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Research article

Adaptive patch searching strategies in fragmented landscapes

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Abstract. The search strategies dispersers employ to search for new habitat patches affect individuals' search success and subsequently landscape connectivity and metapopulation viability. Some evidence indicates that individuals within the same species may display a variety of behavioural patch searching strategies rather than one species-specific strategy. This may result from landscape heterogeneity. We modelled the evolution of individual patch searching strategies in different landscapes. Specifically, we analysed whether evolution can favour different, co-existing, behavioural search strategies within one population and to what extent this coexistence of multiple strategies was dependent on landscape configuration. Using an individual-based simulation model, we studied the evolution of patch searching strategies in three different landscape configurations: uniform, random and clumped. We found that landscape configuration strongly influenced the evolved search strategy. In uniform landscapes, one fixed search strategy evolved for the entire spatially structured population, while in random and clumped landscapes, a set of different search strategies emerged. The coexistence of several search strategies also strongly depended on the dispersal mortality. We show that our result can affect landscape connectivity and metapopulation dynamics.

Key words: adaptive modelling, dispersal, evolution, fragmented landscapes, genetic algorithm, individual-based model, metapopulations, patch searching strategies

Introduction

Dispersal is a key factor driving the dynamics of spatially structured populations and metapopulations (Roff, 1986; Denno *et al.*, 1991; Hanski *et al.*, 1994; Hess, 1996; Anderson and Danielson, 1997; Frank and Wissel, 1998; Thomas, 2000; Johst *et al.*, 2002) and therefore plays a central role in the viability of such populations. Dispersal of animals in fragmented landscapes can be divided into several processes: (1) the emigration of individuals from a habitat patch, (2) movement through a more or less inhospitable environment and (3) immigration into a new habitat patch (Ims and Yoccoz, 1997; Stamp, 2001). These processes are influenced by animal behaviour and physiology (Stamp, 2001): the propensity to leave a habitat patch (Merckx *et al.*, 2003), the behavioural search strategy applied to locate a new habitat patch (Conradt *et al.*, 2000, 2001), and the distance from which individuals can detect new habitat patches (Yeomans, 1995; Zollner and Lima, 1997; Conradt *et al.,* 2000; Zollner, 2000).

The search strategies individuals employ to search for new habitat patches have been shown to affect individual search success (Cain, 1985; Duvall and Schuett, 1997; Duvall *et al.,* 1997; Zollner and Lima, 1999) and subsequently landscape connectivity (Keitt *et al.,* 1997; Wiens *et al.,* 1997; Heinz *et al.,* 2005) and metapopulation viability (Heinz *et al.,* in press). Previous modelling studies have compared different fixed search strategies regarding their search success (Duvall *et al.,* 1997; Zollner and Lima, 1999, 2005; Conradt *et al.,* 2003) and their consequences on metapopulation dynamics (Heinz *et al.,* in press). However, empirical studies show that individuals within one species do not necessarily apply one species-specific fixed movement pattern, but rather a range of different behavioural strategies (Ball *et al.,* 2001; Mauritzen *et al.,* 2001; Merckx *et al.,* 2003; Austin *et al.,* 2004; Heinz, 2004; Merckx and Van Dyck, submitted). In some species, this is due to the fact that individuals are separated into two distinct morphs with different dispersal abilities (dispersal polymorphism; Harrison, 1980; Roff, 1986; Denno *et al.,* 1991). However, even in the absence of distinct morphological differences a variety of behavioural strategies have been found within the same species (de Bono and Bargmann, 1998; Ball *et al.,* 2001; Mauritzen *et al.,* 2001; Merckx *et al.,* 2003; Austin *et al.,* 2004; Merckx and Van Dyck, submitted) and even within the same population (Heinz, 2004). Different patch searching strategies within one population have been found for the grey seal *Halichoerus grypus* (Austin *et al.,* 2004) and the butterfly *Proclossiana eunomia* (Heinz, 2004).

Differences in dispersal behaviour may be associated with sex or age, although in some cases, the reason is less clear. Austin *et al.* (2004) found that neither sex nor age explained all the variation found in the search strategies of grey seals. Individual variation in patch searching strategy may result from learning or a behavioural plasticity that allows adjusting strategies according to information individuals obtain about the landscape. However, this is less likely to explain behavioural differences observed in small, short-living animals like butterflies (Heinz, 2004; Merckx and Van Dyck, submitted). Intra-specific behavioural differences between butterfly populations (*Pararge aegeria*) coming from different landscapes in crossing habitat boundaries and different foraging strategies in the nematode *C. elegans* have been found to depend on heritable variation (de Bono and Bargmann, 1998; Thomas, 1998; Merckx *et al.*, 2003). Many studies indicate that the movement of individuals is influenced by the structure of the landscape (Crist *et al.*, 1992; Gustafson and Gardner, 1996; Wiens *et al.*, 1997; McIntry and Wiens, 1999; Goodwin and

Fahrig, 2002; Pe'er *et al.*, in press; Tuck and Hassall, 2004). Optimal foraging theory has shown that the best strategy for deciding when to leave a patch depends on the spatial distribution of patches (Iwasa *et al.*, 1981). Several authors have suggested that intra-specific variation in dispersal behaviour could result from different landscape structures (Ball *et al.*, 2001; Mauritzen *et al.*, 2001). Modelling studies on the evolution of dispersal rates predict that co-existence of high- and low dispersal rates is favoured by landscape heterogeneity (Cohen and Levin, 1991; McPeek and Holt, 1992; Doebeli and Ruxton, 1997; Mathias *et al.*, 2001). Theoretical and empirical investigations thus indicate that habitat heterogeneity is a driving factor in the evolution of dispersal polymorphism (Roff, 1990; Denno *et al.*, 1991; Roff and Fairbairn, 1991; Langellotto and Denno, 2001).

In this study, we investigated evolutionary robust patch searching strategies of dispersing individuals in three different landscapes: uniform, random and clumped. We analysed whether and under what conditions evolution can favour different, co-existing, behavioural search strategies within one (meta-) population. In particular, we focused our analysis on whether landscape configuration alone (in this study determined by the distance between habitat patches only) can affect different search strategies within one population. We discuss the implications of our results for metapopulation analyses and for the recent discussion of genetic differentiation by dispersal.

Model description

An individual-based model (IBM), written in C++, was developed to investigate optimal search strategies for finding habitat patches in a fragmented landscape. The binary landscape (100 × 100 spatial units) consisted of 16 circular habitat patches in an otherwise inhospitable matrix. Patches were assumed to be equally sized (diameter = 4 spatial units) and to be equally suitable for dispersing individuals. In the beginning of a simulation, individuals were randomly assigned to habitats and then forced to emigrate from their natal habitat patch i to search for a new habitat. Each individual applied a search strategy based on a random walk strategy modified by two behavioural parameters: (1) the correlation degree r determining the straightness of random walk and (2) a bias g shifting the walk in one orientation. Individuals were considered to be successful if they reached a new habitat without depleting their energy reserves, leaving the landscape, or dying while travelling in the interpatch matrix. Based on the successfully arriving individuals, a new population (or generation) of individuals was created and then all individuals were again forced to emigrate to locate another habitat. The previous generation was removed from the model. These processes were repeated for every simulated generation.

The IBM contains a genetic algorithm (GA; Holland, 1975) that uses the theory of natural selection to find solutions to a given problem. In this model, the GA was used to find the best combination of the two behavioural parameters to maximise the arrival success of dispersing individuals. By simulating numerous generations, where one generation inherited the behavioural strategy of the successful individuals of the previous generation, the search strategies most able to deal with the properties of the modelled landscape became increasingly more common. This approach has the advantage that it does not require the modeller to assume *a priori* defined behavioural strategies since evolutionary sound strategies will emerge during the course of a simulation. Genetic algorithms have been widely used in the field of artificial life to evolve behavioural rules (see review Mitchell and Forrest, 1995) and to study behavioural and life-history strategies in animals (Huse *et al.*, 1999; Strand *et al.*, 2002).

Landscape

We used three different distributions of habitat patches: uniform, random and clumped. In the uniform landscapes, habitat patches were evenly spaced with a 25-unit distance between neighbouring patch centres. Patch positions in the random landscapes were determined by randomly selecting x- and y-coordinates from a uniform distribution. If two patches overlapped, the location of the second patch was resampled. Clumped landscapes were generated by first randomly selecting three clump centres. The other 13 patches were, one by one, randomly distributed in the landscapes. If a patch was not within a certain neighbourhood-distance to another patch (10 spatial units) it was resampled.

A 300-unit buffer zone was created around the patch containing area. This buffer zone gave the individuals an opportunity to return to the patch-containing area before reaching the landscape edge. If they encountered the edge of the landscape, they were considered dead. Using absorbing borders rather than reflecting or periodic ones (Adler and Nuernberger, 1994; Schumaker, 1996) seemed, in our case, the most biologically reasonable, as real landscapes do not necessarily have edges between patch-containing and empty matrices that are apparent to dispersing animals. As individuals were tracked during the total dispersal time, substituting one individual that would run out of the landscape by another entering would be pointless (as is typically done in models with periodic border conditions).

Movement

Each individual in the simulation was described by two state-variables; natal patch and position in the landscape matrix (x,y). Furthermore, individuals were described by the two behavioural parameters affecting the patch searching strategy.

The search strategy was based on a (correlated) random walk with a constant step length of two spatial units. Deviation in direction from the previous bearing was determined by turning angles (α). Turning angles were influenced by two behavioural parameters: a correlation degree (r) determining the straightness of the random walk and a bias (g), shifting the average turning angle towards one side.

$$\alpha_i = \alpha_{i-1} + \theta(r) + g \tag{1}$$

The random angles (θ) were drawn from a wrapped Cauchy distribution (Batschelet, 1981; Haefner and Crist, 1994; Zollner and Lima, 1999). The straightness of random walk depended on the mean vector length of the Cauchy distribution, so that for $r = 0$ there was no correlation between steps while for $r = 1$ individuals walked in a straight line.

After leaving their natal patch in a random direction, individuals moved through the landscape applying their search strategy. While moving, individuals faced the risk of dying in the matrix due to limited energy reserves and a (non-starvation) risk of mortality. The mortality risk was modelled by a per-step probability of dying, as is done in various models (Pulliam *et al.*, 1992; Zollner and Lima, 1999; Tischendorf, 2001). We ran our simulations with 6 different per-step mortalities (0.000, 0.001, 0.005, 0.01, 0.015, 0.02). Energy reserves were modelled by the maximum step number (20,000 steps) an individual can take before starving.

We assumed that individuals were able to detect new patches within a certain distance. (Perceptual range; Yeomans, 1995; Zollner and Lima, 1997; Conradt *et al.*, 2000; Zollner, 2000). If a patch came within the perceptual range of an individual (radius of 2 spatial units), the individual travelled to that patch and remained there; this excluded the natal patch. If there was more than one patch within the perceptual range, the individuals choose a patch at random. The number of steps an individual needed to reach a patch was counted.

Reproduction

After all individuals had either found a patch or died, reproduction occurred. We assumed that only individuals fulfilling the chosen fitness criteria could reproduce. Of all individuals reaching a habitat patch, two were randomly chosen. Each individual was then tested against the fitness criteria:

reproduce if:

$$\frac{s_i}{\sum_{i=1}^{N}(s_i)/N} \geq \Phi \qquad (2)$$

where Φ is a randomly drawn number between 1 and 2, N is the total population size of the patch, and s_i the number of steps individual i needed to arrive. All individuals with a step number less than the average were able to reproduce if they were chosen; for individuals with an above average step number the probability to reproduce decreased with increasing step number. If an individual failed to fulfil the criteria, it was resampled from the patch population. When both individuals fulfilled the criteria they produced one offspring. We repeated the process of selecting parents (with replacement) and performing reproduction until a fixed number of offspring per patch (100 individuals) was reached. If a habitat patch was not reached by any individual, no reproduction took place in this patch. If just one individual reached a habitat patch, we allowed reproduction to occur. Since we did not intend to study population dynamics but rather wanted to find good behavioural search strategies, this seemed appropriate. The probability of an individual reproducing was higher in patches reached by few individuals. The fitness criterion was chosen as it entails two important aspects of evolution: (i) only successful dispersers can reproduce and (ii) within the group of successful dispersers, the probability of reproduction increases with decreasing number of steps needed to find the patch. The second aspect reflects the fact that dispersers that reach a patch using fewer steps than average can spend more time in the patch and have more energy reserves left to reproduce. The fitness criterion was based on the population average rather than on a fixed level as this ensures that there is a continuous selection pressure on the number of steps an individual needs to reach a patch, even when search strategies get better adapted.

Offspring inherited the average parameter value of the correlation degree r and the bias g of both parents; taking the average gave the same result as randomly choosing only one of the partners' genes. Mutations in the inherited behavioural parameters could also take place and were determined in the model by (i) the probability of a mutation occurring (prob. = 0.2) and (ii) a mutation step picked from a randomly drawn number in the range [–0.3, 0.3] for r and g. While developing the model, we found these values applicable for allowing changes in the population's gene pool without producing too much noise.

Simulation

Each simulation was initialised by placing 100 individuals in each of the 16 patches. Every individual was initialised with a random correlation degree [$0 < r < 1$] and (if investigated) a random bias [$-\pi < g < \pi$]. The simulations were run for 200–350 generations, depending on the time needed to arrive at stable behavioural parameters. For each landscape type and mortality risk, we performed 5 replicate simulations. For the uniform landscapes, we simulated the same configuration for all 5 replicates while we used 5 different random or clumped landscapes. In some simulations, only the correlation degree r was evolved ($g = 0$ at all times), while in other simulations, both variables, r and g, were evolved simultaneously. We recorded the mean correlation degree and mean bias of the whole metapopulation (i.e. all individuals of all patches), as well as the mean correlation degree and mean bias of each patch (i.e. all individuals residing at one patch).

Results

Metapopulation search strategy

Using the correlation degree between turning angles (r) as the only determinant of the movement behaviour, we found a high correlation degree evolved as the best strategy (between $r = 0.6$ and $r = 0.85$) in the uniform and random landscapes. In the clumped landscapes, a relatively low correlation degree was favoured ($r \approx 0.45$). In both the uniform and random landscapes, the evolved correlation degree increased with increasing mortality risk. The correlation degree varied little among replicates after 350 generations (Fig. 1a), which indicated that the evolutionary stable behavioural parameter was found.

Using both the correlation degree (r) and the turning angles bias (g) to determine the search strategy, a high correlation degree evolved again in uniform and random landscapes (between $r = 0.6$ and $r = 0.85$; exception: uniform landscape with mortality 0.000 $r \approx 0.22$), while a lower correlation degree emerged in the clumped landscape (between $r = 0.4$ and $r = 0.6$; Fig. 1b). The turning angles bias was distinctly higher in the clumped and random landscapes (between $r = 0.13$ and $r = 0.2$) than in the uniform ($r \leq 0.1$). The evolved turning angle bias must be interpreted in connection with the results for correlation degree. A given value for the bias parameter will have greater influence on the resulting search path as the correlation degree increases. This explains the lack of a clear trend for the bias in the clumped landscapes regarding mortality. The large variation in the evolved bias parameter between replicates further indicates that there exists no strong evolutionary force towards one bias value as long as the evolved correlation degree is low. In the random landscape, the bias increased for the highest level of mortality, while for the uniform landscapes, the bias decreased slightly with increasing mortality.

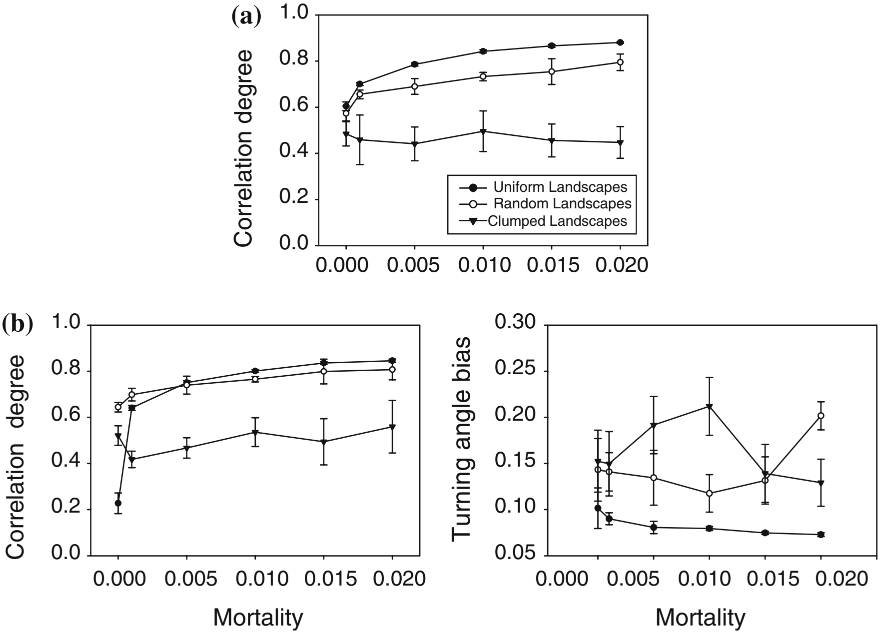

Figure 1. The evolved mean search strategy of the whole population: (a) only the correlation degree is evolved, (b) both correlation degree and bias in turning angle are evolved.

Search strategy on patch level

Concentrating firstly only on *r*, all patches evolved similar mean correlation degrees within all mortality regimes in the uniform landscape; however, large variation in mean correlation degrees emerged for higher mortality regimes in the random landscapes (Fig. 2). This evolutionary path is seen even more clearly in the clumped landscape; at the highest mortality level, three distinct values of correlation degrees emerged during the simulation. When no mortality risk during dispersal was assumed, no differences in correlation degree evolved in either landscape type.

We further examined whether the emerged differences between patches were related to attributes of the landscape. Our simulated landscapes were structured only by the configuration of habitats. A common measurement relating animals' movement to habitat configuration can be obtained by calculating the distance to the nearest neighbouring patches into account (Schumaker, 1996). Hence, we calculated the mean distance between every patch and its two nearest neighbouring patches and tested whether the emerged correlation degree found for a patch could be related to this value. In the random landscape, the correlation degree of patches increased with increasing distance to the next two

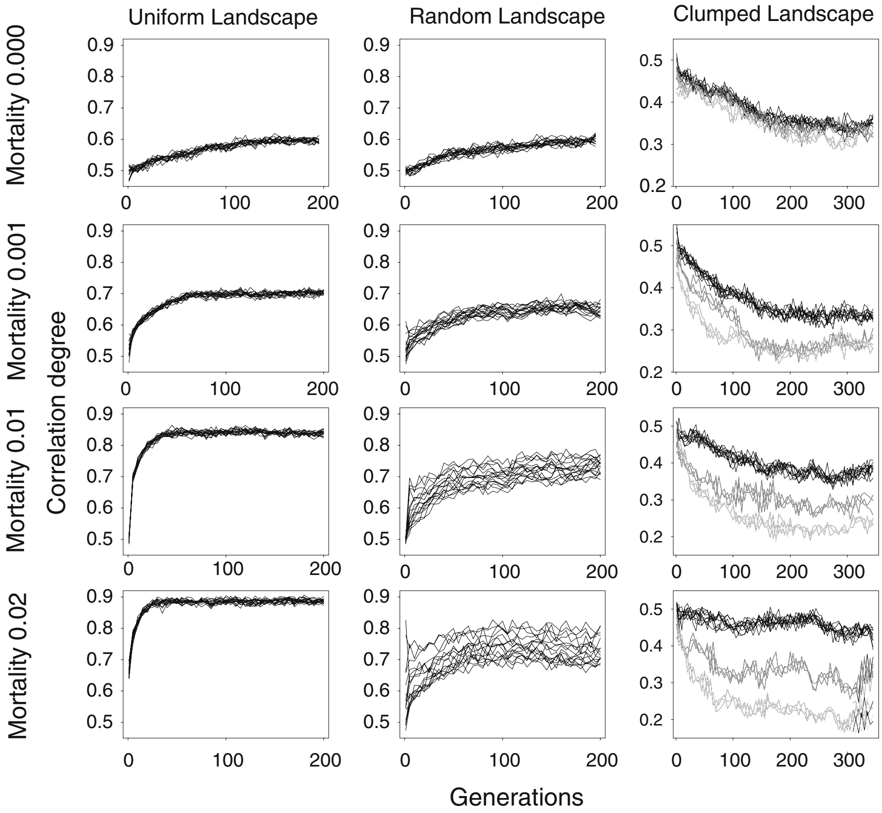

Figure 2. The correlation degree of the single patches under different mortality rates. Each line represents a patch and different line colours in the clumped landscape mark patches that belong to the same clump. In the uniform landscape, all patches evolve to a similar correlation degree for all mortality risks. In the random and clumped landscape, different patches evolve to different correlation degrees, especially when the mortality risk is high.

neighbours and increased with increasing mortality risk (Fig. 3a). For all mortality risks, a linear regression analyses provided a good fit to the data. In the clumped landscape, no dependence of correlation degree on distance to the two next neighbours could be found (Fig. 3b). Within two clumps, the distance of patches to the next two neighbours only varied between 5 and 10 units, making a correlation difficult to detect. However, the evolved correlation degree of a patch was strongly related to the correlation degree of the other patches within a clump. This can be seen in Figure 2 where we marked different patches with different line colours according to which clump they belong to.

When both correlation degree and bias were allowed to evolve simultaneously, the correlation degree evolved to the same values for all patches in the uniform landscape, but differences existed between patches in the random landscape. The bias decreased in these landscapes from the random

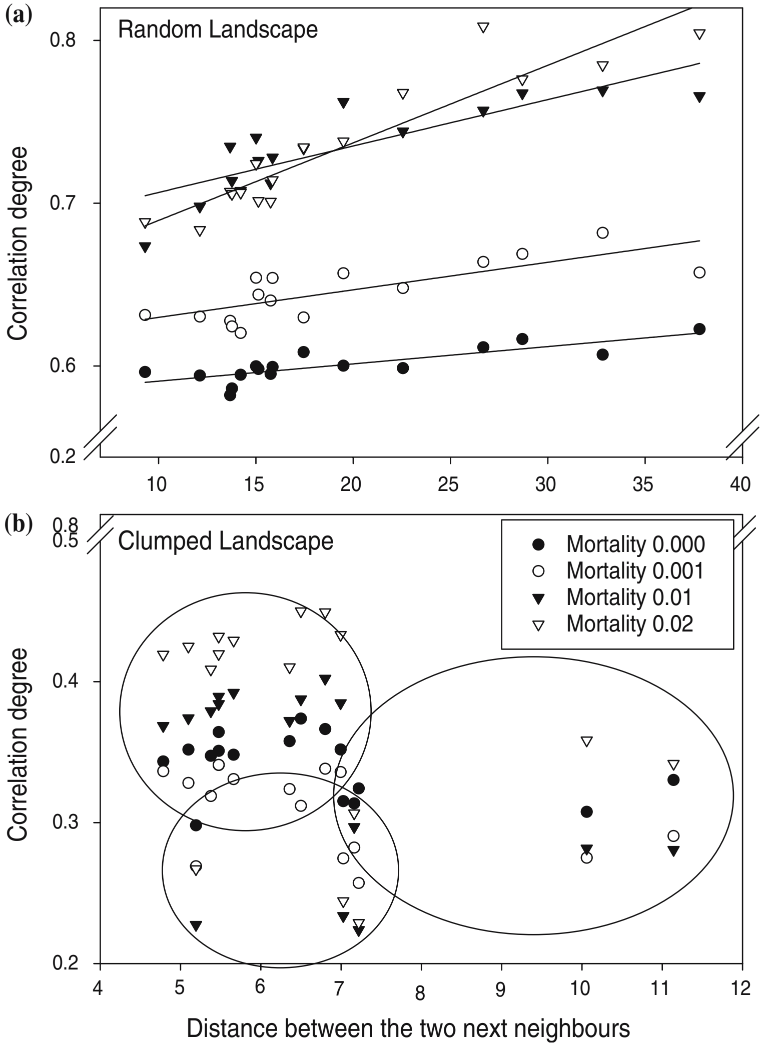

Figure 3. Evolved correlation degree related to the distance to the two next neighbours in: (a) random landscape, where a clear linear relationship exists between the two variables (mortality 0.000: $r^2 = 0.66$; mortality 0.001: $r^2 = 0.59$; mortality 0.01: $r^2 = 0.70$; mortality 0.02: $r^2 = 0.87$; for all mortalities $p < 0.001$), and (b) clumped landscape, where the correlation degree has similar values for all patches within one clump (marked by the large circles) and cannot be related to the distance between the two next neighbours (for all mortalities $p > 0.5$).

initialisation value to a small value and differences did not exist between patches. The results of the clumped landscape were different (Fig. 4). Without mortality, we did not find a clear differentiation between patches. For all other mortality rates, patches were different compared to each other with respect to both correlation degree and bias. In contrast to the first experiment, the correlation degree evolved in different directions from the random initialisation; it

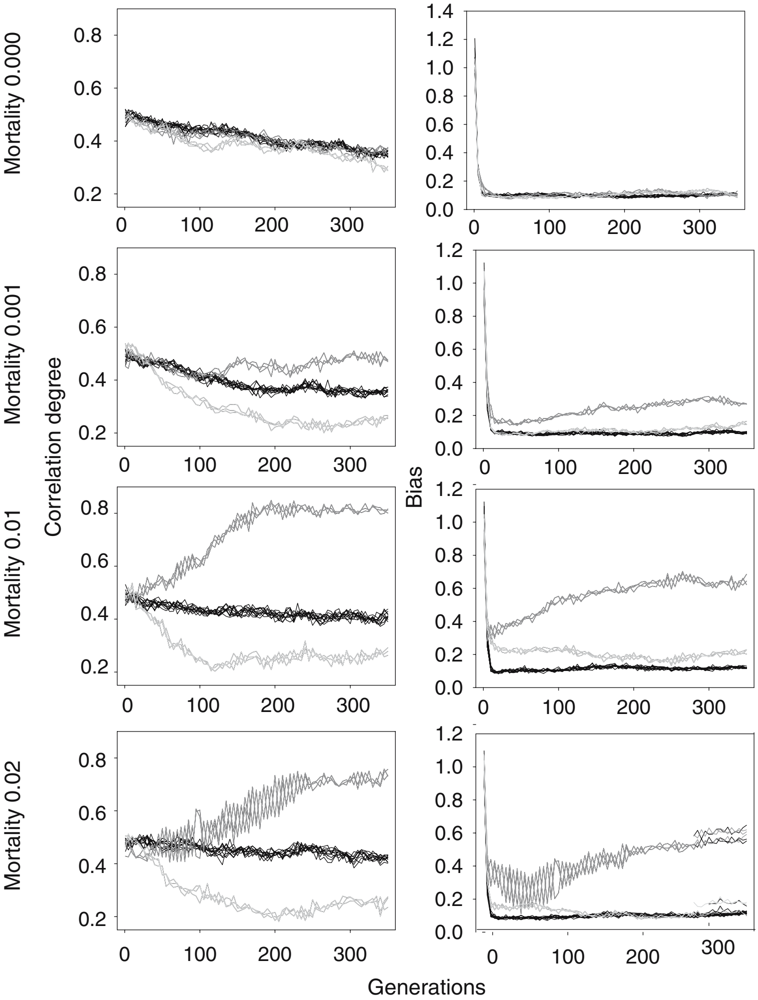

Figure 4. Correlation degree (left) and turning angle bias (right) evolution in different patches of the clumped landscape. Each line represents a patch and different line colours mark patches that belong to the same clump.

decreased in one clump, increased in another, and did not change in the last. The high correlation degree found in one clump corresponded with a high value in the bias. This relatively high bias in combination with a high correlation degree leads to a more looped path including small circles.

The degree to which individuals migrate between clumps was found to be dependent on two factors: the predation risk regime and generation number. Figure 5 shows low risks of predation result in a greater exchange of individuals between clumps and in fewer migrations by individuals between clumps with increasing simulation time.

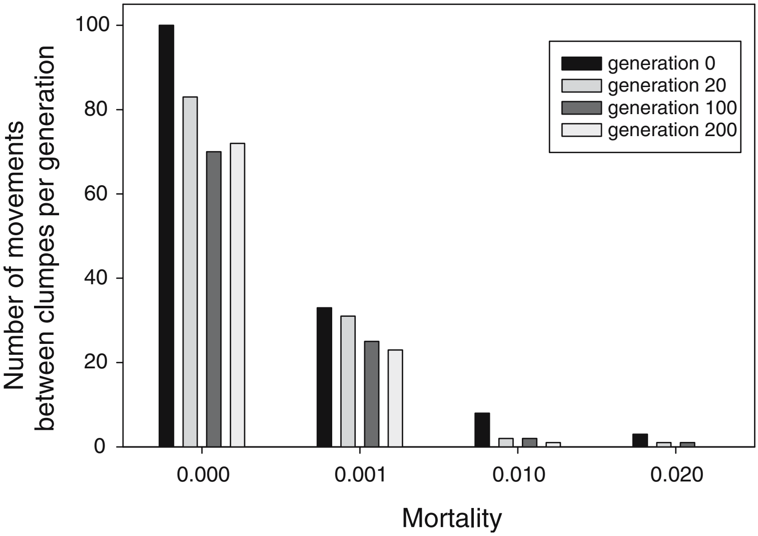

Figure 5. The number of movements between different clumps at different generations and mortality levels.

Discussion

Evolved search strategy

The mean correlation degree of the metapopulation evolved to the highest value in uniform landscapes, slightly lower in random landscapes, and distinctly lower in clumped landscapes. The correlation degree of the random walk increased with higher mortality risk. Qualitatively, these findings match the results obtained by Zollner and Lima (1999). Quantitatively, however, our results predict, on average, a lower correlation degree. The main reason for this variation may be due to differences in the modelled landscape, especially as Zollner and Lima (1999) assumed a much larger area than modelled here. An individual starting from the centre of their modelled habitat, moving in a straight line, will need 550 steps to reach the edge of the patch containing area; this is 22 times more than in our model. Consequently, our modelled individuals have a greater risk of leaving the patch containing area without finding a patch when employing a straightline search strategy. Whereas theoretical considerations suggest a straight search to be the best (Dusenbery, 1992), variation in parameters such as patch density, total number of patches, border conditions, and finite vs. infinite landscapes have previously been shown to affect the optimal correlation degree of random walk (Cain, 1985; Duvall *et al.*, 1997; Zollner and Lima 1999).

The bias, constantly shifting the turning angles of random walk towards one side, developed only to a certain degree in some patches of the clumped landscape and not in the other landscapes. In combination with certain values for the correlation degree, the bias resulted in a looping search strategy where individuals moved in small circles. Such a type of movement has been observed for a variety of animals (Hoffmann, 1983; Bell, 1985; Müller and Wehner, 1994; Durier and Rivault, 1999; Conradt *et al.*, 2000; Bengtsson *et al.*, 2004; Wiktorsson *et al.*, 2004). If a simple rule such as a bias in a correlated random walk can emulate apparent systematic search strategies such as a looping strategy, we might expect to observe such systematic search strategies more frequently in nature – even for organisms with rather poor perceptive or orientation abilities. In a simulation study, Conradt *et al.* (2003) found that a search strategy where individuals move in loops and return to the starting point was especially advantageous in clumped landscapes.

Variability between search strategies on patch level

In the uniform landscape, all patches evolved the same search strategy. However, in the random and clumped landscape, the search strategy evolved towards distinctly different values between patches (with different values for the correlation degree in both landscapes, and different values for the bias in turning angles in the clumped landscape only). These differences within one spatially structured population are purely induced by the configuration of the landscape. In the random landscape, we found that the evolved correlation degree of a subpopulation is correlated with the distance to the next two neighbouring patches. The system thus seems to optimise the search strategy in order to increase the success of finding one of the next neighbouring patches. Several studies found evidence that moving to neighbouring patches can be a favourable strategy. Limiting movement to the closest 3–4 patches was found to be optimal in a study on foraging strategies of hummingbirds (Pyke, 1981) and bighorn sheeps (Gross *et al.*, 1995) as well as on movement strategies for finding mating partners of geckos (Gruber, 2002). Gruber and Henle (2004) found that the movement of geckos between trees could best be described with the rule ‘go to the next 3 neighbours’.

In our study, the level of per-step mortality risk is the key factor to understanding the evolution of a ‘migrate to one of the next neighbouring patches’ strategy, while the spatial configuration of neighbouring patches determines the evolved correlation degree for individuals moving in-between neighbouring patches. A high predation risk acts as reproductive barrier by strongly limiting the flux of individuals between non-neighbouring patches.

In the clumped landscape, there was no correlation between the distance to the next neighbours and the evolved correlation degree. The correlation degree of a patch is related to the correlation degree of the other patches within a clump; the value within a clump may depend on the number of patches and the patch configuration of the clump. Within one clump, the distances between all patches are rather small, and the probability of reaching one of the other patches within a clump is quite high. Selection, therefore, favours searching for other patches within a clump rather than leaving the clump to search for patches outside. To accommodate this, the correlation degree of random walk evolves to a low value and the exchange between the different clumps clearly decreases. As in the random landscape, a higher per-step mortality rate strengthens this trend.

In reality, natural selection is likely to act on more than the two behavioural parameters investigated here. It is thus possible that the effect of model parameters such as mortality would have less impact on the evolved search strategies if other means of reducing the mortality risk (e.g. dusk/dawn migration, short migration steps with long pauses) were available. In future investigations such scenarios might yield interesting insights into more species-specific problems.

We assumed one fixed level of energy reserves and did not investigate the effect of different energy reserves. Energetic constraints were found to influence the optimal search strategy (Zollner and Lima, 1999) and to favour search strategies were resources can be replenished (Conradt *et al.*, 2003). A more exhaustive study of how search strategies are affected by the relationship between energy reserves, step length and distance between patches would be appealing.

Implications for metapopulation dynamics and genetic differentiation

The adaptation of search strategies to the configuration of the landscape can lead to a strong exchange between some patches, but to a lower exchange with others. We have seen that in the random landscape the correlation degree of individuals within a patch evolves in correspondence with the distance to the two next neighbours, while in a clumped landscape it is correlated with the other patches within a clump. The exchange of individuals between patches within a clump increases, while the exchange to outside patches decreases. If we had only concentrated on the mean search strategy of the whole population, such local search strategy adaptations would have been missed.

If local search strategies are shaped by evolution in such a way that individuals only migrate between neighbouring patches, this will have consequences for the connectivity of the landscape and for the viability of metapopulations. Some patches will be more isolated from each other than the mean movement pattern over the landscape would imply. This kind of isolation is not visible from the landscape features as, for example, isolation due to barriers between patches. However, it can strongly affect colonisation rates of patches and therefore metapopulation viability. How strongly metapopulation viability is influenced by this 'hidden' isolation is difficult to tell. This will be a challenge for future work.

Evolved search strategies differed strongly between landscape configurations. If landscapes configuration changes on short time scales, for example due to human activities, individuals will be poorly adapted to the new environment. Removing a neighbouring patch in a random landscape where search strategies has evolved towards finding the nearest neighbouring patch, can result in an unexpected strong decrease of search success. This underlines the need to consider individual behaviour adequately in conservation management.

Our results also contribute to the recent discussion about how new species are formed (Tautz, 2003). Only in the last years, researchers have been able to show that speciation is possible without geographical isolation (Kondrashov and Kondrashov, 1999; Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003). Recently, empirical studies showed that non-random dispersal as a consequence of landscape heterogeneity facilitates genetic differentiation (Coltman, 2005; Garant *et al.*, 2005; Postma and van Nordwijk, 2005). In our model, patches are not isolated from each other *per se*, although few individuals survive a long migration at the highest per-step mortality regime. Due to the adaptation of dispersal strategies some patches become better connected while others become less. Hence, the adaptation of locally optimised search strategies will increase the isolation of some patches to a level where no or very little exchange of genetic material can occur. This can lead to speciation within a metapopulation by splitting it into several groups of isolated patches.

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