Report

On Spatial Resolution in Habitat Models: Can Small-scale Forest Structure Explain Capercaillie Numbers?

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ABSTRACT. This paper explores the effects of spatial resolution on the performance and applicability of habitat models in wildlife management and conservation. A Habitat Suitability Index (HSI) model for the Capercaillie (*Tetrao urogallus*) in the Bavarian Alps, Germany, is presented. The model was exclusively built on non-spatial, small-scale variables of forest structure and without any consideration of landscape patterns. The main goal was to assess whether a HSI model developed from small-scale habitat preferences can explain differences in population abundance at larger scales. To validate the model, habitat variables and indirect sign of Capercaillie use (such as feathers or feces) were mapped in six study areas based on a total of 2901 20 m radius (for habitat variables) and 5 m radius sample plots (for Capercaillie sign). First, the model's representation of Capercaillie habitat preferences was assessed. Habitat selection, as expressed by Ivlev's electivity index, was closely related to HSI scores, increased from poor to excellent habitat suitability, and was consistent across all study areas. Then, habitat use was related to HSI scores at different spatial scales. Capercaillie use was best predicted from HSI scores at the small scale. Lowering the spatial resolution of the model stepwise to 36-ha, 100-ha, 400-ha, and 2000-ha areas and relating Capercaillie use to aggregated HSI scores resulted in a deterioration of fit at larger scales. Most importantly, there were pronounced differences in Capercaillie abundance at the scale of study areas, which could not be explained by the HSI model. The results illustrate that even if a habitat model correctly reflects a species' smaller scale habitat preferences, its potential to predict population abundance at larger scales may remain limited.

INTRODUCTION

Habitat models, in general, and habitat suitability index (HSI) models, in particular, are among the most widely used wildlife management tools in North America (Verner et al. 1986, Van Horne and Wiens 1991, Brooks 1997). In Europe, habitat models are receiving increasing attention (Storch 1996, Kuhn 1998) as the need for practical evaluation methods for land management and conservation practice has become recognized (Link et al. 1996). Typically, habitat models are used to assess the suitability of an area as a habitat for one or several target species. A HSI model summarizes the conceptual understanding of the habitat relationships of the target species, based on literature reviews, expert opinion, or research studies. A set of habitat variables is identified and combined into a series of simple equations. The resulting HSI score ranges between 0 for unsuitable and 1 for optimal habitat suitability. Ideally, a HSI model should be validated by comparing the model output with population data from independent sites before it is put into use. HSI scores allow one to

compare differences among sites, over time, or between management scenarios. The procedures of HSI model development and testing have been summarized by Schamberger and O'Neil (1986), Van Horne and Wiens (1991), Morrison et al. (1992), and Brooks (1997).

Species–habitat relationships include several hierarchical levels of spatial scale, and different habitat features may be relevant to a species at different scales (Bissonette 1997). Thus, habitat variables used successfully to predict a species' response at one scale may fail at another. Habitat models, however, rarely consider the potential effects of scale (e.g., Hamel et al. 1986, Laymon and Reid 1986, Van Horne and Wiens 1991). The spatial resolution underlying HSI models depends on the resolution of the species–habitat concept used for model development. Being planning rather than research tools, most HSI models are not built on direct investigations, but on whatever information is at hand. Therefore, resolution will often result from the available data set rather than from purposeful design.

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Hence, many HSI models are applied with the underlying assumption that wildlife–habitat relationships are consistent throughout all levels of scale (Hamel et al. 1986). The implications of this assumption for model application have rarely been assessed (Schulz and Joyce 1992). This is the general problem that I address in this paper.

There is good evidence that both small-scale and landscape-scale characteristics of the habitat are significant predictors of the presence and abundance of vertebrate species (Mazerolle and Villard 1999). In the past, however, landscape-scale features such as habitat fragmentation have not been a common consideration in wildlife habitat models (Temple and Wilcox 1986). Most models are built on a species' preferences for smaller scale habitat features such as vegetation or soil characteristics (e.g., Van Horne and Wiens 1991, Picozzi et al. 1992). This is the resolution at which wildlife–habitat relationships most commonly have been perceived and described (Temple and Wilcox 1986), and is also the resolution of the data most commonly available to land use managers. This is also true of the Capercaillie (*Tetrao urogallus*), a grouse of the boreal and montane forests of Eurasia. In central Europe, the Capercaillie is regarded as an indicator of intact mountain forest communities (Müller 1978, Scherzinger 1989, Marti 1993). The species is considered to be a habitat specialist with close affinity to old conifer forest rich in bilberry, *Vaccinium myrtillis* (Rolstad and Wegge 1987, Klaus et al. 1989, Picozzi et al. 1992). In the past, descriptions of Capercaillie habitat needs have almost exclusively addressed vegetation structure at the forest stand level, and accordingly, habitat management measures for Capercaillie have primarily focused on stand structure (Storch 1997*b*). Because of its relatively large spatial requirements, with annual home ranges of several hundred hectares in size, the Capercaillie is susceptible to forest fragmentation (Rolstad and Wegge 1987, 1989, Storch 1995*a*). Although the Capercaillie's habitat preferences at the forest-stand level can be described by a small set of variables (Picozzi et al. 1992, Storch 1995 *a*), it is unclear whether Capercaillie presence and abundance can actually be explained by small-scale habitat structure. This is the specific question that I address in this paper.

In this study, I aim to determine whether species presence and abundance can be predicted without reference to the landscape context. I explore whether a habitat model based on small-scale habitat preferences can explain (1) presence or absence of signs of Capercaillie use at the scale of 5-m sample plots, and (2) differences in Capercaillie abundance between mountain ranges, i.e., local populations. I present a HSI model for Capercaillie habitat evaluation that is exclusively built on variables at the forest-stand level (such as canopy cover and ground vegetation height), without any consideration of landscape features (such as patch size or juxtaposition). I assess whether, at the local scale, HSI scores are related to the chances of finding signs of Capercaillie use (such as feathers or feces), and thus correctly reflect Capercaillie habitat preferences at the forest-stand level. Because the frequency of Capercaillie signs may also depend on habitat features at larger spatial scales, I also assess the relationship between incidence of signs and HSI scores aggregated over areas of various sizes, up to 2000-ha study areas. Lastly, I explore whether the inclusion of landscape patterns as explanatory variables may improve the predictability of Capercaillie presence and abundance.

In most central European countries, the Capercaillie is listed in the Red Data Books of endangered species (Storch 2000). Human land use, and particularly forestry, greatly influences the structure and dynamics of Capercaillie habitats and is considered the main cause of declining Capercaillie numbers during the past decades (Rolstad and Wegge 1989, Klaus and Bergmann 1994). Therefore, integrating forestry practices and Capercaillie habitat preservation is a major conservation challenge (Storch 2000). Standardized and practical methods that allow objective evaluation and monitoring of habitat suitability are needed (see also Picozzi et al. 1992). In the Alps, Capercaillie habitat is managed primarily by local State foresters or small, private forest owners, and descriptions of forest stands are the kind of data typically available. Thus, the major motivation for developing the HSI model for Capercaillie was to create a tool for habitat suitability assessment at the stand level that could be used in forest planning and management.

METHODS

Study areas

The Alps have the widest distribution of Capercaillie in central Europe. The species occurs throughout alpine forests, but population density varies locally (Storch 2001; A. Zeitler, *personal communication,* I. Storch, *unpublished data*). In the Bavarian Alps in southernmost Germany, the landscape is characterized

by mountain ranges reaching altitudes of 1000–3000 m and covering areas of typically 50–100 km², separated by farmland valleys at 600–900 m altitude and up to a few kilometers wide, and with treelines at 1300–1800 m. In this landscape, the distribution of Capercaillie is spatially structured, with distinct local populations on separate mountain ranges. Juvenile dispersal and adult movement distances reported from throughout the species' range (Storch and Segelbacher 2000), as well

as telemetry results from the Bavarian Alps (Storch 1995*a*; I. Storch, *unpublished data*) suggest that only a few birds move between these ranges. Preliminary microsatellite data indicate that Capercaillie populations on neighboring mountain ranges differ genetically (G. Segelbacher and I. Storch, *unpublished data*).

Fig. 1. Location of the six study areas in southern Germany, and sampling design within each study area. A 200 x 200 m grid of sample plots was laid over each area. Habitat variables were recorded within a 20 m radius to calculate HSI scores. As an index of Capercaillie use, presence or absence of signs such as feathers and feces was recorded within a 5 m radius. To assess habitat suitability and Capercaillie abundance for 100-, 400-, and 2000-ha areas, data for all sample plots were aggregated.
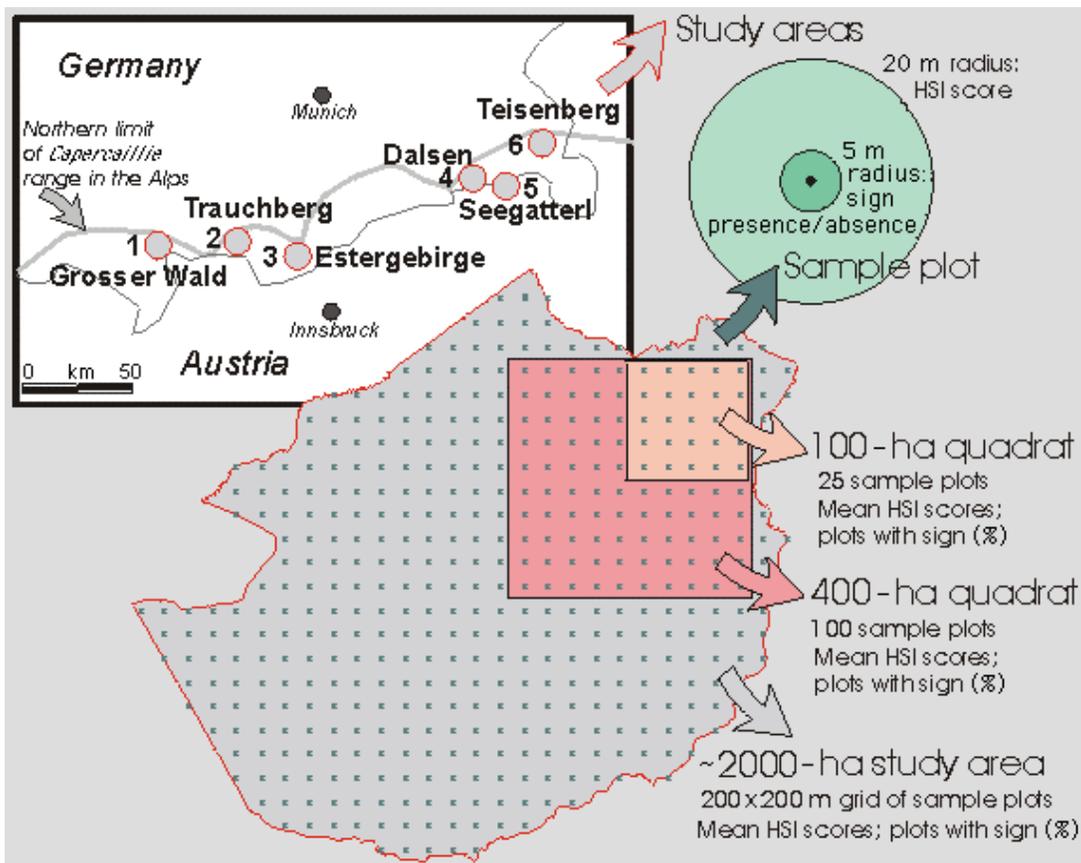
The climate in the Bavarian Alps is moist and temperate, with mean annual temperatures of about 5°C, mean annual precipitation of 1500–2200 mm, wet summers, and snow-rich winters. Intensive forestry practices have influenced Capercaillie habitats for more than 200 years (Klaus et al. 1989).

I selected six mountain ranges in the Bavarian Alps that covered much of the geology, climate, vegetation, and forest management practices found in the region

(see Fig. 1). From previous experience, Capercaillie densities on the six ranges were assumed to span from very low (Trauchberg) to very high (Teisenberg) for the Bavarian Alps. The northern edges of three ranges (Grosser Wald, Trauchberg, and Teisenberg) followed the border between the mountain forests and the dairy-farming lowlands to the north of the Alps; this borderline also coincides with the northern edge of the alpine range of the Capercaillie. The other three ranges were surrounded by forest and Capercaillie habitats on

all sides. On each range, a study area of about 2000 ha was established (see Table 1); the size of the areas was based on a compromise between logistic limitations and statistical needs, and followed administrative or natural boundaries. Forests covered 60–95% of the mountain ranges and ≥90% of all study areas, and were dominated by spruce (*Picea abies*) mixed with varying percentages of beech (*Fagus sylvatica*) and fir

(*Abies alba*). All areas were state-owned forest managed by the Bavarian State Forest Service, except for one-third of the Estergebirge study area, which was community and privately owned. Even-aged management and, locally, long-term single-tree management were the predominant sylvicultural practices, creating fine-grained forest mosaics with stands of 1–50 ha.

Table 1. The six study areas in the Bavarian Alps from west to east (compare with Fig. 1).

Study area	Size (ha)	Total plots[a]	Capercaillie abundance[b] (%) [no. plots]	Altitude range (m)	Forest 5 km [c] (%)	Forest 10 km [d] (%)	Mean cluster[e] (no. plots)	Bilberry cover mean ± 1 SD (%)
1 Grosser Wald	1800	435	3.0 [13]	950–1700	74	48	0.64	17 ± 21
2 Trauchberg	1800	448	1.8 [8]	850–1600	95	76	0.00	7 ± 13
3 Estergebirge	2800	690	6.4 [44]	900–1800	93	85	1.09	11 ± 11
4 Dalsen	1200	291	2.3 [5]	650–1600	63	52	0.00	2 ± 7
5 Seegatterl	2900	642	3.7 [24]	700–1600	69	78	1.21	9 ± 15
6 Teisenberg	1900	467	9.2 [43]	700–1350	93	62	1.68	8 ± 15

[a] Number of sample plots per study area.
[b] Index; Percentage of sample plots [*n*] with Capercaillie sign.
[c] Landscape variable FOREST5KM; percentage of forest cover in a 5 km radius circle around the center of the study area.
[d] Landscape variable FOREST10KM; percentage of forest cover in a 10 km radius circle around the center of the study area.
[e] Landscape variable HSI1NN; mean number of plots in each cluster of adjacent sample plots with HSI_{year} scores ≥0.8.

Model development

I developed a HSI model for Capercaillie in the Bavarian Alps based on smaller scale habitat variables that have previously been shown to significantly influence Capercaillie habitat use (Storch 1993*a, b*, 1994). Capercaillie have seasonally distinct habitat needs. In winter, they feed on conifer needles and spend most of their time on trees, whereas in summer they prefer habitats with abundant ericaceous shrubs, particularly bilberry, *Vaccinium myrtillis* (Storch 1995*b*), for food and cover. Therefore, distinct winter and summer habitat suitability indices, HSI_{wi} and HSI_{su}, were constructed and combined into an index of habitat suitability throughout the year, HSI_{year}. I verified the model using two existing data sets from the same study area, radio-tracking data from 1988–1992 and data on indirect Capercaillie signs from 1992

(G. Schwab, *unpublished data*). The process of model development and verification are described in Appendix 1.

Model validation

For statistical analyses, I used SPSS Version 9.0.1 and SPSS version 10.0, unless stated otherwise. Tests were two-tailed throughout ($\alpha = 0.05$). I use the terms habitat use, selection, preference, availability, and quality according to Hall et al. (1997).

Database

Habitat variables and signs of Capercaillie use were mapped in the six study areas between July and September 1997. This timing was chosen because, in summer, Capercaillie males do not aggregate at leks as

they do from late autumn through spring, and thus, the bird's range use within a mountain range is not affected by social attraction (Storch 1995*a*). Furthermore, Capercaillie molt during summer and indirect signs are most abundant.

A grid of sample points 200 m apart was laid over a 1:10000-scale forestry map of each area, resulting in approximately 500 points per study area and a total of 2901 points for the whole study (see Fig. 1). Around

these points, a set of habitat variables (Appendix 1). To estimate habitat suitability of the closer surroundings of each sample plot, I aggregated HSI scores for each plot and its eight nearest neighboring plots into mean scores (NN-HSI); excluding marginal plots, i.e., those with fewer than eight neighbors. To assess habitat suitability for 100-, 400-, and 2000-ha areas, the HSI scores for all sample plots within these areas were aggregated into mean HSI scores (100-HSI, 400-HSI, AREA-HSI).

Table 2. Variables sampled in 20 m radius plots within Teisenberg forest stands (1989–1990) and in the six study areas (1997; see Table 1) in the Bavarian Alps.

Variable	Definition
Elevation above valley or forest/farmland edge	1 (<100 m), 2 (100 to <300 m), 3 (300 to <500 m), 4 (500 to <700 m)...
Steepness of slope	mean [in degrees]
Successional stage	clearcut or young regeneration; thicket; pole stage; middle-aged forest; old forest; mixed, single-stem managed; nonforest cover types
Canopy cover	percentage of forest floor covered
Occurrence of gaps in canopy	wider than canopy height; yes/no
Type of stand	conifer; conifer/deciduous; deciduous (according to Forest Service categories)
Occurrence of preferred winter feeding trees	fir or pine except *Pinus mugo;* yes/no
Cover of forest regeneration	percentage of forest floor covered
Cover of bilberry	percentage of forest floor covered by *Vaccinium* spp.
Height of ground vegetation	mean height of dominating layer (cm)
Sign of Capercaillie use	tracks, feathers, feces, dustbaths; yes/no

To obtain an index of Capercaillie use, presence or absence of Capercaillie signs such as feathers, feces, tracks, or dust baths was recorded during a 15-min search in a 5 m radius sample plot (see Fig. 1). However, Capercaillie are rare in the Bavarian Alps, they use large home ranges (Storch 1993*a, b,* 1994,

1995), and their feces and feathers disintegrate rapidly in the moist summer climate. Thus, absence of signs from a sample plot is not equivalent to avoidance by Capercaillie. Among sample plots, the probability of finding signs was used as an *index of Capercaillie habitat use.* The frequency of Capercaillie signs,

however, not only is a function of habitat preference, but also is influenced by population density. Therefore, at larger areas, the percentage of sample plots with signs can also be viewed as an *index of Capercaillie abundance.*

Habitat preferences

The HSI model uses information on Capercaillie habitat preferences to assess habitat suitability. Accordingly, HSI scores should be correlated with habitat selection; that is, preferred habitat types (those used more often than expected based on their availability) should score higher than habitats avoided (used less than expected) by the birds. As a first step of model validation, I therefore assessed Capercaillie summer habitat selection in relation to HSI scores.

I grouped the sample plots from all study areas into 10 intervals according to their HSI_{su} score (as in Table 3). For each interval, I aggregated the HSI_{su} scores of all sample points into a mean HSI_{su} score and calculated the percentage of sample plots with Capercaillie signs as an index of habitat use. To assess area-specific

differences, I repeated the same procedure for those four study areas with at least 3% sample plots with signs. To avoid small sample sizes, I grouped each study area's sample plots into five HSI classes (instead of 10 intervals) according to their HSI_{su} scores (as in Table 3). For each HSI interval, and for each study area and HSI class, respectively, I calculated the mean HSI_{su} score, the relative availability (*A*) within the study areas (the percentage of all sample plots), the relative utilization (*U*) by Capercaillie (the percentage of all Capercaillie signs found), and Ivlev's electivity index (*I*) as $I = (U - A)/(U + A)$ (Krebs 1989). Ivlev's index varies from -1.0 to +1.0, with positive values indicating preference, negative values avoidance, and 0 indicating random use. I then related Ivlev's index to the mean HSI scores across the 10 HSI intervals (see Fig. 2) and the five HSI classes (see Fig. 3), respectively, using linear regression analysis. I used a GLM (general linear modeling) univariate ANOVA (dependent variable: Ivlev's index; covariate: mean HSI_{su} score; fixed factor: STUDY AREA) to test for study-area-specific differences in habitat selection across the five HSI classes.

Table 3. To explore Capercaillie habitat use in relation to model results, HIS scores were grouped into 10 intervals and five classes, respectively, which indicate excellent, good, fair, moderate, and poor habitat suitability.

HSI score	HSI interval	HSI class	Habitat suitability
[1.0–0.9]	1	**1**	excellent
]0.9–0.8]	2		
]0.8–0.7]	3	**2**	good
]0.7–0.6]	4		
]0.6–0.5]	5	**3**	fair
]0.5–0.4]	6		
]0.4–0.3]	7	**4**	moderate
]0.3–0.2]	8		
]0.2–0.1]	9	**5**	poor
]0.1–0]	10		

Note: Left-hand brackets preceding the intervals indicate that the highest value is not included in the interval; i.e.,]0.9–0.8] is equivalent to an interval of 0.8 to <0.9.

Habitat use at the scale of sample plots

I used logistic regression analysis to assess whether presence or absence of Capercaillie signs was related to HSI scores.

In a first step, I assessed the relationship between Capercaillie signs (response variable) and HSI scores at the scale of individual sample plots. To consider study area-related differences, I added STUDY AREA as a categorical explanatory variable. I assessed which of HSI_{su}, HSI_{wi}, or HSI_{year} offered the best explanation of Capercaillie incidence by comparing the measure of residual deviance (-2log-likelihood) between alternative models, and by backward elimination of explanatory variables in logistic models including all three seasonal HSI scores.

Because the assumption of independence of the individual sample plots in the logistic regression could be disturbed by the spatial structure of the data, an alternative logistic model was also estimated. To take into account the spatial correlation structure, a marginal GEE (generalized estimating equations) model (see Diggle et al. 1994) was fitted using the procedure GENMOD of the package SAS (SAS Institute 2000). There, the spatial correlation structure of the outcome variable was modeled by assuming constant association of the individual samples in one 100-ha quadrat and assuming independence between the 100-ha quadrats. Compared to standard logistic regression, estimated parameters were almost identical, with slightly larger confidence intervals. This was also true for other choices of the association structure. Thus, the results were not significantly influenced by the spatial structure of the data, and results from standard logistic regression are reported throughout this paper.

Habitat use at larger scales

In the next step, to test model performance at larger spatial scales in relation to Capercaillie signs, I aggregated HSI scores calculated for individual sample plots into mean HSI scores for each sample plot and its eight nearest neighboring plots (0.6 x 0.6 km, i.e., nine sample plots; NN-HSI), for 100-ha (1 x 1 km, i.e., 25 sample plots; 100-HSI) and 400-ha (2 x 2 km, i.e., 100 sample plots; 400-HSI) quadrats, and for the entire approximately 2000-ha study areas (AREA-HSI) (see Fig. 1), respectively, equivalent to about 7%, 20%, 75%, and 400% of the annual home range size of Capercaillie in the Bavarian Alps: 550±52 ha, mean ±

1 SE; range 130–1210 ha (Storch 1995*a*). For all aggregated HSI scores, I also calculated coefficients of variation (CV).

At each resolution, I used logistic regression to assess the relationship between Capercaillie signs (response variable) and mean HSI scores (NN-HSI, 100-HSI, 400-HSI, and AREA-HSI, respectively; explanatory variable). At the scales of nearest neighbors, 100-ha and 400-ha quadrats, I also included the coefficient of variation (CV) in HSI scores to assess potential effects of HSI score variability, and added STUDY AREA as a categorical variable to test for study area-related differences. For all scales, I assessed which of the aggregated HSI_{su}, HSI_{wi}, or HSI_{year} scores offered the best explanation of Capercaillie incidence by comparing the measure of residual deviance (-2log-likelihood) between alternative models, and by backward elimination of explanatory variables in logistic models including all three seasonal HSI scores. Finally, I included variables from all spatial scales (HSI, NN-HSI, 100-HSI, 400-HSI, and AREA-HSI) into a logistic regression, and assessed significant effects on Capercaillie use by backward elimination ($\alpha = 0.05$).

To allow for direct comparisons across scales, all cases were excluded from logistic regression for which at least one of the variables used showed missing values. Thus, logistic models were based on $N = 2340$ sample plots (see Table 4), and model fit can be directly compared across scales by the measure of residual deviance (see, e.g., McCullagh and Nelder 1989).

Effects of landscape patterns

To explore potential effects of landscape patterns at the scale of study areas on the presence and abundance of Capercaillie, I included the following variables in logistic regression analyses: the mean number of plots in each cluster of adjacent sample plots with HSI_{year} scores ≥ 0.8 (HSI1NN), and the percentage of forest cover in circles of 5 km (FOREST5KM) and 10 km (FOREST10KM) radius, respectively, around the center of each study area (see Table 1). I tested for correlations between these variables, AREA-HSI and its CV, and Capercaillie abundance (percentage of plots with sign per study area) using standard least square linear regressions.

First, I introduced the landscape variables in addition to AREA-HSI and its CV as predictors of Capercaillie abundance at the scale of study areas into the logistic

regression model. Then, I recalculated the basic logistic regression models for all other scales (HSI, NN-HSI, 100-HSI, 400-HSI, respectively; see Table 4) by replacing the categorical variable AREA (study area) with those landscape variables that had shown significant effects at the scale of study areas (HSI1NN, FOREST5KM) (see Table 5). Finally, I repeated the regression with HSI variables from all spatial scales (HSI, NN-HSI, 100-HSI, 400-HSI, and AREA-HSI; see Table 4) with HSI1NN and FOREST5KM instead of AREA. At all steps, I assessed significant effects by backward elimination of explanatory variables (α = 0.05).

RESULTS

Habitat preferences

Across the 10 intervals of HSI scores, Ivlev´s electivity index increased from poor to excellent habitat suitability (R^2=0.96, $P <$ 0.001) (Fig. 2). Habitats with HSI scores above 0.5 were preferred (i.e., used more often than expected from their availability), and those with scores below 0.5 were avoided (used less than expected). The same held for the study areas analyzed separately (Fig. 3). The poorer fit for area 1 probably was due to the small number (N = 13) of Capercaillie signs found. A GLM univariate ANOVA including areas 1, 3, 5, and 6 showed that there were no study-area-specific differences (F = 0.672, 3 df, P = 0.583) in habitat preferences across the five HSI classes.

Habitat use at the scale of sample plots

The chances of finding Capercaillie signs at the scale of individual sample plots were strongly related to habitat suitability scores according to the HSI model presented. A logistic regression analysis revealed a close relationship between HSI_{su} scores and presence of Capercaillie signs. In each of the six study areas, the mean HSI_{su} scores of plots with Capercaillie signs were greater than the mean scores of all plots. However, significant study-area-specific differences in the chances of finding Capercaillie signs were not explained by HSI; e.g., for a given HSI score, the chances of finding signs were almost eight times greater in area 6 than in area 1 (Model 1, Table 4).

Fig. 2. Performance of the HSI model for Capercaillie at the level of sample plots. Capercaillie habitat preference, as expressed by Ivlev´s electivity index, increased across the 10 intervals of summer habitat suitability. Ivlev´s index and the mean HSI scores per interval were closely correlated (weighted least square linear regression; Pearson´s R²). *N* values (no. sample plots per interval) are given below the *x*-axis.
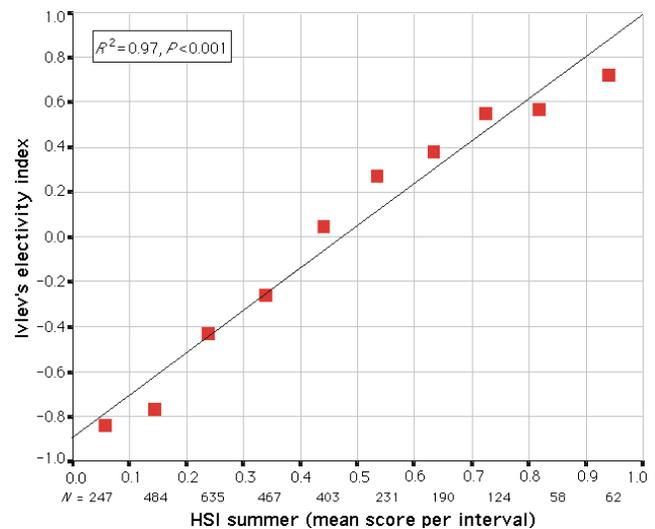
Fig. 3. Relation between HSI scores and Capercaillie habitat preference at the sample plot level for individual study areas. In all areas, mean HSI scores and Ivlev´s electivity index were correlated across the five classes of summer habitat suitability (weighted least square linear regressions; Pearson´s R²); differences between study areas were nonsignificant (see *Results: Habitat preferences*). Data points are color-coded for the different study areas. In study areas 2 and 4, Capercaillie signs had been too rare for individual analysis.
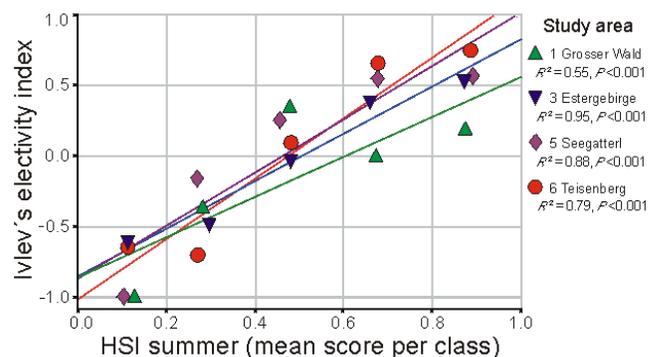
Table 4. Stepwise logistic regression models (regression coefficient B) explaining the presence or absence of Capercaillie signs at individual sample plots ($n = 2340$) from HSI scores at various scales (HSI$_{su}$, NN-HSI $_{year}$, 100-HSI$_{year}$, and 400-HSI $_{year}$, AREA-HSI$_{year}$, respectively; Models 1–5) and study area (AREA; reference = Area 1). The coefficients of variation in HSI scores had been entered into Models 2–5, but showed no significant effects. In Model 6, HSI scores from all scales were considered as explanatory variables entered: (HSI$_{su}$, NN-HSI$_{year}$, 100-HSI$_{year}$, and 400-HSI$_{year}$, AREA; reference = Area 1). For all models, variables were selected by backward elimination.

Model and variables	(scale)	B	1 SE	df	Odds ratio exp(B)	P	Change in deviance	Residual deviance (-2log-likelihood)
1) Sample plot								689.0
HSI$_{su}$		4.75	0.47	1	115.6	0.000	108.5	
AREA				5		0.000	37.1	
Area 2		0.34	0.59		1.41			
Area 3		1.18	0.40		3.26			
Area 4		1.61	0.65		5.02			
Area 5		0.71	0.46		2.03			
Area 6		2.04	0.42		7.69			
Constant		- 6.31	0.47			0.002		
2) Sample plot and 8 nearest neighbors								713.6
NN-HSI$_{year}$		6.55	0.73	1	700.3	0.000	82.7	
AREA				5		0.000	44.1	
Area 2		0.49	0.59		1.63			
Area 3		1.08	0.40		2.94			
Area 4		1.93	0.66		6.87			
Area 5		0.72	0.46		2.05			
Area 6		2.26	0.42		9.55			
Constant		- 6.92	0.53			0.000		
3) 100-ha quadrat								720.9
100-HSI$_{year}$		7.76	0.90	1	2345.1	0.000	76.7	
AREA				5		0.000	25.6	
Area 2		- 0.37	0.58		0.69			
Area 3		- 0.04	0.42		0.96			
Area 4		1.11	0.63		3.04			
Area 5		0.01	0.46		1.01			
Area 6		1.18	0.42		3.27			
Constant		- 6.50	0.49			0.000		
4) 400-ha quadrat								757.5

400-HSI$_{year}$	8.91	1.40	1	7398.4	0.000	40.1	
AREA			5		0.000	26.9	
Area 2	- 0.30	0.58		0.74			
Area 3	- 0.06	0.43		0.95			
Area 4	1.25	0.65		3.50			
Area 5	0.15	0.45		1.16			
Area 6	1.18	0.42		3.27			
Constant	- 6.85	0.62			0.000		
5) 2000-ha study area							828.2
AREA-HSI$_{year}$	4.79	1.49	1	119.8	0.001	10.4	
Constant	- 4.84	0.57			0.008		
6) All scales							671.6
HSI$_{su}$	3.60	0.56	1	36.43	0.000	42.04	
NN-HSI$_{year}$	4.18	1.02	1	65.28	0.000	17.43	
AREA			5		0.000	34.33	
Area 2	0.46	0.47		1.59			
Area 3	0.62	0.42		1.86			
Area 4	0.34	0.59		1.40			
Area 5	1.89	0.42		6.60			
Area 6	1.90	0.66		6.68			
Constant	- 7.30	0.55			0.001		

Significant logistic regression models could also be achieved when using HSI$_{wi}$ or HSI$_{year}$, and STUDY AREA as independent variables. However, as should be expected because Capercaillie signs had been sampled in summer, residual deviance (-2log-likelihood; 689, HSI$_{su}$; 746, HSI$_{wi}$; 705, HSI$_{year}$) showed the best model fit for HSI$_{su}$. A logistic regression with STUDY AREA and with HSI$_{su}$, HSI$_{wi}$, and HSI$_{year}$ as explanatory variables showed that HSI$_{wi}$ ($P = 0.76$) and HSI$_{year}$ ($P = 0.77$) provided no additional explanation.

To visualize Capercaillie habitat use in relation to HSI scores, I grouped the sample plots from all study areas into 10 intervals according to their HSI$_{su}$ score (as in Table 3). For each interval, I aggregated the HSI$_{su}$ scores of all sample plots into a mean HSI$_{su}$ score and plotted the percentage of plots with signs against the mean HSI$_{su}$ scores per HSI interval (Fig. 4). Because habitat use, i.e., the probability of finding Capercaillie signs, increased with HSI scores, from poor habitat (HSI scores 0–0.1) to excellent habitat (0.9–1), I concluded that the HSI model adequately depicts Capercaillie habitat preferences.

However, some differences between the study areas in the frequency of finding Capercaillie signs could not be explained by different HSI scores. To illustrate these area-specific differences, I repeated the same procedure for each of the six study areas by grouping the sample plots into five HSI classes according to their HSI$_{su}$ scores (as in Table 3). For each area and HSI class, I aggregated HSI$_{su}$ scores of all sample points to a mean HSI$_{su}$ score, and calculated the percentage of sample plots with Capercaillie signs as an index of habitat use. For each area, I plotted the

percentage of sample plots with signs against the mean HSI_{su} scores per HSI class (Fig. 5). The logistic model (Model 1, Table 4) was used to compute regression lines. Study-area-specific differences in addition to HSI scores became obvious.

Fig. 4. Performance of the HSI model for Capercaillie at the smallest scale. The regression line is based on a logistic model with HSI_{su} as explanatory variable. For illustration, the data were aggregated across the 10 intervals of summer habitat suitability. *N* values (no. sample plots per interval) are given below the *x*-axis (total *N* = 2901).
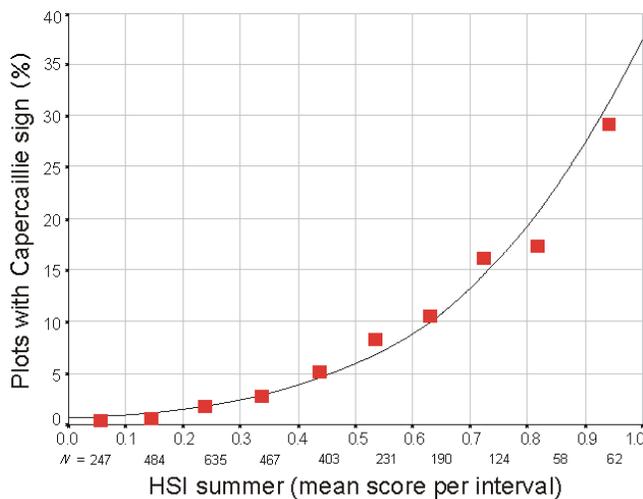
Habitat use at larger scales

Presence or absence of Capercaillie signs at a sample plot was also significantly related to mean HSI scores aggregated at the scales of nearest neighbors, 100-ha quadrats, 400-ha quadrats, or study areas; CVs of aggregated HSI scores had no significant effect at all scales. In general, the percentage of plots with signs was larger and, accordingly, Capercaillie were more abundant, in areas with greater HSI scores. However, at all scales there were significant study-area-specific differences in Capercaillie abundance that could not be explained by the HSI model. As indicated by the values for residual deviance and change in deviance, model fit and the explanatory power of the HSI scores deteriorated across scales (Models 1–5, Table 4).

For nearest neighbors, 100-ha quadrats, and 400-ha quadrats, Capercaillie use was significantly ($P < 0.001$) related to the aggregated HSI_{su}, HSI_{wi}, and HSI_{year} scores (Models 2–4, Table 4). In contrast to the

analysis at the scale of sample plots, which had revealed the closest fit for HSI_{su} scores, Capercaillie use was best explained by aggregated HSI_{year} scores (i.e., NN- HSI_{year}, 100-HSI_{year}, 400-HSI_{year}, AREA-HSI_{year}). At these larger scales, residual deviance showed the best model fit for HSI_{year}, and logistic regression with aggregated HSI_{su}, HSI_{wi}, and HSI_{year} as explanatory variables did not reveal significant additional effects of HSI_{su} or HSI_{wi}. For the six 2000-ha study areas, Capercaillie abundance was significantly related to AREA-HSI_{wi} ($P = 0.005$) and AREA-HSI_{year} ($P = 0.002$) scores. Residual deviance showed the best model fit for aggregated HSI_{year} scores, and a logistic regression with AREA-HSI_{year} and AREA-HSI_{wi} showed that the latter variable had no significant effects in addition to HSI_{year} (Model 5, Table 4).

Fig. 5. Relation between HSI scores and Capercaillie habitat use at the sample plot scale for individual study areas. Regression lines show area-specific results of a logistic regression model with HSI_{su} and study area as explanatory variables (total *N* = 2901 sample plots). For illustration, the data were aggregated across five classes of summer habitat suitability (see Table 3 for explanation) and for each study area. Data points are color-coded for the different study areas.
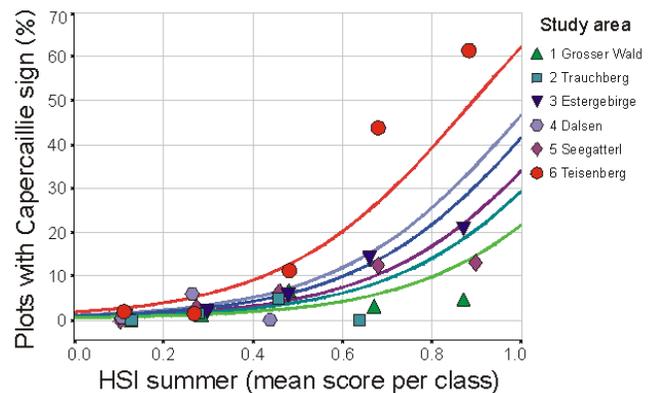
To visualize the relationship between mean HSI scores and Capercaillie abundance, I plotted the percentage of sample plots with signs against mean HSI scores for 82 100-ha and 28 400-ha quadrats for which > 50 and > 20 sample plots, respectively, had been mapped, and for the six study areas (Fig. 6), together with regression lines according to the logistic models 3–5 presented in Table 4>.

Fig. 6. Performance of the HSI model for Capercaillie at larger scales. HSI scores for all sample plots within 100-ha, 400-ha, or 2000-ha areas, respectively, were aggregated into a mean HSI score. The percentage of sample plots within a 100-ha, 400-ha, or 2000-ha areas, respectively, is an index of Capercaillie abundance within that area. Regression lines are based on the logistic models in Table 4. Data points are color-coded for the different study areas.
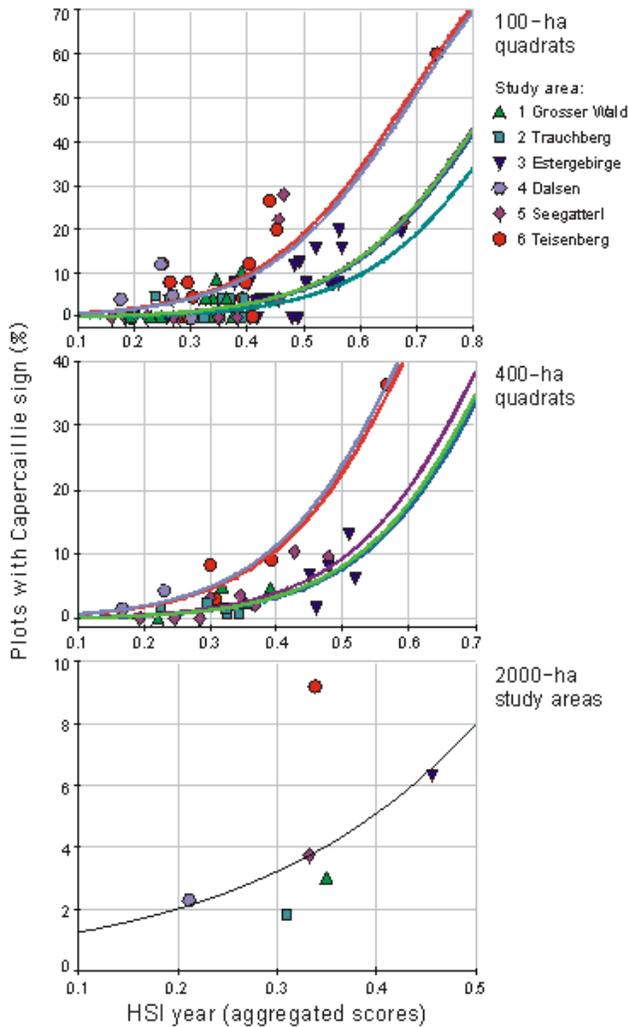
A logistic regression model including HSI variables from all scales indicated significant positive effects on Capercaillie use for HSI and NN-HSI, positive, but nonsignificant effects of 100-HSI and 400-HSI, and a significant negative effect of AREA-HSI. As the latter result cannot be interpreted ecologically, AREA-HSI was removed from the analysis, and instead STUDY AREA was included as a categorical variable. Backward elimination of variables resulted in a model

with significant effects of HSI, NN-HSI, and STUDY AREA, and larger scale aggregated HSI scores did not provide further information (Model 6, Table 4). Residual deviance of the resulting model was only slightly better than residual deviance of the basic model with HSI and STUDY AREA (Model 1, Table 4).

Because of the obvious correlation between scale-specific HSI scores, a multi-colinearity problem occurs and results should be interpreted with caution. Note, however, that the statistical tests used in the backward elimination procedure are still valid in the presence of correlation of the covariates.

Effects of landscape patterns

Lastly, I tested the landscape variables extent of clusters of excellent habitat (HSI1NN) and the percentage of forest cover within a mountain range (FOREST5KM) and its surroundings (FOREST10KM) as predictors of Capercaillie presence and abundance. The three variables were not significantly intercorrelated, nor were they correlated with AREA-HSI. A stepwise linear regression with the three landscape variables, AREA-HSI$_{year}$ and its CV as predictors revealed that HSI1NN explained 76% (least square linear regression; Pearson's R^2, $P = 0.023$, $N = 6$) of the variation in Capercaillie abundance at the scale of study areas; the other variables showed no significant additional effects.

When the landscape variables were introduced in addition to AREA-HSI and its CV as predictors of Capercaillie signs at the scale of study areas, logistic regression showed a significant negative effect of AREA-HSI. Becauses this result cannot be interpreted ecologically, AREA-HSI was excluded from the analysis. Backward elimination of the remaining variables resulted in a model with significant effects of HSI1NN and FOREST5KM (Model 5, Table 5). As indicated by the values for residual deviance, the fit and the explanatory power of this model was slightly better than those for the basic model with AREA-HSI as explanatory variable (Model 5, Table 4). Thus, the extent of clusters of plots with excellent HSI scores (HSI1NN) and the percentage of forest cover within a mountain range (FOREST5KM) offered the best explanation for Capercaillie presence and abundance at the scale of study areas. Note, however, that this result is based on $n = 6$ study areas only and should be interpreted as preliminary.

Table 5. Logistic regression models, as in Table 4, explaining the presence or absence of Capercaillie signs at individual sample plots ($n = 2340$) from HSI scores at various scales. In contrast to the models in Table 4, the landscape variables HSI1NN (extent of excellent HSI clusters) and FOREST5KM (percentage of forest cover within mountain ranges) were entered instead of the categorical variable AREA (study area) (Models 1–4, 6). These landscape-scale variables offered the best explanation for Capercaillie abundance at the scale of study areas (Model 5, variables entered: AREA-HSI year, CV-AREA-HSI year, HSI1NN, HSI11, FOREST5KM, FOREST10KM). All models resulted from backward elimination of variables.

Model (scale) and variables	*B*	1 SE	df	Odds ratio exp(*B*)	*P*	Change in deviance	Residual deviance (-2log-likelihood)
1) Sample plot							700.7
HSI$_{su}$	4.40	0.45	1	81.6	0.000	102.2	
HSI1NN	0.97	0.26	1	2.63	0.000	16.5	
FOREST5KM	0.02	0.01	1	1.02	0.036	4.6	
Constant	- 8.02	0.98			0.000		
2) Sample plot and 8 nearest neighbors							731.4
NN-HSI$_{year}$	6.35	0.76	1	573.2	0.000	77.9	
HSI1NN	1.05	0.27	1	2.86	0.000	16.7	
Constant	- 6.88	0.49			0.001		
3) 100-ha quadrat							731.4
100-HSI$_{year}$	6.67	0.80	1	784.4	0.000	72.7	
HSI1NN	0.86	0.27	1	2.37	0.002	10.6	
Constant	- 6.70	0.45			0.000		
4) 400-ha quadrat							765.1
400-HSI$_{year}$	4.39	1.46	1	80.4	0.003	9.15	
CV 400-HSI$_{year}$	- 0.02	0.01	1	0.98	0.012	6.86	
HSI1NN	0.97	0.26	1	2.63	0.000	14.5	
Constant	- 4.78	0.90			0.000		
5) 2000-ha quadrat							803.0
HSI1NN	0.98	0.21	1	2.678	0.000	26.2	
FOREST5KM	0.02	0.01	1	1.023	0.022	5.5	
Constant	- 6.04	0.87			0.002		
6) All scales							691.2
HSI$_{su}$	3.36	0.52	1	28.90	0.000	40.23	
NN-HSI$_{year}$	3.23	0.88	1	25.34	0.000	14.20	
HSI1NN	1.03	0.28	1	2.80	0.000	14.74	
Constant	- 7.04	0.49			0.001		

As a next step, I replaced the categorical variable STUDY AREA with the two landscape variables, HSI1NN and FOREST5KM, and recalculated the basic logistic regression models (see Table 4) for all other scales (HSI, NN-HSI, 100-HSI, and 400-HSI, respectively). Backward elimination of variables revealed positive effects of the extent of excellent HSI clusters (HSI1NN) on Capercaillie incidence at all scales (Models 1–4, Table 5), whereas forest cover within mountain ranges (FOREST5KM) had a significant influence only at the scale of sample plots (Model 1, Table 5). Only at the 400-ha scale did the coefficient of variation in HSI scores show an effect (Model 4, Table 5). For the analysis including HSI variables from all scales (Model 6, Table 4), replacement of STUDY AREA by the landscape variables resulted in a model with HSI, NN-HSI, and HSI1NN (Model 6, Table 5).

Although landscape variables contributed to the presence of Capercaillie signs, HSI scores remained the most powerful predictor at all scales below the scale of study areas. Also, as residual deviance remained poorer for the alternative models (Models 1–4, 6, Table 5) compared to their equivalents with STUDY AREA (Models 1–4, 6, Table 4), the landscape variables considered could not fully explain the study-area-related differences. Nevertheless, because the extent of clusters of excellent habitat explained 76% of the variation in Capercaillie abundance among study areas, landscape patterns certainly had major influence on the density of local populations at the scale of mountain ranges.

DISCUSSION

Conservation biology faces the dilemma that nature protection often requires almost immediate decisions regarding questions as complex as the natural systems they address. In this situation, HSI models provide a rapid and simple habitat assessment tool, and are frequently applied in natural resource management. At the same time, they are criticized because of their simplicity and lack of scientific rigor (Schamberger and O'Neil 1986, Brooks 1997). With HSI models, there seems to be a discrepancy between a great practical value and a poor scientific reputation. Scientific approaches to model testing and reviewing can significantly improve model performance and reliability in management activities (Schamberger and O'Neil 1986, Van Horne and Wiens 1991, Brooks 1997). The HSI model for Capercaillie presented in this paper provides an example of the limitations and

the potential for misunderstanding that are involved when applying a model at scales different from the scale of the information used for its development. The Capercaillie model was exclusively built on nonspatial, small-scale variables of forest structure and without any consideration of larger scale features such as the extent and juxtaposition of habitat patches. First, the model's representation of Capercaillie habitat preferences at the forest-stand level was assessed. Then, Capercaillie habitat use was related stepwise to HSI scores at different spatial scales from 20 m radius sample plots to 2000-ha areas. The performance of the model at the different scales illustrates several points:

1. Among sample plots, Capercaillie use was closely related to HSI model scores, and Capercaillie selected high-score habitats in all study areas. Apparently, the model adequately described the species' habitat preferences at the scale of forest stands. This congruence of model and data supports the mechanistic and deterministic understanding of ecosystem processes that still is common among land management practitioners. Based on the model's power in reflecting *Capercaillie habitat preferences* at the scale of forest stands, managers will tend to automatically expect close links between the habitat and *Capercaillie abundance* at larger spatial scales.

2. Incidence of Capercaillie sign was best predicted from HSI scores at the small scale, but was also related to HSI scores aggregated at various larger scales. Thus, habitats preferred by Capercaillie indeed supported greater numbers of birds. However, model fit deteriorated at coarser resolutions. Most importantly, the great differences in the abundance of Capercaillie populations among mountain ranges could not be explained by the HSI model, but were related to landscape patterns. Quite evidently, both forest structure and landscape patterns should be considered to explain Capercaillie presence and abundance.

3. The overall HSI score can be viewed as an indicator of the vegetation-related components of carrying capacity. The model's power to predict population abundance, however, is limited. In general, HSI models can be expected to account for about half of the variation in species abundance (Morrison et al. 1992). This does not mean that habitat is irrelevant: habitat suitability, as defined in the model, is a prerequisite but not a guarantee for

good Capercaillie populations. Because it depicts the Capercaillie's small-scale habitat preferences, the model can be used for preserving and creating high habitat suitability, and thus provides an effective tool for habitat managers in the Bavarian Alps.

Model development

The model was developed using variables of small-scale forest structure that the Teisenberg telemetry study (Storch 1993*a, b*) had revealed as having significant effects on Capercaillie habitat use. This study showed that, at the local scale, the model is valid in the forests of the Bavarian Alps. Because of the relatively narrow habitat preferences of Capercaillie throughout their distribution range (see Storch 2001), applicability of the model beyond the northern Alps is likely, but remains to be tested. Possible examples of variables that may play a role in some higher parts of the Alps are microclimate and exposure. Two of the model variables, steepness of slope and forest regeneration, showed little variation among and within the study areas. Their contribution to the overall HSI score remains to be tested at further sites.

Throughout the Bavarian Alps, Capercaillie rarely use the lower elevations, even where they provide optimal habitat structure (Storch 1993*a, b,* 1994, this study; A. Zeitler, *unpublished data*). This may be related to an altitudinal gradient in predation risk decreasing from the farmland valley bottoms, which support high numbers of generalist predators, uphill to the mountain peaks. In other parts of their range (e.g., in the boreal forest), Capercaillie do use lowland areas. Thus, Capercaillie may not select elevation per se. Rather, elevation in the Alps may actually index distance to farmland and, thus, predation pressure. This should be considered when interpreting model results.

The percentage of sample plots with Capercaillie signs was used as an index to Capercaillie use in the model tests. Because plots were sampled in summer, Capercaillie signs reflect habitat use in summer, but not winter. This showed in the closer relationship between the frequency of Capercaillie signs and HSI_{su} than HSI_{wi} or HSI_{year} scores at the scale of sample plots. The winter model has been verified by telemetry data from a single study area. Applications of the winter model therefore should be done with caution. The frequency of Capercaillie signs, however, is not only a function of habitat preference, but also it depends on population density, which is influenced by

habitat quality in all seasons. This is reflected by the fact that, at larger spatial scales (nearest neighbors, 100-, 400-ha quadrats, study areas), HSI_{year} was the best predictor of the frequency of Capercaillie use and, thus, population density.

The HSI model and Capercaillie habitat preferences

Capercaillie habitat use at the scale of individual sample plots was closely related to habitat suitability scores according to the HSI model presented: habitat preferences, as expressed by Ivlev's electivity index, increased from poor to excellent habitat suitability, the probability of finding signs increased with HSI scores, and a sample plot's HSI was the variable with the strongest effect on the presence or absence of Capercaillie signs. Although bird–habitat relationships may vary with population density (e.g., O'Connor 1986), habitat selection by Capercaillie with regard to HSI scores was consistent across all study areas. From all this, I conclude that the HSI model correctly describes Capercaillie habitat preferences at the scale of forest stands in the Bavarian Alps.

The HSI model and Capercaillie abundance

There is little doubt that small-scale habitat factors such as those included in the HSI model do have a major influence on Capercaillie abundance (Picozzi et al. 1992, Klaus and Bergmann 1994, Storch 1995 *b*). However, Capercaillie populations may also be limited by larger scale habitat features. Telemetry has revealed that Capercaillie prefer larger old-forest stands over small ones (Storch 1997*b*), that home range size is inversely related to the amount of preferred habitat (Wegge and Rolstad 1986, Storch 1995*a*), and that forest fragmentation leads to increased predation risk (Gjerde and Wegge 1989, Wegge et al. 1990, Storch 1997*a*).

Aggregating HSI scores masks smaller scale variation in habitat quality. An area that consists of medium-quality habitat throughout receives the same score as an area with 50% optimal and 50% unsuitable habitat. The latter area will score the same regardless of the distribution and grain of the optimal and unsuitable patches. Evidently, these cases are not necessarily the same to a Capercaillie, as indicated by the positive relationship between the size of clusters with excellent suitability and Capercaillie presence and abundance. The extent and juxtaposition of habitat patches may thus lead to differences that cannot be explained by

mean HSI scores as produced by the present model. Capercaillie populations may also be influenced by landscape patterns at scales beyond those studied: In Finland, variation in local Capercaillie breeding success is best explained by landscape characteristics within areas of 100 km² (Kurki et al. 2000); in particular, the percentage of farmland in the landscape negatively affects breeding success in grouse (Kurki and Lindén 1995, Kurki et al. 2000). Capercaillie populations are assumed to disappear as forest fragmentation exceeds a critical threshold (Rolstad and Wegge 1987). Thus, there is evidence that Capercaillie population density may be influenced by habitat factors that range across spatial scales from forest stands to landscapes of 100 km² and beyond.

Because the present HSI model does not include any assumptions regarding landscape patterns, the deterioration of fit with increasing spatial scale may be related to increasing effects of landscape-scale habitat features. At the scale of study areas, variables of landscape pattern better explained Capercaillie presence and abundance than did aggregated HSI scores. Furthermore, across all scales, the results revealed major study-area-specific differences in factors other than small-scale forest structure. The model's limitations to predicting between-area differences in population density became most obvious on Teisenberg (area 6), where Capercaillie were more abundant than in any other study area. Habitat selection with regard to HSI classes did not differ from that in other study areas, and Capercaillie habitat use was related significantly to HSI scores. However, in comparison with the other areas, Teisenberg's greater Capercaillie abundance could not be derived from forest structure alone. Explanations may lie in differences in landscape patterns (e.g., Teisenberg had the largest clusters of high-quality habitat (HSI1NN)), predation pressure (e.g., losses of artificial nests were lower than elsewhere (I. Storch, *unpublished data*), and social attraction (e.g., Teisenberg holds the largest lek of the region, which may lead to immigration of juveniles from neighboring mountain ranges).

There is no evidence that local Capercaillie populations noticeably fluctuate between years in the Bavarian Alps. On Teisenberg, Capercaillie abundance probably had remained on a similarly high level at least throughout the 1990s: a first census in parts of the area in 1992 had resulted in signs at 11.6% of 809 random sample plots (G. Schwab, *unpublished data*). The 1997 count on Teisenberg (this study) was replicated in 1999 and 2000; the results were similar

(signs at 9.2% vs. 9.9% vs. 12.0% of 467 plots; Friedmann chi² = 3.61, *P* = 0.2) (I. Storch, *unpublished data*). For all six study areas, the observed differences in the frequency of Capercaillie signs agreed with the differences in Capercaillie numbers perceived by local hunters and foresters. Therefore, it can be assumed that the index of Capercaillie abundance used in this study reliably reflected differences in population density among study areas. These differences could not be fully explained by the HSI model.

Speculation

The study-area-specific differences found suggest that Capercaillie abundance in the Bavarian Alps needs to be explained at the level of local populations, i.e., at the scale of mountain ranges. The six mountain ranges studied differed with regard to landscape pattern within the study areas and within the wider surroundings (see Table 1). They might also have differed in local climate (Slagsvold and Grasaas 1979, Moss 1985), predation pressure (Klaus 1985), human disturbance (Menoni et al. 1989, Zeitler 1995), or other factors that may affect Capercaillie populations. In this study, I could only begin to explore potential influences of landscape patterns on Capercaillie abundance. To finally delineate which landscape-scale habitat variables do have significant effects on Capercaillie population density in the Bavarian Alps, a greater sample of mountain ranges must be compared.

Some studies suggest that landscape pattern, per se, only affects population survival when there is <20–30% of suitable habitat in the landscape (Andrén 1994, Fahrig 1998). In the Bavarian Alps, >50% of the landscape is forested. Accordingly, landscape pattern should not have major effects on Capercaillie, and population size should be linearly related to the percentage of suitable habitat (Andrén 1994). Because aggregated HSI scores were closely related to the percentage of suitable habitat (e.g., HSI ≥0.6), this clearly is not the case (this study). However, for species that are able to use different landscape elements (such as the different forest types and ages in the Alps) to various degrees, Andrén et al. (1997) argue that the numerical response to landscape pattern will depend on overall landscape composition, and cannot be predicted from the percentage of one habitat type alone. Also, one must not neglect that landscape pattern may have major effects on the distribution and abundance of predators within the habitat (Kareiva 1987).

In the Bavarian Alps, forested mountain ranges are separated by densely settled dairy-farming valleys. In addition, various percentages of the mountain ranges have long been cleared for summer pastures for cattle. The farmland valleys, and perhaps also, to a lesser degree, the upland pastures, favor high densities of generalist predators such as red foxes (*Vulpes vulpes*) and corvids (*Corvus corone, Corvus corax, Pica pica*). Preliminary evidence from experiments with artificial nests supports the hypothesis that predation pressure may be increasing with decreasing distance from farmland and pastures (Tschunko 2000). This may explain why Capercaillie avoid lower elevation forests in the vicinity of farmland, even where habitat structure is optimal (I. Storch, *unpublished report*). Thus, the interspersion of forest, farmland, and pastures may lead to large-scale edge effects (see Laurance 2000) that affect Capercaillie population density, even if >20–30% of the landscape is suitable as Capercaillie habitat.

Conclusions

Despite its limitations at larger scales, the model presented in this paper may be a valuable management tool. As long as the minimum spatial requirements (see van Horne and Wiens 1991) for a Capercaillie population (see Storch 1995*b,* Grimm and Storch 2000) are met, it allows a land manager to assess the forest-structure-related potential of the area of interest for the Capercaillie, to recognize the spatial distribution of habitats of different suitability, to compare the expected effects of various management scenarios on habitat suitability, and to monitor changes in habitat suitability and distribution over time. In the Alps and elsewhere in central Europe, Capercaillie habitat management is typically planned at the scale of forest stands within forest districts of some hundred to some thousand hectares in size. The data typically available to managers are stand descriptions, with variables of small-scale forest structure. The HSI model allows the evaluation of habitat suitability using these variables. It incorporates habitat features that are significantly influenced by forestry and, thus, can be addressed through habitat preservation measures. Other regulating factors of Capercaillie population dynamics are beyond human control (e.g., climatic stochasticity), or are difficult to influence (e.g., predation pressure). By maximizing habitat suitability based on HSI scores computed with the present model, a manager may improve an area's habitat-related carrying capacity for Capercaillie. It is important to comprehend, however, that improving habitat

suitability will not inevitably result in increasing Capercaillie numbers (see Morrison et al. 1992).

The example of the Capercaillie illustrates that, although a habitat model may correctly describe a species' smaller scale habitat preferences, its potential to predict the species' abundance at larger spatial scales will probably remain limited. In part, this is related to the narrow concepts of habitat and carrying capacity used in many HSI models: typically, they are restricted to vegetation-related components of carrying capacity, although populations may be influenced by a variety of other intrinsic and extrinsic factors as well (Morrison et al. 1992). Also, wildlife–habitat relationships are often hierarchical (Bissonette 1997) and therefore rarely consistent throughout all levels of spatial scale (Hamel et al. 1986, Schulz and Joyce 1992). The findings of this study support the conclusion of a recent review by Mazerolle and Villard (1999) that both small-scale and landscape-scale characteristics of the habitat should be included in models explaining and predicting the distribution and abundance of vertebrate species. The inclusion of landscape characteristics will enhance the performance and predictive power of habitat models and, thus, may contribute to the success of the conservation and management strategies to which they are applied.

Responses to this article can be read online at:
http://www.consecol.org/vol6/iss1/art6/responses/index.html.

APPENDIX 1. The Capercaillie habitat model

Model assumptions

Under the HSI approach, the habitat conditions defined as optimal are those that allow the greatest carrying capacity for the target species (Schamberger and O´Neil 1986). The concepts of carrying capacity and habitat suitability underlying this present model reflect those factors of habitat structure that satisfy life-history needs, determine habitat preferences, and influence the distribution of Capercaillie. This narrow, operational definition does not include other factors that may impact the distribution and abundance of Capercaillie, e.g., predation or climate (Schamberger and O´Neil 1986). In general, such factors could be included in HSI models. However, for in the Alps, in general, and the study areas, in particular, data are lacking that would allow the inclusion of habitat factors other than vegetation.

The Capercaillie model uses information on habitat preferences to assess habitat suitability. The underlying assumption, which is commonly and perhaps uncritically made in Capercaillie conservation practice, is that habitat preferences reflect habitat quality (for definitions of habitat-related terms used, see Hall et al. 1997) and thus are related to reproductive success and/or survival, and finally to carrying capacity and population density (Van Horne and Wiens 1991). Although there is some preliminary evidence for a positive relationship between Capercaillie habitat preferences and survival (Gjerde and Wegge 1989, Storch 1994, 1997*a*), this assumption has not been formally tested. This study provides further evidence that habitats that provide small-scale structures preferred by Capercaillie indeed support greater numbers of birds.

Model development

I describe the processes of constructing and testing the HSI model using the terminology of Van Horne and Wiens (1991; see also Brooks 1997): *model development* (to identify, construct, and combine a set of habitat variables into a series of equations to calculate an overall HSI score), *verification* (to match the model operations and output to the data set used for model construction), and *validation* (to match the model output to an independent dataset that was not used in model development).

As is commonly done with HSI models, the model was constructed based on a combination of research data and expert opinion (Morrison et al. 1992). I identified a set of habitat variables that had been shown to significantly influence Capercaillie habitat use in a five-year (1988–1992) telemetry study of 24 male and 16 female Capercaillie in the 50-km² Teisenberg area of the Bavarian Alps (Storch 1993*a, b,* 1994). Because the model should be applicable throughout the Bavarian Alps, variables were included that were believed to influence Capercaillie elsewhere, but that had not been relevant on Teisenberg. For better applicability, variables were defined in order to match the measures used in stand descriptions by the Bavarian State Forest Service whenever possible. These are the kinds of data typically available for forest management decisions in the Alps and elsewhere in central Europe.

Based on the Teisenberg telemetry results (Storch 1993*a, b,* 1994) and experience from other areas in the Bavarian Alps (I. Storch, *unpublished data,* A. Zeitler, *personal communication*), a suitability index (SI) function was constructed for each model variable, describing the assumed relationship between the variable and Capercaillie habitat use by values between 1 (optimal) and 0 (unsuitable) (see Fig. A1). Some variables may reduce, but not exclude, habitat suitability; in such cases, minimum SI scores were set >0. SIs were then combined into simple equations to calculate overall HSI scores. Scores for winter (HSI_{wi}) and summer (HSI_{su}) habitat suitability were calculated separately and then combined in an annual HSI score (HSI_{year}).

Fig. A1. Suitability index (SI) functions for the variables of the HSI winter model (above) and the HSI summer model (below). A high SI score indicates preference, low scores avoidance of the habitat by Capercaillie. For successional stage, clearcuts < 1ha in size received greater SI succession scores that clearcuts > 1 ha; for canopy cover, SI canopy scores were greater if gaps existed, e.g., due to snowbreak or windthrow; for stand type, SI scores were greater if fir or pine trees existed, the preferred winter food sources of Capercaillie (dark vs. light bars).
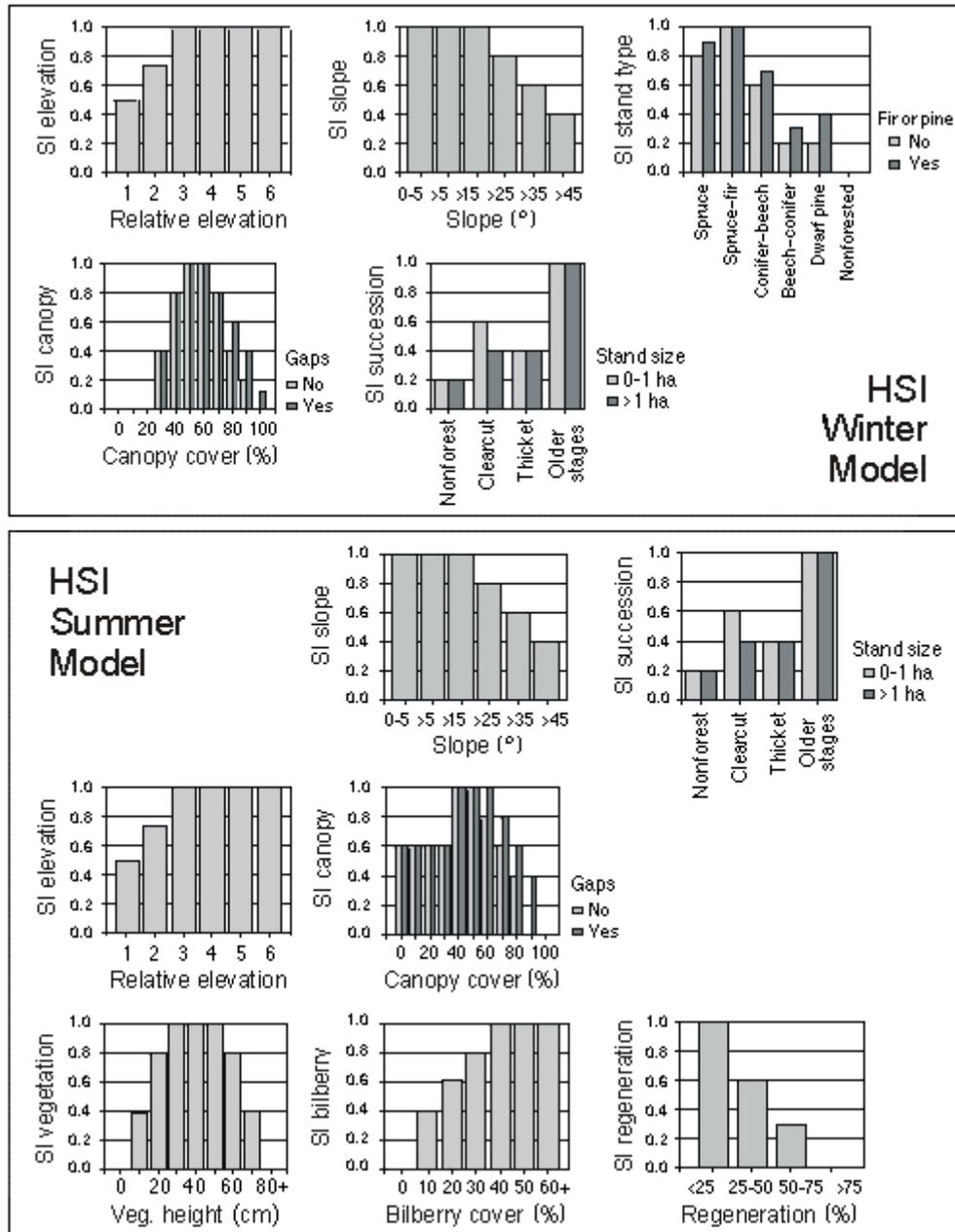
The mathematical ways of combining the variables' SIs were chosen to reflect their assumed role in Capercaillie habitat relationships (Van Horne and Wiens 1991). Multiplication of SI scores results in a large potential influence of each individual variable, and a zero score for any SI will lead to a zero overall HSI score; such variables function as limiting factors. The arithmetic mean is used if variables are assumed to be compensatory; their SIs contribute equally to the overall score. The geometric mean is used if the SIs are assumed to be partly compensatory, but the overall value is weighed by the smallest SI.

Model variables and suitability index functions

Capercaillie have seasonally distinct habitat needs. In winter, they feed on conifer needles and spend most of their time on trees, whereas in summer they prefer habitats with abundant ericaceous shrubs, particularly bilberry, *Vaccinium myrtillis* (Storch 1995*b*), for food and cover. For the purpose of the model, "winter" represents the time period with a snow layer, and "summer" represents the snow-free periods, although during spring and autumn, Capercaillie may show intermediate habitat preferences. Males, females, and broods show the same general patterns of habitat use (Storch et al. 1991, Storch 1993*a, b,* 1994, 1995*a*). Distinct winter and summer habitat suitability indices, HSI_{wi} and HSI_{su}, were constructed to reflect the seasonal habitat preferences of Capercaillie. Eight habitat variables were included in the model. Suitability index (SI) functions for the variables in the HSI winter model and the HSI summer model are shown in Fig. A1. Below, I sketch Capercaillie habitat preferences in the Bavarian Alps as a rationale for the development of suitability indices for each model variable, based on results from Teisenberg (Storch et al. 1991, Storch 1993*a, b,* 1994, 1995*a,* 1997*a*) and other work (A. Zeitler, *unpublished data,* I. Storch, *unpublished data*).

1) Steepness of slope (SI_{slo}): Capercaillie rarely use steep terrain and prefer level ground and moderate slopes. This holds for both sexes, throughout the year, and independently of habitat. Because steepness of slope is not likely to completely exclude Capercaillie use, the minimum score is 0.4.

2) Relative elevation (SI_{ele}): Capercaillie avoid the lower elevations, regardless of habitat structure. Elevation <300 m (score 0.75) and <100 m (score 0.5) above the farmland valley floor will reduce habitat suitability. (However, refer to the main text section *Discussion: Speculation* for a discussion of the relevance of elevation as a habitat variable.)

3) Successional stage (SI_{suc}): Capercaillie are forest obligates. They largely avoid open areas such as alpine pastures or meadows (score 0.2). In even-aged managed forests, they prefer pole-stage and older stands (score 1); the canopy cover and ground vegetation of a stand, however, are more important than its age. Capercaillie rarely use thickets or large clearcuts (score 0.4), but use small clearcuts (<1 ha) more often (score 0.6).

4) Canopy cover (SI_{can}): Moderate canopy cover is a prerequisite for a rich ground vegetation. Capercaillie prefer somewhat denser cover (±60%) in winter than in summer (±50%) (score 1), and may even use dense stands if a few gaps exist in the canopy, e.g., due to snowbreak or storm. Therefore, dense stands with gaps scored higher than those without. Stands with canopy cover <20% may be used in summer (score 0.6), but rarely in winter (score 0).

5) Type of stand (SI_{typ}): The classification of stands followed the system used by the Bavarian State Forest Service, which only considers the major tree species; e.g., a stand with 95% spruce and 5% fir is classified as "spruce". In winter, Capercaillie strongly prefer to feed on pine (*Pinus sylvestris*) or fir (*Abies alba*) needles. Availability of a few pine or fir trees in a stand is sufficient for preferred winter habitat. Therefore, sample plots with pine or fir received higher scores than plots without. Capercaillie avoid stands dominated by deciduous trees as winter habitat.

6) Bilberry and other Vaccinium *shrubs* (SI_{bil}): In summer, Capercaillie show a strong affinity to a well-developed ground vegetation rich in ericaceous shrubs, especially bilberry. Bilberry is a major food plant of Capercaillie in the snow-free seasons. It is rich in insects for chicks, and it provides optimal hiding and thermal cover for adults and broods. Cover by bilberry and other *Vaccinium* species of >40% was considered optimal (score 1).

7) Vegetation height (SI_{veg}): Capercaillie prefer a ground vegetation 30–50 cm high (score 1), tall enough to hide in but short enough to watch out of. Vegetation <10 cm and >70 cm was considered as unsuitable (score 0).

8) Forest regeneration (SI_{reg}): If forest regeneration (young trees >0.5 m high) covers 25–50% of the forest floor, conditions for Capercaillie deteriorate (score 0.6); if forest regeneration covers >75% of the forest floor,

conditions become unsuitable for the Capercaillie (score 0).

Combining the variables

The index for Capercaillie winter habitat suitability was calculated based on the variables successional stage, canopy cover, type of stand, slope, and elevation:

$$HSI_{wi} = (SI_{suc} * SI_{can}) * (SI_{typ} * SI_{slo})^{1/2} * SI_{ele}.$$

The major component of HSI_{wi} is stand structure, expressed by successional stage and canopy cover, each of which can be limiting ($SI_{suc} * SI_{can}$). Slope and stand type may both reduce the suitability of a stand, but, due to their SI functions, cannot result in a zero overall score $(SI_{typ} * SI_{slo})^{1/2}$. Relative elevation ($SI_{ele}$) may significantly reduce habitat suitability.

The index for summer habitat suitability included the variables successional stage, canopy cover, bilberry cover, regeneration cover, vegetation height, slope, and elevation:

$$HSI_{su} = 0.25 * \{(SI_{suc} * SI_{can}) + (2\ SI_{bil} * SI_{reg}) + SI_{veg})\} * SI_{slo} * SI_{ele}.$$

Three components are assumed to have compensatory effects on HSI_{su}: stand structure ($SI_{suc} * SI_{can}$), ground vegetation type ($2\ SI_{bil} * SI_{reg}$), and ground vegetation height (SI_{veg}). The component assumed to be most important, ground vegetation type, is given double weight. As with stand structure (see HSI_{wi}), both variables contributing to ground vegetation type (bilberry cover and regeneration cover) can be limiting. The last two components, slope (SI_{slo}) and elevation (SI_{ele}) may each reduce habitat suitability, but because of their SI functions, they cannot lead to a zero overall score.

An index of habitat suitability throughout the year, $HSI_{year} = (HSI_{wi} * HSI_{su})^{1/2}$, was calculated as the geometric mean of the winter and summer index, because both winter and summer habitat may be limiting Capercaillie abundance. Among the 2901 sample plots from the six study areas, the scores for HSI_{wi} and HSI_{su} varied widely and were positively correlated ($r = 0.58$, $P<0.001$, Spearman rank correlation).

An example for the calculation of HSI scores is provided in Table A1.

Model verification

I used two existing data sets from the Teisenberg study area for model verification: the telemetry data from 1988 to 1992 (Storch 1993*a, b,* 1994) on which the model was based, and data on indirect Capercaillie signs mapped between July and September 1992 (G. Schwab, *unpublished data*). Data on habitat structure for Teisenberg forest stands had been collected in 1989–1990 (see Storch 1993*b* for methods; see Table 2 for variables).

For 403 forest stands, I calculated HSI scores and the area-corrected number of radio locations (number per hectare) separately for winter (*N* = 3586 radio locations; Storch 1993*a*) and summer (*N* = 3656; Storch 1993*b*). Data were pooled for all radio-tagged birds because their habitat selection had not differed individually (Storch 1993*a, b*). I grouped forest stands into five HSI classes according to Table 3. For each HSI class, I calculated the mean HSI score for all stands, used the percentage of stands with at least one radio location per hectare as an index of the probability of Capercaillie use.

For 169 forest stands in the central part of Teisenberg, data on indirect Capercaillie signs had been sampled at 809 random plots (*c*. 1 plot/ha; ≥3 plots per stand). Plots were 5 m in radius, and the presence or absence of tracks, feathers, dustbaths, or feces had been recorded during a 15-min search (G. Schwab, *unpublished data*). As previously described, I grouped forest stands into five HSI classes, calculated mean HSI scores for all stands per class, and used the mean percentage of plots with sign per stand as an index of the probability of Capercaillie use.

Table A1. How to calculate an HSI score? An example is given with habitat mapping results from one sample point. The according SI scores for winter and summer, respectively, are taken from Fig. A1. HSI winter, HSI summer, and HSI year scores are then calculated according to the equations given below.

Variable	Mapping result	SI code	Score winter	Score summer
Elevation above valley or forest edge	400 m	ele	1.0	1.0
Steepness of slope	30°	slo	0.8	0.8
Successional stage	middle-aged forest	suc	1.0	1.0
Canopy cover	70%	can	0.8	0.6
Occurrence of gaps in canopy	no			
Type of stand	spruce	typ	0.9	-
Occurrence of preferred feeding trees	yes			
Cover of forest regeneration	<25%	reg	-	1.0
Cover of bilberry	20%	bil	-	0.6
Height of ground vegetation	20 cm	veg	-	0.8

$HSI_{wi} = (SI_{suc} * SI_{can}) * (SI_{typ} * SI_{slo})^{1/2} * SI_{ele} = (1.0 * 0.8) * (0.9 * 0.8)^{1/2} * 1.0 = 0.68$

$HSI_{su} = 0.25 * \{(SI_{suc} * SI_{can}) + (2\ SI_{bil} * SI_{reg}) + SI_{veg})\} * SI_{slo} * SI_{ele} = 0.25 * \{(1.0 * 0.6) + (2 * 0.6 * 1.0) + 0.8)\} * 0.8 * 1.0 = 0.52$

$HSI_{year} = (HSI_{wi} * HSI_{su})^{1/2} = (0.68 * 0.52)^{1/2} = 0.59$

If the HSI model adequately depicts Capercaillie habitat preferences, habitat use should increase from HSI class 5 (poor habitat) to class 1 (excellent habitat). This could be shown using simple Spearman rank correlations between mean HSI score and Capercaillie use: mean HSI scores within the five HSI classes were significantly related to the two indices of Capercaillie use calculated from telemetry data (winter and summer) and indirect signs (summer), respectively (Table A2). The greater the HSI score, the more proof of Capercaillie use had been found. Thus, one may conclude that, for the data set on which the model was based, the HSI classes adequately reflected the probability of Capercaillie use at the level of forest stands.

Table A2. Distribution of winter and summer telemetry relocations of Capercaillie (1988–1992; data reanalyzed from Storch 1993*a, b*) and indirect Capercaillie sign (1992), by HSI class among forest stands in the Teisenberg study area.

HSI class	Score	Description	Indices of habitat use by Capercaillie								
			Stands with $\geq$ 1 telemetry location/ha (%)						Plots with indirect sign (%)		
			Winter			Summer			Summer		
			Mean	95% CI	n	Mean	95% CI	n	Mean	95% CI	n
1	[1.0–0.8]	Excellent	36.0	25–47	75	75.0	36–114	8	40.5	9–72	7
2	]0.8–0.6]	Good	27.1	15–39	59	44.4	4–85	9	30.0	0–86	5
3	]0.6–0.4]	Fair	13.2	5–21	76	42.2	30–55	64	17.8	7–28	32
4	]0.4–0.2]	Moderate	9.9	2–17	71	22.8	16–30	145	14.5	7–22	52
5	]0.2–0.0]	Poor	4.9	1–9	122	11.3	7–16	177	6.4	3–10	73

Notes: For each of the use indices (telemetry in winter, HSI_{wi}, telemetry in summer, HSI_{su}, and indirect sign in summer, HSI_{su}), Spearman correlations were significant: all R_S = 1.0; all $P \leq 0.001$. Left-hand brackets preceding the score intervals indicate that the highest value is not included in the interval; i.e.,]0.8–0.6] is equivalent to an interval of 0.6 to <0.8. Sample size (n) is the number of stands.

LITERATURE CITED

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355-366.

Andrén, H., A. Delin, and A. Seiler. 1997. Population response to landscape changes depends on specialisation to different landscape elements. *Oikos* **80**:193-196.

Bissonette, J. A. 1997. Scale-sensitive ecological properties: historical context, current meaning. Pages 3-31 *in* J. A. Bissonette, editor. *Wildlife and landscape ecology: effects of pattern and scale.* Springer-Verlag, New York, New York, USA.

Brooks, R. P. 1997. Improving habitat suitability index models. **25**:163-167.

Diggle, P. J., K. Y. Liang, anf S. L. Zeger. 1994. *Analysis of longitudinal data.* Carendon Press, Oxford, UK.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**:273-292.

Gjerde, I., and P. Wegge. 1989. Spacing pattern, habitat use and survival of capercaillie in a fragmented winter habitat. *Ornis Scandinavica* **20**:219-225.

Grimm, V., and Storch, I. 2000. Minimum viable population size of capercaillie *Tetrao urogallus:* results from a stochastic model. *Wildlife Biology* **6**:219-225.

Hall, L. S., P. R. Krausman, and M. L. Morrision. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* **25**:173-182.

Hamel, P. A., N. D. Cost, and R. M. Sheffield. 1986. The consistent characteristics of habitats: a question of scale. Pages 121-128 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, Wisconsin, USA.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* **326**:388-390.

Klaus, S. 1985. Predation among capercaillie in a reserve in Thuringia. *Proceedings of the International Symposium on Grouse* **3**:334-346.

Klaus, S., A. V. Andreev, H.-H. Bergmann, F. Müller, J.

Porkert, and J. Wiesner. 1989. *Die Auerhühner.* Die Neue Brehm-Bücherei. Band 86. Westarp Wissenschaften, Magdeburg, Germany.

Klaus, S., and H.-H. Bergmann. 1994. Distribution, status and limiting factors of capercaillie in central Europe, particularly in Germany, including an evaluation of reintroductions. *Gibier Faune Sauvage* **11**:57-80.

Krebs, C. J. 1989. *Ecological methodology.* Harper and Row, New York, New York, USA.

Kuhn, W. 1998. *Flächendeckende Analyse ausgewählter ökologischer Parameter.* Europäische Hochschulschriften: Reihe 42, Band 23. Peter Lang Europäischer Verlag der Wissenschaften, Frankfurt, Germany.

Kurki, S., and H. Lindén. 1995. Forest fragmentation due to agriculture affects the reproductive success of ground-nesting black grouse *Tetrao tetrix. Ecography* **18**:109-113.

Kurki, S., A. Nikula, P. Helle, and H. Lindén. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* **81**:1985-1997.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? *Trends in Ecology and Evolution* **15**:134-135.

Laymon, S. A., and J. A. Reid. 1986. Effects of grid-cell size on tests of a spotted owl HSI model. Pages 93-96 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, Wisconsin, USA.

Link, F.-G., H. Reck, and M. Theis. 1996. *Bewertungen im Naturschutz.* Beiträge der Akademie für Natur- und Umweltschutz Baden-Württemberg 23, Stuttgart, Germany.

Marti, C. 1993. *Merkblatt: Waldwirtschaft und Auerhuhn.* Bundesamt Umwelt Wald Landschaft (BUWAL) and Schweizerische Vogelwarte, Sempach, Switzerland.

Mazerolle, M. J., and M.-A. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience* **6**:117-124.

McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models.* Second edition. Chapman and Hall, London, UK.

Menoni, E., C. Novoa, and E. Hansen. 1989. Impact de station de ski alpin sur des population de Grand Tétras dans les Pyrénées. *Actes Colloque National de l'Association Francaise des Ingenieures Écologues en collaboration avec la Societé d'Écologie* **5**:427-449.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. *Wildlife–habitat relationships.* University of Wisconsin Press, Madison, Wisconsin, USA.

Moss, R. 1985. Rain, breeding success and distribution of capercaillie and black grouse in Scotland. *Ibis* **128**:65-72.

Müller, F. 1978. Rauhfußhühner als Biotopindikatoren. Pages 57-68 *in* R. Hofmann, editor. *Jagd und Hege Ausbildungsbuch II.* Ferdinand Euke Verlag Stuttgart, Germany.

O'Connor, R. J. 1986. Dynamic aspects of avian habitat use. Pages 235-240 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, Wisconsin, USA.

Picozzi, N., D. Catt, and R. Moss. 1992. Evaluation of capercaillie habitat. *Journal of Applied Ecology* **29**:751-762.

Rolstad, J., and P. Wegge. 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. *Oecologia* **72**:389-394.

Rolstad, J., and P. Wegge. 1989. Capercaillie populations and modern forestry—a case for landscape ecological studies. *Finnish Game Research* **46**:43-52.

SAS Institute. (2000) *SAS /STAT software: Changes and enhancements.* Release 8.1 . SAS Institute, Cary North Carolina, USA.

Schamberger, M. L., and L. J. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pages 5-10 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, Wisconsin, USA.

Scherzinger, W. 1989. Endangered bird-species of woodland, habitat pretensions and their integration in natural succession. *Stapfia* **20**:81-100.

Schulz, T. T., and L. A. Joyce. 1992. A spatial application of a marten habitat model. *Wildlife Society Bulletin* **20**:74-83.

Slagsvold, T., and T. Grasaas. 1979. Autumn population size of the capercaillie in relation to weather. *Ornis Scandinavica* **10**:37-41.

SPSS. 1999. *SPSS advanced models.* Version 10.0. SPSS, Chicago, Illinois, USA.

Storch, I. 1993*a.* Patterns and strategies of winter habitat selection in alpine capercaillie. *Ecography* **16**:351-359.

Storch, I. 1993*b.* Habitat selection of capercaillie in summer and autumn: Is bilberry important? *Oecologia* **95**:257-265.

Storch, I. 1994. Habitat and survival of Capercaillie nests and broods in the Bavarian Alps. *Biological Conservation* **70**:237-243.

Storch, I. 1995*a.* Annual home ranges and spacing patterns of Capercaillie in central Europe. *Journal of Wildlife Management* **59**:392-400.

Storch, I. 1995*b.* Habitat requirements of capercaillie. *Proceedings of the International Symposium on Grouse* **6**:151-154.

Storch, I. 1996. Bewertung von Landschaften für Wildtiere. *Beiträge der Akademie für Natur- und Umweltschutz Baden-Württemberg* **23**:113-128.

Storch, I. 1997*a.* Male territoriality, female range use, and spatial organization of capercaillie leks. *Wildlife Biology* **3**:149-161.

Storch, I. 1997*b.* The importance of scale in habitat conservation for an endangered species: the capercaillie in central Europe. Pages 310-330 *in* J. A. Bissonette, editor. *Wildlife and landscape ecology: effects of pattern and scale.* Springer Verlag, New York, New York, USA.

Storch, I. 2000. *Status Survey and Conservation Action Plan 2000–2004: Grouse.* IUCN, Gland, Switzerland and Cambridge, UK.

Storch, I. 2001. Capercaillie. BWP Update. *Journal of Birds of the Western Palearctic* **3**:1-24. [Oxford University Press, Oxford, UK.]

Storch, I., and G. Segelbacher. 2000. Genetic correlates of spatial population structure in central European capercaillie and black grouse: a project in progress. *Wildlife Biology* **6**: 305-310.

Storch, I., C. Schwarzmüller, and D. von den Stemmen. 1991. The diet of capercaillie in the Alps: a comparison of hens and cocks. Pages 630-635 *in* S. Csanyi and J. Ernhaft, editors. *Transactions of the XXth Congress of the International Union of Game Biologists.* University of Agriculatural Sciences, Gödöllö, Hungary.

Temple, S. A., and B. A Wilcox. 1986. Predicting effects of habitat patchiness and fragmentation. Pages 261-262 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, Wisconsin, USA.

Tschunko, E. 2000. *Die Höhenverteilung des Prädationsrisikos von Bodenbrütern im Bergwald der Bayerischen Alpen und des Fichtelgebirges.* [Altitudinal patterns of predation risk on ground-nesting birds in the mountain forests of the Bavarian Alps and the Fichtelgebirge.] Thesis. University of Würzburg, Würzburg, Germany.

van Horne, B., and J. A. Wiens. 1991. Forest bird habitat suitability index models and the development of general habitat models. *Fish and Wildlife Research* **8.** U.S. Fish and Wildlife Service, Washington, D.C., USA.

Verner, J., M. L. Morrison, and C. J.Ralph, editors. 1986. *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates.* University of Wisconsin Press, Madison, Wisconsin, USA.

Wegge, P., I. Gjerde, L. Kastdalen, J. Rolstad, and T. Storaas. 1990. Does forest fragmentation increase the mortality rate of capercaillie? Pages 448-453 *in* S. Myrberget, editor. *Transactions of the XIXth Congress of the International Union of Game Biologists.* Norwegian Institute for Nature Research, Trondheim, Norway.

Wegge, P., and J. Rolstad. 1986. Size and spacing of capercaillie leks in relation to social behavior and habitat. *Behavioural Ecology and Sociobiology* **19**:401-408.

Zeitler, A. 1995. Skilauf und Rauhfusshühner. *Ornithologischer Beobachter* **92**:227-230.