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RESEARCH ARTICLE

What you see is where you go? Modeling dispersal in mountainous landscapes

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Abstract Inter-patch connectivity can be strongly influenced by topography and matrix heterogeneity, particularly when dealing with species with high cognitive abilities. To estimate dispersal in such systems, simulation models need to incorporate a behavioral component of matrix effects to result in more realistic connectivity measures. Inter-patch dispersal is important for the persistence of capercaillie (*Tetrao urogallus*) in central Europe, where this endangered grouse species lives in patchy populations embedded in a mountainous landscape. We simulated capercaillie movements with an individual-based, spatially explicit dispersal model (IBM) and compared the resulting

connectivity measure with distance and an expert estimation. We used a landscape comprising discrete habitat patches, temporary habitat, non-habitat forests, and non-habitat open land. First, we assumed that dispersing individuals have perfect knowledge of habitat cells within the perceptual range (null model). Then, we included constraints to perception and accessibility, i.e., mountain chains, open area and valleys (three sub-models). In a full model, all sub-models were included at once. Correlations between the different connectivity measures were high (Spearman's $\rho > 0.7$) and connectivity based on the full IBM was closer to expert estimation than distance. For selected cases, simple distance differed strongly from the full IBM measure and the expert estimation. Connectivity based on the IBM was strongly sensitive to the size of perceptual range with higher sensitivity for the null model compared to the full model that included context dependent perceptual ranges. Our heuristic approach is adequate for simulating movements of species with high cognitive abilities in strongly structured landscapes that influence perception and permeability.

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Introduction

The ability of animals to move between habitat fragments is a key determinant of the viability of spatially structured populations and metapopulations (e.g., Levins 1970; Hanski et al. 1994; Hess 1996; Frank and Wissel 1998). However, our empirical understanding of the movements of animals across landscapes is limited and quantification of dispersal is difficult (Zollner and Lima 1999), especially for vertebrates with large spatial requirements (Koenig et al. 1996; Martin et al. 2006). Therefore, simulation models have become a cost-effective approach to understand and predict the effect of dispersal on population dynamics (e.g., Tischendorf 1997; Wiegand et al. 1999; Pfenning et al. 2004; Kramer-Schadt et al. 2004).

As a first approximation, spatially explicit population models included dispersal rates based on simple connectivity measures, such as distance-dependent functions or buffer measures (Hanski 1994; Zollner and Lima 1999; Vos et al. 2001; Moilanen and Nieminen 2002). Such measures assume a simple landscape consisting of discrete habitat patches embedded in a hostile but homogeneous matrix. In most cases, however, the matrix is a mosaic of different land cover types that may affect the movement behavior of animals and thus metapopulation dynamics (Ricketts 2001; Vandermeer and Carvajal 2001; Wiegand et al. 2005; Bender and Fahrig 2005). Matrix heterogeneity, for example, had important effects on dispersal movement properties of Iberian Lynx at the individual scale, and these translated to large effects on the population scale (Revilla et al. 2004). Mooij and DeAngelis (2003) and Wiegand et al. (2005) found evidence that dispersal models that include relevant landscape details were preferable over simpler models that ignore basic information on the system.

In addition to matrix heterogeneity, the individual ability to perceive suitable dispersal paths and habitats affects connectivity. One element of matrix heterogeneity, topography, has so far received little attention in modeling dispersal (Pe'er et al. 2006). Topography, however, should obviously not be ignored in mountainous landscapes because it is likely to have a strong

influence on the individual's ability to perceive suitable dispersal paths and habitats and, in turn, on connectivity (cf. Lima and Zollner 1996; Alderman et al. 2005). Ecologists studying and modeling animal dispersal have commonly assumed that individual movements arise from a predefined set of local decision rules operating within a static isotropic perceptual range (e.g., Kramer-Schadt et al. 2004; Fernandez et al. 2006). However, anisotropic perceptual ranges can arise from animal orientation to environmental stimuli. Therefore, Olden et al. (2004) propose using context-dependent perceptual ranges by adapting the perception window to matrix heterogeneity. Here we use this approach for modeling dispersal of capercaillie in the Swiss Alps.

The endangered capercaillie (Storch 2000) is an example for a species living in a patchy environment that is stamped by varying land use types and topography, and where connectivity is difficult to assess *ad hoc*. Capercaillie is a forest grouse species with specialized habitat preferences (e.g., Schroth 1992) and large spatial requirements (e.g., Storch 1995). Capercaillie populations are declining in most of their central European range (Storch 2000), as habitat loss and fragmentation have resulted in mostly small populations with different degrees of connectivity or complete isolation (Klaus 1994; Storch 2000). Although capercaillie populations in Central Europe seem not to follow classical metapopulation dynamics (extinction and re-colonization are extremely rare events), dispersal between the sub-populations is important because it reduces the extinction risk of small populations (Grimm and Storch 2000) and maintains genetic connectivity (Segelbacher et al. 2003a; Jacob 2006).

Very little is known about long-distance movement behavior and about dispersal rates between capercaillie populations. Mark-recapture data from Finland from the 1950s are still the best data-set on dispersal distances (Koivisto 1963). Telemetry studies have provided only anecdotic data on dispersal events (Storch 1995). In the case of capercaillie in central Europe, using simple connectivity measures for exchange rates between patches (e.g., distance or buffer measures, cf. Bollmann et al. submitted) probably is an unreasonable simplification because of the complicated

pattern of topography and land cover types that form dispersal corridors and barriers. In conservation practice in Switzerland, inter-patch connectivity is currently intuitively estimated by experts (Mollet 2006).

The aims of this study were to assess the effect of perceptual range, topography and matrix heterogeneity on connectivity estimates and to get a more realistic and impartial measure of inter-patch connectivity than with simple distance or expert estimations. We adopted an individual-based, spatially explicit approach (Grimm and Railsback 2005) allowing the individuals to assess the landscape structure around them and use this information to decide on the direction and distance of movement steps. Our approach is based on the heuristic assumption that capercaillie must have certain knowledge of the surrounding landscape and are probably able to perceive habitat types visually. We expected the connectivity measure based on our individual-based model to differ substantially from simple inter-patch distances and to correspond closely with expert estimations. We then discuss the consequences of differences between the connectivity measures for the conservation of the capercaillie in central Europe.

Methods

Study area and species data

Capercaillie in Switzerland is structured into five independent populations in three mountainous areas (Mollet et al. 2003). In this study, we use data from two of the five populations: eastern Pre-Alps (region 4a) and northern part of eastern Central Alps (region 4b) and southern part of eastern Central Alps (Engadin, region 5; Fig. 1). Within each population, we find a few relatively large and stable core populations and a number of small surrounding populations. The study regions differ significantly in terms of topography, forest distribution, tree species composition and land use. The areas inhabited by capercaillie range in elevation from 1,000 to 1,800 m above sea level in the region 4a, and from 1,200 to 2,200 m above sea level in the regions 4b and 5. There is a

climate gradient from more atlantic in the region 4a with cold-temperate winters and wet summer months to more continental in the region 5 with a relatively low precipitation rate, cold winters but warm and dry summers. A patchy pattern of forest, pasture and mires is typical for the Pre-Alps (region 4a), whereas large contiguous and mostly conifer-dominated forests spread along the valley slopes in the Alps (regions 4b and 5).

Species data originated from three different data sources: First, three national surveys in 1971, 1985 and 2001 provided information on distribution and rough figures of abundance (Mollet et al. 2003). Second, capercaillie populations were surveyed in large areas within the regions 4a, 4b and 5 using a systematic plot sampling. Additionally, populations in some parts of the regions 4a and 5 were investigated by regional experts with systematic plot sampling and lek counts. All these data combined result in reliable information on patch occupancy (Bollmann et al. submitted) and a rough estimate of population sizes. Only very few and occasional data on dispersal events are available for the study area.

Landscape map

As a spatially explicit framework, we use a landscape map discerning four different habitat types: discrete habitat patches, temporary habitat, additional (non-habitat) forest area and non-habitat open land. The habitat patches stem from a statistical habitat distribution model built with presence–absence data and a set of landscape variables describing aspects of topography, climate, vegetation and human disturbance (Graf et al. 2005). The dependence of patch occupancy on size and configuration of the patches has been analyzed in Bollmann et al. (submitted). As temporary habitat, we assume all additional forested area above 1,000 m above sea level, areas that could be used temporarily by capercaillie individuals but not for overwintering, mating and reproduction. The landscape maps were generated from the land cover database 1992/97 (BFS GEOSTAT) and a digital elevation model (DHM25 © 2004, SWISSTOPO, DV033594). The landscape maps were prepared as grids with a resolution of 500 m to evenly scale

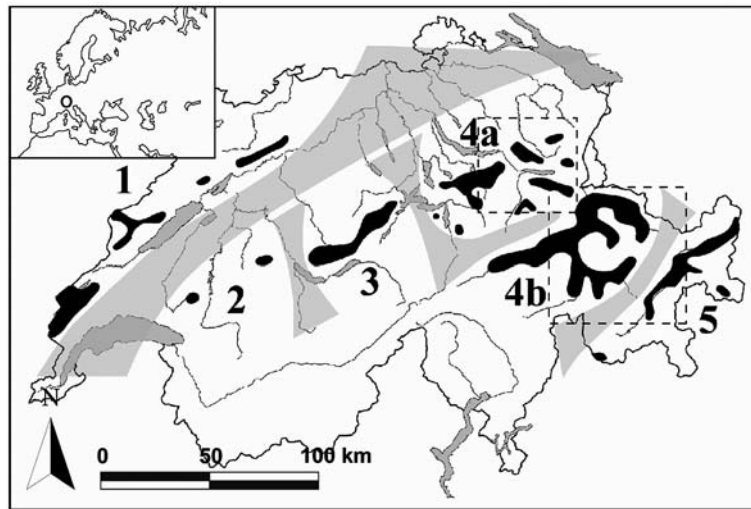


Fig. 1 Capercaillie regions in Switzerland (dark grey areas; from Mollet et al. 2003); (1) Jura Mountains, (2) western Pre-Alps, (3) central Pre-Alps, (4a) eastern Pre-Alps, (4b) northeastern central Alps, (5) Engadin. Barriers dividing capercaillie range into five independent populations are indicated in light grey. This study used data from

the regions 4a, and 4b. The capercaillie areas in dark grey are simplified for better illustration; in real, the potential habitat is much more fragmented (see Fig. 2). The rectangle areas indicated with dashed lines were used as test regions (Fig. 2)

with the mean size of an annual home range of 5 km^2 (Storch 1995; 5 km^2 equals 20 cells).

Simulation model description

Our individual-based model simulates the movements of capercaillie individuals between discrete habitat patches. With this model, we intended to capture the overall movements of capercaillie between two mating seasons ignoring the daily movements within the home ranges. For each run, we placed a variable number of capercaillie individuals into selected habitat patches or patch clusters, let all of them move a variable number of steps and assessed the resulting movement pattern.

In the initialization, three different grids are computed: patch number information, habitat map (habitat patches, temporary habitat, additional forest, and matrix) and a digital elevation model. Capercaillie individuals are placed into selected patch clusters (cf. Fig. 2) and within the patches each individual is assigned to a randomly chosen, exact location (a specific grid cell). The movement procedure for each individual involves four steps.

First, the perception window is defined as the square area around the present location of the individual with an edge length of two times the perception range (parameter p_range , Table 1) plus one cell. The patch and temporary habitat cells available within the perception window (potential destination cells) represent the initially assumed perfect knowledge of the individuals. Second, we test the direct accessibility of the potential destination cells by inspecting the land-cover types and topography on a straight line between the present location and all the potential destination cells. If a certain cell is inaccessible from the present location, it is deleted from the potential destination cells. In addition, all cells within the patch where the capercaillie is located are assumed to be accessible because the individual could walk to the new location without leaving the patch of suitable habitat. Third, the new location of the individual is selected randomly from the accessible destination cells. Fourth, the individual decides on whether to stay at this new location or to move on further: if the new location was not a breeding patch but only temporary habitat then the individual moves on. If the new location was within a suitable patch,

Fig. 2 Test regions used for sensitivity analyses and for comparison of connectivity measures. Region (a) covers parts of the capercaillie region 4a, Region (b) covers parts of capercaillie regions 4b and 5 (see Fig. 1). Numbered polygons identify patch clusters

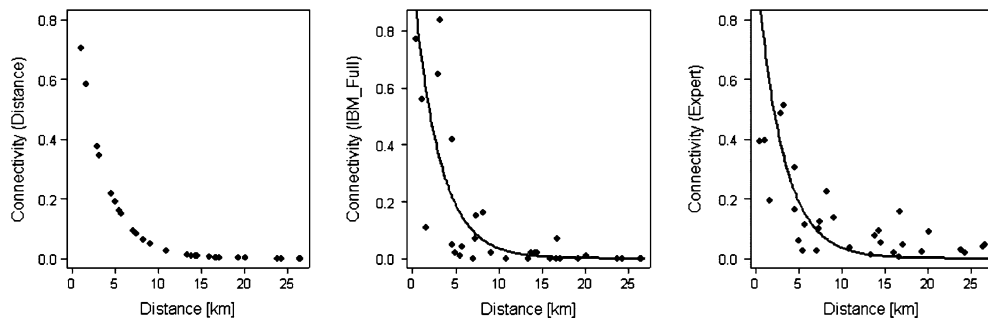
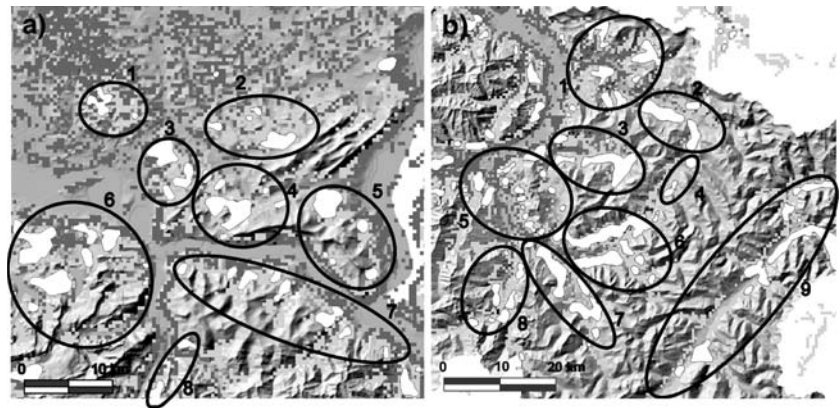


Fig. 3 Comparison of the distance-based connectivity measure (left) with the one based on the individual-based dispersal model (middle) and the expert estimations

(right). The function $M = \exp(-D/3000)$, where M = connectivity and D = distance, is included in the two graphs on the right

Table 1 Model parameters

Parameter	Abbreviation	Default	Unit
Perception range; size of square perceptual window in number of grid cells; the default of 15 equals a perceptual range of 7.5 km from the start cell, the entire perceptual window has a diameter of 15.5 km (7.5 times 2 plus 1 cell; cell size = 0.5 m)	<i>p_range</i>	15	Number of cells
Probability to stay in a patch; an individual can take several movement steps during one time-step; the decision whether to stay in a patch or to move on depends on <i>p_stay</i>	<i>p_stay</i>	0.5	Index
Effect of topography; elevation difference to start location is measured for all cells between start location and potential end locations; the higher the maximum difference the lower the accessibility (Eq. (1); see Methods)	<i>c_top</i>	20	Index
Effect of land cover; number of open cell between start location and potential end locations is measured; the larger the number of open cells, the lower the accessibility (Eq. (2); see methods)	<i>c_lc</i>	7.5	Index
Effect of valleys; an index for valley depth and width is measured for the route from a start location to all potential end locations; the higher the valley index, the lower the accessibility (Eq. (3); see methods)	<i>c_va</i>	15	Index

the individual stays with a constant probability (parameter p_{stay}).

Accessibility test

The test for direct accessibility of the potential destination cells includes three sub-models: topographic barriers (IBM_TOP), effect of open area (IBM_LC) and effect of valleys (IBM_VA). The sub-model “topographic barriers” inhibits direct movements over mountain chains and is based on two assumptions, one related to landscape heterogeneity and one related to perceptual abilities: First, we assume that flying over a mountain chain would involve high energetic costs and a high predation risk for a bird like capercaillie that is specialized for quick but short flights (Klaus et al. 1986). Second, we assume that the field of vision will govern the direction and length of movements of capercaillie individuals. Visual perception is well-developed in capercaillie (Klaus et al. 1986) and other grouse species (e.g., Klaus et al. 1990; Aspbury and Gibson 2004) and is definitely used for orientation during flights. Forest areas behind a mountain chain are not visible and therefore will not be accessible in one movement step. Topographic barriers are defined as cells with an elevation higher than the present location of the individual (please note that this rule was only applied for inter-patch movements; uphill movements within patches were not constrained because capercaillie are known to easily climb by walking, Klaus et al. 1986). The larger the difference in elevation is the lower the probability that the potential destination cell is chosen by the individual. This probability assumes a logistic function of the elevation difference:

$$Y = -\exp(1 + 0.1*(c_{top}*x - 50))/ (1 + \exp(1 + 0.1*(c_{top}*x - 50))) - 0.018 \quad (1)$$

where the probability Y between 0 and 1 is a function of the elevation difference x with parameter c_{top} that defines the location of the s-shaped curve in x -direction. The numbers “0.1” and “-50” define the shape and location of the curve, and “-0.018” was applied to make the curve pass through the origin.

The submodel “effect of open area” is based on the assumption that crossing a large distance without forest will mostly be avoided. Therefore, we count the number of open cells between the present location and the potential destination cells. The number of open cells accounts for a certain probability for the exclusion of potential destination cells based on a logistic function:

$$Y = -\exp(1 + 0.1*(c_{lc}*x - 50))/ (1 + \exp(1 + 0.1*(c_{lc}*x - 50))) - 0.018 \quad (2)$$

where the probability Y between 0 and 1 is a function of the number of open cells x with parameter c_{lc} .

Capercaillie probably fly across large and deep valleys. Such movements involve a risk of predation by raptors and thus will be rare. The submodel “effect of valleys” uses a combined index of valley depth and width. This index is calculated in two steps. First, a mean is calculated from the two elevation values at the present location and a potential destination cell. Second, the elevation values for the cells between the start and the destination cell are subtracted from the mean and the resulting positive values are summed up and divided by 1,000. The larger the index, the higher the probability of cell removal following a logistic function (analogously to topography and land-cover):

$$Y = -\exp(1 + 0.1*(c_{va}*x - 50))/ (1 + \exp(1 + 0.1*(c_{va}*x - 50))) - 0.018 \quad (3)$$

where the probability Y between 0 and 1 is a function of the valley depth and width (x) with parameter c_{va} .

Model parameterization

As there were only anecdotic dispersal data available for the study area, we first parameterized the model based on expert knowledge and literature review by narrowing down the plausible parameter ranges.

The size of the perception window (parameter *perception range*) defines the maximum distance that can be made by capercaillie in one movement

step. Thus, it also defines the maximum width of open area without temporary habitat that can be crossed by capercaillie. In the literature, we found maximum inter-patch distances made by capercaillie in central Europe of 10 km (Storch and Segelbacher 2000; D. Thiel, personal communication). In Norway and Russia, spring summer movements of up to 6 km were observed (Hjeljord et al. 2000). We chose 7.5 km as the default perception range accounting for a window area of about 96 km².

The default values of the parameters c_{top} , c_{lc} and c_{va} involve a high uncertainty associated to the lack of specific data from field studies. Therefore, we chose plausible values attending to expert opinion. For the effect of topography, we assumed that elevation “barriers” higher than 200 m hamper the perception and accessibility of areas behind (default $c_{top} = 20$). There is evidence that distances up to 4 km of open area are crossed regularly (Storch, personal communication). The effect of open area is parameterized accordingly ($c_{lc} = 7.5$), reaching a cell removal probability of 0.9 for at least 4 km of open area. For setting the default of the effect of valleys, we assessed the range of values of the index of valley depth and width. We chose a default of c_{va} ($c_{va} = 15$) allowing only occasional movements over main valleys (width > 3 km, elevation difference between capercaillie habitat and valley bottom >800 m).

The probability to stay in a patch (parameter p_{stay}) defines the number of steps made by an individual in one time step. The smaller the probability, the more steps will the individuals take and thus the more individuals will disperse over long distances. We chose a default value for p_{stay} of 0.5.

Sensitivity analysis

For the local sensitivity analysis and the sensitivity analysis of the parameter *perception range* we used a number of example situations in test region (a). We applied two different procedures for estimating the influence of parameter variation on values of inter-patch connectivity (i) and on dispersal distance (ii). For (i), we let 1,000

individuals start in a certain source patch cluster and assessed the number of individuals arriving in the surrounding patch clusters (Fig. 2a). Example situations were (A) ratio between movements from the largest patch of patch cluster 4 (Amden) to patch clusters 2 and 3 (Schwägalp/Regelstein), (B) ratio between movements from the largest patch of patch cluster 4 (Amden) to patch clusters 3 and 7 (Regelstein/ Highway SG), (C) ratio between movements from the largest patch of patch cluster 5 (Wildhaus) to patch clusters 4 and 2 (Amden/ Schwägalp), (D) Movements from the largest patch of patch cluster 4 (Amden) to patch cluster 5 (Wildhaus), (E) Movements from the largest patch of patch cluster 5 (Wildhaus) to patch cluster 4 (Amden). The numbers of arriving individuals per patch cluster were averaged over 100 simulation runs. We consciously chose extreme values of parameter variation (up to 40% of default; Table 2) because they entail a high degree of uncertainty. This procedure did not apply to the evaluation of dispersal distance (ii), because the dispersal distance strongly depends on the choice of the start patch, i.e., on how a patch is embedded in the landscape. Therefore, we initialized a number of individuals per habitat patch in parts of region 4a. The number of individuals was chosen proportional to the size of the patches, with a total sum of 559 individuals. Mean, median and maximum dispersal distance was averaged over 100 simulation runs.

Connectivity measures

The concept of connectivity has been used in different ways in landscape ecology and metapopulation biology (Tischendorf and Fahring 2000; Moilanen and Hanski 2001). We calculated connectivity between habitat patches or patch clusters as the probability r_{ij} of a certain patch j being reached by an emigrant from a certain patch i (Heinz et al. 2005). For this analysis, we let 1,000 individuals start from a source patch cluster and assessed the number of individuals arriving at all potential target patch clusters surrounding the source cluster (Fig. 2).

Table 2 Local sensitivity analysis for arrival of individuals at a selection of patches/ patch clusters (Fig. 2a, Situations A–E) and for dispersal distance (mean, median, max) measured in test region a (Fig. 2a); Upper (–) and lower

(+) deviation from default; Local sensitivity defined as $(\text{Difference } Y / \text{Default } Y) / (\text{Difference } X / \text{Default } X)$, where Y is the response variable and X the parameter value

Parameter	Default (+,-)	A+	A–	B+	B–	C+	C–	D+	D–
<i>p_range</i>	15 (20,10)	0.12	0.91	–0.89	–1.30	0.66	0.10	–0.91	–1.34
<i>p_stay</i>	0.5 (0.7, 0.3)	–0.03	0.59	0.07	–0.03	–0.11	–0.27	0.48	1.05
<i>c_top</i>	20 (25, 15)	–0.20	0.40	–0.77	0.85	0.16	–1.28	0.03	0.24
<i>c_lc</i>	7.5 (10, 5)	0.75	1.72	–2.40	–1.22	–0.46	–0.80	0.71	0.81
<i>c_va</i>	15 (20,10)	0.22	0.63	–7.12	–1.71	0.11	–0.42	0.26	0.30
		E+	E–	Mean+	Mean–	Median+	Median–	Max+	Max–
<i>p_range</i>	15 (20,10)	–0.37	–1.20	0.55	0.19	0.33	0.19	0.38	0.17
<i>p_stay</i>	0.5 (0.7, 0.3)	0.69	1.16	–0.47	–0.28	–0.56	–0.04	–0.54	–0.24
<i>c_top</i>	20 (25, 15)	0.43	0.08	–0.14	–0.15	–0.19	–0.02	–0.15	0.02
<i>c_lc</i>	7.5 (10, 5)	0.95	0.82	–0.55	–0.43	–0.69	–0.10	–0.53	–0.40
<i>c_va</i>	15 (20,10)	0.49	–0.02	–0.09	–0.11	–0.06	–0.01	–0.16	–0.06

As source patch clusters, we chose the patch clusters 4 and 5 in test region (a) and the clusters 4 and 6 in test region (b). This resulted in a total of 30 connectivity values. In addition, we measured edge-to-edge distances between the patch clusters for the two test regions. These raw distance values were then transformed with an exponential function: $M = \exp(-D/b)$ (Kitching 1971), where M was the resulting connectivity value, D were the raw distances and b was a constant represents the average distance that is made by dispersing individuals. We chose $b = 3,000$ m (cf. Storch and Segelbacher 2000).

To compare model estimates with expert opinion, we collected expert estimation of dispersal for the same situations (Fig. 2) resulting in 30 connectivity values. Four Swiss capercaillie experts had to answer the question where they would expect 100 dispersing individuals to arrive. We compared the three different types of connectivity measures using rank correlations (Spearman’s ρ). Because the 30 connectivity values were not independent, we repeated a random selection of 10 out of 30 for 100 times and calculated mean correlation and standard deviation (Table 3). Additionally, we arbitrarily chose a subset of 10 samples for which we expected a difference between distance and the individual-based model because high mountain chains or large valleys separate start from target patch clusters.

Table 3 Spearman’s rank correlations between the three different types of connectivity measures: connectivity based on edge-to-edge distances (Distance), expert estimation (Expert) and on the individual-based model with different submodels included (IBM_NULL, IBM_TOP, IBM_LC, IBM_VA, IBM_FULL)

Variables	Spearman’s ρ	
	Mean	SD
Distance vs. IBM_NULL	0.82	0.11
Distance vs. IBM_TOP	0.76	0.12
Distance vs. IBM_LC	0.81	0.10
Distance vs. IBM_VA	0.81	0.10
Distance vs. IBM_FULL	0.74	0.15
Expert vs. IBM_NULL	0.74	0.14
Expert vs. IBM_TOP	0.86	0.08
Expert vs. IBM_LC	0.85	0.09
Expert vs. IBM_VA	0.77	0.15
Expert vs. IBM_FULL	0.92	0.04
Distance vs. Expert	0.64	0.18

Results

Connectivity

The three different approaches (distance, expert estimation, individual-based dispersal model) produced highly correlated connectivity measures (Spearman’s $\rho > 0.7$, cf. Table 3). In particular, the distance measure was closest to the null model (Spearman’s $\rho = 0.82$) that assumes complete knowledge within the perception window without considering land cover and topography. Including the sub-models for topography, land

cover and valleys made model-based connectivity values deviate more from the distance-based connectivity, with decreasing values of Spearman's ρ for valleys (0.81), land cover (0.81), topography (0.76), and the full model (0.74), respectively (see also Figs. 4 and 5). The expert estimation was strongly correlated with the full model (Spearman's $\rho = 0.92$) but only moderately with the distance measure (Spearman's $\rho = 0.64$).

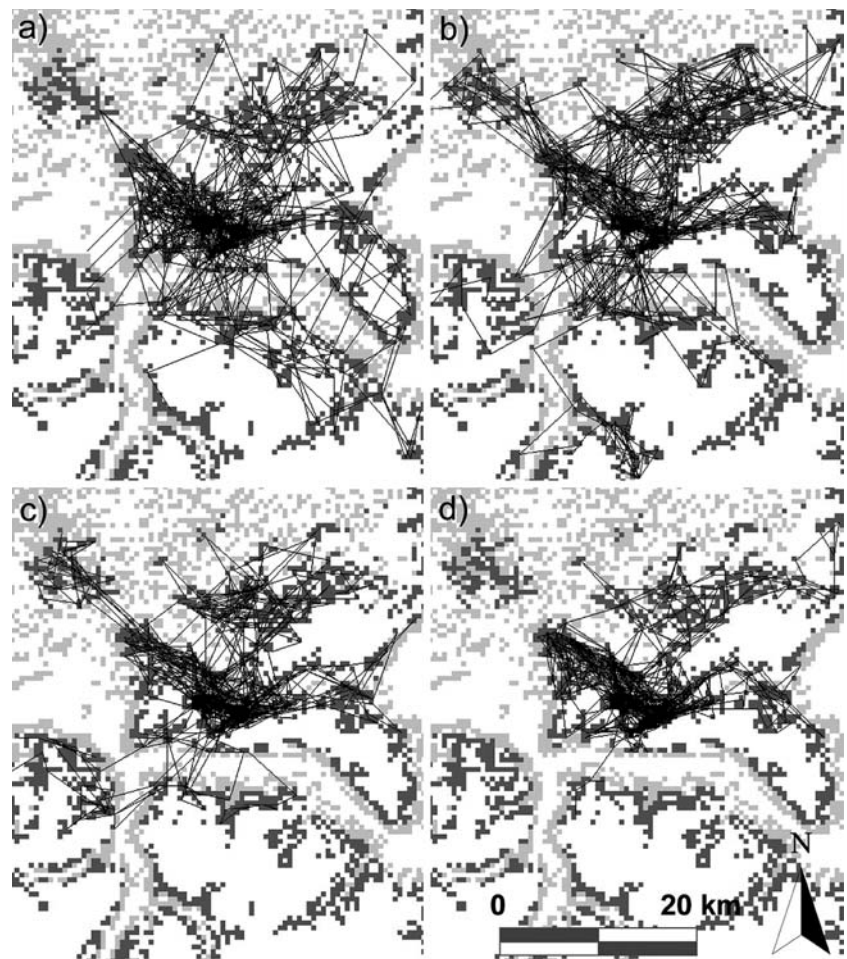
All these correlation values seem to be quite high. However, we found different results for an arbitrarily selected subset of 10 situations, for which we expected a difference between distance and the individual-based model because high mountain chains or large valleys separate start from target patch clusters. For this special case, rank correlations were low between the distance measure and the five measures based on the

dispersal model (Spearman's $\rho < 0.2$) but high between the expert estimation and the measure based on the full model (Spearman's $\rho = 0.94$).

Sensitivity analyses

With some exceptions, the effect of parameter variation on the response variable (inter-patch connectivity or dispersal distance) was smaller than the degree of parameter variation (sensitivity values < 1 , Table 2). However, lower values of *perception range* than the default influenced connectivity strongly (see also Fig. 5). Variation of the probability to stay in a patch (p_{stay}) had low influence on the relative connectivity values, i.e., the ratio of connectivity values for two patches (situations A–C). But it affected the absolute values for single patches (D, E) with

Fig. 4 Illustration of the effect of sub-models on the simulated movements of capercaillie individuals starting at one source patch. Black lines indicate the movements of 100 individuals, with habitat patches and temporary habitat shown by dark grey cells and additional forest by light grey cells. **(a)** IBM without additional effects included (null model), **(b)** IBM with effect of topography, **(c)** IBM with effects of topography and land-cover and **(d)** full IBM with effects of topography, land-cover and valleys included



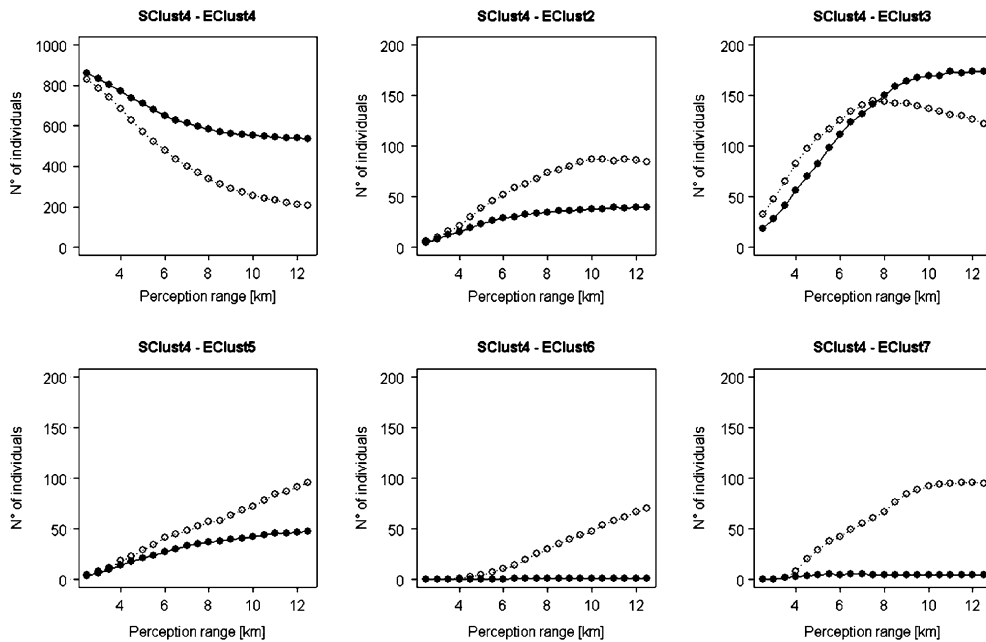


Fig. 5 Sensitivity analysis of the perceptual range; number of individuals arriving in six different end-patch clusters from start-cluster 4 (Fig. 2a); empty circles: null model

(without effect of topography, land-cover and valleys), filled circles: all effects included (default parameter values used; see Table 2)

small values of p_{stay} promoting dispersal. The model was sensitive to the effect of topography (c_{top}) when there was a mountain chain between two patches limiting dispersal (situation C). The effects of land-cover and valleys affected the model output in situations where a wide and deep valley or a large amount of open area separated a target patch from a source patch (mainly situation B). Mean, median and maximum distances were only weakly affected by varying the values of all parameters (sensitivity values <0.7). Dispersal distance for default parameters averaged at 4.8 km (sd = 0.2) and maximum distance was 25.6 km (sd = 4.1 km).

An additional sensitivity analysis was performed to assess the model response to variation of the parameter *perception range* over a range from 5 to 25 cells (2.5 km to 12.5 km; Fig. 5). The perception range has a strong influence on patch connectivity and this influence is not linear but reveals threshold behavior due to landscape structure. The strongest influence is observed for small values of perception ranges (2.5–7.5 km), due to valleys that can only be crossed when the

perception range exceeds valley width. The model is less sensitive to values of perception range between 7.5 km and 12.5 km, and this is particularly true for the full model. In general, the model output is less sensitive to variation in perception range when all sub-models are activated. The rules may inhibit variation in this case, i.e., they restrict the movement possibilities of the individuals.

Discussion

The modeling approach

Capturing the dispersal pattern of species like capercaillie in mountainous, diversely structured landscapes seems to demand a complex modeling approach. As a species with high cognitive abilities (Klaus et al. 1986), capercaillie will decide on movement path and distance based on its perception of the landscape, i.e., its field of vision. However, our heuristic approach is relatively simple. We use a square perception

window as a baseline concept and assume that the individual has perfect knowledge of the landscape within the window. Then we reduce the window by testing each cell for accessibility or visibility, respectively. Doing so, we adopt the concept of context-dependent perceptual ranges that has recently been proposed by Olden et al. (2004). Also, we account for matrix effects on dispersal success (cf. Revilla et al. 2004; Wiegand et al. 2005), which is a problem that needs further attention (With 2004). Revilla et al. (2004) identify the need to incorporate a behavioral component of matrix use in models of inter-patch connectivity. Our individual-based approach provides a practical solution by making inter-patch movements depend on topography and matrix heterogeneity via individual, context-dependent perceptual ranges.

Species specific movement characteristics define the type of simulation approach to be chosen for dispersal models. In mammal studies, a common approach is to simulate hourly or daily movements via some correlated random walk routine where individuals move continuously from cell to cell (e.g., Kramer-Schadt et al. 2004). Dispersal of resident birds such as the capercaillie can not be captured with a continuous sequence of steps of equal size because their movement pattern is different. Capercaillie individuals do not move much most of the time (especially in winter and during reproduction), but in between they may make discrete movements over varying distances (Klaus et al. 1986; Storch 1995). This type of movement is well-captured with our approach to allow the individuals to make a number of discrete steps of varying size within the perceptual range.

Our approach was heuristic in the sense that we did not have empirical data for model calibration but captured intuitive knowledge of capercaillie experts with impartial dispersal rules (Starfield 1990). Using these rules, we simulated how a large forest bird may use information on the landscape in decisions regarding movement and patch selection. Thus, we include more biological detail than do simple connectivity measures, which may make our model more reliable (cf. Mooij and DeAngelis 2003).

Comparison of connectivity measures

We found that the connectivity measure based on our IBM differed from the distance-based measure but was very similar to the expert estimation. In particular, the more options (rules) we included in the model, the more the connectivity measure deviated from the distance-based measure and the closer it was to the expert estimation. This indicates that we were successful in translating the expert knowledge to impartial dispersal rules.

Distance was a reliable estimate for connectivity in many situations. However, for special situations where dispersal barriers occur between two patch clusters the model-based connectivity measures differed substantially from distance. In such situations, landscape structure may constrict dispersal to few connections that are crucial for maintaining the metapopulation structure and thus the viability of the species in that region.

Apart from properties of the source and target populations, two factors influence the degree to which the dispersal pattern of a certain species deviates from simple distance. The first factor is landscape structure. In a plain landscape with continuous habitat, connectivity will mainly depend on the configuration of the habitat patches making distance an adequate connectivity measure (but see Pfenning et al. 2004). However, in regions with rugged topography and a strongly structured landscape with varying permeability, dispersal will deviate from distance. Second, the ability of a species to move through a landscape and its cognitive abilities to react to visual perception of the landscape will influence the dispersal pattern (Lima and Zollner 1996; Alderman et al. 2005). For very mobile species with generalist habitat use or for species with low cognitive abilities, distance may be an adequate measure of connectivity. However, if dealing with a habitat specialist with limited movement abilities, topography and matrix composition can influence the dispersal pattern significantly. Our findings support the important caveat that when dealing with an endangered species, management actions based on simple distance measures may be ineffective because they neglect matrix heter-

ogeneity and species perceptual ranges that may influence the movement patterns substantially.

Parameterization, validation, sensitivity analysis

The sensitivity analyses show that the model output and thus the predicted connectivity values depend strongly on the parameterization of the model, i.e., on the strength of the dispersal rules. Therefore, we have to be careful about the interpretation and application of our results. The evaluation of the model with dispersal data is an important task before applying the model in any conservation action plan. However, validation of such models is difficult because appropriate data are hardly available (e.g., With 2004). The solution will probably be in the use of patterns derived from indirect movement data that can help to reduce the plausible parameter range (e.g., Wiegand et al. 2003) and thus to calibrate dispersal models. Useful patterns may arise from population genetics (Segelbacher et al. 2003a, b; Jacob 2006), telemetry (Storch 1995; Kramer-Schadt et al. 2004) or mark-recapture data (Koivisto 1963). The emerging science of geographical genetics (Epperson 2003) is particularly promising for confirming dispersal patterns predicted by individual-based models. Our dispersal model could be used to produce hypotheses on genetic affinities among populations that could then be tested with DNA analyses.

Management implications

Individual-based dispersal models may compensate for the lack of field data on inter-patch connectivity (Tischendorf 1997). Our dispersal model produces a similar connectivity pattern to that estimated by capercaillie experts. This result is not surprising because we implemented the dispersal rules based on expert knowledge. But it indicates that we translated the expert knowledge successfully into the dispersal rules. Our model provides quantifiable connectivity envelopes that are impartial, reproducible and consistent over space and time. As such, our model (if validated) may be directly used for the national species action plan (Mollet 2006). In combination with a

model on population dynamics it may help to assess the influence of management strategies on the long-term survival of capercaillie in central Europe. Our approach with context-dependent perceptual ranges could serve as a pragmatic example of how to incorporate a behavioral component of topography and matrix use into dispersal models. Thus, our approach can also be used to model dispersal of other species that use information on the structure of the landscape and constraints to habitat detection to decide on their movements.

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