# A Model for Evaluating the 'Habitat Potential' of a Landscape for Capercaillie Tetrao urogallus: A Tool for Conservation Planning

Authors: Braunisch, Veronika, and Suchant, Rudi

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# A model for evaluating the 'habitat potential' of a landscape for capercaillie *Tetrao urogallus*: a tool for conservation planning

**Veronika Braunisch & Rudi Suchant**

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Most habitat models developed for defining priority conservation sites target areas currently exhibiting suitable habitat conditions. For species whose habitats have been altered by land use practices, these models may fail to identify sites with the potential of producing suitable habitats, if management practices were modified. Using capercaillie *Tetrao urogallus* as an example, we propose a model for evaluating the potential of ecological conditions at the landscape level to provide suitable habitat at the local scale. Initially, we evaluated the influence of selected landscape parameters on the structural characteristics of vegetation relevant to capercaillie. Then we used capercaillie presence data and an ecological niche factor analysis (ENFA) to identify landscape and land use variables relevant to capercaillie habitat selection. We also studied the effect of scale on predictive model quality. Despite high variance, correlations between landscape variables and forest structure were detected. The greatest influence on forest structure was recorded for climate and soil conditions, which were also found to be the best predictors of capercaillie habitat selection in the ENFA. The final model, retaining only two landscape variables (soil conditions and days with snow) and three land use variables (proportion of forest, distance to roads and forest-agricultural borders), explained a high degree of capercaillie habitat selection, even before considering patch size and connectivity. By restricting the analyses to areas with stable subpopulations and a set of relatively stable landscape variables capable of explaining habitat quality at a local scale, we were able to identify areas with long-term relevance to conservation of capercaillie.

*Key words: capercaillie, conservation, ecological niche factor analysis, habitat model, 'habitat potential', landscape scale, Tetrao urogallus*

*Veronika Braunisch & Rudi Suchant, Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, Wonnhaldestr. 4, 79100 Freiburg im Breisgau, Germany - e-mail address:veronika.braunisch@forst.bwl.de (Veronika Braunisch); rudi.suchant@forst.bwl.de (Rudi Suchant)*

*Corresponding author: Veronika Braunisch*

Given the limited area within central Europe suitable as wildlife habitat, and the resultant need to integrate wildlife ecology concerns into landscape planning, it is important to ask: "Which areas are relevant to an endangered species?" Yet, how should priority areas for conservation measures be defined? Considering only areas where an endangered species is currently present is obviously not sufficient, although this is still common practice in nature conservation and landscape planning. The development of increasingly powerful geographic information systems and the growing availability

of digital landscape data in recent years have promoted the creation of large-scale habitat models for the identification of species-relevant sites (e.g. Mladenoff & Sickley 1998, Kobler & Adamic 2000, Schadt et al. 2002, Graf et al. 2005, Zajec et al. 2005). Most of these models are based on a comparison between currently inhabited and uninhabited areas and the identification of relevant habitat parameters, followed by the delimitation of potentially suitable habitats. However, for declining species whose habitats are massively influenced by anthropogenic land use and silvicultural practices, such approaches may be of limited use, as they analyse and extrapolate only a momentary state in an ongoing dynamic process. For example, no decision can be made as to whether the areas with currently suitable habitat conditions are the outcome of past or present management or whether the habitat conditions are a natural result of the prevailing ecological conditions (e.g. climate, soil conditions and topography) and thus have a high potential to remain suitable in the future.

Because of its broad spatial and specific habitat requirements (e.g. Klaus et al. 1989, Storch 1993a,b, 1995), and owing to its function as an umbrella species (e.g. Suter et al. 2002), the capercaillie *Tetrao urogallus* is a popular model species for the analysis of species-habitat interrelationships. This tetraonid is indicative of structurally rich and continuous boreal and montane forest habitats (Scherzinger 1989, 1991, Boag & Rolstad 1991, Storch 1993b, 1995, Cas & Adamic 1998, Simberloff 1998). Within these forested habitats, the geographic distribution of the capercaillie corresponds largely to the spatial pattern of forest fragmentation and the prevailing climatic conditions.

The Black Forest in southwestern Germany holds the largest capercaillie population in Central Europe outside the Alps. Up until the end of the 19th century, the capercaillie was present down into the lowlands. There, secondary habitats had been created by intensive use of forests, including grazing, which opened the forests, and raking of litter for use in stables, which removed nutrients (especially nitrogen) from the soil and led to a change in tree species composition (Suchant 2002, Gatter 2004). Partly as a result of the deterioration of these secondary habitats (Gatter 2004), the capercaillie population has continually declined over the last 100 years and is now limited to higher altitudes (Suchant & Braunisch 2004).

The habitat requirements of capercaillie have been investigated in the past, primarily at the local level (e.g. Gjerde et al. 1989, Rolstad 1989, Helle et al. 1990, Storch 1993a,b, 1995, Schroth 1995, Wegge et al. 1995). In view of the capercaillie's spatial requirements, variables occurring at the landscape level have recently been considered (Ménoni 1994, Sachot 2002, Storch 2002, Suchant 2002, Graf et al. 2005). The purpose of our study was to identify the ecological conditions at a landscape scale that define the preconditions for the development of suitable capercaillie habitat at a local scale. Therefore, we focused on indirect variables (Austin & Smith 1989, Austin 2002), which may replace a combination of different resources in a simple manner and which are more stable and less susceptible to anthropogenic influences than resource variables (Guisan et al. 1999). We hypothesised that a habitat model restricted to a small set of such landscape variables, analysed in areas where subpopulations of capercaillie were stable, would allow us to identify areas with a long-term potential for producing and maintaining suitable habitat. We chose different methodological steps to answer the following questions: 1) which landscape variables support the development of suitable capercaillie habitat at a local scale, 2) which landscape and land use variables are relevant to habitat selection by capercaillie and on which spatial scale must they be considered, and 3) to what extent can a model, based on the resultant variables, explain the distribution of capercaillie?

## Material and methods

### Study area

The study area encompasses the Black Forest, a low forested mountain range in southwestern Germany covering ca 7,000 $km^2$. The elevation ranges within 120-1,493 m a.s.l. Capercaillie are currently present on about 510 $km^2$ at the higher altitudes, with 258 cocks counted in 2003 (Braunisch & Suchant 2006). We distinguished three main capercaillie regions: the southern, northern and eastern Black Forest subregions.

### Capercaillie data

The capercaillie has been continuously monitored in the Black Forest since 1988. Every five years its distribution is mapped, using all direct and indirect evidence of capercaillie presence provided by foresters, hunters, ornithologists and our research personnel. Furthermore, the locations of lekking

Table 1. Landscape and land use variables (landscape scale) used in modelling capercaillie 'habitat potential'. Among the reasons for omitting variables from the reduced model (righternmost column), 'Correl.' means that correlation r was ≥ 0.7 and 'Insufficient contr.' that the contribution to marginality and specialisation was < 0.2.

| Variable category | Variable description | Code | Unit | Data source | Reason for omission from reduced model |
|---|---|---|---|---|---|
| *Landscape variables* | | | | | |
| Climate | Number of days per year with snow cover > 10 cm | snowd | days | DEM | Retained |
| | Average annual temperature | tempyear | °C | German met. service | Correl. with snowd |
| | Duration of the vegetation period (temperature > 10 °C) | vegdur | days | German met. service | Correl. with snowd |
| | Potential sunshine duration (April - September) | soldur | hours | DEM, SAGA-gis model | Insufficient contr. |
| | Potential solar radiation (April - September) | solrad | kWh/m$^2$ | DEM, SAGA-gis model | Insufficient contr. |
| Soil conditions | Soil conditions, evaluated according to their potential to support suitable forest types | scval | index (1-15) | Soil condition database | Retained |
| Topography | Slope | slope | degree | DEM | Ecological plausibility & insufficient contr. |
| | Topographic exposure | topex | (+/−) degree + 1000 | DEM | Insufficient contr. |
| *Land-use variables* | | | | | |
| Forest | Proportion of forest | foall | % of area | Landsat 5 | Retained |
| | Proportion of coniferous and mixed forest | fcomi | % of area | Landsat 5 | Correl. with foall |
| | Proportion of forest-agriculture border area (200 m width) | agfor | % of area | Landsat 5 | Retained |
| Agriculture | Proportion of agriculture | agall | % of area | Landsat 5 | Correl. with foall |
| | Distance to agriculture | agdist | m | Landsat 5 | Correl. with agall |
| Settlements | Proportion of settlements and urban area | urb | % of area | Landsat 5 | Correl. with stdist |
| | Distance to settlements and urban area | urbdist | m | Landsat 5 | Correl. with stdist |
| Linear infrastructure | Proportion of area influenced by roads (plus 100 m buffer) | stall | % of area | ATKIS | Correl. with stdist |
| | Proportion of roads (plus 100 m buffer) weighted according to average traffic/day | sttra | % of area* traffic-index | ATKIS/Ministry of Traffic | Correl. with stdist |
| | Distance to roads | stdist | m | ATKIS | Retained |

places are mapped and the number of cocks counted annually (Braunisch & Suchant 2006). For our analyses, we randomly sampled 1,600 presence points, with at least 300 m between points to reduce bias from spatial autocorrelation. The proportion of records selected from each subregion (south, north and east) corresponded to the mean proportion of cocks counted in each area. In addition, to restrict the landscape analyses to areas with 'stable' subpopulations of birds, we included only records from patches that had been consecutively mapped as 'inhabited' since 1988.

## Landscape and land use variables

The landscape-scale variables tested in the model (Table 1) were subdivided into two categories: 'landscape' and 'land use' variables. 'Landscape' variables are environmental factors that are expected to affect the composition and structure of forests and other vegetation. They therefore define the natural potential of the landscape for the development of suitable habitat. 'Land use' variables in contrast, describe the current distribution of forest and human land-use features and, therefore, may define the area that is currently available for use by capercaillie.

The landscape variables included characteristics of climate, soil conditions and topography. As the restriction of central European capercaillie populations to the higher altitudes of montane regions (Klaus et al. 1989, Storch 2000) is a consequence of climate, rather than altitude, we compared three climate variables correlated with altitude: 1) 'average annual temperature', 2) 'duration of the vege-

tation period' and 3) 'number of days with >10 cm snow cover', calculated according to Schneider & Schönbein (2003). In addition, 'potential sunshine duration' and 'potential solar radiation' during the vegetation period (April-September) were modelled according to Böhner et al. (1997).

Analyses of soil conditions were based on a soil condition database. Soil texture, soil type, humus type, nutrient status and hydrological regime were evaluated separately with respect to their potential to support selected capercaillie habitat structures, including ground vegetation dominated by bilberry *Vaccinium myrtillus*, nutrient-poor forest types dominated by conifers or pines, bogs and wet forests. The variables were then aggregated into a soil condition index using an expert model (V. Braunisch, M. Wiebel, H.G. Michiels & R. Suchant, unpubl. data).

Topographic exposure was determined using the topex-index (Wilson 1984), which qualifies a point's position relative to the surrounding terrain. The topex-to-distance index employed here was calculated as the sum of angles to the ground within a fixed distance, measured for each of the eight cardinal directions (Mitchell et al. 2001). A distance of 2,000 m was chosen because Hannah et al. (1995) found this topex to be strongly correlated with the probability of windfall events, which favour open forest structures.

Land use variables describe the availability and spatial distribution of existing land use features (forest, forest fragmentation and agricultural areas), including the distribution of possible sources of disturbance (settlements and linear infrastructures). A distinction was made between 'forest' in general, which grouped all available forest categories, and 'coniferous and mixed forest', which excluded purely deciduous forest.

As a measure of forest fragmentation, we calculated a 200-m wide forest-agricultural border zone, which included a 100-m buffer on either side of the forest edge. As intensive agriculture (arable fields, orchards and grassland) is very rare in the Black Forest and the map of 'intensive agriculture' would have neglected the minimum criteria for statistical normality, it was pooled with non-intensively used grassland and pastures.

To the potential sources of disturbance, i.e. settlements and linear infrastructures, we added a 'disturbance' buffer of 100 m. Two different maps were constructed for linear infrastructures. On the first map, depicting the fragmentation effect of roads, we pooled all road categories (e.g. main roads, county roads and rural roads) and railways. On the second map, highlighting the disturbance effect of roads, the different road categories were weighted according to average traffic density.

We prepared raster maps with a $30 \times 30$ m grid for all variables. As the two climate variables 'average annual temperature' and 'duration of the vegetation period' were only available at a resolution of 1 $km^2$, we produced an additional map depicting 'number of days with >10 cm snow cover' at this 1-$km^2$ resolution for a separate comparison. To determine the spatial scale at which a variable performed best, we calculated the mean value for each variable within circular moving windows of 10, 100, 500 and 1,000 ha. These scales correspond to the size of an average forest stand (10 ha), the size of a small (100 ha) and large (500 ha) individual capercaillie home range, and to the average size of an occupied habitat patch in the study area (1,000 ha). As multinormality was required, all variables were normalised using the Box-Cox standardising algorithm (Box & Cox 1964, Sokal & Rohlf 1981). Maps were prepared in ArcView (ESRI 1996) and converted to IDRISI.

## Habitat structure data

Data on habitat structure at a local scale were taken from the national forest inventory. The sampling strategy was based on a $2 \times 2$ km Gauss-Krüger grid. The corner of each grid cell represented the centre of a $150 \times 150$ m square, the corners of which in turn each marked the centre of a sample plot. A total of 4,308 sample plots were distributed over the afforested parts of the study area, with selected habitat structure variables mapped within different radii around the sample plot centre (Table 2). The influence of landscape variables on vegetation structure was tested using multiple linear regression (STATISTICA, StatSoft 1999).

## Statistical methods

### *Modelling approach*

Multivariate approaches to modelling habitat suitability or to predicting species presence (e.g. logistic regression) usually require presence-absence data. The ecological niche factor analysis (ENFA; Hirzel et al. 2002), based on Hutchinson's (1957) concept of the ecological niche, compares the conditions of sites with proved species presence against the conditions of the whole study area, requiring only presence data. All predictor variables included in the model are transformed to an equal number of un-

Table 2. Habitat structure variables relevant for capercaillie at local scale tested for correlation with the landscape variables listed in Table 1 and the size of the sample plots in which they were mapped.

| Category | Forest structure variable | Unit | Sample unit |
|---|---|---|---|
| Forest type | Conifer dominated forest types | Yes/no | Forest stand containing the centre of the sample plot |
| | Pine dominated forest types | Yes/no | Forest stand containing the centre of the sample plot |
| Forest age | Old forest | (years > 70) yes/no | Forest stand containing the centre of the sample plot |
| Forest structure | Density (related to ideal crown projection and ha) | Index | Sample plot (r = 25 m) |
| | Increment (10 years) | $m^3$/year ha | Sample plot (r = 25 m) |
| | Windfall (10 years) | Yes/no | Sample plot (r = 25 m) |
| Ground vegetation | Ground vegetation coverage | Index | Sample plot (r = 10 m) |
| | Bilberry coverage | % coverage (4 classes) | Sample plot (r = 10 m) |

correlated and standardised factors. The first factor explains the species' marginality (M = the difference between the average conditions within areas with species presence and those in the entire study area), which defines the location of the species' niche in relation to the range of available conditions. It also explains part of the specialisation (S = the ratio between the standard deviation (SD) of the conditions in the entire study area and the SD of the conditions where the species is present), which defines the niche breadth. The subsequent factors explain the rest of the specialisation.

*Variable and scale selection*

Initially an ENFA was performed including all variables at all spatial scales. Then we calculated a multi-scale model including all variables, each at the scale where it performed best and compared this with four single-scale models, including all variables at the same scale (10, 100, 500 and 1,000 ha).

To obtain a simple final model without losing too much information, we selected the best of the aforementioned models and reduced the initial set of variables using the following criteria. A variable was only included in the final model if 1) it made a sufficient contribution to marginality or specialisation (> 0.2), 2) it showed the same algebraic sign in the coefficient value of the marginality factor (indicating avoidance or preference) at all spatial scales, and 3) it was ecologically plausible. In addition, if bivariate correlation between any two remaining variables exceeded a threshold of 0.7, the variable with the lower contribution to specialisation and marginality was discarded.

*Landscape model of 'habitat potential'*

We defined 'habitat potential' as the capacity of landscape conditions to give rise to suitable capercaillie habitat. Some areas of the landscape may already exhibit suitable habitat, others might be capable of producing such habitats, depending on management practices and natural evolution of the vegetation. We calculated an index to 'habitat potential' using the 'area-adjusted median algorithm with an extreme optimum' for the marginality part of the first factor. This modification of the median algorithm (Hirzel & Arlettaz 2003a) was especially developed for species existing at the edge of their natural distribution range (Braunisch et al. submitted). The number of significant factors retained for the calculation of 'habitat potential' was chosen according to the broken-stick model (MacArthur 1960, Hirzel et al. 2002). Indices of 'habitat potential' ranged from 0 (unsuitable for capercaillie) to 100, with low values representing suboptimal areas.

*Model validation*

For model evaluation we applied a 10-fold area-adjusted frequency cross validation (AAFCV; Fielding & Bell 1997). The model quality was quantified using the continuous Boyce index (Hirzel et al. 2006). In addition, we calculated the 'regular' Boyce index (Boyce et al. 2002), the absolute validation index (AVI), which calculates the proportion of evaluation points occurring in the predicted core habitats, and the contrast validation index (CVI), which compares this value with the value that could be expected from a random model (Hirzel & Arlettaz 2003b, Hirzel et al. 2004).

## Results

### Landscape variables - habitat structure

Although parameter values varied greatly between sample plots, multiple regression analysis showed significant correlations between landscape condi-

tions and forest structure (Table 3). The greatest influence was recorded for the variables 'days with snow' (snowd) and 'soil conditions' (scval), which affect the forest type, and bilberry cover in particular. Among the landscape variable, these two variables were also found to be the best predictors of capercaillie habitat selection in the ENFA (Table 4).

### Effect of scale selection on models

Of all the models, including those with the full set of descriptors and those with reduced variable sets, the 10-ha single-scale models always provided better results in the AAFCV than either the corresponding single-scale models with lower resolutions (Table 5) or the multi-scale models. Therefore, the 10-ha scale was chosen for variable selection and identification of sites with 'habitat potential'.

### Variable selection, marginality and specialisation

The contribution of the different variables to marginality and specialisation for the 10-ha single-scale model is shown in Table 4. The marginality factor also explains the highest degree (28.9%) of the specialisation. This indicates a quite narrow niche breadth for the variables that most differentiate capercaillie habitats from the average conditions in the study area.

Of the landscape variables, snowd (days with snow cover) exhibited the highest contribution to both marginality and specialisation. In the separate comparison (only one significant factor, therefore M = S) it also performed better (coefficient value: 0.632) than the two other altitude-correlated climate variables vegdur (0.569) and tempyear (0.526), which were therefore excluded from further analyses. The second most important variable was scval (soil conditions). However, although capercaillie areas are characterised by a much higher soil condition index than average, the degree of specialisation is rather moderate. The other landscape variables (topex, slope, soldur and solrad) revealed only weak contributions to both marginality and specialisation.

Concerning the land use variables, capercaillie shows highest marginality in relation to distances to roads (stdist), agricultural areas (agdist) and settlements (urbdist), but it is most specialised in the selection of areas with a high abundance of forest (foall) and in the avoidance of agricultural areas (agall). The similar absolute values for these two variables are not surprising, as they are highly neg-

Table 3. Results of least square regression correlation between landscape and forest structure variables. The first row shows the multiple R. The algebraic sign[1] of the standardised regression coefficient β (subsequent rows) indicates whether a variable's contribution is positive or negative. The number of asterisks indicates the level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. β-values > 0.2 are italicised.

| Category | | Forest type | | Forest age | Forest structure | | | Vegetation coverage | |
|---|---|---|---|---|---|---|---|---|---|
| Variable | | Conifer-dominated | Pine-dominated | Proportion of old forest | Density | Growth capacity | Frequency of windthrow | Bilberry | Ground vegetation |
| | Unit | Number of sample plots | Number of sample plots | Years | Index | Increment $m^3$/ year ha | Number of sample plots | % coverage | Index |
| Level P-value of multiple R | | 0.31*** | 0.23*** | 0.10*** | 0.12*** | 0.17*** | 0.16*** | 0.55*** | 0.23*** |
| Days with snow > 10 cm | Day | *0.246**** | -0.121*** | | | -0.091*** | -0.066*** | *0.311**** | 0.038* |
| Potential solar radiation | $kWh/m^2$ | -0.058** | 0.047** | 0.057** | 0.066* | | | | -0.076*** |
| Potential sun-shine duration | Hour | | | | | | 0.096*** | | |
| Soil conditions | Index | 0.097*** | *0.217**** | 0.070*** | -0.077*** | -0.104*** | 0.084*** | *0.342**** | 0.082*** |
| Topographic exposure[1] | Index | | -0.109*** | | 0.066* | 0.080* | -0.089*** | 0.047 | 0.072** |
| Slope | Degree | -0.103*** | | | | -0.088** | | -0.121*** | *-0.218**** |

[1]Low values indicate high topographic exposure.

Table 4. Contribution of the landscape and land use variables to marginality, specialisation and explained information[1] by the significant first four factors (out of 16) in the 10-ha single scale model. The variables are represented by their code as shown in Table 1. Positive values in the marginality factor indicate preference and negative values indicate avoidance. Variables are sorted by category (landscape and land use) and decreasing value of coefficients on the marginality factor. Contributions to marginality, explained specialisation and explained information > 0.2 are italicised. For the topographic exposure variable (topex), low values indicate high topographical exposure and high values indicate topographical depressions. Therefore, the minus sign in the coefficient on the marginality factor indicates preference for exposed sites.

| | F1 | F2 | F3 | F4 | F1-F4 | F1-F4 |
|---|---|---|---|---|---|---|
| Factor | Marginality (28.9%) | Specialisation (22.2%) | Specialisation (19.2%) | Specialisation (8.9%) | Contribution to explained specialisation (79.2%) | Contribution to explained information (89.6%) |
| snowd | *0.442* | -0.077 | 0.093 | -0.013 | *0.207* | *0.338* |
| scval | *0.310* | 0.000 | 0.020 | -0.008 | 0.119 | *0.226* |
| topex | -0.078 | -0.012 | -0.001 | -0.010 | 0.033 | 0.058 |
| slope | 0.064 | 0.016 | -0.013 | 0.014 | 0.033 | 0.050 |
| soldur | 0.016 | 0.005 | -0.018 | 0.019 | 0.014 | 0.015 |
| solrad | 0.003 | 0.001 | 0.001 | 0.006 | 0.002 | 0.003 |
| agdist | *0.333* | 0.005 | -0.105 | 0.006 | 0.149 | *0.252* |
| stdist | *0.320* | 0.009 | 0.005 | 0.000 | 0.121 | *0.232* |
| urbdist | *0.313* | -0.012 | 0.018 | -0.031 | 0.125 | *0.230* |
| fcomi | *0.303* | -0.022 | 0.001 | 0.006 | 0.120 | *0.222* |
| agall | *-0.273* | 0.626 | 0.791 | -0.552 | *0.529* | *0.386* |
| foall | *0.270* | 0.775 | 0.549 | -0.704 | *0.528* | *0.384* |
| agfor | *-0.228* | 0.008 | -0.220 | 0.051 | 0.145 | 0.191 |
| stall | -0.198 | -0.008 | -0.032 | -0.014 | 0.098 | 0.154 |
| sttra | -0.186 | 0.011 | 0.031 | 0.129 | 0.093 | 0.145 |
| urb | -0.151 | -0.007 | 0.033 | -0.398 | 0.110 | 0.133 |

[1]Explained information = ½ (1*contribution to marginality + 0.792 * contribution to specialisation).

atively correlated ($r > 0.9$). In addition, the results show a strong avoidance of areas bordering agricultural land (agfor). With regard to linear infrastructure, the distance to roads was more important than the density of roads, independently of whether traffic density was included or not.

Based on the criteria described, only two landscape variables (snowd and scval) and three land use pattern variables (foall, stdist and agfor) were retained for the final model to calculate the indices of habitat potential. The reasons for omitting the other variables are given in Table 1.

## Landscape 'habitat potential' models

The indices to 'habitat potential' (Fig. 1) were calculated on the basis of the five most important variables. Three significant factors accounted for 94.2% of the explained specialisation and 97.1% of the explained information. Global marginality was high (1.145), indicating that capercaillie habitats differed greatly from average conditions in the study area. Global specialisation (2.601) and tolerance (0.384) indicate a relatively narrow niche breadth. With only five variables, a large degree of capercaillie habitat selection at the landscape

Table 5. Results of the area-adjusted k-fold cross-validation for single and multi-scale models with the full descriptor set, and for the final model (10-ha scale) with the reduced descriptor set. Correlations between modelled 'habitat potential' and area-adjusted frequency of capercaillie presence points are given by the continuous Boyce index ($B_{cont}$, ± SD) and the 'regular' Boyce index ($B_{4bins}$, ± SD), both ranging from -1 (wrong model) to 1 (good model). The capacity to predict the spatial pattern of capercaillie distribution is provided by the absolute validation index (AVI, ± SD) and the contrast validation index (CVI, ± SD), both ranging between 0 (random model) and 0.5 (good model). SD = standard deviation.

| Model type<br>Full descriptor set | Scale | $B_{cont}$ | SD | $B_{4bins}$ | SD | AVI | SD | CVI | SD |
|---|---|---|---|---|---|---|---|---|---|
| Single scale_10 | 10 | 0.83 | 0.23 | 0.82 | 0.24 | 0.52 | 0.20 | 0.44 | 0.20 |
| Single scale_100 | 100 | 0.58 | 0.36 | 0.78 | 0.27 | 0.50 | 0.08 | 0.38 | 0.08 |
| Single scale_500 | 500 | 0.76 | 0.27 | 0.70 | 0.32 | 0.52 | 0.24 | 0.43 | 0.23 |
| Single scale_1000 | 1,000 | 0.56 | 0.51 | 0.64 | 0.39 | 0.51 | 0.29 | 0.42 | 0.28 |
| Multi_scale | Multi | 0.61 | 0.43 | 0.72 | 0.33 | 0.52 | 0.24 | 0.43 | 0.24 |
| Reduced descriptor set (final model) | | | | | | | | | |
| Landscape habitat potential (5 variables) | 10 | 0.70 | 0.44 | 0.78 | 0.27 | 0.52 | 0.24 | 0.45 | 0.24 |

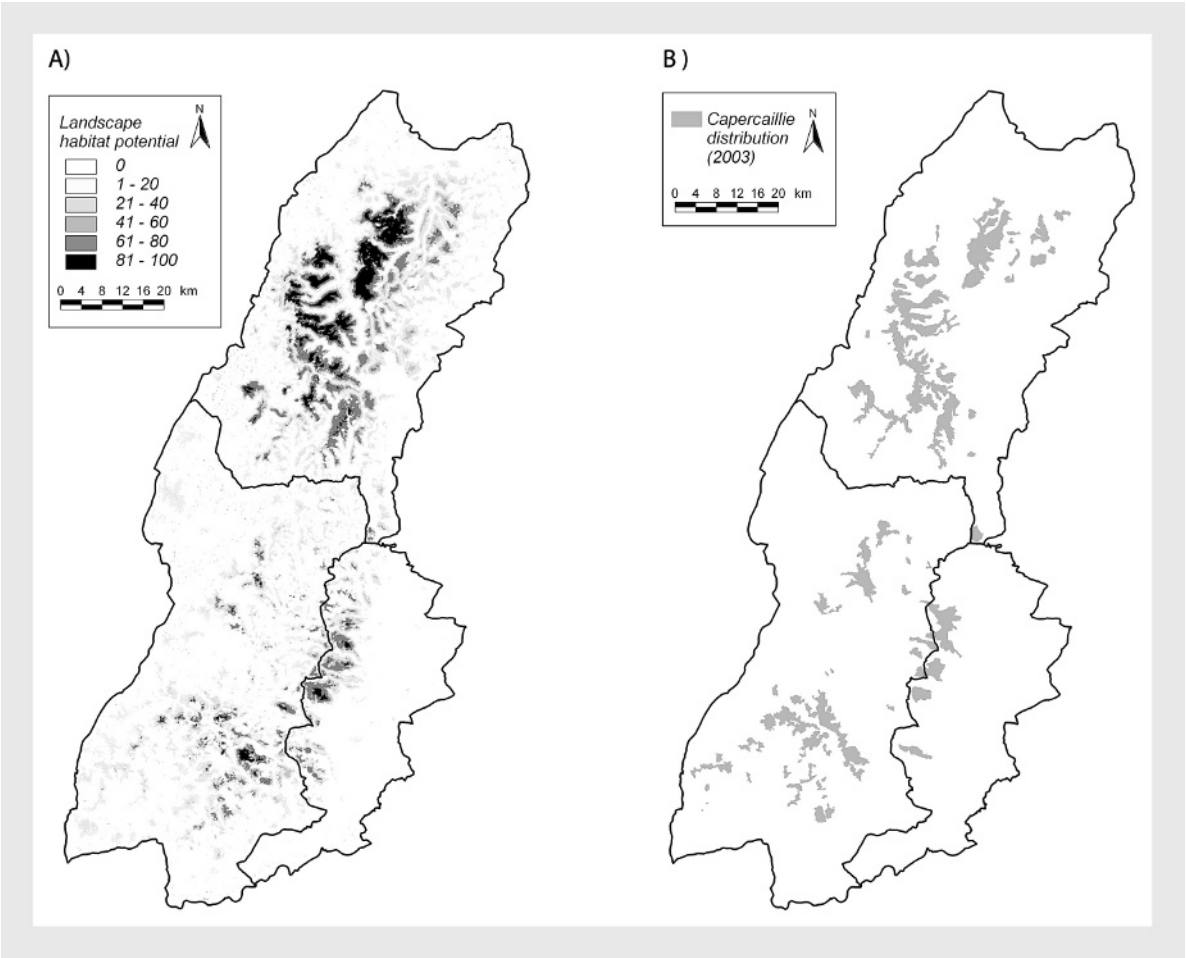


Figure 1. Landscape 'habitat potential' for capercaillie in the Black Forest, Germany, before considering patch size and connectivity (A), compared with current capercaillie distribution mapped in 2003 (B).

scale could be explained. The reduction in number of variables led to only a moderate decrease in model quality compared to the full descriptor set, which was reflected by a decrease in the Boyce indices and an increase in the standard deviation (see Table 5).

### Indices of 'habitat potential' vs capercaillie distribution

Although the distribution pattern of the 'habitat potential' in the study area closely matched the areas of actual capercaillie presence (see Fig. 1), great differences between the three subregions became apparent (Fig. 2) when comparing the 'habitat potential' values within the capercaillie areas mapped in 2003.

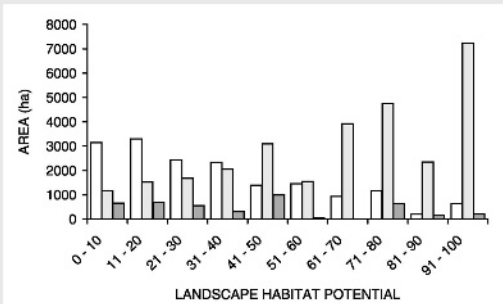


Figure 2. Distribution of the landscape 'habitat potential' in the areas currently inhabited by capercaillie (mapped in 2003), differentiated according to the different subregions (□: southern; ■: northern; ■: eastern) of the Black Forest, Germany.

## Discussion

### Modelling approach

In view of the increasing conflict between human activities and the need to protect habitats of endangered species, concepts are required for optimising the use of limited spatial and financial resources. Therefore, predictive species-habitat models have become a popular planning instrument. However, as they are based on comparisons of the observed current distribution of a species and the current state of its habitat, the models are by default static and assume an equilibrium between environment and species distribution (Guisan & Zimmermann 2000). Such equilibrium, however, seldom corresponds to reality (Pickett et al. 1994). Natural dynamics and continuously changing anthropogenic land use, as well as far reaching effects of historical processes, continue to affect the spatial patterns of animal-habitat relationships. Yet, the incorporation of such processes in dynamic simulation models is very difficult (e.g. Lischke et al. 1998, Guisan & Zimmermann 2000) and frequently unrealisable in the context of applied nature conservation issues. Our approach was, therefore, to identify areas with a long-term potential for producing and maintaining suitable habitat for capercaillie by exhausting the possibilities of a static resource selection model. To minimise the aforementioned problems of static models we considered three aspects: First, the sample locations were restricted to areas with stable subpopulations. Second, we focused on comparatively stable indirect predictor variables for habitat quality, and third, an ENFA, requiring only presence data, was preferred over a logistic regression model to reduce the influence of 'false' absence data. Such false data may arise from anthropogenic impacts producing unsuitable habitat structures at a local scale in areas where the prevailing landscape conditions are in fact suitable. The applicability and transferability of the methods to other species and regions was another important criteria for choosing the ENFA approach, as reliable absence data are often unavailable in practical conservation management.

### Influence of landscape and land use variables on capercaillie habitat selection

The landscape descriptors identified as being important for capercaillie in the Black Forest resembled those of other investigations (Suchant 2002, Sachot 2002, Graf et al. 2005). Therefore, we will only discuss deviations from these results and new findings in this paper.

Our study is the first to examine the explanatory power of different elevation-correlated climate variables. The variable 'number of days with $>$ 10 cm snow cover' was found to perform slightly better than the other two altitude-correlated variables, vegdur and tempyear. This may be due to areas with a longer duration of snow cover being more susceptible to snow damage, which may promote the creation of open and structured habitat conditions. Furthermore, snow cover may also reduce predator population densities in winter and enhance the possibilities for saving energy by resting in snow 'igloos'.

The influence of soil conditions on capercaillie habitats has received little attention, despite the fact that they impact the species composition of trees and ground vegetation, as well as the growth rate of plants, especially bilberry, which is a key source of food for capercaillie (e.g. Storch 1993a). Graf et al. (2005) integrated only sites with extreme soil conditions (moors and wet forests) into their model, whereas we used a graded weighting of soil conditions for the first time.

Forest fragmentation is reportedly linked to a reduction in reproductive success because of increased predation in areas bordering agricultural land (e.g. Andrén & Angelstam 1988, Kurki et al. 2000, Storch et al. 2005). In our study capercaillie apparently avoided such border areas. However, we could have underestimated the possible positive influence of small, non-intensively used open land areas, as we considered neither the size of the agricultural areas nor the distinction between intensive and non-intensive land use.

### Impact of spatial scale

As different environmental variables impact species at different spatial scales (Freemark & Merriam 1986, Levin 1992), multi-scale approaches are becoming increasingly common (Bissonette 1997). Graf et al. (2005) found that better model results can be obtained for a generalised linear model when the variables are integrated at the scale at which they make the highest contribution to the explained variance in univariate models. In the case of an ENFA, such a selection of variables can be difficult, as their contribution to the explained information depends on the other variables integrated into the model.

Two aspects must be distinguished when determining the 'optimal' scale: 1) the influence of scale

on the explanatory power of individual variables for habitat selection and 2) the influence of the selected variable scales on the overall quality of the model results. Hirzel et al. (2004) quantified the performance of the same variables on different spatial scales in the context of an ENFA for the bearded vulture *Gypaetus barbatus*. They found that in the case of generalised variables quantifying the availability of a resource within a predefined area, the contribution to marginality and specialisation mostly increased with spatial scale. Zajec et al. (2005) compared the results of single-scale ENFA models comprising the same set of variables, but with different spatial resolutions, and found that model quality decreased with an increase in scale. Both, seemingly contradictory phenomena, also apply in our investigation. However, a multi-scale model containing all variables at the scale where they performed best failed to provide better results than the 10-ha single scale model. As an analysis of landscape-scale patterns by simply calculating the mean availability of a resource within a circular moving window implies a high degree of generalisation, it may lead to misclassification of small unsuitable landscape structures (e.g. roads, small settlements and arable fields). Consequently the predictive power of a model containing such highly generalised variables is low.

Nevertheless, in view of the spatial requirements of capercaillie, the availability and distribution of 'habitat potential' at the landscape scale cannot be ignored. Therefore, we would suggest a two-step approach. First, select, as we did, the high-resolution 10-ha single-scale model for the quantification of the 'habitat potential'. Second, to select priority sites for practical habitat management, one should retain only those patches with 'habitat potential' that are large enough to be inhabited by capercaillie, and which theoretically can be reached by the birds. Although we do not present the results here, we tested this procedure by selecting only patches of 'habitat potential' at least 100 ha in size, including smaller ones only if within 100 m of patches of $\geq$ 100 ha. This 100-m threshold was chosen after an evaluation of all currently inhabited patches. Furthermore we excluded all uninhabited patches $>$ 10 km from inhabited patches, because 10 km corresponds to the mean dispersal distance of capercaillie (Myrberget 1978, Rolstad et al. 1988, Ménoni 1991, Swenson 1991, Storch 1993b, cited in Storch & Segelbacher 2000). This procedure improved the predictive power of the model and had the following advantages: 1) a high degree of accuracy is achieved, which improves applicability, and 2) locations with high potential but which are too small to serve as habitat can be considered for subsequent biotope network models.

**Model results and consequences for management**

Our results support earlier findings suggesting that with a small number of landscape parameters most of the capercaillie distribution can be predicted (Suchant 2002, Graf et al. 2005). Most habitats in the Black Forest with high indices of 'habitat potential' are currently occupied by capercaillie. There are, however, evident differences between the subregions. In the southern part, the 'habitat potential' is generally lower and highly fragmented, and capercaillie are found in both high- and low-potential sites. Nevertheless, especially in this region, the spatial pattern of population decline coincides with the spatial distribution of lacking or low 'habitat potential' (V. Braunisch & R. Suchant, unpubl. data). In contrast, in the northern part, where the capercaillie distribution is mainly restricted to high potential habitats, the population has remained more or less stable over the last 20 years (Braunisch & Suchant 2006).

Given that in sites with high indices of 'habitat potential' the prevailing landscape conditions favour the development of suitable habitat, concentrating habitat improvement measures on these sites leads not only to an ecological but also an economical optimisation of conservation efforts. Optimisation will be achieved particularly in areas where forest management has created unsuitable habitats. The graduated series of 'habitat potential' indices simplifies the selection of priority areas, particularly when trying to satisfy predefined area requirements, e.g. for a minimum viable population (Hovestadt et al. 1992). The model also provides location-specific information for the location of protected areas (especially Natura 2000) and the spatial planning of conservation measures and land-use activities (especially silviculture, tourism and wind energy). However, the model could be improved by considering in greater detail the functional connectivity between patches and the long-term changes in landscape conditions (e.g. climate change and nitrification).

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