movement (Crist et al., 1992). This is an example of how movement patterns may vary among different terrains. We adapted our model to these perceptions. Our individuals only express an alternating movement pattern between random walk and directed walk on the patch hedgerow. Outside of the hedgerow they move faster and in a more directed fashion. The parameters for the movement step length and step angle are drawn from probability distributions. The movement parameters for all patch types are summarised in Table 1.

Boundary behaviour: how carabids perceive boundaries is hardly known. However, it is of particular interest for our model what an individual might perceive as a barrier, what it really does after encountering a barrier or to what extent a boundary is permeable. Tannigel (1991) found for *A. parallelepipedus* strongly reduced movements into adjacent fields. We refer to this finding and use our experience of *A. parallelepipedus* to model hypothetical boundary behaviour. As we know, *A. parallelepipedus* prefers dry ground and avoids direct sunlight. It is decisive too, that *A. parallelepipedus* is active at dusk. The boundary between hedgerows and cereal fields is characterised by an extreme contrast between vegetation cover and often by a small strip of grass. At dusk the grass margin would be dewy in contrast to the interior of the hedgerow. For these reasons we assume the boundary between hedgerow and surrounding to be a barrier for 80% of our modelled individuals. We label 20% of the individuals as being able to cross this boundary after ten encounters. All other individuals return after encountering the boundary by adding an extra angle of $\pi/2$ or $-\pi/2$ to the previous step angle so that the individuals return to the hedgerow.

Mortality: the probability of dying for *A. parallelepipedus* mainly depends on food supply and shelter from predators. We assume the best conditions to be within original habitat but also within hedgerows. Here we use a mortality rate of 10% of all individuals over the whole simulation time. The dying individuals are randomly chosen. For individuals moving outside the hedgerow the situation deteriorates. We model different maximum survival times between 2 and 10 days for the different patch types for surrounding (Table 1). We reset the counter for the survival time if an individual attains the hedgerow again after leaving it.

4. Results

4.1. Transition probability in space and time

We define the transition probability as the proportion between the number of individuals attaining the sink at the right end of the hedgerow and the initial number of individuals. The transition probability is a spatio-temporal measure because of the spatial relationship between source and sink, whereas time has to be regarded as being just as significant as the spatial dimensions of the hedgerow. We present the results depending on each of the three variables, hedgerow length, hedgerow width and simulation time separately in Fig. 3(a–c) by fixing two of them in each case. Fig. 3(a) shows the decline of the transition probability with increasing hedgerow length. The shape of the curve is as expected, and as generally known for distance dispersal rates (Wolfenberger, 1946). The essential point is that the transition probability approaches zero at about 100 m for common hedgerow widths. This result clearly corresponds to what we know about the maximum immigration distances of silvicolous carabids into hedgerows (Irmler et al., 1996).

There exists a positive relationship between the width of the hedgerow and the transition probability, as can be seen in Fig. 3(b). The asymptotic levelling up of the transition probability seems to be a general characteristic. The more general models of Soulé and Gilpin (1991) and Tischendorf and Wissel (1997) produce a similar relationship. Note that the transition probability rises to an upper level which is strongly determined by the hedgerow length and more generally by the overall velocity of the moving individuals.

We followed the number of the individuals within each patch during simulation to obtain information about the temporal change of their spatial distribution within the different patches of the landscape model. The dependence of the transition probability on time for differently proportioned hedgerows is represented in Fig. 3(c). This result makes clear that the time is as significant for the transition probability as the spatial dimensions of the hedgerow. While the transition probability generally increases linearly with time, both the delay after which the first individuals arrive at sink and the rate of arriving individuals per time unit depend on the geometrical proportion of the hedgerow. In particular the different slopes of the rising transition probabilities indicate varying landscape resistance for moving individuals. From this we can conclude that both hedgerow length and width determine landscape resistance or connectivity. One might compare this with an effect of friction. In longer hedgerows the movement velocity decelerates due to the increase of this effect.

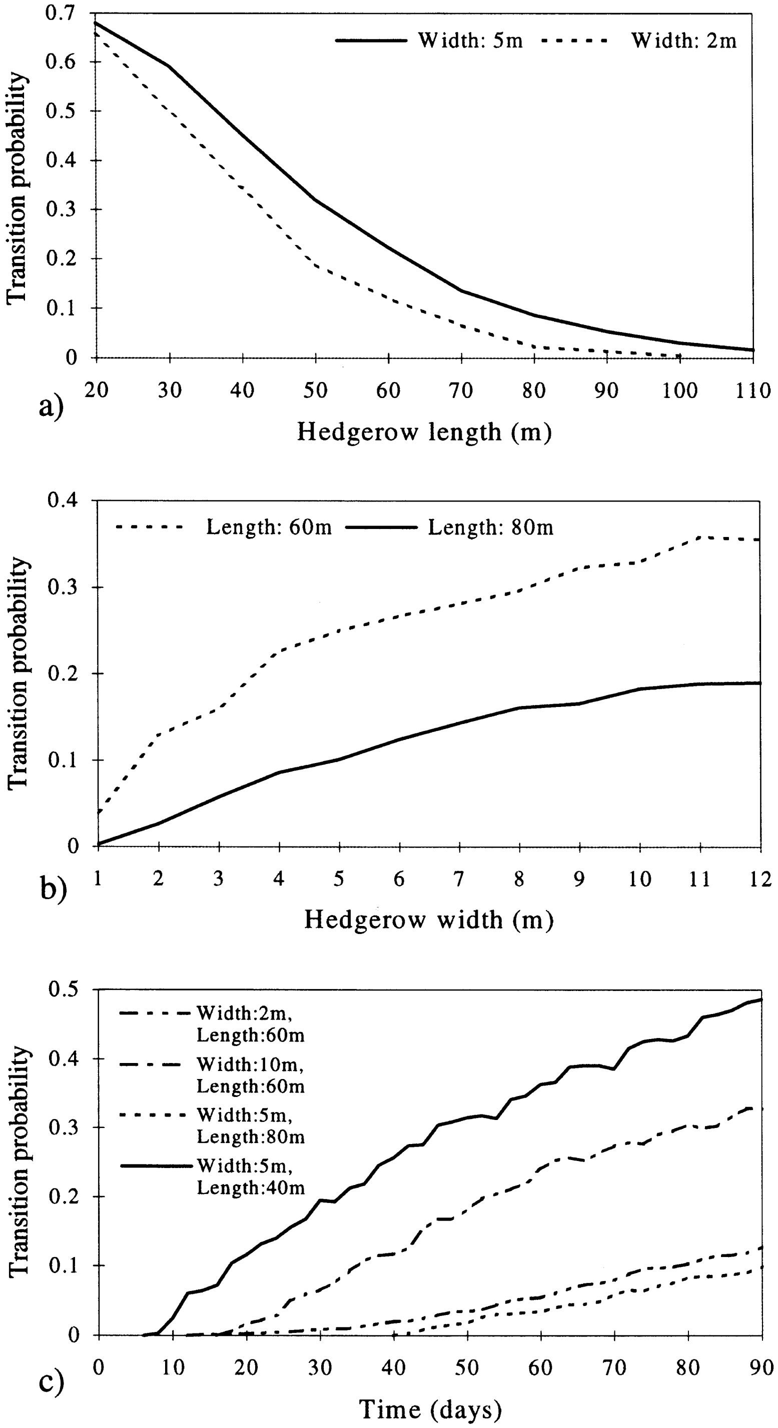
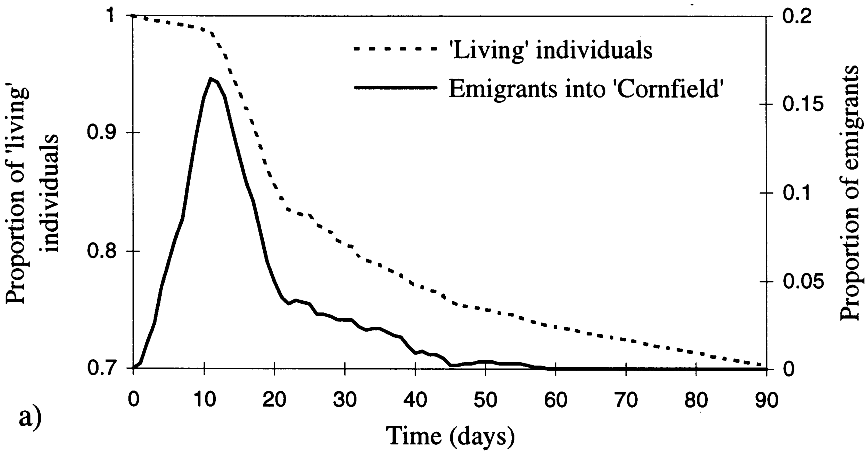


Fig. 3. Transition probability, measured as the proportion of individuals attained at the sink patch depending on the hedgerow dimensions and simulation time. (a) The maximum immigration distances do not exceed much more than about 100 m within one seasonal period of movement activity; (b) asymptotic increase of the transition probability with increasing width. The upper level is determined by the corresponding length or the overall movement velocity; (c) the transition probability increases linearly with time for all hedgerow proportions. The different slopes of the lines indicate different resistances for the moving individuals.



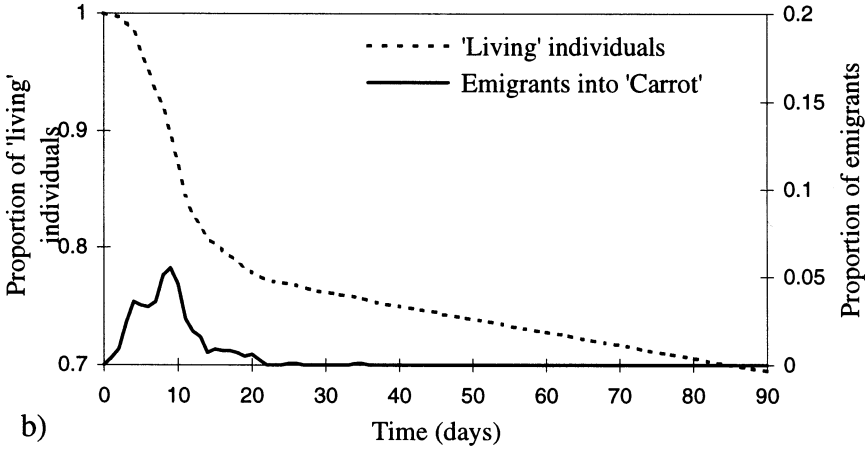


Fig. 4. Dynamic of the emigration into two different patch types of surrounding followed by the decline of the emigrated individuals due to the restricted survival times on the surrounding patch types. These curves correspond to equal configurations of the landscape model (width, 5m; length, 90 m). (a) Peak of emigrants after about 10 days followed by the mortality after 10 days of emigration. The number of all individuals is reduced synchronously; (b) the process of emigration is interrupted by mortality after just 2 days. Hence, the peak is smaller and the probability of returning into the hedgerow is reduced. The process of emigration is finished after about 20 days in contrast to about 45 days as in 4(a).

4.2. Significance of boundary behaviour

Because we assumed the boundary between hedgerow and cornfield to be permeable for 20% of all individuals, the loss caused in particular for the resulting transition probability must be investigated. We follow the number of emigrants into the cornfield and observe their temporal variation together with the decline of the whole number of individuals. Fig. 4(a) shows a peak of emigrants on cornfield by 0.17 after about 500 time steps, which corresponds to a real time of 10 days. Hence most of the labelled (bold) individuals emigrate into the cornfield within a very short period of time, despite the fact that crossing was enabled after ten encounters. After this steep rise the curve falls steeply again synchronously with the decline of the total number of individuals. This indicates that all the emigrated individuals died because of the modelled survival time on the cornfield of 480 time steps (10 days, see Table 1). From the two curves in Fig. 4(a) we can conclude that the frequency of boundary encounters within a hedgerow is very high. As a consequence all potential emigrants will leave the hedgerow early and most of them will probably get lost if the conditions within the surrounding are inhospitable. Hence the permeability of the boundary directly influences the transition probability.

We also found that the returning angle at the boundary between hedgerow and surrounding strongly influences the transition probability for all hedgerow proportions. We executed additional simulations with a returning angle of π so that the modelled individuals returned in the opposite direction. The transition probability was reduced by 90%. It is not possible to state a uniform relationship for this reduction because it changes with the proportion of the hedgerow. However, we have to consider the returning behaviour as a model parameter which significantly influences transition probability.

4.3. Significance of landscape composition

The effect of landscape composition depends on the influence of the different patch types of surrounding on both the movement behaviour and the survival time of the emigrated individuals. We change the landscape composition by subsequently assigning the two other patch types fallow and carrot to the original patch type of the surrounding, cornfield. As a result the parameters for the movement behaviour and the survival time change (Table 1). We consider movements of *A. parallelepipedus* across fallow to be much faster than on cornfield. We assume *A. parallelepipedus* to move similarly on carrot than on cornfield. For both changes the survival time is reduced by 8 days since food supply and shelter are perceived worse than on cornfield.

Because we do not change the boundary permeability between hedgerow and surrounding, only the 20% labelled individuals are affected by this change in landscape composition. The question is whether the changed movement behaviour and the changed survival time on surrounding would reduce the potential loss of the 20% emigrants. As one might predict, these parameter changes could hardly increase the probability of returning into the hedgerow, in particular because of the reduced survival time. Also the increased movement velocity on fallow combined with the higher degree of autocorrelation reduce the probability of returning to the hedgerow. Our simulation results confirm this supposition. Fig. 4(b) shows the same relationship as Fig. 4(a) but for the patch type carrot instead of cornfield. The peak of the emigrants is smaller and the period of emigration is shorter than in Fig. 4(a), because the modelled individuals die much faster after emigration. At the end of the simulations the total number of individuals is reduced by about 30%. Hence, all potential emigrants get lost and the transition probability remains unaffected by the changed landscape composition.

5. Discussion

It is a critical but crucial question for landscape ecology whether it is possible to extrapolate information about organism's movement behaviour on small scales toward larger scales in space and time by movement modelling. This question arises since experimental studies dealing with trapping or tracing organisms are restricted in different ways. Firstly, such experiments are restricted in space and time. Secondly, tracing studies which provide the most insight into the movement behaviour of individual organisms are very protracted and labour intensive and therefore limited to a small number of organisms. Finally, field studies are carried out in one specific landscape configuration, yet conservation plans need information about the consequences of changing landscape structures on movements and their outcomes. From this point of view the modelling of movement behaviours within heterogeneous landscapes could build a bridge between the results of experimental studies and the information needed for critical management decisions. So far, there is not very much evidence that modelling could carry out this task. Only few attempts have been made (Kareiva and Shigesada, 1983; McCulloch and Cain, 1989; Johnson et al., 1992a; Vermeulen, 1995; Wiens et al., 1997). While some of them failed to predict the observed and quantified aspects of the movements (Johnson et al., 1992a; Kareiva and Shigesada, 1983), other models could fit the observed displacements (Vermeulen, 1995). Our work is a further attempt along this line. Our model clearly predicted the known maximum immigration distances into hedgerows for a typical forest ground beetle.

What are the differences between the models and the evaluated measures responsible for the differing success in the prediction of movement outcome?

Johnson et al. (1992a) considered two critical assumptions in their model: (1) beetle movements were strictly confined to areas of bare soil and (2) the description of the movements as a correlated random walk. The first assumption has been relaxed in our model but also for instance in that of Vermeulen (1995). The modelled individuals move differently according to the given patch type and express special reactions at boundaries. Hence, the landscape heterogeneity induces an adequate heterogeneous behaviour of the modelled individuals. This aspect is increasingly considered as important for more realistic movement models as for instance by Johnson et al. (1992b) and Turchin (1991). However, the modification of the second assumption of Johnson et al. (1992a) remains a difficult task. For the sake of tractability of the model and its evaluation, a correlated random walk seems to be one common compromise to describe individual movements. Attempts have been made (Marsh and Jones, 1988; Cain, 1991) to examine the effects of differences in movement models on the long-term displacements. It was difficult to distinguish the different movement models by their output because of the high magnitudes of the S.D. of the mean or mean squared displacements. This implies that detecting an adequate distinguishable movement process in short-term studies is a difficult task. For simulation models dealing with movements within heterogeneous landscapes every attempt to include explicit movement motivations such as memory, orientation and navigation would dramatically increase the modelling input, because this observation level would incorporate very much detailed information into the model. We are aware of one model dealing with memory-based movement decisions within a heterogeneous landscape (Folse et al., 1989). However, it has not been validated against empirical data.

Another factor important for the predictive power of the movement models is the response variable against which the model is evaluated. As we have found in other models (Tischendorf and Wissel, 1997), the mean value of distance frequency distributions does not well represent the displacement of the modelled individuals. Most of our evaluated displacement frequency distributions and also those of Vermeulen (1995) or some of Marsh and Jones (1988) are heavy- or long-tailed, producing high magnitudes of S.D. as mentioned above. Thus, the evaluation of these frequency distributions by the mean value alone may be misleading. In most cases there is no correlation between the maximum distances and the mean values (Vermeulen 1995). The predictive power of the model proposed by Johnson et al. (1992a) was evaluated by comparing the mean squared displacements and the mean first-passage time (after crossing a given circle centered on the origin of the walk). An evaluation based on frequency distributions might provide more detailed information about the reasons for the deviations between modelling results and empirical data.

After this more general discussion we will concentrate on the model presented in this paper. The question remains, what did we learn from this model and what are the most important results? Besides the satisfactory prediction of the maximum immigration distance into hedgerows, we have shown how the transition probability depends on the width of a hedgerow and time. So far, time has not been properly considered to be an important factor for transition through corridors. As Fig. 3(c) shows, the proportions of the hedgerow influence the temporal increase of the transition probability. The different slopes of these lines indicate a different resistance for the moving individuals. In hedgerows the organisms are often confronted with the boundary. If they do not leave the hedgerow they change their movement direction, which causes a delay. This delay increases with decreasing width and increasing length, because the organisms encounter the boundary more often. The linear increase of the transition probability with time permits a transformation to other activity periods of organisms.

The most critical model parameters are those defining behaviour at boundaries. Our results are very sensitive to both boundary permeability and the angle with which the individuals return. The total permeability of the boundary would cause the loss of almost all individuals. Consequently, the transition probability at sink would be reduced dramatically. Estimating this permeability parameter becomes more complicated if organisms are not as well adapted to a certain vegetation cover as the species we have chosen. In such cases the capability of orientation or detection depending on a certain distance would strongly influence the probability of returning to the hedgerow after leaving it and thus the permeability of the boundary. Modifying the returning angle causes a reduction of the transition probability by up to 90%. Despite the unlikelyhood of an organism returning in the opposite direction after encountering a boundary, this extreme modification shows the maximum possible impact on the result.

Finally we would like to draw attention to the scale of the modelled movement pattern. We had to rescale the movement data (as explained above), because step sizes should be smaller than the smallest geometric features of the landscape model. This has to be considered for field studies if the data are intended for use in simulations within various landscape configurations. If the subsequent rescaling of the experimental data fails, the original resolution of the movement data is an impeding factor for simulations dealing with the influences of landscape heterogeneity on displacements of moving individuals.

6. Conclusion

Our model clearly estimates the maximum immigration distances of forest carabids like *A. parallelepipedus* into hedgerows as known by trapping experiments. The measured transition probability approaches zero at about 100 m for common hedgerow widths. From this point of view the transition through longer hedgerows can only be accomplished by more than one generation. Hence, the hedgerow itself has to provide habitat qualities necessary for reproduction if it is to act as a corridor. Our model indicates boundary behaviour to be important to the transition probability. The permeability of the boundary becomes a critical factor, in particular if species show a more indifferent behaviour than specialists such as *A. parallelepipedus*. In such cases additional sources of movement motivation such as orientation have to be included in models dealing with movements within more than one habitat type.

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