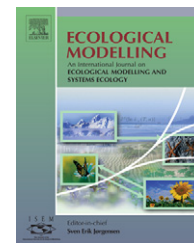


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Incorporating the perceptual range of animals into connectivity models

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ABSTRACT

The perceptual range of an animal towards different landscape elements affects its movements through heterogeneous landscapes. However, empirical knowledge and modeling tools are lacking to assess the consequences of variation in the perceptual range for movement patterns and connectivity. In this study we tested how changes in the assumed perception of different landscape elements affect the outcomes of a connectivity model. We used an existing individual-based, spatially explicit model for the dispersal of Eurasian lynx (*Lynx lynx*). We systematically altered the perceptual range in which animals recognize forest fragments, water bodies or cities, as well as the probability that they respond to these landscape elements. Overall, increasing the perceptual range of the animals enhanced connectivity substantially, both qualitatively and quantitatively. An enhanced range of attraction to forests had the strongest impact, doubling immigration success; an enhanced range of attraction to rivers had a slightly lower impact; and an enhanced range of avoidance of cities had the lowest impact. Correcting the enhancement in connectivity by the abundance of each of the landscape elements in question reversed the results, indicating the potential sensitivity of connectivity models to rare landscape elements (in our case barriers such as cities). Qualitatively, the enhanced perception resulted in strong changes in movement patterns and connectivity. Furthermore, model results were highly parameter-specific and patch-specific. These results emphasize the need for further empirical research on the perceptual capabilities of different animals in different landscapes and conditions. They further indicate the usefulness of spatially explicit individual-based simulation models for recognizing consistent patterns that emerge, despite uncertainty regarding animals' movement behavior. Altogether, this study demonstrates the need to extend the concept of 'perceptual ranges' beyond patch detection processes, to encompass the wide range of elements that can direct animal movements during dispersal through heterogeneous landscapes.

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1. Introduction

Dispersal is a key element in the dynamics and persistence of spatially structured populations. The decision-making pro-

cess by which animals respond to the landscape during dispersal affects spatial patterns and biological processes at multiple spatio-temporal scales (Wiens, 2001; Schooley and Wiens, 2003; Olden et al., 2004b). Therefore, understanding

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animal-landscape interactions in the context of movement, dispersal and connectivity has been the focus of an increasing number of theoretical and empirical studies in ecology (Taylor et al., 1993; Taylor, 2000; With et al., 1997; Tischendorf and Fahrig, 2000a,b). Paramount to understanding movement decisions is the perceptual range of a given animal to its surroundings, defining the sensory information window to which an animal can potentially respond (Lima and Zollner, 1996). The perceptual range influences the probability of detecting new patches, as well as the duration of searches (Lima and Zollner, 1996; Zollner and Lima, 1997), thereby affecting connectivity, the distribution of species across space (Kennedy and Gray, 1993; Ranta et al., 1999) and their response to fragmentation (Zollner, 2000; Olden et al., 2004b; Olden, 2007).

In considering how the perceptual range affects connectivity one difficulty stems from the fact that the perceptual range varies not only between species (Zollner, 2000; Olden, 2007) but also for a given species across time, e.g. due to variation in cloud cover or moonlight illumination (Yeomans, 1995; Zollner and Lima, 1999a; Schooley and Wiens, 2003) or across space, e.g. in response to variations in vegetation structure (Schooley and Wiens, 2003) or chemical cues (Yamazaki and Kamykowski, 2000). Further, directional elements such as wind (Schooley and Wiens, 2003; Schooley and Branch, 2005), water currents (e.g. Olden et al., 2004a), polarized light (Yeomans, 1995), topographical gradients and gradients of soil moisture (Rothermel, 2004) can also bias the directionality within which habitat patches can be perceived. Consequently, with the accumulation of empirical evidence it becomes clearer that our knowledge of this complicated factor is insufficient, and that current empirical methodologies to tackle it may still be limited. Here, simulation models can serve as a powerful tool to investigate how different assumptions (or new information) about animals' perception could affect our understanding of movement, connectivity and population dynamics in heterogeneous landscapes.

Thus far, most dispersal and connectivity models incorporated the perceptual range simply as a distance from which habitat patches can be recognized, rather than as a trait of the response to the attributes of complex heterogeneous landscapes (Yamazaki and Kamykowski, 2000; Turner et al., 1994; Gustafson and Gardner, 1996; Wiegand et al., 1999; Zollner and Lima, 1999b; Kramer-Schadt et al., 2004). Recently, several modeling studies attempted to focus more explicitly on the perceptual range of animals in heterogeneous landscapes: Cramer and Portier (2001) explored how land-use patterns of Florida Panthers change when altering the assumed perceptual distance within which animals can identify conspecifics. Olden et al. (2004) used a conceptual model to demonstrate that the perceptual range should be divided into three components: the distance, horizon and breadth. Vuilleumier and Perrin (2006) compared different cognitive abilities which affect patch detection and connectivity in the context of metapopulations. Graf et al. (2007) and Alderman and Hinsley (2007) took into consideration the impacts of topography, and particularly topographical barriers, on perception and consequently on connectivity.

However, two problems are common to most modeling approaches taken so far. The first is that dispersal models tend to neglect small-scale landscape gradients and overem-

phasize habitat-edge processes (e.g. Ovaskainen and Cornell, 2003; Vuilleumier and Perrin, 2006). The second problem is that perception is mostly addressed in the context of habitat patch detection, rather than as an attribute of the response to environmental stimuli. The importance of this refinement lies in the fact that landscape elements that can serve as directing cues may occur throughout the landscape, and, while they could often lead animals into new habitats, at times they may also be unreliable and lead them into dead-end routes. A better understanding of the role of perception in connectivity would thus be achieved if one considered the senses that dominate the response of animals to their surroundings (Schooley and Wiens, 2003; Vuilleumier and Metzger, 2006), and the consequences in terms of movement decisions (Cramer and Portier, 2001). Therefore, it may be imperative to address the perceptual range of animals within the context of the multiple small-scale landscape elements that can direct dispersal and influence connectivity.

One main question in this context is whether variation in perceptual ranges, for instance due to our insufficient knowledge of the animals' capacities and limitations of perception, can affect movement and connectivity patterns to an extent that indeed demands serious consideration of this complex factor. One way to address this question is to investigate the sensitivity of an existing connectivity model to changes in the assumed perception of various small-scale features in a given landscape. Particularly, we focused on two components of perception: the range within which animals can perceive different landscape elements, and the strength of their response to these. To this end, we used a spatially explicit, individual-based model for the Eurasian lynx (*Lynx lynx*) in Germany. This model was calibrated with field data and consists of both a movement component and a demographic component, running on realistic landscapes with discrete landscape types (Schadt et al., 2002b; Kramer-Schadt et al., 2004, 2005). Our study focuses on three landscape elements that are known to invoke a behavioral response in Eurasian lynx during dispersal, and are likely to be 'perceived' from large distances, but the perception of these elements was not considered in the original model. These elements are forests and waterbodies, which should attract dispersers (in search for sheltered habitats), and cities, which the lynx are known to avoid (Breitenmoser and Bättig, 1992; Breitenmoser et al., 1993; Kramer-Schadt et al., 2004). We tested how the response to each of these elements can affect connectivity, given different assumptions about (a) the perceptual range and (b) the intensity of response to them. We discuss the implications of our results for landscape management and conservation.

2. Methods

2.1. The original model

We used an individual-based model which consists of three main components: a landscape providing the grid for the spatially explicit simulation (Schadt et al., 2002b), a dispersal sub-model (Kramer-Schadt et al., 2004) and a component for simulating territory selection and population demography (population sub-model; Kramer-Schadt et al., 2005). To explore

Table 1 – Parameter values for the demographic and the dispersal sub-models (Kramer-Schadt et al., 2005)

Sub-model	Symbol	Model parameter value or range
Demographic sub-model		
Reproduction rate (=prob. of giving birth)	P_{birth}	0.75
Annual mortality probability of residents	M_{res}	0.1 (translates into ~13% annual mortality rate)
Dispersal sub-model		
Correlation factor	P_C	0.5
Probability of stepping into matrix	P_{matrix}	0.03
Maximum number of steps per day	s_{max}	45
Exponent of step distribution	x	11
Daily mortality probability of dispersers	M_{disp}	0.0007 (translates into 22% annual mortality rate)

Each day, each dispersing lynx is assigned a certain number of movement steps s based on a probability $P(s)$ using a power function with an exponent x and parameter s_{max} that determines the maximum number of steps that a dispersing lynx can cover during a single day:

$$P(s) = (1 - ((s - 1)/(s_{\text{max}} - 1)))^x.$$

the influence of perceptual range on lynx population colonization patterns, we altered the dispersal sub-model based on published and unpublished data (see Section 2.2.1). Parameters of the original model that were not changed in this study are summarized in Table 1.

2.1.1. Landscape sub-model

The basic map categorized the landscape as breeding, dispersal, matrix or barrier habitat with a cell size of 1 km². Breeding habitat refers to large forested areas and other natural and semi-natural land-use types. All forested areas and breeding habitats can be used by animals as dispersal habitat. Barriers consist of urban areas and lakes, and are never used. The remaining areas, such as pastures and agricultural lands, are summarized as 'matrix': areas that, although not strictly avoided by dispersing lynx, are only used occasionally.

2.1.2. Population sub-model

At the beginning of each model time step (year), the number of resident and non-resident males and females on the landscape map are determined. All non-residents older than 1 year disperse and search for territories. The spatially explicit processes of dispersal and territory selection in the model depend upon local habitat quality within the immediate surrounding of the animals' location (see Section 2.1.3). If dispersing individuals survive, they settle or continue dispersing in the following year. Next, each resident female whose territory is overlapped by that of a male reproduces with a certain probability (P_{birth} , Table 1). Both P_{birth} and the annual mortality of residents (M_{res} , Table 1) are based on published data from lynx populations in fragmented landscapes (Ferrereras et al., 1992; Jedrzejewski et al., 1996; Breitenmoser-Würsten et al., 2001; Schmidt-Posthaus et al., 2002). In the final step, the age and status (i.e. disperser or resident) of each surviving individual are determined.

2.1.3. Dispersal sub-model

The original movement module was calibrated with field data from dispersing lynx collected in the Swiss Jura Mountains (Breitenmoser et al., 1993). The spatial unit of dispersal is one movement step, i.e. 1 km² grid cell. In each step, individuals survey their eight-cell neighborhood and make decisions based on this information. Their choice of direction is com-

prised of two components: the probability of leaving preferred dispersal habitat by stepping into the matrix (P_{matrix} , Table 1), and a correlation factor determining the probability of continuing with the same direction as their previous movement within a day (P_C , Table 1). The hierarchy is a preference of dispersal habitat over a persistent movement forward, with the first direction of every day chosen randomly (Kramer-Schadt et al., 2004; Revilla et al., 2004). Each day, a certain number of movement steps (s) is assigned, based on model calibration with field data (Table 1). If an animal has stepped into the matrix, it is assigned a 'memory' of its last location in a dispersal habitat, toward which it returns should it fail to find a dispersal habitat cell within 10 steps. A daily mortality probability is included (M_{disp} , Table 1), resulting in an annual mortality of dispersers of about 22%. We note that the mortality probability M_{disp} is landscape-independent, due to the absence of sufficient field-data regarding mortality risks in different landscape types. For instance, though road mortality is an important risk factor, we found it too complex to be investigated within the scope of this study. For some assessments of the impacts of road mortality on lynx dispersal success see Kramer-Schadt et al. (2004) and Klar et al. (2006).

2.2. Alteration of the dispersal sub-model

2.2.1. Biological reasoning

The response to water bodies (including rivers, streams, ravines and lakes) was incorporated due to the possible use of dense vegetation along them as shelter during dispersal. For example, a radio-transmitting lynx crossed a landscape assumed hostile and exposed while moving between forest fragments. Inspection at the site indicated the presence of a small stream, easily missed by a coarse-grained landscape model, that may have been used as a safe dispersal habitat (Palomares, 2001). Animals can potentially arrive at some water bodies and forest patches by following topographical inclinations, a directing cue used by various animals (Shkedy and Saltz, 2000; Lowe, 2003; Pe'er et al., 2004; Dolev, 2006). Small fragments of forests that are not considered in coarse-grained maps (e.g. Kramer-Schadt et al., 2005) were incorporated too, as they can provide shelter for dispersing animals. The incorporation of big cities was based on the knowledge that nocturnal felines tend to avoid light (e.g. Beier,

1995). Therefore, the avoidance of cities can be based on perceiving the gradual increase in light, noise and traffic density while approaching them (Cramer and Portier, 2001).

2.2.2. Movement rules

To cope with the lack of empirical knowledge regarding the perceptual ranges of lynx towards the hypothesized landscape elements, we confined the response to directing gradients only to the dispersal sub-model, and only to cells in which animals are already moving through open landscapes (i.e. the matrix). Hence, their basic movement is defined by the original model, meaning that we did not alter the movement and dispersal rules within forests. Neither did we make any changes to parameters of the model that determine the tendency of animals to remain in any given cell during dispersal.

The alteration of the original model was made by incorporating two parameters: the perceptual range (hereafter PR) for the three landscape elements, and the intensity of response (hereafter IOR) to these elements. PR was defined as the distance from which an animal can potentially perceive a certain element. In order to enable the alteration of the assumed perceptual range, we incorporated three landscape matrices which depicted the distance from each cell in the landscape to the closest forest, water body and city (see Section 2.2.3). If any distance value within the neighboring eight cells was smaller than the investigated PR, animals could sense this specific landscape element and respond to it with a per-step probability IOR. The probability IOR is necessary due to various confining factors, such as competing sensory cues or local barriers to dispersal. It ranges from 0 (no response) to 1 (always respond). The response itself was manifested in a directed movement: toward the neighboring cell with the lowest distance value in the case of forests or water bodies, or toward the cell with the highest distance value in the case of cities. In cases where two or more factors were analyzed simultaneously, we determined the avoidance of cities to be dominant over the attraction to forests and rivers, and the attraction to forests to be dominant over the attraction to water bodies. Importantly, if an animal took a directed movement in a given step, this did not affect its next movement decision unless the correlation factor (P_C , see Table 1) determined the next movement direction to follow the previous ('directed') one. To ensure that animals would not stay in non-breeding (but attracting) elements, we determined that responding to any of the three elements could not lead the animals to stay in the same cell, or prolong the duration of dispersal.

2.2.3. Landscape maps

We used a realistic landscape map, 258 km \times 275 km in size, depicting a heterogeneous landscape in central Germany. The area includes several large forest patches (e.g. the Harz, where lynx were reintroduced in the year 2000) as well as highly fragmented areas and a few large regions dominated by intense human activity, mainly agriculture and settlements (Fig. 1). In addition to the original landscape map, we created three matrices depicting the different distances from each cell in the landscape to the closest forest, water-body and city. In order to preserve local-scale landscape elements such as small forest fragments and streams while maintaining the resolution of the original model for comparability with the original

model (see Online Appendix), we utilized 250 m resolution maps, which were aggregated into 1 km² cell-size matrices by assigning the value of the 250 m cell with the minimum distance value. This was done under the assumption that if a forest patch or a stream is present anywhere within a cell of 1 km², it can be recognized and utilized by the lynx (see Haller and Breitenmoser, 1986). We note that the values within the resulting distance matrices could vary along a continuum of values, depending on the location of the minimum-value cell within the original 250-m cell matrices. Further details on the production of the distance matrices are provided in an Online Appendix.

2.2.4. Parameterization and simulation runs

In the absence of empirical knowledge on the actual perceptual range (PR) and intensity of response (IOR) of the lynx to the three landscape elements, we explored these parameters by varying them systematically over a wide range of values. This systematic exploration of parameters can be considered as a 'sensitivity analysis', allowing us to obtain a more general understanding of the sensitivity of the model to these parameters. The PR for each directing element was varied from 0 m (no response, i.e. the original or 'null' model) to 3000 m in steps of 500 m. The upper boundary of 3000 m was chosen as it extends the average net daily distance covered by lynx, which is approximately 2000 m (Kramer-Schadt, unpublished analysis derived from Breitenmoser et al., 1993). The IOR to each element was varied from 0 (no response, i.e. the null model) to 1 (always respond when within the perceptual range) in steps of 0.1. We repeated each parameter combination 100 times. Each simulation started with the introduction of 15 males and 15 females to the Thuringian Forest (patch 1 in Fig. 1), and lasted 50 years. This initial number corresponds with a minimum viable population (i.e. extinction risk <5% in 50 years) at the source patch, ensuring a continuous source of dispersing animals. To measure connectivity we used the mean number of individuals arriving at the different patches (labeled 1–12 in Fig. 1), a value which was found to be highly correlated with colonization success (inverse first order regression on $1 - \lambda$ where λ represents the rate of population increase, $R^2 = 0.919$).

3. Results

3.1. Sensitivity analysis

For forests, a systematic increase in IOR led to a monotonic increase in the overall number of successful immigrants, yet with a certain saturation when IOR reached values of 0.6–0.9 (Fig. 2a). This saturation was evident from the fact that an inverse-exponential regression between the number of successful immigrants and the IOR yielded higher R^2 than a linear fit, for all values of the PR (results not shown). We found that all models with $IOR \geq 0.3$ differed significantly from the null model of $IOR = 0$ (Tukey post hoc analysis, comparing model results of each IOR value to the null model, using $PR \geq 1000$ m). Altering the PR systematically revealed a threshold effect in which immigration success first increased with PR, and then remained unchanged for all PR values ≥ 1000 m (Fig. 2b; ANOVA

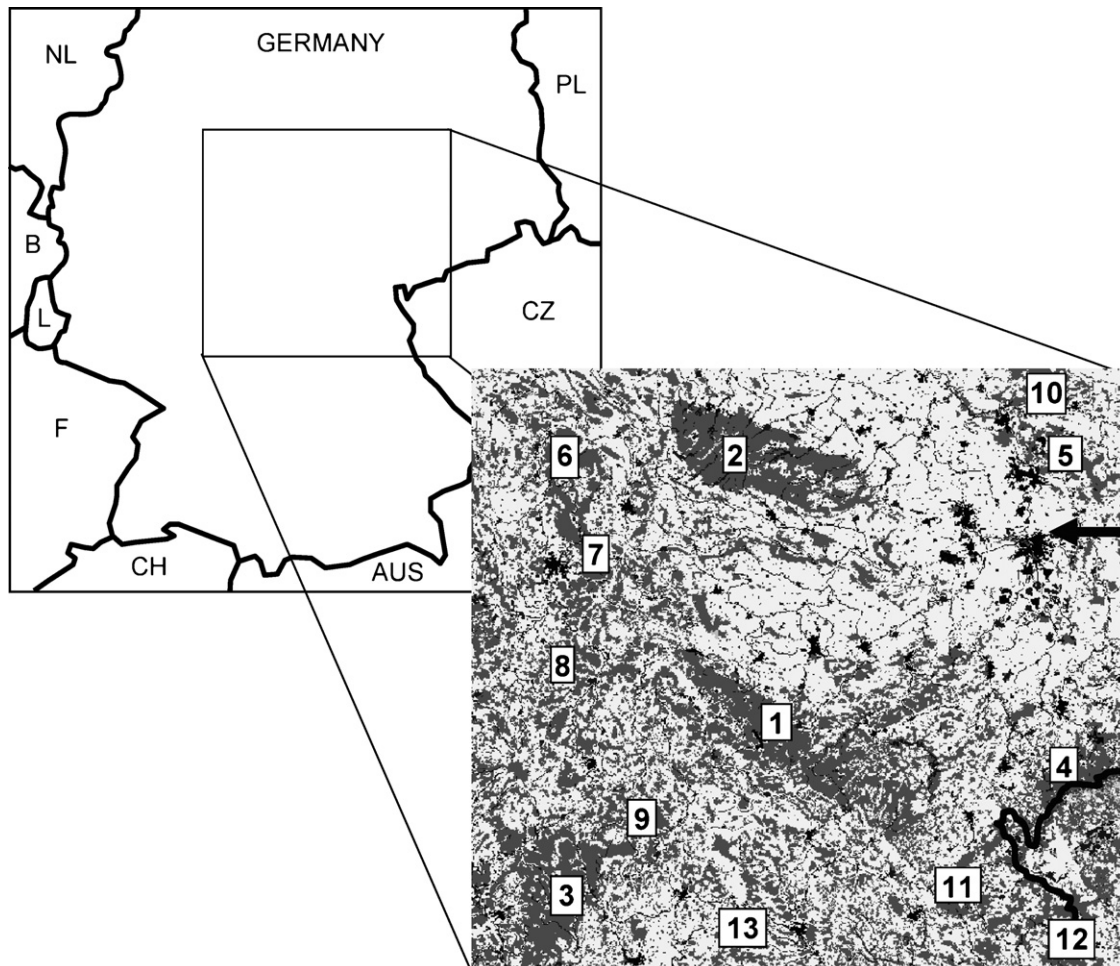


Fig. 1 – Land-use map of the area investigated in this study. Black = cities, rivers and lakes; Gray = forests and woods; White = matrix (mainly agricultural fields). Numbers represent the forest patches within this region, of which patches 1–4 (Thuringian Forest, the Harz, Spessart and the Erz Mountains, respectively) are defined by the habitat map as source patches (i.e. capable of supporting a population). NL: The Netherlands; B: Belgium; L: Luxembourg; F: France; CH: Switzerland; PL: Poland; CZ: Czech Republic; AUS: Austria. The arrow indicates the city of Leipzig with about 500,000 inhabitants.

for $PR \geq 1000$ m was found insignificant). At its best results ($IOR=0.9$, $PR=1000$ m), the response to forests doubled the total number of successful immigrants with respect to the null model.

For rivers, increasing IOR systematically enhanced the number of successful immigrants, starting to diverge significantly from the null model at $IOR \geq 0.5$ (Fig. 2c; Tukey post hoc analysis for $PR \geq 1500$ m). Again, a certain saturation effect was found in which the enhancement of immigration success was no longer significant for $IOR > 0.7$ (Fig. 2c; GLM for $IOR > 0.7$ with $PR > 2000$ m was found insignificant). A systematic exploration of the PR revealed that the enhancement of immigration success occurred only above a threshold value of $PR = 1000$ m, whereas further increase in PR beyond 1500 m did not enhance immigration success further (Fig. 2d). At its maximum impact ($IOR=0.8$, $PR=3000$ m), the response to rivers had an almost similar impact to that of forests, nearly doubling the number of successful immigrants.

An increase in the response to cities had a positive impact on immigration success. However, a visual inspection of the

pattern revealed an increase in immigration success only for $IOR > 0.3$ (Fig. 2e), and a significant divergence from the null model occurred only when $IOR \geq 0.7$ (Tukey post hoc analysis for PR values ≥ 2000 m). A systematic increase in the PR had a positive impact on immigration success, but the graphical pattern was weaker and seemed to depend on a combination of PR and IOR . Indeed, in a regression analysis for the impact of IOR on immigration success with different PR values, we found that the slope was significant only when PR exceeded 1000 m (results not shown). The maximum effect of the response to cities on immigration success, occurring at $IOR=1$ and $PR=3000$ m, was lower than that of forests and water bodies, increasing the number of successful immigrants by 36%.

An enhanced perception of two out of the three directing elements (forests plus water bodies or cities, water bodies plus cities) added, at most, only 6–21% more immigrants (depending on the combination of factors) to the maximum number of immigrants that could be obtained from the enhanced perception of one factor alone (results not shown). This means that

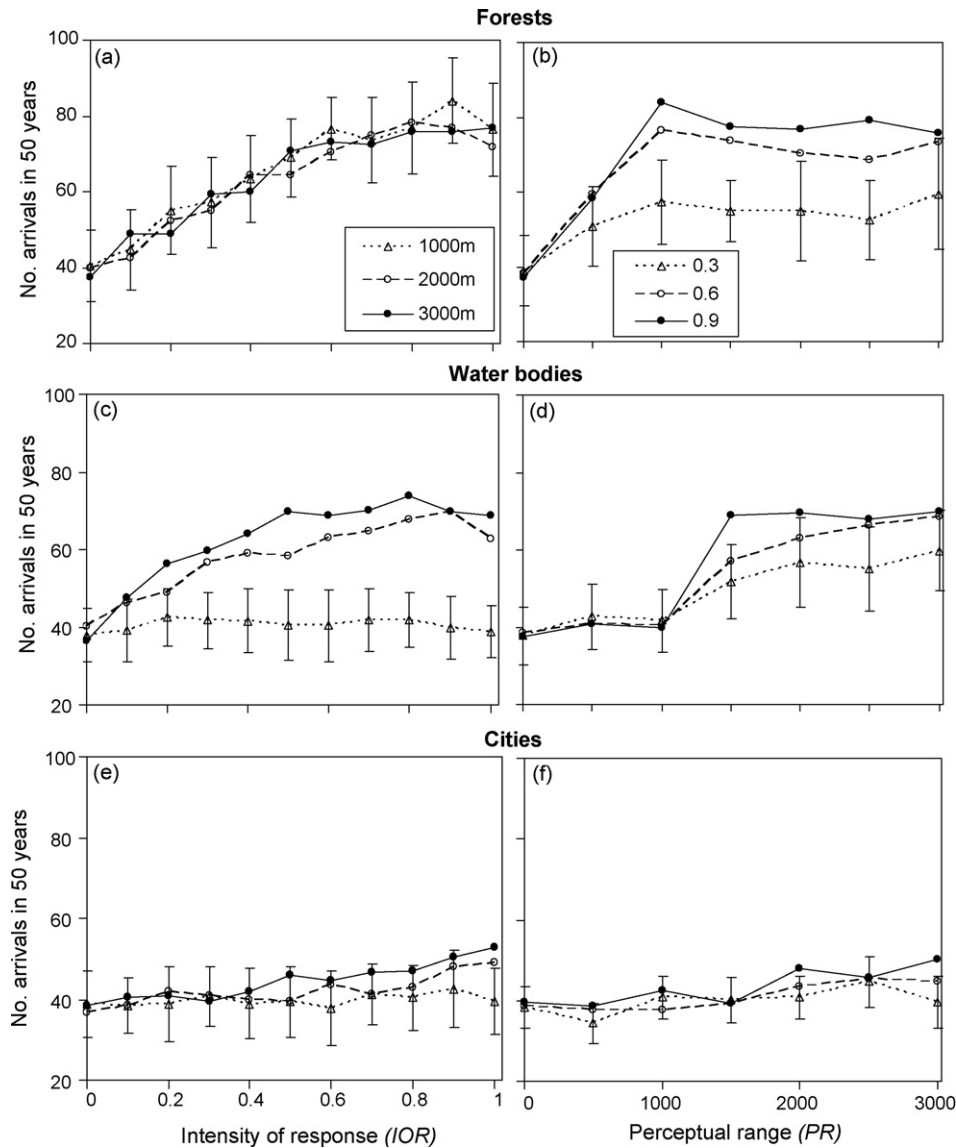


Fig. 2 – The average number of arrivals at all forest patches during 50 years, starting from the Thuringian Forest, plotted against the intensity of response (IOR) and the perceptual range to forests (a and b, respectively), water bodies (c and d) and cities (e and f). Results in (a, c and e) are given for PR values of 1000 m (empty triangles, dotted lines), 2000 m (empty circles, dashed lines) and 3000 m (full circles, full lines). For simplicity of the graphs, S.D. bars are given for a PR = 1000 m, representing similar scales for other PR values. Results in (c, d and f) are given for IOR values of 0.3, 0.6 and 0.9, with S.D. bars for IOR = 0.3.

an enhanced perception to two factors did not substantially improve connectivity compared with an animals' enhanced perception to only one factor, and neither did any two factors negate each other to reduce immigration success.

3.2. Enhanced perceptual range increases the availability of directing elements

To obtain a better understanding of how the perceptual range affects connectivity, one needs to consider that increased perceptual range will increase the functional 'availability' of an element—namely, the number of cells in which a response to that element can occur. To investigate whether this is

the reason for the increase in connectivity, we depicted the 'availability' of each landscape element against the PR to this element. We found that for forests, the most abundant directing element studied in this specific landscape, increasing PR resulted in the availability of the landscape increasing from 58 to 93%, with saturation when the PR reaches 1500 m (Fig. 3a). For rivers, the increase in 'availability' increased steeply with the PR. This can be explained by the linear shape of rivers, as well as by the relatively sparse and regular distribution of water bodies across the landscape. For cities, the least abundant element and the most spatially clustered, the increase in PR had only little effect on availability, enhancing it from 3 to 9% of the landscape.

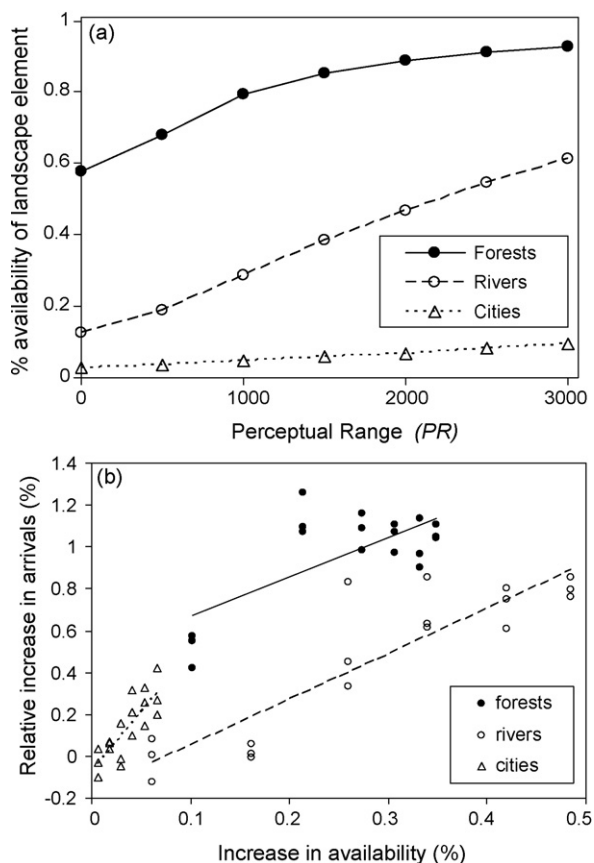


Fig. 3 – (a) The number of successful arrivals at all patches in 50 years vs. the assumed perceptual range, with an intensity of 0.9 response to forests (full circles, full line), water bodies (empty triangles, dashed line) and cities (empty triangles, dotted line). Results for other intensities of response show similar trends. S.D. bars are given for cities only, representing similar orders of magnitude for forests and water bodies. (b) The proportion of landscape that is covered by a given landscape element or capable of orienting the animals toward that element or away from it (see Section 3.2), against the hypothetical perceptual range of the animals for that element, for forests (full circles, full line), water bodies (empty circles, dashed line) and cities (empty triangles, dotted line). (c) The increase in total number of arrivals (relative to number of arrivals in the null model) vs. the increase in availability of a landscape element due to the increase in perceptual range for forests (full circles), water bodies (empty circles) and cities (empty triangles). Lines represent the best-fit regression lines. The results in (c) are given for the entire range of PR and for IOR values of 0.8, 0.9 and 1. These provided the three highest immigration success values within a range where the results were found to be unaffected by IOR.

A visual comparison of the patterns depicted in Fig. 2b, d and f with the patterns of ‘availability’ presented in Fig. 3a reveals a dissimilarity which suggests that the increase in ‘availability’ alone cannot explain the increase in connectivity. To explore this dissimilarity more deeply, we depicted the relative increase in connectivity against the relative increase

in availability due to the increased PR for each landscape element (Fig. 3b). This is under the assumption that, if connectivity is attributed to the availability of an element, then one should expect a linear relation between availability and immigration success. We found that the increase in ‘availability’ best explains the increase in immigration success due to rivers (linear regression, $R^2 = 0.804$, $P < 0.001$), less so for cities ($R^2 = 0.666$, $P < 0.001$) and least for forests ($R^2 = 0.506$, $P = 0.001$). In the case of forests, excluding the PR of 500 m resulted in a weak, near-significant impact of ‘availability’ on immigration success ($R^2 = 0.195$, $P = 0.1$), and the regression slope was negative. This emphasized that, once a threshold PR is reached, the further increase in the availability of forests due to higher PR does not contribute to immigration success. The slopes of the regression lines can provide a first indication of the strength of impact of each of the factors, normalized with respect to their availability: cities had the strongest impact (slope = 5.69), rivers had a lesser impact (slope = 2.159) and forests had the lowest impact (slope = 1.878) on connectivity with respect to the increase in ‘availability’. Thus, adjusting the impact of each directing element with its availability yielded opposite results to those of the overall impact in terms of the per-unit effect of each landscape element on connectivity.

3.3. Distance-dependent results

Plotting the total number of successful immigrants against the net distance from each of the patches to the patch of origin revealed a diminishing arrival probability with increasing distance, but the pattern was somewhat scattered (Fig. 4a). Fitting an inverse-exponential equation to the results of the null model explained 76% of the variability in the number of successful arrivals ($R^2 = 0.7631$, $P < 0.001$). The response to forests increased the number of arrivals at some patches, but decreased it at others. The trend of change in immigration success for each of the patches in response to altering the IOR was affected by the specific value of the IOR rather than by distance from the patch of origin (Fig. 4b). Consequently, the strength of the distance-dependence pattern (as indicated by the R^2 of an inverse-exponential equation) did not show a monotonous trend with respect to altering IOR, but instead it increased between $0 < IOR < 0.4$ and then diminished when IOR increased beyond 0.7 (Fig. 4c).

Both the IOR to each of the factors (e.g. to forests) and to a lesser extent the PR to this element affected the arrival probability differently at each of the patches, resulting in different response curves (Fig. 5). However, we note that for most of the patches the highest number of successful immigrants was obtained for medium to high ranges of IOR (results not shown), a result that relates to the unimodal trend of the strength of the distance dependence with respect to IOR as explained above (Fig. 4c).

3.4. Movement patterns

To visualize the impacts of the response to each directing element in terms of movement patterns, we plotted the average number of times that each cell was ‘visited’ by individuals in the course of the 100 simulation repeats. One can see that the response to forests, at its best, distributes individuals

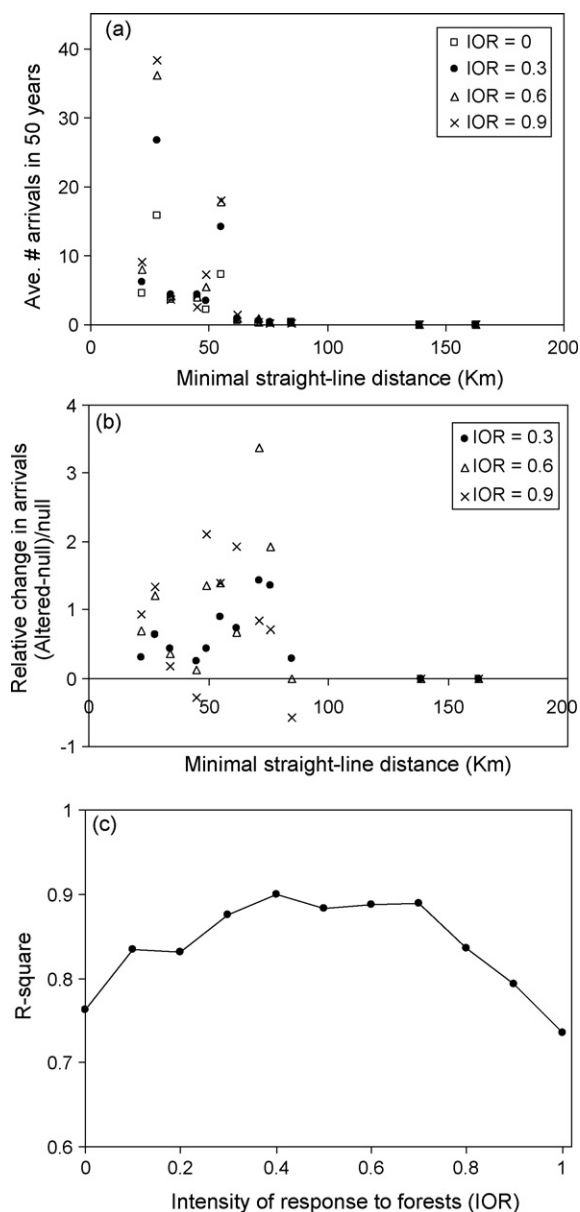


Fig. 4 – (a) The total number of successful immigrants from the Thuringian Forest to all other patches in 50 years, vs. the minimal straight-line distance of each of the patches from the Thuringian Forest (the patch of origin). Results are given for several values of IOR to forests: IOR = 0 (no response; empty squares); 0.3 (full circles); 0.6 (empty triangles) and 0.9 (x marks). All results are given for a perceptual range of 2000 m. (b) The difference in number of arrivals between the altered model and the null model ((altered – null)/null) for each of the patches against the distance from the patch of origin, for different IOR to forests: IOR = 0.3 (full circles); 0.6 (empty triangles) and 0.9 (x marks). (c) The R^2 of an inverse-exponent regression between the number of arrivals and the minimal aerial distance between the patch of origin (Thuringian Forest) and each of the patches, plotted against the intensity of response to forests.

over the landscape more evenly than the null model (Fig. 6b versus Fig. 6a, respectively). In particular, note a patch that was considered unreachable by the null model (as well as by Kramer-Schadt et al. (2005)), but received dispersers when incorporating the response to forests (Fig. 6b, arrow 1). In the Harz, the null model predicted that individuals arrive from the west, whereas the response to forests brought dispersers both from east and west (Fig. 6b, arrow 2). The figure also reveals some patches that received a lower proportion of the immigrants than in the null model (e.g. Fig. 6b, arrow 3).

While the response to forests caused a more scattered distribution of the animals across the landscape, the response to water bodies caused the formation of ‘clusters’ of cells that were visited frequently, probably along rivers. In some cases, routes that were frequently visited by dispersers did not lead to any patch (Fig. 6c, arrows 4 and 5)—suggesting a higher tendency to be trapped at dead-end routes. The response to water bodies also seemed to lead individuals away from the Harz, reducing the relative number of immigrants that arrived at the Harz in comparison to their relative number in the null model (Fig. 6c, arrow 6).

The spatial patterns resulting from responding to cities did not differ strongly from the null model. However, one can recognize that the large urban area south-east of the Harz (see Fig. 1) was completely avoided, whereas all other models predicted that it should be utilized by at least some dispersers (Fig. 6d, arrow 7). Importantly, the model with avoidance of cities was the one yielding the highest proportion of arrivals at the Harz (Fig. 6d, arrow 8).

To summarize, the visualization of visitation patterns reveals that the response to each of the landscape elements in question did not only affect the overall quantity of dispersers but also their movement patterns and consequently their distribution across the landscape.

4. Discussion

Our study demonstrates that different perceptual ranges of animals toward important landscape elements may alter connectivity to a great extent, both quantitatively—in terms of the number of successful immigrants, and qualitatively—in terms of connectivity patterns. Quantitatively, in this study increasing the assumed perceptual range of forests and water bodies could as much as double immigration success with respect to a null model. To a certain extent, this result reinforces previous models that concentrated on patch-perception for it demonstrates that connectivity is enhanced if larger perceptual ranges are assumed (Zollner and Lima, 1999b; Graf et al., 2007). Notably, an enhanced distance within which cities were avoided added 36% to the number of successful immigrants although cities cover only 3% of the landscape studied. This indicates that the predicted number of successful immigrants may be particularly sensitive to the perceptual range of rare landscape elements.

Qualitatively, we found that simulation results were patch-specific and parameter-specific, depending both on the perceptual range of the animals and on the intensity of their response to each of the landscape elements (Figs. 2 and 3). Changes in these two behavioral parameters affected con-

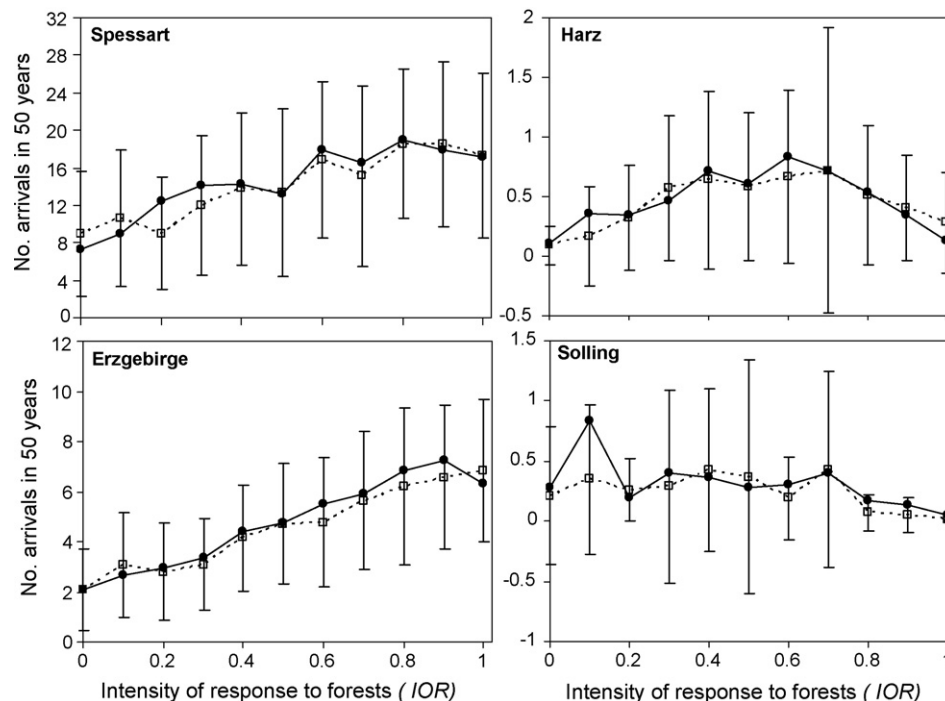


Fig. 5 – The number of arrivals at a given patch during 50 years starting in the Thuringian Forest plotted against the intensity of response to forests, for four patches: (a) Spessart (55 km from origin, patch 3 in Fig. 1a); (b) Erz Mountains (49 km, patch 4); (c) the Harz (71 km, patch 2); and (d) Solling (85 km, patch 6). Results are given for a perceptual range PR of 1000 m (empty squares, dashed line) and 2000 m (full circles, full lines). S.D. values are given for a PR of 1000 m, representing similar scales for a PR of 2000 m.

nectivity differently at different patches, thus altering the allocation of immigrants between patches. This is in agreement with previous models, showing that animal response to landscape heterogeneity alters connectivity patterns and metapopulation structures (Gustafson and Gardner, 1996; Vuilleumier and Perrin, 2006). Another important qualitative finding was that, due to the alteration of the assumed perceptual range, some patches that were considered unreachable in the null model became reachable in the altered model (Fig. 6b, arrow 1), indicating the potential forming of Virtual Corridors—i.e. routes of channeled movements whose structure may be complex and unintuitive (Pe'er et al., 2005). In other cases, however, the response to a directing element led animals into dead-end routes (e.g. Fig. 6c, arrows 4 and 5) emphasizing that directing stimuli may also be unreliable, leading animals into blind corridors—as illuminated for instance by Vuilleumier and Perrin (2006).

To summarize, our quantitative and qualitative results suggest that connectivity models may be highly sensitive to elements that have the capacity to invoke a strong behavioral response within relatively large ranges. Given the rarity of empirical studies that specifically address decision-making processes during dispersal (Bakker and Van Vuren, 2004; Pe'er et al., 2004; Revilla et al., 2004), our study indicates that it is imperative to expand empirical knowledge on the ranges in which different animals can detect different landscape elements, as well as the conditions that affect the strength of their response to these elements.

4.1. Underestimating directed movements

To a great extent, the enhancement of connectivity originates from increasing the proportion of the landscape within which animals perform directional movements. Therefore, models that underestimate the number of directed movements in the landscape are likely to provide poorer predictions of connectivity patterns than models that can take into account the real abundance of directed movements (Malanson, 2003; Pe'er et al., 2005). Further, Pe'er et al. (2005) further pointed out that current models tend to confine animal-landscape interactions to a small proportion of the landscape, namely the borders between landscape types (Gustafson and Gardner, 1996; Schippers et al., 1996; Schadt et al., 2002a; Kramer-Schadt et al., 2004; Ovaskainen, 2004; Vuilleumier and Perrin, 2006). Since enhanced perceptual ranges can increase the number of directed movements, incorporating these factors should receive high priority for the improvement of dispersal and connectivity models.

4.2. Rethinking about perception

Olden et al. (2004) recognized the need to dissect the perceptual range of habitat patches into different components. Our work provides an additional contribution to the field by demonstrating the need for further expansion of the concept of perceptual ranges beyond the limits of patch detection, so as to encompass the response of animals to various directing

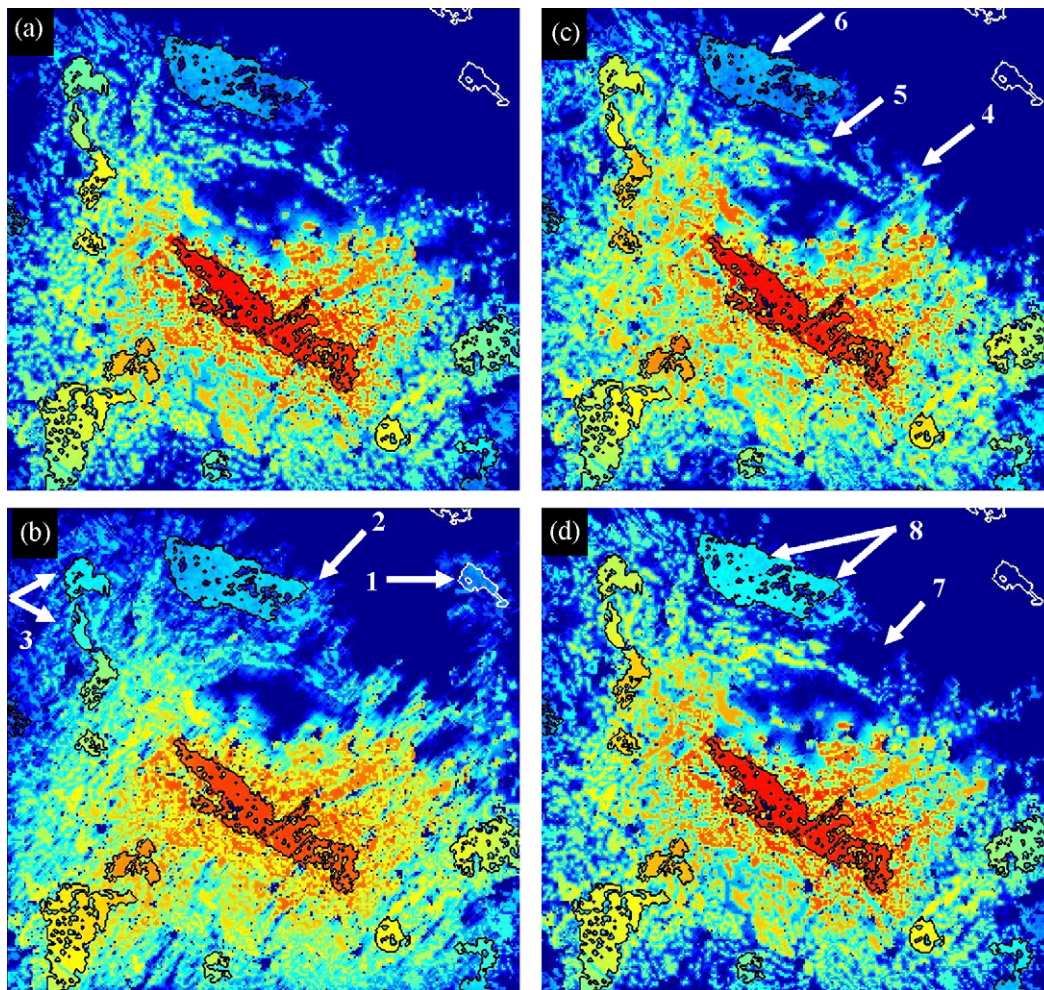


Fig. 6 – The relative number of visits to each cell in the landscape, represented by colors (red = many visits, yellow = medium number of visits, light blue = few visits; dark blue = no visits). The edges of suitable habitats for reproduction (patches) are depicted by blue polygons. (a) The null model; (b) response to forests = 0.9, PR = 2000 m. (c) IOR to water bodies = 0.9, PR = 2000 m. (d) IOR to cities = 1, PR = 2000 m. Arrows indicate areas of divergence between the different models (b–d) and the null model (a) (see text).

stimuli during dispersal. Conceptually, we suggest differentiating between “patch-detection capabilities” and “perception of landscape elements” (or stimuli) in order not to impose our knowledge of the landscape on our model animals. We cannot assume that animals simply know the location, size or quality of habitat patches prior to moving into them. Instead, we should consider that their movement in heterogeneous landscapes is constantly affected by multiple cues, directing them toward some elements and away from others.

4.3. Implications for understanding ecological patterns

In this study, we developed a novel, behavior-based, mechanistic approach for incorporating the response of animals to different small-scale environmental cues. Thus, we kept the ‘landscape’ parameter fixed and concentrated on a systematic exploration of quantitative and qualitative patterns that are of main focus in conservation: namely the patterns that occur within a given landscape and often at the

level of the single patches. Performing analyses over multiple neutral landscapes was beyond the scope of this study, partly because perception itself may alter between landscapes. However, our parameter-specific and patch-specific results indicated that the outcomes in the patch level depended on the attributes of the landscape surrounding each of the patches. Hence, changes in perception are likely also to yield landscape-dependent responses. Understanding the nature of such responses may be fundamental for conservation theory, as it can enable us to understand the relationship between animals’ perception and their response to fragmentation. Further theoretical and empirical investigations, and especially comparisons between various landscapes differing in the level of habitat loss and fragmentation, may reveal how species-specific differences in perception can explain responses to fragmentation (see Zollner, 2000; Zollner and Lima, 2005; Olden, 2007). Thereby, it may provide the tools to explain empirical patterns – such as change in the behavior of a species with fragmentation levels – which are thus far left

unexplained (e.g. Bélisle et al., 2001; Bélisle and St. Clair, 2001). Similarly, it may be of importance to investigate how different perceptual abilities affect the structure, functioning and persistence of metapopulations in different heterogeneous landscapes.

4.4. Implications for conservation

Models are increasingly used not only for understanding biological patterns but also as powerful decision-support tools to focus conservation efforts. In particular, one may wish to identify habitat types that are crucial for connectivity, or, alternatively, to detect focal areas or landscape elements that can be manipulated. Our modeling approach may provide an opportunity for doing so. Depicting the spatial patterns that result from the four model scenarios (the null model vs. the response to each landscape element) indicates localities where animals are likely to pass regardless of model parameters (hence, corridors or Virtual Corridors that should be preserved), as well as localities where animals fail to pass regardless of model parameters (hence, barriers). For example, we found that the agro-industrial landscapes south-east of the Harz are a substantial barrier to dispersal regardless of our uncertainty about the perceptual capacities of the lynx. Thus, landscape modifications in this region have a high potential to enhance dispersal and connectivity. A logical next step would be to alter specific landscape cells in the model (e.g. create patches of woods) and examine which modifications yield the highest impact on connectivity.

Since economic and practical limitations require optimizing the choice of landscape parcels for protection or restoration, it may be paramount to consider the possible contribution of each landscape parcel, or each type of landscape, to connectivity. Such an insight can be gained through correcting the impact of each landscape element with its abundance in the landscape, thereby allowing a better understanding of the potential impact of each unit of a given landscape element to connectivity. In this study, we found rare landscape elements – cities and to a lesser extent water bodies – to have a relatively stronger impact on connectivity than forests. Therefore, we can suggest directing conservation efforts towards manipulating the presence of such elements, or the spatial gradients associated with them. For instance, since nocturnal animals such as the lynx may be sensitive to illumination during night (e.g. lighting along roads and crossroads), one may wish to consider the use of illumination for manipulating dispersers towards corridors or away from dead-end routes, as a more immediate and perhaps also more cost-effective tool than restoration of forest parcels.

4.5. Dispersal models for predictive purposes

Very often, the results of connectivity models are summarized into one-dimensional graphs, depicting the distance-dependent probability of arriving at different patches (i.e. dispersal kernels). This approach may not be invalid: even in our study, 76% of the variation in immigration success between patches could be explained simply by the distance from the patch of origin. However, we suggest great caution in assuming that it is the distance which determines con-

nectivity or isolation. The response to landscape gradients may easily result in a considerable divergence from distance-dependence patterns (Pe'er, 2003; Pe'er et al., 2006), and the results of our work emphasize that one cannot intuitively predict whether the response to a certain directing element would enhance or diminish distance-dependence patterns. Therefore, for predictive purposes in the context of conservation we strongly recommend a two-dimensional approach, in which plotting the spatial patterns that result from simulation models (namely by counting the number of “visits” of animals in each cell) can be used for identifying barriers and corridors for dispersal.

4.6. From model to reality

Both empirical studies and further theoretical work are clearly needed for assessing the perceptual ranges of different animals, to different landscape elements, in various conditions and landscapes. In particular, there is a need to develop methodologies for obtaining realistic values for the movement parameters explored in this study. Two approaches can be used for doing so. The first is the use of detailed telemetry data on the dispersal movement of individuals, to examine movement decisions through turning angles and step-lengths with respect to distance from various landscape elements (see Pe'er et al., 2004; Revilla et al., 2004). The second approach is to analyze connectivity patterns, for example by means of the allocation of dispersers among different patches, and investigate what parameter values best predict these patterns ('pattern-oriented modeling', Railsback, 2001; Grimm et al., 2005). Both approaches can yield powerful methodologies for model testing and deriving information on realistic movement parameters.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2007.11.020.

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