

## Effects of cognitive abilities on metapopulation connectivity

Séverine Vuilleumier and Nicolas Perrin

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Connectivity among demes in a metapopulation depends on both the landscape's and the focal organism's properties (including its mobility and cognitive abilities). Using individual-based simulations, we contrast the consequences of three different cognitive strategies on several measures of metapopulation connectivity. Model animals search suitable habitat patches while dispersing through a model landscape made of cells varying in size, shape, attractiveness and friction. In the blind strategy, the next cell is chosen randomly among the adjacent ones. In the near-sighted strategy, the choice depends on the relative attractiveness of these adjacent cells. In the far-sighted strategy, animals may additionally target suitable patches that appear within their perceptual range.

Simulations show that the blind strategy provides the best overall connectivity, and results in balanced dispersal. The near-sighted strategy traps animals into corridors that reduce the number of potential targets, thereby fragmenting metapopulations in several local clusters of demes, and inducing sink–source dynamics. This sort of local trapping is somewhat prevented in the far-sighted strategy. The colonization success of strategies depends highly on initial energy reserves: blind does best when energy is high, near-sighted wins at intermediate levels, and far-sighted outcompetes its rivals at low energy reserves.

We also expect strong effects in terms of metapopulation genetics: the blind strategy generates a migrant-pool mode of dispersal that should erase local structures. By contrast, near- and far-sighted strategies generate a propagule-pool mode of dispersal and source–sink behavior that should boost structures (high genetic variance among- and low variance within local clusters of demes), particularly if metapopulation dynamics is also affected by extinction–colonization processes.

Our results thus point to important effects of the cognitive ability of dispersers on the connectivity, dynamics and genetics of metapopulations.

*S. Vuilleumier, Inst. of Environmental Science and Technology, Swiss Federal Inst. of Technology of Lausanne, CH-1015 Lausanne, Switzerland. Present address: Fish Ecology and Evolution, Eawag, Seestrasse 79, CH-6047 Kastanienbaum, Switzerland (severine.vuilleumier@eawag.ch). – N. Perrin, Dept. Ecology & Evolution, Univ. of Lausanne, CH-1015 Lausanne, Switzerland.*

Owing to the progressive fragmentation of natural habitats, connectivity among habitat fragments has emerged as a major issue in conservation biology. Connectivity affects not only the dynamics of metapopulations through rescue effects and recolonization of extinct patches, but also their genetics, by preventing inbreeding depression and maintaining the evolutionary

potential of small and isolated demes (Fahrig and Merriam 1985, Henein and Merriam 1990, Hansson 1991, Hastings 1991, Taylor et al. 1993, Driscoll 1998, Lande 1998, Akçakaya 2000, Hanski and Ovaskainen 2000, Couvet 2002). The main determinants of connectivity must therefore be accounted for, if fragmented populations are to be managed properly.

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Connectivity obviously depends on properties of the landscape matrix between habitat patches (Dunning et al. 1992, Taylor et al. 1993, Gustafson and Gardner 1996, Couvet 2002). These properties, however, cannot be considered independently of dispersing organisms: travel paths, travel time and dispersal costs actually result from the interaction between animal behavior and landscape structure (Turner 1989, Moilanen and Hanski 2001). The central question thus becomes: How do behavioral decision rules translate into spatial patterns of movements within complex landscapes? (Reed and Dobson 1993, Curio 1996, Lima and Zollner 1996, Ulfstrand 1996, Sutherland 1998, Reed 1999, Caro 1999, Anthony and Blumstein 2000). This is not an easy question, owing not only to our limited understanding of the behavioral mechanisms involved (Lima and Zollner 1996), but also to the practical difficulties in tracking individual organisms in the field (Koenig et al. 1996, Tischendorf 1997).

Computer simulations provide a possible alternative approach, allowing investigations on the potential effect of animal cognitive abilities and decision rules on metapopulation connectivity and colonization probability (Delmers et al. 1995, Backer 1996, Lima and Zollner 1996, Schippers et al. 1996, Schumaker 1996, Carter and Finn 1999, Tischendorf and Fahrig 2000, Moilanen and Hanski 2001). Simulations of animal dispersal have already been conducted by linking a model landscape with a model animal, characterized by behavioral rules and constraints such as habitat affinity (With and Crist 1995, With et al. 1997, 1999) or physiological states (Blackwell 1997, Wu et al. 2000). Such simulations have indeed already been used to assess animal movements (Berg 1993, Sobol 1994, Gustafson and Gardner 1996, With et al. 1997, Farnsworth and Beecham 1999, Bergman et al. 2000) and to provide guidelines for landscape and wildlife management (Lindenmayer and Possingham 1996, Thulke et al. 1999).

These models, however, are limited in terms of information content regarding landscape structure and cognitive abilities of dispersing individuals. In the present paper, we combine a landscape model containing explicit information on the positions, shapes and properties of landscape features that might act as support for dispersal, together with an animal model containing information on the physiological state and cognitive abilities of animals during dispersal. This combination allows simulating a variety of rules of movement, leading to complex interactions between individual and landscape features. Specifically, the simulations presented here were aimed at evaluating the influence of different cognitive abilities and physiological states (energy reserves) on metapopulation connectivity in a fragmented landscape.

## Material and methods

### Landscape model

When dealing with animal movement, landscape is usually represented as a grid of regular cells to which attributes are assigned (Gustafson and Gardner 1996, Lindenmayer and Possingham 1996, Tischendorf 1997, Grimm 1999, Thulke et al. 1999, Wissel 2000). However, the regular geometry of the grid may limit the representation of landscape features (Laurini and Thompson 1992). Linear features such as rivers or roads, in particular, that may strongly influence dispersal, are poorly dealt with in grid-data format. Refining the scale of analysis may somewhat circumvent the problem, but with important drawbacks. Simulation time and data volume increase exponentially with cell numbers, which may prohibit sensitivity analyses (Tischendorf 1997).

Here we use instead a feature-oriented landscape model (Vuilleumier and Metzger, in press), which allows dealing with linear structures and topological relationships among landscape entities without imposing prohibitive computing times. A landscape is represented as a mesh of contiguous spatial entities, irregular in shape and dimension. Two main spatial entities are used: cells (polygons) and frontiers (polylines). Cells are homogeneous areas limited by frontiers. The latter represent linear structures such as rivers or roads, or the transition between two land covers (e.g. borders between forests and fields). Each entity stores as much information as needed to simulate the interaction between an animal and the landscape features, including information on close or distant neighborhood. This allows simulation of dispersal in animals with a variety of cognitive abilities.

### Animal model and simulations

The movements of an animal in a landscape are directed by its searching behavior, mobility constraints, and cognitive abilities. We assumed a model animal in which searching behavior is driven by finding a new suitable habitat patch. Individuals move on the ground across a heterogeneous matrix, and are constrained by energy and mobility. Three dispersal strategies were defined, relying on different levels of cognitive abilities. In the "blind" strategy, the animal has no perception of its environment: cells and frontiers are crossed randomly. In the "near-sighted" strategy, animals have a perception of their immediate environment (neighboring frontiers and cells) and direct movement accordingly. In the "far-sighted" strategy, animals can detect suitable habitats within a given perceptual range (in addition to immediate surroundings). None of these cognitive abilities allowed animals to learn during dispersal. Distant perception (far-sighted strategy) is certainly widespread among higher vertebrates, including most birds and

some mammals (Blough 1971, Etienne et al. 1996, Zollner 2000). Short-sighted strategy might better characterize lower vertebrates and some invertebrates with active dispersal, which only perceive their neighboring environment (Zollner and Lima 1997, Gillis and Nams 1998). Random dispersal is a common assumption for plants (Pearson and Dawson 2005) and might also characterize invertebrates with passive dispersal.

Interactions between animal and landscape features were mediated by three major attributes of cells and frontiers: their attractiveness (AC and AF, respectively, value between 0–1), the possibility to be crossed ( $p_c$  value 1: yes and value 0: no), and the energy cost paid while crossed (see below). The transition probability  $p_{ij}$ , from cell  $i$  to cell  $j$  (through the frontier  $ij$ ) was applied as follows. First, each frontier  $ij$  was attributed a probability of being crossed, depending on its attributes and those of the adjacent cell  $j$ , as well as on animal cognitive ability. In the blind strategy, this probability  $p_{ij,b}$ , only depended on the relative length of the frontier  $l$ :

$$P_{ij, b} = P_c \frac{l_j}{\sum l_k} \quad (1)$$

In the near-sighted strategy, the transition probability,  $P_{ij,n}$ , depended on its relative attractiveness times that of the adjacent cell  $j$ :

$$P_{ij,n} = P_c \frac{A_{F_j} A_{C_i}}{A_{F_k} A_{C_k}} \quad (2)$$

In the far-sighted strategy, finally, the near-sighted rule applied, unless a suitable habitat appeared at a distance  $d_{is}$  within the animal perceptual range  $R$ . In that case, the path presenting the shortest Euclidian distance to the habitat was chosen (i.e. a probability of 1 was attributed to the corresponding frontier, and 0 to all others).

In order to avoid oscillations, animals were not allowed to return to the cell they just left (i.e. the corresponding probability was also set to zero). Probabilities were normalized in order to sum up to one, and pseudorandom numbers were then used to decide which frontier was finally crossed.

When leaving their patch of origin, animals were attributed a fixed amount of energy, progressively used up as cells and frontiers were crossed. Each time-step, an individual had to move from one cell to another. The cost of crossing a cell was calculated as the product of its intrinsic cost (varying with land use; see Appendix 1) by the distance covered. The animal died if energy stores were burnt out before a suitable habitat was reached. Otherwise (new patch reached before death), the run was counted as a successful colonization event, and the path, as well as its ecological cost (total energy spent while traveling) were recorded.

Dispersal was simulated in realistic settings, corresponding to a highly fragmented countryside landscape in Switzerland, in which 13 habitat patches were identified (forest fragments). For each strategy, 50 000 individuals were released in succession from each of the 13 habitat patches, and an arbitrary allocation of 50 000 energy units was made to each individual (in our settings, one unit of energy allowed an individual to cross one meter in an homogenous agricultural cell). The far-sighted strategy was allowed a 100 m perceptual range.

## Connectivity measurements

The results of simulations, in terms of connectivity among habitat patches, were described by the following measurements:

- 1) The colonization success from patch  $i$  to patch  $j$  ( $P_{ij}$ ) measures the proportion of individuals leaving patch  $i$  that successfully reach patch  $j$ . This measure is asymmetric (i.e.  $P_{ij}$  may differ from  $P_{ji}$ ). The overall colonization success of a strategy is the proportion of individuals leaving a patch that successfully reach one of the other patches.
- 2) The flow of individuals between two patches  $i$  and  $j$  is the sum of the two positive unidirectional colonization successes ( $P_{ij} + P_{ji}$ ). High flows have consequences in terms of population genetics (low differentiation among local demes).
- 3) The balance at a given patch is the difference between flows in and out ( $\sum P_{ij} - \sum P_{ji}$ ). Positive values characterize source populations, while negative values characterize sinks. Source–sink dynamics have important consequences in terms of metapopulation viability and genetics.
- 4) The successful colonization events from patch  $i$  to patch  $j$  provide a distribution of ecological costs. The minimal value, median, and standard deviation of these distributions were also used to describe connectivity, since the colonizing success of different cognitive abilities are likely to interact with the amount of energy reserves provided.

## Results

### Colonization success, flow and balance

Simulation results show that the metapopulation structure strongly depends on both cognitive abilities and energy reserves. Among 650 000 runs, the blind strategy generated 241 092 successes (37.1%), the near-sighted strategy 121 617 successes (18.7%), and the far-sighted strategy 247 207 successes (38%). The spatial distribution of flows is provided in Fig. 1. The blind strategy (Fig. 1a)

ensured the highest connectivity, with 89% of the total possible connections realized (each patch was connected with 10.6 other patches) and no spatial substructure.

This contrasts heavily with the near-sighted strategy (Fig. 1b), which realized only 33% of feasible connections (each patch was connected with 4.1 other patches),

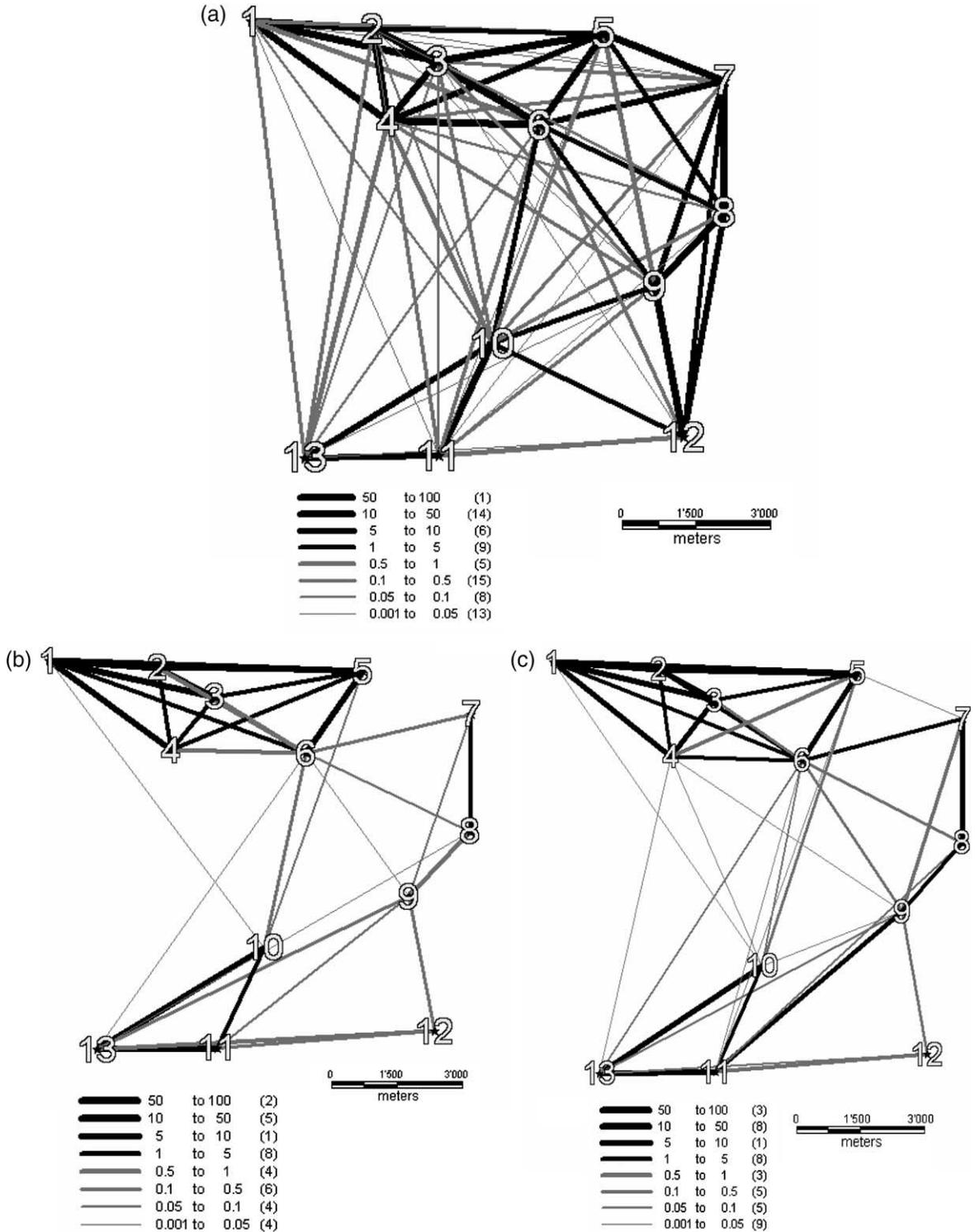


Fig. 1. Spatial representation of the overall exchange of individuals between patches for the blind strategy (a), near-sighted strategy (b) and far-sighted strategy (c). In gray, values of individual fluxes are between 0% and 1%, and in black, values are larger than 1%.

and divided the metapopulation into three poorly connected clusters. The far-sighted strategy (Fig. 1c) was lying in-between, with 42% of feasible connections realized (5.0 connections per patch), and variable connection intensities (low flows between distant patches and high flows between close patches). These differences among strategies were significant ( $\chi^2$  Kruskal–Wallis = 24.47, p-value = 0).

Cognitive strategies also affected source–sink dynamics (Fig. 2). Flows were balanced in the blind strategy, while disequilibrium dynamics prevailed in near- and far-sighted strategies, leading to source–sink behaviors. Substructures also emerged at this level, since the source–sink dynamics were mostly marked in local parts of the landscape (western part; Fig. 2).

The high connectivity resulting from the blind strategy was made possible by the high energy reserves values assigned to dispersers. Indeed, the probability distribution of the median values of ecological costs paid by successful colonizers (Fig. 3) shows that the mode for the blind strategy is very close to the maximum allowed (50 000). By contrast, the short-sighted strategy presents a maximum at 30 000, while the long-sighted strategy does the best at low cost values (less than 10 000). In

other words, the relative success of cognitive strategies strongly depends on the amount of energy available: had we fixed the energy stores at 10 000, then the long-sighted strategy would have provided the highest colonization success.

Finally, colonization success showed stronger correlations with the median, minimum, and standard deviations of the energetic costs distributions in the blind strategy than in the two others (Table 1), highlighting the fact that the near- and far-sighted strategies may provide high colonization probabilities at low ecological costs.

## Discussion

Simulation approaches have already been taken to investigate the consequences of animal dispersal strategies in terms of search efficiency (Zollner and Lima 1999), dispersal patterns (Morales and Ellner 2002), dispersal success (With et al. 1999, King and With 2002) or extinction–colonization balance (Conradt et al. 2003). These approaches were based on a raster system where the perceptual range or distance habitat affinity analysis must correspond to the cell size, or a multiple

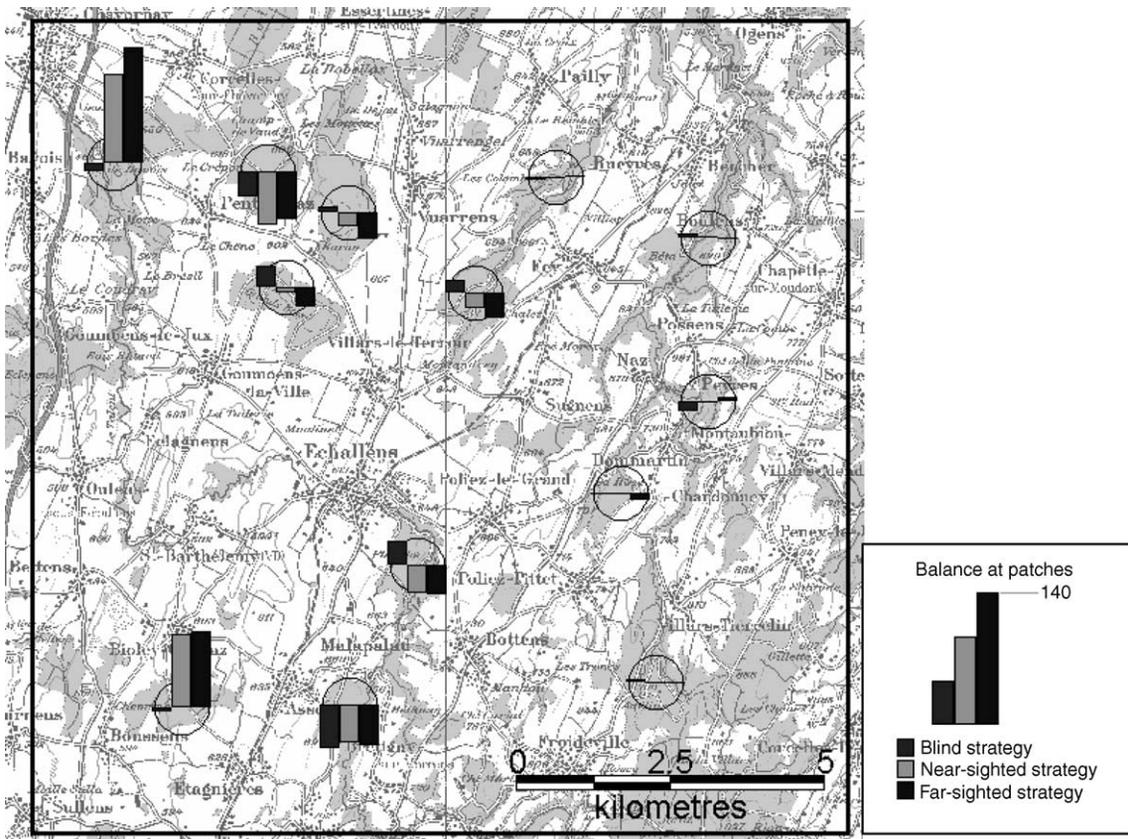


Fig. 2. Balance at each patch (absolute difference between in and out fluxes) for the blind, near-sighted and far-sighted strategies. A positive value represents a net gain of individual and a negative value a net loss.

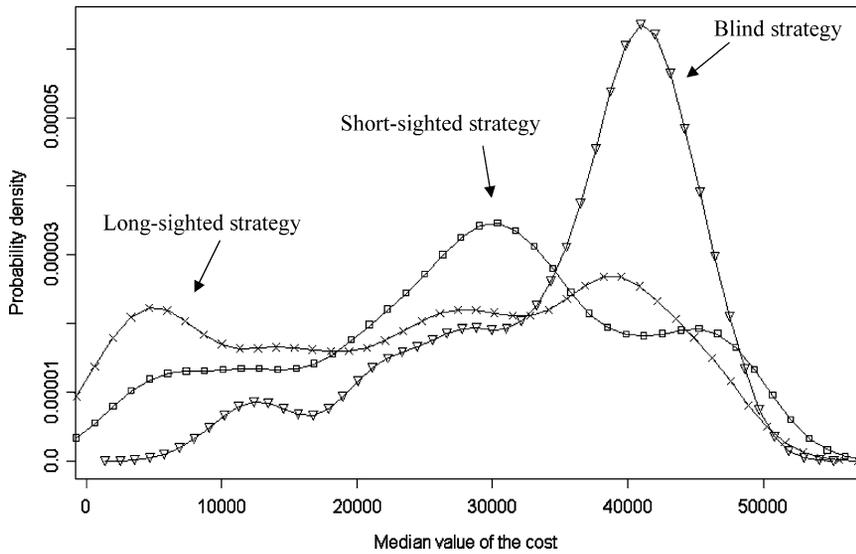


Fig. 3. Probability density functions for the median values of the ecological cost distribution between two connected patches.

thereof (With and Crist 1995, Gustafson and Gardner, 1996, With et al. 1997, 1999, Farnsworth and Beecham 1999, Bergman et al. 2000, King and With 2002) and have used simple dispersal algorithms such as percolation or random walk (be it pure, correlated or biased). Our contribution goes one step further by allowing model organisms a distant perception of landscape elements and a specific knowledge of their environment. Different continuous values (metrics) can be used for patch size, dispersal movement and perceptual range. Our results point to crucial effects of cognitive abilities on several important properties of metapopulations, including overall colonization success, overall landscape connectivity, and balance of exchange (sink–source dynamics).

From our results, the blind strategy did better than the near-sighted and far-sighted strategies on most main counts, at least as long as energy reserves were high enough. Not only did it provide the best colonization success, but it also allowed connecting the whole landscape (Fig. 1a): even the most remote and isolated patches had a non-zero probability of being reached from any other such patch. Flows, furthermore, were balanced, with immigration equilibrating pretty well emigration in most patches (Fig. 2).

By contrast, the near-sighted strategy did the worst under these conditions, providing the lowest colonization

success and overall connectivity (Fig. 1b): strong substructures emerged, with parts of the landscape disconnected from others. Flows, furthermore, were strongly unbalanced, generating a source–sink behavior. The far-sighted strategy appeared intermediate on these counts, though often closer to the near-sighted strategy in general.

Though surprising at first sight, this pattern is readily understood when considering the searching behavior characterizing the three strategies. The blind strategy induces a diffusive prospecting of the landscape. Random dispersal should indeed maximize connectivity, provided energy reserves, mobility, or propagule numbers are high enough. By contrast, the local attraction to neighboring cells that characterizes the near-sighted strategy canalizes dispersal: emigrants are trapped into a limited set of fixed paths determined by local structures and corridors, which fragments the metapopulation into independent substructures. Poorly attractive cells or frontiers have the potential to act as barriers, in effect preventing connection. Differential attractiveness also has the potential to induce asymmetries in paths, resulting in the unequal dispersal and source–sink behavior that characterizes this strategy. In the far-sighted strategy, finally, adding a perceptual range allows targeting suitable habitats from some distance, which partly breaks down the canalizing process. Some patches

Table 1. Kendall's correlation and associated P-value between colonization probability and the median, minimum and standard deviation of ecological cost.

Strategy	Median/Prob.		Min/Prob.		StDev/Prob.	
	Kendall r	P-value	Kendall r	P-value	Kendall r	P-value
Blind	−0.75	0	−0.86	0	0.74	0
Near-sighted	−0.46	0	−0.58	0	0.37	0.0001
Far-sighted	−0.48	0	−0.61	0	0.23	0.0072

may become connected even when separated by poorly-attractive cells or frontiers.

The relative performances of strategies were highly dependent on the initial level of energy. As evident when considering the distribution of ecological costs, the blind strategy was successful only insofar as initial energy was high (50 000 units in our simulations). For medium values (30 000 units), the near-sighted strategy would do best, and for low values (10 000), the far-sighted would outcompete the two others. Better cognitive abilities should thus be selected for as soon as energy reserves (or mobility, or propagule numbers) are limited.

It is worth noting that, in our simulations, unbalanced dispersal (source–sink dynamics) emerged only from the asymmetry in paths and corridors generated by the landscape structure (in interaction with the cognitive abilities of the focal species), and not from local dynamics (good vs bad patches). Coupling our dispersal model with a population dynamics model would presumably unravel other interactions of cognitive abilities with metapopulation dynamics. Similarly, coupling our dispersal model with an evolutionary model would unravel the selective pressures imposed by specific landscape on cognitive abilities. Depending on landscape heterogeneity and energy stores allowed, bet-hedging- or plastic strategies, rather than pure strategies, might be selected for.

Metapopulation genetics is also likely to depend on the cognitive strategies investigated here. The blind strategy should provide the highest effective population size, due to a combination of balanced dispersal and high colonization success. Together with widespread connectivity, this high colonization success should also ensure low genetic differentiation among local demes (low  $F_{st}$  values). In case of extinction–colonization dynamics (to be expected under metapopulation settings) these  $F_{st}$  values should furthermore decrease as extinction rate increases, owing to the migrant-pool pattern of colonization generated by random dispersal (Wade and McCauley 1988, Whitlock and Barton 1997).

By contrast, the near-sighted strategy is expected to induce a high substructure (high  $F_{st}$  among population clusters), further boosted by the source–sink dispersal behavior. Extinction–colonization dynamics should in that case reinforce  $F_{st}$  values, owing to the propagule pool model of dispersal that characterizes this strategy (immigrants in one deme stem from a restricted pool of neighboring demes, Wade and McCauley 1988). The effective size and genetic variance of local demes should therefore be lower than under random dispersal.

Our results also suggest that the relevance of any management action aimed at improving connectivity in fragmented landscape is likely to depend on the cognitive abilities of the species under focus. In particular, the blind strategy appears much less likely to respond to management scenarios. Some cognitive abilities are

obviously required to make full use of corridors. Random dispersers cannot be directed.

Simulation approaches clearly have their limitations (Grimm et al. 1999, Wyszomirski et al. 1999), stemming e.g. from the uncertainty about assumptions (Beven 2000), the sensitivity of results to parameter values (Ruckelshaus et al. 1997), the lack of generality and difficulty in interpreting results (Lorek and Sonnenschein 1999). However, the point must also be made that simulations sometimes provide the only way to address certain questions, including the present one. This is due not only to the practical difficulty of obtaining information on animal dispersal in fragmented landscapes, but more basically to the necessity of isolating the effects of one biological trait (cognitive ability), which, in real organisms, necessarily correlates with a series of life-history traits likely to interfere with connectivity (mobility, energy reserves, propagule numbers, etc). Though details of our simulations certainly depend on specific assumptions on the model organism and landscape features, our main assumptions are general enough that the main results should prove robust, and hold under a variety of ecological and simulation settings.

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## Appendix

Values of attractiveness and cost assigned to landscape spatial entities

Landscape entities	Attractiveness	Cost
Frontiers		
First category road	0.1	6
Second and third category road	0.2	4
Railroad, road bridges, fourth, fifth and sixth category road	0.4	2
Stream	0.4	2
Hedges, fruit trees and rivers	0.6	1
Lake	1	8
Cells		
Rivers	0.4	2
Quarry, fallen rocks, rocks	0.5	1.5
Fruit tree	0.7	0.8
Lake	0	8
Inhabited area	0	8
Cultivated land	0.6	1
Forest, scattered forest, swamp and bush	0.8	0.5