

Diss. ETH No. 15999

Analysis of Capercaillie Habitat at the Landscape Scale Using Aerial Photographs and GIS

A dissertation submitted to the
SWISS FEDERAL INSTITUTE OF TECHNOLOGY ZURICH
For the degree of
DOCTOR OF SCIENCES

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2005

Table of contents

Summary		1
Zusammenfassung		3
General introduction		5
Paper I	The importance of spatial scale in habitat models: capercaillie in the Swiss Alps	15
Paper II	On the generality of habitat suitability models: a case study of capercaillie in three Swiss regions	37
Paper III	Forest and landscape structure variables as predictors for capercaillie occurrence at the scales of forest stands and home-ranges	59
Paper IV	Assessing the influence of patch area, isolation and connectivity on predicting capercaillie occurrence in the Alps	87
Paper V	Using a multi-scale model for identifying priority areas in capercaillie (<i>Tetrao urogallus</i>) conservation	109
Synthesis		117
Appendix		125
Acknowledgements		141
Curriculum vitae		143

Summary

The role of scale in ecology is widely recognized as being of vital importance for understanding ecological patterns and processes. Species respond to their environment at several spatial scales. As a consequence, multi-scale approaches are necessary to better understand species-habitat relationships and for effective conservation of endangered species.

The capercaillie (*Tetrao urogallus*) is an endangered forest grouse species with narrow habitat preferences and large spatial requirements, making it a model organism of both theoretical and practical interest. Whereas past research and conservation efforts concentrated mostly on small spatial scales, recent work has revealed the strong effect of landscape pattern, habitat connectivity and fragmentation on capercaillie populations. In this thesis, the main objectives were (1) to identify the factors affecting capercaillie occurrence patterns at different spatial scales and (2) to provide a spatially explicit basis for population viability analyses.

In the first two papers, we investigated capercaillie habitat at the scale of entire regions. We used presence-absence data as dependent variables and a large set of environmental data derived from country-wide available sources as independent variables. We hypothesized that the ability of both single variable and multivariate models to explain capercaillie occurrence would vary with the spatial scale (grain and extent) of the analysis. Therefore, we varied the grain size (moving window) from 1 to just over 1100 hectares and compared single- with multi-scale models (Paper I). Further, we investigated how the spatial extent of the data used for calibration influenced the performance of habitat models applied to independent data (Paper II).

Generally, we were able to predict capercaillie occurrence successfully with only few landscape variables, such as average temperature, proportion of forest, and topographic position. Thus, the distribution pattern of capercaillie must be strongly driven by landscape-scale processes. In particular, we found the variance explained by the univariate models to vary among the predictors and with spatial scale. Within the multivariate models, the best single-scale model (using all predictor variables at the same scale) was found at the scale equivalent to a small annual home range. The multi-scale model, in which each predictor variable was entered at the scale at which it had performed best in the univariate model, performed slightly better than the best single-scale model. Additionally, we found that habitat models differed significantly between the regions of the Pre-Alps and the Central Alps. The regional models performed very well in the region where they had been calibrated, but poorly to moderately in the other region and in the Jura Mountains that were used as an independent validation area. The model built with pooled data from the Pre-Alps and the Alps classified almost as well in the two regions as the regional models, but clearly better in the Jura Mountains.

In the large-scale approaches of papers I and II, we used only nation-wide available environmental data and neglected forest structure completely. Therefore, we assessed forest structure data from aerial photographs to investigate capercaillie habitat requirements at the scales of forest stands and home ranges (Paper III). Data were assessed in 52 study plots of 5 km² each, and for the two points in time 1960 and 2000. The plots represented three categories of population trends, i.e. “stable”, “declining” and “extinct”. Observational data were used for defining presence and absence grid-cells within the plots to build predictive habitat models with logistic regression. Also in this analysis, we identified marked differences between the regions of the Pre-Alps and the Central Alps. At the scale of forest stands, forest structure variables alone had limited power for predicting capercaillie occurrence. Landscape variables used in papers I and II, however, improved the models significantly. At the home range scale, variables relating to forest structure such as mean canopy cover and proportion of open forest, and the presence areas predicted by the models differed significantly between plot categories. Changes of forest structure between 1960 and 2000 were not large enough to be detected with our coarse method.

As a first step towards a population viability analysis, we analyzed the size and configuration of potentially suitable habitat patches (Paper IV). We derived discrete patches from the presence areas predicted by the multi-scale habitat model from paper 1 and classified them into “occupied” and “not occupied”. Patch size was the most important variable for predicting patch occupancy, followed by the distance to the nearest occupied patch. A connectivity measure, describing the proportion of occupied area within a circular buffer with a radius of 5 km, was not significant.

This thesis has direct relevance for practical conservation. We describe a method how large-scale habitat models (cf. paper I or II) can be used for the spatially explicit planning of conservation efforts in entire regions or countries (Paper V). We propose to combine potential capercaillie habitat derived from the statistical model with actual capercaillie presence data. The resulting map can directly serve as a basis for identifying and classifying priority areas for conservation. In fact, this method has already been used in the National Capercaillie Action Plan of Switzerland.

Zusammenfassung

Die Rolle der räumlichen Skala ist heute anerkannt als wichtiger Faktor für das Verständnis von ökologischen Mustern und Prozessen. Damit ein Organismus an einem bestimmten Ort vorkommen und überlebensfähige Populationen bilden kann, müssen seine Lebensraumansprüche auf verschiedenen räumlichen Ebenen erfüllt sein. Um diesem Aspekt gerecht zu werden, sind Forschungsansätze nötig, welche alle relevanten räumlichen Ebenen berücksichtigen. Nur so können wir Art-Lebensraum Beziehungen besser verstehen und effiziente Werkzeuge für die Erhaltung von gefährdeten Arten entwickeln.

Das Auerhuhn (*Tetrao urogallus*) ist ein waldbewohnendes Raufusshuhn mit hohen Ansprüchen an seinen Lebensraum und gleichzeitig grossem Raumbedarf. In Mitteleuropa sind seine Bestände stark zurückgegangen und die Art wird heute als gefährdet eingestuft. Diese Eigenschaften machen das Auerhuhn zu einem Modell-Organismus von sowohl theoretischem als auch praktischem Interesse. Früher haben sich die Auerhuhnforschung sowie Schutzbestrebungen vorwiegend auf die Struktur und Zusammensetzung von Waldbeständen auf kleinen Flächen konzentriert. Es hat sich jedoch gezeigt, dass auch die Verteilung und Fragmentierung von günstigen Lebensräumen, sowie die Landschaftsstruktur einen starken Einfluss auf Auerhuhnpopulationen haben. Ziel dieser Arbeit war, (1) die entscheidenden Faktoren zu identifizieren, welche das Vorkommen des Auerhuhns auf verschiedenen räumlichen Ebenen beeinflussen, und (2) eine räumlich explizite Grundlage für Populationsstudien zu erarbeiten.

In den ersten beiden Publikationen untersuchten wir den Lebensraum des Auerhuhns auf der Ebene von ganzen Regionen. Aus flächendeckend vorhandenen Geodaten leiteten wir ein ausgewähltes Set von Umweltvariablen ab, um das Verbreitungsmuster des Auerhuhns zu erklären. Dieser Arbeit lag die Hypothese zugrunde, dass die Fähigkeit, das Auerhuhn-Vorkommen vorherzusagen, sowohl bei einzelnen Variablen, als auch bei multivariaten Modellen von der räumlichen Skala abhängt. Um dies zu untersuchen, erhöhten wir einerseits die räumliche Auflösung unserer Analyse (Grösse eines „moving window“) schrittweise von 1 ha bis auf 1100 ha und verglichen Modelle mit Variablen auf einer Skala (uni-skalare Modelle) mit multi-skalaren Modellen (Paper I). Zudem analysierten wir, wie sich die für die Kalibrierung verwendeten Daten auf die Prognose eines Modells in einer unabhängigen Region auswirken (Paper II).

Generell konnten wir das Vorkommen des Auerhuhns mit wenigen Landschaftsvariablen, wie etwa Mittlere Temperatur, Waldanteil oder Topographie, gut erklären. Etwas detaillierter betrachtet, konnten wir feststellen, dass die durch einzelne Variablen erklärte Varianz stark von der räumlichen Skala abhängt. Das multi-skalare Modell, das alle Variablen auf der „optimalen“ Ebene berücksichtigte, erklärte leicht besser als das beste uni-skalare Modell, in dem alle Variablen auf derselben Ebene einfließen; das beste uni-skalare Modell enthielt die

Variablen auf der Ebene eines kleinen jährlichen Streifgebiets (Paper I). Bedeutende Unterschiede ergaben sich zwischen den Modellen für die Voralpen und die Zentralen Alpen. Die regionalen Modelle zeigten sehr gute Prognosewerte in der Region, in der sie kalibriert wurden, erklärten das Auerhuhn-vorkommen aber schlecht bis mittelmässig in der anderen Region sowie im Jura. Das mit kombinierten Daten aus den Voralpen und Alpen kalibrierte Modell klassierte in den beiden Regionen fast ebenso gut wie die regionalen Modelle, dafür aber klar besser im Jura (Paper II).

In den ersten beiden Publikationen verwendeten wir nur Daten, die flächendeckend für die Schweiz vorhanden waren. Dabei waren wir gezwungen, kleinräumige Habitat-Variablen zu vernachlässigen. In einem nächsten Schritt erfassten wir deshalb Waldstruktur aus Luftbildern, um Lebensraumansprüche des Auerhuhns auf den Ebenen von Waldbeständen und Auerhuhn-Streifgebieten zu untersuchen (Paper III). Wir bearbeiteten 52 kreisförmige Untersuchungsgebiete à je 5 km² für die beiden Zeitschnitte 1960 und 2000. In dieser Zeitperiode haben sich die Auerhuhngebiete in der Schweiz unterschiedlich entwickelt. Wir wählten je etwa gleich viele Untersuchungsgebiete in Waldarealen mit stabiler, abnehmender oder erloschener Population (drei Kategorien). Die Untersuchungsgebiete à je 5 km² teilten wir in ein Raster ein und identifizierten vom Auerhuhn besetzte und unbesetzte Rasterzellen. Basierend auf der Präsenz-Absenz Information konnten wir Habitatmodelle mit logistischer Regression berechnen. Generell stellten wir auch in dieser Analyse klare Unterschiede zwischen den Voralpen und den Alpen fest. Auf der Ebene von Waldbeständen konnten die Waldstrukturvariablen das Vorkommen des Auerhuhns nur beschränkt erklären. Die Modelle wurden hingegen deutlich besser, wenn wir auch Landschaftsvariablen integrierten. Auf der Ebene von Streifgebieten (ganze Untersuchungsgebiete) konnten wir deutliche Unterschiede zwischen den Kategorien feststellen, so etwa für die mittlere Bestandesdichte oder den Anteil an lichtem Wald. Die Veränderung der Waldstruktur zwischen 1960 und 2000 war nicht so ausgeprägt, dass wir mit unserer Methode klare Trends gefunden hätten.

Als Grundlage für Populationsuntersuchungen analysierten wir die Grösse und die räumliche Anordnung von diskreten Fragmenten von potentiell Lebensraum (Paper IV). Diese Fragmente (Patches) leiteten wir vom multi-skalaren Modell ab, das wir in Paper I entwickelt hatten. Die Patch-Grösse als wichtigster Faktor und die Distanz zum nächsten besetzten Patch erklärten am besten, ob ein Fragment vom Auerhuhn besiedelt war oder nicht.

Diese Doktorarbeit hat einen direkten Nutzen für die Naturschutzpraxis. Wir haben eine Methode beschrieben, wie grossräumige Habitatmodelle (siehe Paper I und II) direkt in der Planung von Naturschutzmassnahmen verwendet werden können (Paper V). Wir schlagen vor, die potentielle Verbreitung des Auerhuhns (gemäss Habitatmodell) mit den aktuellen Vorkommen zu überlagern. Aus der resultierenden Karte können wir wichtige Flächen für die Förderung des Auerhuhns identifizieren und in Prioritätsstufen klassieren. Diese Methode wurde für die Erarbeitung des Nationalen Aktionsplan Auerhuhn verwendet.

General introduction

Motivation and state of the art

With the increase of human-induced habitat fragmentation, a new question has become quite important in conservation biology: how can subdivided populations persist in such environments (e.g., Hanski & Gilpin 1991; Harrison 1994; Harrison & Fahrig 1995; Storch 1997; Grimm & Storch 2000)? Metapopulation theory (Levins 1969, 1970) proved to be a successful tool for answering these questions (Hansson 1995; Wiens 1996; Harrison & Bruna 1999; Hanski & Ovaskainen 2000), and the relatively young discipline of landscape ecology has helped to put this theory in a spatially explicit framework (Lidicker 1995).

As an important prerequisite for spatially explicit population viability analyses of endangered species, the species-habitat relationship has to be well understood. Traditionally, wildlife ecologists have focused on small spatial scales, but it is now increasingly clear that in many wildlife species demographic and genetic processes are driven by mechanisms operating at the landscape scale (Sjöberg 1996; Bissonette 1997; Baillie et al. 2000; Hanowski et al. 2000; Linden et al. 2000). Thus, conservation goals can be reached only if spatial scale is addressed appropriately (Wiens 1989; Levin 1992). Spatial scale can be differentiated into grain and extent. While grain refers to the finest level of resolution available within a given data set, extent refers to the size of the study area (Turner et al. 1989). Because there is no single correct spatial scale at which to describe species-habitat relationships (Wiens 1989), multi-scale approaches are necessary (Bissonette 1997; Cushman & McGarigal 2004) and are indeed becoming increasingly common (Carroll et al. 1999; Fuhlendorf et al. 2002; Lawler & Edwards 2002; Thompson & McGarigal 2002; Zabel et al. 2003; Fischer et al. 2004). The rapidly advancing GIS technology and new powerful analysis tools have helped to address spatial scale questions in species-habitat relationships (Guisan & Zimmermann 2000; Manly et al. 2002).

The capercaillie (*Tetrao urogallus*) is a Eurasian forest grouse species with narrow habitat preferences (e.g., Schroth 1992; Sjöberg 1996) and large spatial requirements (average home range: c. 550 ha, Storch 1995). This makes it highly susceptible to habitat and landscape changes. Capercaillie populations are declining in most of their central European range (e.g., Storch 2000), as habitat loss and fragmentation have resulted in small populations with different degrees of connectivity or complete isolation (Klaus 1994; Storch 2000). The same holds true in Switzerland, where the remaining population of 900 – 1'100 individuals (Mollet et al. 2003) faces a high extinction risk due to environmental, demographic, and genetic processes. The negative population trend and the role of capercaillie as an umbrella species (Suter et al. 2002; Roberge & Angelstam 2004) have made it a focal species in biodiversity conservation (Keller & Bollmann 2004). As a charismatic bird, it is now getting much

attention from forestry and conservation practice. All these characteristics make capercaillie a model organism of both theoretical and practical interest.

In the past, hunters, scientists and conservationists conceived capercaillie as a sedentary bird with a restricted, predictable home range (e.g., Müller 1974). Thus, capercaillie conservation efforts have been focused on the preservation of microhabitat features at the forest stand scale, and particularly at leks (Stein 1974; Zeimentz 1974; Eiberle 1976; Koch 1978; Weiss et al. 1990). This is partly justifiable because small-scale forest structure has been found to influence capercaillie habitat use substantially. Capercaillie prefer forests with an intermediate canopy cover (e.g., Gjerde 1991; Sjöberg 1996; Storch 2002; Suchant 2002) and a lush ground vegetation cover (e.g., Schroth 1992; Sjöberg 1996), which ideally is dominated by bilberry (e.g., Storch 1993; Suter et al. 2002). However, small-scale habitat features can explain capercaillie occurrence only in part (Storch 2002). Telemetry studies revealed the large spatial requirements of capercaillie (e.g., Rolstad et al. 1988; Storch 1995) and demonstrated that populations are sensitive to macrohabitat alterations such as forest fragmentation or the spatial arrangement of favorable habitat (Wegge & Rolstad 1986; Rolstad et al. 1987; Rolstad & Wegge 1989; Storch 1995). Recent work mainly in Scandinavia has shown that capercaillie populations are in fact substantially driven by landscape-scale processes (Kurki & Linden 1995; Kurki et al. 2000). As a consequence, capercaillie habitat requirements can only be fully understood if they are studied at the entire set of relevant spatial scales (Storch 1997). Thus, multi-scale approaches are necessary (Bissonette 1997; Keppie & Kierstead 2003), especially in regions where the species is endangered (Storch 2000).

Objectives and research questions

The necessity for multi-scale approaches and the profound knowledge of small-scale habitat requirements made me start and concentrate most of my efforts at larger spatial scales. The overall goals of this PhD thesis were to identify the factors affecting capercaillie occurrence at different spatial scales and to provide a spatially explicit basis for population viability analyses.

In particular, the objectives of this thesis were:

1) to investigate capercaillie habitat at different spatial scales:

Can suitable capercaillie habitat be identified based on a landscape ecological parameter set comprising environmental variables, forest structure information, patch size and spatial configuration?

How does spatial scale (grain and extent) influence the ability of single variables and multivariate models to predict capercaillie occurrence?

2) to estimate historical changes of forest and landscape structure relevant to habitat suitability:

How did forest and landscape structure change, expressed by the parameters found to predict habitat suitability for capercaillie?

Can the decline of capercaillie be "predicted" based on the observed changes of forest and landscape variables?

3) to provide a baseline for spatially explicit population viability analyses and for regional concepts for the conservation of capercaillie populations:

Do size and configuration of discrete patches of potentially suitable habitat explain capercaillie patch occupancy?

How can priority areas for the conservation of capercaillie be derived from predictive habitat distribution models?

Thesis structure

This PhD thesis was part of a larger project at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL, which aimed at investigating capercaillie populations in the Swiss Alps and thereby adopting an interdisciplinary approach including landscape ecology, population dynamics and population genetics. Also, we made use of contemporary theoretical work on metapopulations, minimum viable population size (MVP), and landscape ecology. The overall goal of the project was to understand population dynamics of the capercaillie in the Swiss Alps and to quantify the effects that are likely to be responsible for the observed population decline. In the present thesis, I investigated factors affecting the occurrence patterns of capercaillie at different spatial scales.

The study area encompassed large parts of the Northern Pre-Alps and the Eastern Central Alps of Switzerland. These areas contain the so-called capercaillie regions III, IV and V, respectively (Figure 1, Mollet et al. 2003). We chose this large-scale design because we expected capercaillie-habitat relationships to differ between the regions that cover a climatic gradient from a maritime climate in the Pre-Alps to a continental climate in the inner-alpine valleys of the Central Alps. We believe that this cross-regional approach is a major strength of our project, because the results of studies using data from one single region (e.g., Storch 2002; Suchant 2002; Sachot et al. 2003) may be influenced by peculiar regional conditions.

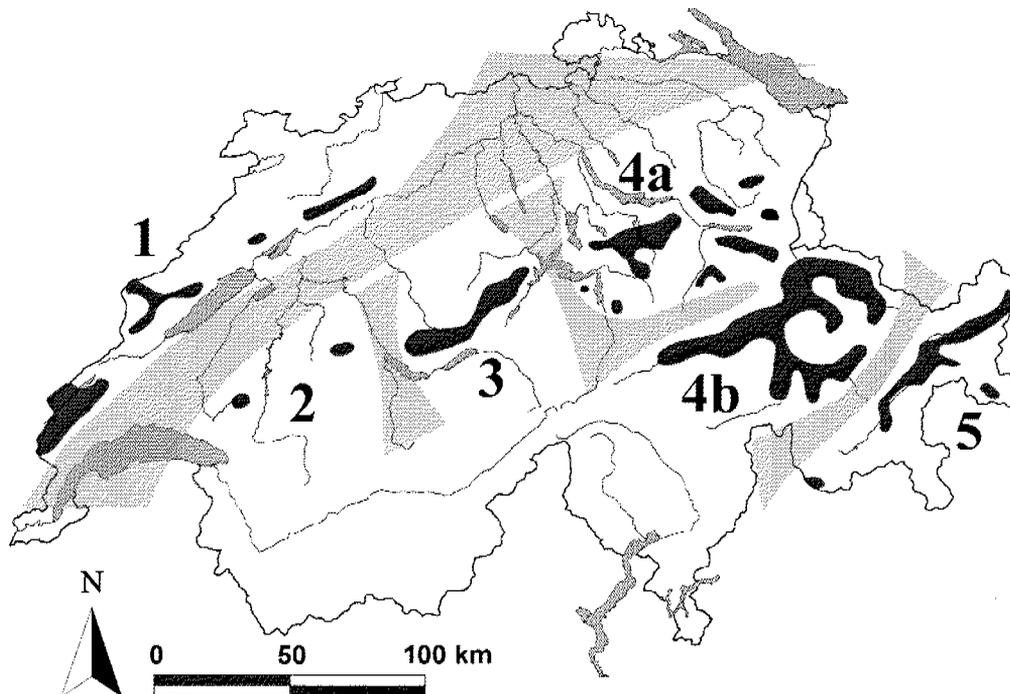


Figure 1. Range of capercaillie in Switzerland 2001 (dark shading). The numbers indicate the five isolated populations, i.e. Jura (1), western Pre-Alps (2), central Pre-Alps (3), eastern Pre-Alps (4a), northeastern Central Alps (4b) and southeastern Central Alps (5). Figure from Mollet et al. 2003.

In the first part of this thesis (Paper I and II), we analyzed capercaillie habitat at the scale of entire regions. For these analyses, we had to confine on environmental data with country-wide coverage as independent variables. As dependent variable, we had presence-absence data for large parts of the study area derived from observational data from different sources (national survey, cantonal inventories, local experts, own surveys; Appendix I). Data from the Jura Mountains were used only for validation purposes. In this part of the thesis, we held the scale and coding of presence-absence data constant but varied both the grain size (moving window) of the independent variables and the overall extent of the analysis (region).

In a first step, we varied grain size from 1 ha to just over 1100 ha and compared the ability of single variables and of single- and multi-scale models to predict capercaillie occurrence.

Paper I: The importance of spatial scale in habitat models: capercaillie in the Swiss Alps

Then, we varied the spatial extent by building separate models for the two regions of the northern Pre-Alps and the eastern Central Alps. These two models were compared with a model built with pooled data from both regions, and all models were validated using data from the Jura Mountains.

Paper II: On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions

Such large-scale models have a drawback in that they often describe indirect species-habitat relationships and thus possibly are of limited value for understanding processes that actually determine species distribution patterns. Therefore, when adopting a larger-scale approach, factors describing the habitat per se should ideally be included. Yet, if important habitat features at the stand scale such as percentage of bilberry cover had to be assessed over large areas, it could only be done if personal and financial resources were almost unlimited. Therefore, habitat models at the landscape scale have to include variables that can be measured easily at the regional level, e.g., using remote sensing techniques. Therefore, we assessed forest structure from aerial photographs within 52 study plots of 5 km² each, representing three categories of population trends, i.e. “stable”, “declining”, and “extinct”. Then, we adopted a two-scale analysis approach to investigate the habitat requirements of capercaillie at the scale of forest stands (400m² cells within study plots) and home ranges (entire study plots).

Paper III: Forest and landscape structure variables as predictors for capercaillie occurrence at the scales of forest stands and home-ranges

One major goal of this thesis was to provide a spatially explicit basis for population viability analyses. Such analyses normally rely on a set of discrete habitat patches distributed in a matrix of unsuitable habitat with information on either presence-absence (incidence,

occupancy) or species abundance. We identified discrete patches of potentially suitable habitat from the multi-scale model built in paper I and classified them as occupied or unoccupied patches. Then, in a first step towards a population viability analysis, we investigated to which extent the size and configuration of the habitat patches predicted patch occupancy.

Paper IV: Assessing the influence of patch area, isolation and connectivity on predicting capercaillie occurrence in the Alps

The results of this thesis have direct implications for conservation efforts. Capercaillie populations in Switzerland have declined strongly over the past decades and the remaining population is down at only 900 – 1000 individuals (Mollet et al. 2003). Conservation actions have mostly been taken at the scale of forest stands and did not halt the ongoing decline. Therefore, a National Species Action Plan is under construction. This action plan will contain maps specifying areas of different priority for conservation that were derived from the habitat models built in Paper I. A simplified description of the method for priority setting is described in Paper V.

Paper V: Using a multi-scale model for identifying priority areas in capercaillie (Tetrao urogallus) conservation.

The results of this thesis provided new insights on the habitat requirements of capercaillie at different spatial scales, and they have implications for conservation practice. Also, they elucidated a number of drawbacks, strengths and problems of statistical habitat modeling in general and logistic regression in particular. Thus, overall discussion, conclusions and methodological aspects are treated in a synthesis chapter.

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Paper I

The importance of spatial scale in habitat models: capercaillie in the Swiss Alps

In press as:

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Abstract

The role of scale in ecology is widely recognized as being of vital importance for understanding ecological patterns and processes. The capercaillie (*Tetrao urogallus*) is a forest grouse species with large spatial requirements and highly specialized habitat preferences. Habitat models at the forest stand scale can only partly explain capercaillie occurrence, and some studies at the landscape scale have emphasized the role of large-scale effects. We hypothesized that both the ability of single variables and multivariate models to explain capercaillie occurrence would vary with the spatial scale of the analysis. To test this hypothesis, we varied the grain size of our analysis from 1 to just over 1100 hectares and built univariate and multivariate habitat suitability models for capercaillie in the Swiss Alps.

The variance explained by the univariate models was found to vary among the predictors and with spatial scale. Within the multivariate models, the best single-scale model (using all predictor variables at the same scale) worked at a scale equivalent to a small annual home range. The multi-scale model, in which each predictor variable was entered at the scale at which it had performed best in the univariate model, did slightly better than the best single-scale model. Our results confirm that habitat variables should be included at different spatial scales when species habitat relationships are investigated.

Key words – *Tetrao urogallus*, conservation, landscape analysis, spatial scale, multi-scale habitat model, logistic regression, Switzerland.

Introduction

Wildlife research and management have traditionally focused on small spatial scales. More recently, it has been recognized that animals, particularly birds, also respond to habitat factors at coarser spatial scales (Freemark and Merriam 1986). Because each species responds to the environment at a unique range of scales (Levin 1992), there is no single correct spatial scale at which to describe species-habitat relationships (Wiens 1989). Thus, multi-scale approaches are necessary (Bissonette 1997; Cushman and McGarigal 2004) and are indeed becoming more and more common in studies of species-habitat relationships (Carroll et al. 1999; Fuhlendorf et al. 2002; Lawler and Edwards 2002; Thompson and McGarigal 2002; Zabel et al. 2003; Fischer et al. 2004). Many studies, however, are conducted at a few arbitrary chosen scales (e.g. Zabel et al. 2003; Johnson et al. 2004), only few include a discrete range of scales (Fuhlendorf et al. 2002; Lawler and Edwards 2002), and very few investigate species-habitat relationships along a continuous range of scales (Thompson and McGarigal 2002).

The rapidly advancing GIS-technology and new powerful statistical tools have helped to address spatial scale questions in species-habitat relationships (Guisan and Zimmermann 2000; Manly et al. 2002). Generalized Linear Models (GLM) are one of the most widespread statistical approaches in habitat modeling (e.g. Mladenoff and Sickley 1998; Sachot et al. 2003; Gibson et al. 2004). As they do not require response variables that are normally distributed, and since they allow non-constant variance functions to be modeled, they are more flexible than the classical least-square regression (Guisan and Zimmermann 2000). A special case of GLM is the Logistic Regression, where the response variable is dichotomous (Hosmer and Lemeshow 1989; Manly et al. 2002). As data on species distributions are often restricted to the information of presence-absence, logistic regression is extensively used in habitat modeling of various taxonomic groups (Mladenoff and Sickley 1998; Carroll et al. 1999; Mace et al. 1999; MacFaden and Capen 2002; Berg et al. 2004; Gibson et al. 2004).

An excellent model organism for investigating the importance of spatial scale in habitat selection is the capercaillie (*Tetrao urogallus*, Tetraonidae, Aves; Storch 1997). This large forest grouse species has specialized habitat preferences (e.g. Schroth 1992; Sjöberg 1996) and extensive spatial requirements (average home range: c. 550 ha, Storch 1995), both making it highly susceptible to habitat and landscape changes. Capercaillie populations are declining in most of their central European range (e.g. Klaus et al. 1986; Storch 2000a), as loss and fragmentation of suitable habitats have split populations into smaller units loosely connected or even completely isolated. This is especially true in Switzerland, where the remaining population of 900 – 1000 individuals (Mollet et al. 2003) faces a high risk to become extinct due to environmental, demographic, and genetic processes.

In capercaillie, most research as well as conservation measures so far have focused on the forest stand scale (e.g. Klaus et al. 1985; Schroth 1992). Telemetry studies in Scandinavia and in Central Europe have revealed that spatial requirements of capercaillie are extensive (Wegge and Larsen 1987; Storch 1995), and they have shown that capercaillie populations are also sensitive to the spatial configuration of preferred habitats and to forest fragmentation (Rolstad and Wegge 1989). Recent work showed that capercaillie populations are strongly driven by landscape-scale processes (Storch 1997; Kurki et al. 2000). These processes, however, have only partly been addressed in predictive habitat modeling designed for large spatial scales. The habitat models for capercaillie at the landscape scale that are presently available either do not address spatial scale explicitly (Sachot et al. 2003), do not include spatial variables (Storch 2002) or do not include different spatial scales in a single statistical model (Suchant 2002). Uncovering larger-scale habitat relationships is an important research need in those regions where the species is endangered (Storch 2000b), and analyses should be conducted at multiple scales (Keppie and Kierstead 2003).

In the present study, we analyzed the species-habitat relationships of capercaillie at different spatial scales by varying the grain size. We hypothesized that the predictive power of single variables would vary with the spatial scale of analysis so that an optimum scale could be determined for each predictor variable. Therefore, we expected multi-scale models (every variable entered at its best-explaining scale) to perform better than single-scale models where all variables are entered at the same scale. To test this hypothesis, we built univariate and multivariate habitat suitability models using presence-absence data of capercaillie in the Swiss Pre-Alps and Alps and a large set of environmental predictors.

Methods

Study area

The study area comprises 4500 km² of forest-dominated landscape within the Northern Pre-Alps and the Eastern Central Alps in Switzerland, ranging in altitude from 400 m a.s.l. to 3500 m a.s.l. (Figure 1) The upper tree line on average is at about 2000 m a.s.l. Deciduous trees (mostly beech *Fagus sylvatica*) dominate the forests in the lower zones (400 – 1000 m a.s.l.), mixed forests prevail at intermediate altitudes (800 – 1400 m a.s.l.), and conifer trees such as silver fir (*Abies alba*), norway spruce (*Picea abies*) and mountain pine (*Pinus mugo*) form the forests at higher altitudes (1200 – 2200 m a.s.l., Steiger 1994).

In the Swiss Alps, capercaillie inhabit conifer-dominated forests at altitudes of about 1000 to 2200 m a.s.l. Most of the capercaillie populations in the Northern Pre-Alps (comprising ca. 280 individuals) and about half of the populations of the Eastern Central Alps (comprising ca. 180 individuals) are included within the study area. Particularly in the Northern Pre-Alps, capercaillie abundance has decreased strongly in the past decades (Mollet et al. 2003). Loss of

suitable habitat, human disturbance and increasing predator abundance are generally thought to be the major reasons.

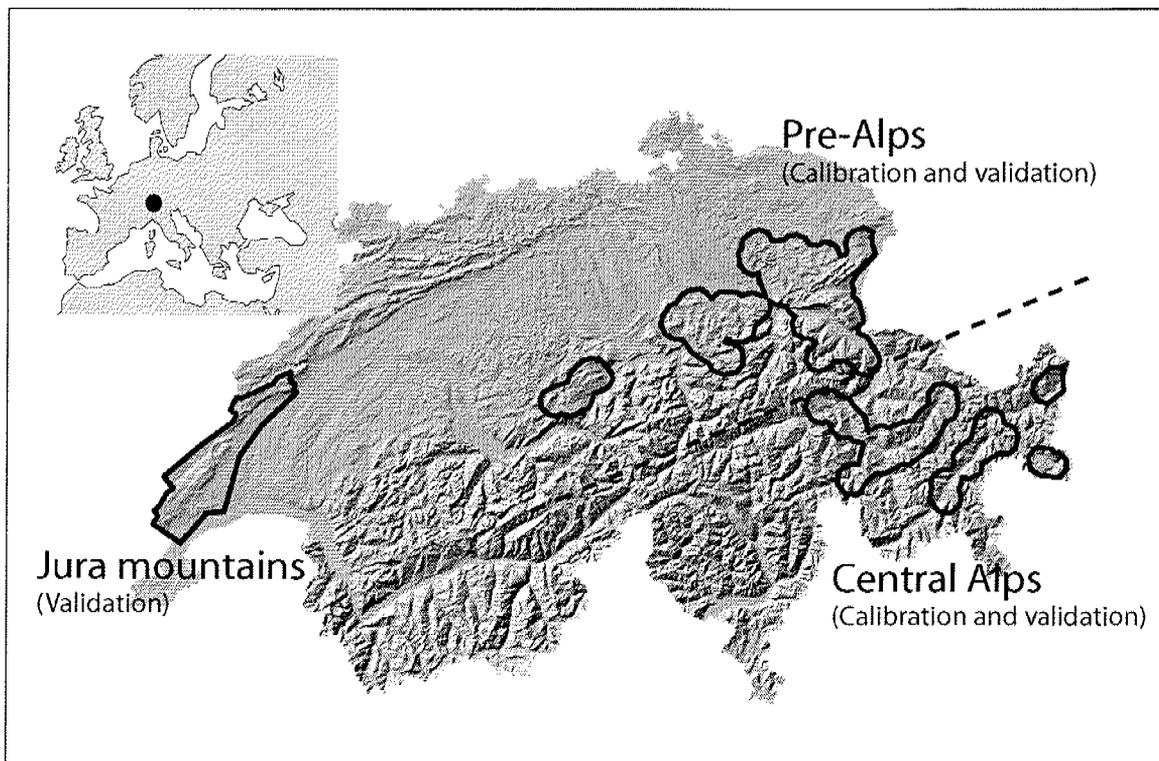


Figure 1: Study area; the study regions do not contain the whole capercaillie distribution in Switzerland; the dashed line separates the two regions of the northern Pre-Alps and the eastern Central Alps.

Modeling design

Presence-absence data and environmental variables were processed in grid format with a cell size of 1 ha. We defined cells as “presence” if they contained at least one capercaillie record. These records came from our own fieldwork and from several regional inventories (Appendix I). They include sightings and indirect evidence of capercaillie presence (faeces, feathers, footprints, etc.). Not all presence cells were used in the analyses, as their clumped distribution could have led to autocorrelation problems. Therefore, we reduced the number of cells by applying thiesen polygons (ARC/INFO 8.3), so that the minimum distance between any two presence cells was at least 500 m.

As the records are mainly from winter and spring surveys the areas with observations can be interpreted as core areas of capercaillie distribution. In late winter and early spring, capercaillie concentrate near the leks. Summer and autumn ranges contain the winter and spring ranges but also additional areas close to the winter ranges (Hess, pers. comm.). Therefore, we placed a buffer of 1 km around all observations to include the winter and summer ranges to a large degree. This leads to a minimum buffer area of about 3 km², which equals about the size of the home range of a capercaillie individual, as home range size in

telemetry studies ranged from 1 km² (only summer home range, Rolstad et al. 1988) up to 5.5 km² (Storch 1995). Using this method, we also avoid that actual presence cells (where no record was obtained) are erroneously classified as absence.

Absence cells used in the analysis are a randomly selected subset of cells with a minimum distance of 500 m. They additionally have a minimum distance of 1 km and a maximum distance of 5 km to the next presence cell. The latter rule ensured that only those areas are included that are located within a realistic dispersal distance from actual capercaillie populations (Storch and Segelbacher 2000; Segelbacher et al. 2003). By doing so, we implicitly assume habitat suitability to be the reason for the absence of capercaillie, not large-scale population effects.

Since both presence and absence cells tend to show a clumped distribution, spatial autocorrelation has to be considered. If autocorrelation was a problem, one would expect the residuals from the fitted models to be spatially correlated (Augustin et al. 1996). We investigated the spatial dependence of the residuals of all the multivariate models by calculating Moran's I (Moran 1948) in the software R 1.7.1. (package: spatial dependence SPDEP) at the level of the first neighbor. Another alternative would have been to account for spatial autocorrelation in the models by including an extra covariate describing whether the species is present or absent in the neighborhood of a site (Smith 1994; Augustin et al. 1996). However, this would have made it impossible to apply the models in areas where capercaillie distribution was mapped incompletely.

Environmental variables

A large set of environmental parameters that could possibly influence capercaillie occurrence, and which were available area-wide for the whole country were used as independent variables (Table 1). The 30 variables express aspects of topography, climate, habitat and human disturbance.

Topography is supposed to influence the habitat quality of capercaillie, for instance, indirectly by influencing forest structure (Roth et al. 1975; Suchant 2002) or directly by affecting the ability of capercaillie to avoid predators. As parameters representing different aspects of topography, we used altitude, slope (steepness) and topographic position. The topographic position is a measure to express the exposure of a location in space compared to the surrounding terrain. Positive values express relative ridges, hilltops and exposed sites, negative values, on the other hand, stand for sinks, gullies, valleys or toe slopes. The topographic position was calculated in GIS by applying circular moving-windows with increasing radii to a digital elevation model (DEM; DHM25 © 2004, SWISSTOPO, DV033594; Zimmermann and Roberts 2001).

Table 1: *Environmental variables.*

Variable description	Abbreviation	Unit (Range)	Dropped because of correlation ($r_s > 0.5$) with
Altitude	DEM	m	TAVE
Slope (Steepness)	SLOPE	degrees	
Topographic position	TOP	unitless	
Potential direct solar radiation in April	SDIR	kJ/day	
Precipitation (June)	PREC	0.1 mm/month	
Average temperature (June)	TAVE	°C*100	
Proportion of forest	PFOR	%*4 (0–25)	
Density of forest edges	FE	%*4 (0–25)	
Distance to forest edges	DFE	m	
Forest type	FT	4 categories	FTC
Coniferous forest ratio	CFR	index	FTC
Proportion of coniferous forest (cat. 1 and 2)	CF	%*6.25 (0–16)	PFOR
Coniferous forest (cat. 1 and 2)	FTC	0/1	
Deciduous forest (cat. 3 and 4)	FTD	0/1	TAVE
Proportion of mires and wet forests	MIRE	%*4 (0–25)	
Distance to mires and wet forests	DMIRE	m	
Total density of roads and trails (cat. 1–6)	RO	m/ha	TAVE
Density of motorable roads (cat. 1–4)	ROD	m/ha	TAVE
Distance to roads and trails	DRO	m	DROD
Distance to motorable roads	DROD	m	
Distance to alpine ski runs	DSKI	m	
Density of settlements	SETTL	0/1	TAVE
Distance to settlements	DSETTL	m	DROD
Distance to farmland used all year	DAGRY	m	DROD
Distance to farmland used seasonally	DAGRS	m	TAVE
Distance to farmland	DAGR	m	PFOR
Proportion of farmland	AG	%*4 (0–25)	TAVE
Proportion of farmland used all year	AGY	%*4 (0–25)	
Proportion of farmland used seasonally	AGS	%*4 (0–25)	DROD

Local climate is an important factor affecting reproduction of capercaillie, with dry and warm weather in early summer reducing chick mortality (Moss et al. 2001). We used average temperature, precipitation and potential direct solar radiation as parameters to characterize the climate. Temperature and precipitation were derived from the national network with recording stations at different altitudes. We used long-term monthly means of average June temperature (°C) and precipitation (mm) for the period of 1971–2000. Temperature and precipitation were spatially interpolated using a DEM as described in Zimmermann and Kienast (1999). Instead of using aspect as many other studies do (Sachot et al. 2003), we used potential direct solar radiation to represent local climate. To calculate this variable from the DEM, the method developed by Kumar et al. (1997) was used, which incorporates topographic shading effects.

Spatial vegetation patterns are a crucial factor influencing population density, home range size, mortality and reproductive success of capercaillie (Wegge and Rolstad 1986; Storch 1994, 1995; Kurki et al. 2000; Baines et al. 2004). Thus, we included variables describing the distribution of forest, forest type, distance to forest edge and forest edge density, abundance of and distance to mires. Forest structure and field layer information were not included because we did not have area-wide data. The variables “proportion of forest”, “forest edge density” and “distance to forest edge” stem from a grid data set (1 = forest, 0 = not forested; cell size 20 m) derived from thematic pixel maps (PK25 © 2004, SWISSTOPO, DV033594; scale of 1:25'000). Cells were defined as forest edge when either the focal cell was forest and at least one of the surrounding cells was not forest, or the focal cell was not forest and at least one surrounding cell was forest. The dataset “forest type” (WMG25, BFS GEOSTAT) was derived from satellite images (Landsat-5, Thematic Mapper) by an automated maximum likelihood classification. For this classification, the Swiss National Forest Inventory (NFI) was used as reference data. “Forest type” is available in four different categories: conifer forest (Cat. 1), conifer-dominated mixed forest (Cat. 2), deciduous-dominated mixed forest (Cat. 3), and deciduous forest (Cat. 4). Sixty percent of the reference cells were classified correctly, and only 10 percent were not assigned at least to the neighboring class of the reference data. In the variable “proportion of mires and wet forest” we combined data from the two inventories of mires and fens (Swiss Federal Research Institute WSL) with data denoting the wet areas from the vector25 dataset (Vector25 © 2004, SWISSTOPO, DV033594). The categories included are mires in open land, mires with bushes, mires in closed forests and mires in open forests. The original vectorized data were converted into grids with 20 m cell size. The values in the final 100 m (1 ha) grid represent the number of 20 m cells defined as moor, swamp or any other wetland.

Disturbances by tourism and leisure activities are generally assumed to negatively affect capercaillie populations (Storch 2000a). Disturbance by human activities was expressed through the presence of roads, alpine ski runs and settlements. The vector25 dataset (Vector25 © 2004, SWISSTOPO, DV033594) provides six different categories of roads. We combined categories one to four into “motorable roads”, categories five and six to “not-motorable

trails". In the variable "settlements", all cells defined as settlements (area statistics 1992/97, BFS GEOSTAT, resolution 1 ha) were included for the calculation of an index of settlement density. In "distance to settlements", we only included clusters of grid cells with built-up areas of at least four hectares. Thus, single houses with low or almost no disturbance effect were ignored for calculating the distance to settlements.

Farmland in the neighborhood of suitable habitats is supposed to negatively affect the reproductive success of woodland grouse species because it promotes high abundances of generalist predators (Kurki and Linden 1995). We employed the land-use data of the Swiss Federal Agency for Statistics (area statistics 1992/97, BFS GEOSTAT; resolution 1 ha) and distinguished between seasonally used areas (alpine meadows and pastures) and farmland used during the whole vegetation period (meadows, pastures, arable fields, horticultural areas, orchards, and vineyards).

We prepared all independent variables in grid format with a cell size of one hectare. With a moving window analysis (ARC/INFO 8.3), we varied the grain size in our analyses by calculating mean, sum or majority values for a circular neighborhood of each grid cell for each environmental variable. The window size was increased stepwise from 1 ha up to just over 1100 ha. We included six window sizes, hereafter called "spatial scales": 1, 13, 113, 253, 529, and 1129 ha. The three larger spatial scales (253, 529, and 1129 ha) have a biological meaning, representing 0.5-, 1- and 2-times the size of an average home range of capercaillie (Storch 1995). The uneven numbers are due to the moving window algorithm that is working with entire grid cells. When summarizing the variables at the different scales we calculated sum values for density of settlements, majority values for forest type, coniferous and deciduous forest, and mean values for all other variables. Our approach leads to some overlap of the analysis windows at the larger spatial scales (scale of 113 ha: 13 %, scale of 253 ha: 27 %, scale of 529 ha: 44 %, scale of 1129 ha: 63 %).

Statistical modeling

Logistic regression models

Logistic regression (Manly et al. 2002; Menard 2002) was used for all habitat modeling using the software SPSS 11.0. Following Hosmer and Lemeshow (1989), we used a binomial error distribution, and a logit link function. In all multivariate models, we applied both stepwise backward and stepwise forward procedures to find robust models (Menard 2002). As in most studies of habitat modeling (Pearce and Ferrier 2000), we use a threshold of $P = 0.05$ for the decision of keeping or omitting a predictor variable. In all modeling, we included untransformed variables, as normality is not required, and error terms are allowed to have non-Gaussian distributions (Guisan and Zimmermann 2000). By plotting the frequency distribution of the predictor variables both for presence and absence plots, we evaluated the type of response. In the case of a unimodal response, the squared predictor variables were

included in the univariate and multivariate analyses as well (Guisan and Zimmermann 2000; Schröder 2002).

Variable reduction

Multicollinearity of independent variables can cause problems in logistic regression models (Menard 2002). Fielding and Haworth (1995) suggested that a correlation higher than 0.7 is critical. We applied an even more stringent threshold value of 0.5 in order to get simple models with only few variables. If Spearman's rank correlation exceeded this value, the variable with no (or less) direct influence on capercaillie populations was omitted from the analysis. For instance, of the pair "altitude" and "average temperature" ($r_s > 0.8$), we dropped altitude and retained average temperature. The latter may directly control vegetation types (e.g., coniferous vs. deciduous forest), whereas altitude would be a surrogate parameter with only regional validity (e.g., in Switzerland the lower altitudinal limit of capercaillie distribution is at 800 m a.s.l., whereas in Fennoscandia it is at sea level). Independent variables with low predictive power in univariate models (R-square Nagelkerke < 0.05) were omitted (e.g. potential direct solar radiation, precipitation, density of forest edges, distance to motorable roads and distance to alpine ski runs). Additionally, the algebraic sign of the coefficient of a variable had to be the same in the multivariate model as in the univariate model, and it had to be ecologically plausible. Otherwise, the variable was omitted (e.g., proportion of farmland used all year).

Calibration and validation

For assessing the model fit, we used the R-square by Nagelkerke (R^2_N , Nagelkerke 1991), which gives a measure of the variance in the dependent variable that is explained by the independent variables. R^2_N is not sensitive towards the number of variables included in the model. Therefore, we also provide the Akaike Information Criterion AIC (Boyce et al. 2002; Rushton et al. 2004) that helps to identify the model that accounts for the most variation with the fewest variables.

For validating the models, we used measures based on a confusion matrix (Fielding and Bell 1997; Guisan and Zimmermann 2000; Boyce et al. 2002). A confusion matrix contains the predicted and observed presences and absences based on a fitted model. From this matrix, a large number of different measures can be derived. We use the correct classification rate (CCR), the positive predictive power (PPP), the negative predictive power (NPP) and Kappa-statistics (Monserud and Leemans 1992). Kappa measures the actual agreement minus the agreement expected by chance; it takes values between 0 and 1 (0.00–0.05 = no agreement, 0.05–0.20 = very poor, 0.20–0.40 = poor, 0.40–0.55 = moderate, 0.55–0.70 = good, 0.70–0.85 = very good, 0.85–0.99 = excellent, 0.99–1 = perfect agreement). We used Kappa both at a threshold of 0.5 ($K_{0.5}$) and at the optimized threshold (K_{opt}). To determine the optimized threshold, we calculated Kappa for all possible threshold values from 0.01 to 0.99. Because all these measures depend on a particular threshold, we also use the Receiver Operating

Characteristic (ROC, Deleo 1993). The area under the ROC function (AUC) is usually taken to be an important index because it provides a single measure of overall accuracy that is not dependent upon a particular threshold (Fielding and Bell 1997; Boyce et al. 2002). AUC can take values between 0 and 1. A value of 0.8 for the AUC means that for 80 % of the time a random selection from the positive group will have a score greater than a random selection from the negative group.

Modeling procedure

In a first step, we calculated univariate models for all predictor variables at each spatial scale. By comparing the accuracy of all these models using R^2_N , we defined the best scale for every predictor variable; in other words, we searched for the scale at which the variable best explained the variance in the species occurrence. In a next step, we calculated a number of multivariate models. First, we built models including all variables at one single scale (single-scale models). Second, we used the information from the univariate analyses and included every predictor variable at its best-explaining scale (multi-scale model). Here, one could have favored other approaches to build a multi-scale model. We preferred our approach because of its mechanistic character: the choice of the scale of a variable is not depending on correlations with other variables. Both the single-scale and the multi-scale models were calibrated on a combined dataset from the Alps and the Pre-Alps ($N = 822$; $N_{Pres} = 322$, $N_{Abs} = 500$) and evaluated on set-aside data from the same area ($N = 662$; $N_{Pres} = 300$, $N_{Abs} = 362$). All models were additionally tested using an independent dataset from the Jura Mountains ($N = 500$, $N_{Pres} = 200$, $N_{Abs} = 300$). This population is spatially separated from our study area by a distance of at least 85 km (Figure 1).

We applied a minimum distance from absence to presence cells to reduce false absences. To test the degree to which this buffer influenced model predictions, we decreased the buffer size stepwise (1000 m, 750 m, 500 m) and thereby allowed absence points to be located closer to capercaillie observations (in the validation data set). By reducing buffer size in the validation, we wanted to test whether the models still predict capercaillie occurrence accurately. As the areas within the buffer are highly likely to be used at least temporarily by capercaillie, we did not want to use these areas as absence nor as presence area for model calibration.

Model predictions

All multivariate models were applied in GIS (ARC/INFO 8.3) by combining the predictor grids as defined by the model equations. This leads to grids with floating values from 0 to 1, which define the probability of a grid cell of being occupied by capercaillie (1 = Presence, 0 = Absence). By reclassifying the grids using an accurate threshold value of 0.5, we produced maps with predicted presence and absence that can be interpreted as potential habitat maps.

The proportion and spatial distribution of predicted presence areas was investigated using Patch Analyst 2.2 (Elkie et al. 1999), a software for calculating landscape metrics based on

FRAGSTATS (McGarigal et al. 2002). We provide data on the mean proportion of predicted presence area, number of patches and mean patch size.

Results

Univariate models

We defined the best scale for every independent variable by comparing their explained variance (R^2_N) in univariate logistic regression models at all six spatial scales analyzed (Figure 2). Some variables performed best at small scales (e.g. topographic position, coniferous forest), others at large scales (e.g. proportion of forest). Other variables were not sensitive towards the observed spatial scale (e.g. average temperature). Variables that had the highest predictive power in univariate models were “proportion of forest”, “average temperature” and “coniferous forest” ($R^2_N = 0.44, 0.47, \text{ and } 0.29$, respectively).

Multivariate models

To calibrate the multivariate models, we retained eight independent variables that were not highly inter-correlated and had a minimum R^2_N of 0.05 in the univariate models. We also included the squared term of four variables to account for unimodal responses to capercaillie presence-absence. Generally, all multivariate models (single-scale and multi-scale) performed well on data from the calibration area that were set aside for validation ($0.76 < K_{05} < 0.85$; $0.94 < \text{AUC} < 0.96$; Table 2).

Table 2: Accuracy of single-scale models (Scale0–Scale19) and the multi-scale model; accuracy measures for model fitting (AIC, R^2_N) and validation (K_{05} , K_{opt} , CCR₀₅, AUC).

Model	Scale [ha]	Model fitting		Validation on dataset from the Prealps and Alps (N = 662)				Validation on dataset from the Jura Mountains (N=500)			
		AIC	R^2_N	K_{05}	K_{opt}	CCR ₀₅	AUC	K_{05}	K_{opt}	CCR ₀₅	AUC
Scale0	1	537	0.684	0.760	0.788	0.881	0.940	0.434	0.623	0.694	0.896
Scale2	13	488	0.723	0.794	0.807	0.897	0.947	0.463	0.617	0.712	0.903
Scale6	113	436	0.762	0.836	0.851	0.918	0.955	0.426	0.610	0.690	0.895
Scale9	253	411	0.781	0.839	0.866	0.920	0.957	0.427	0.483	0.700	0.821
Scale13	529	466	0.741	0.830	0.872	0.915	0.957	0.434	0.472	0.700	0.826
Scale19	1129	579	0.649	0.836	0.851	0.918	0.952	0.323	0.534	0.624	0.866
Multi-scale		415	0.778	0.845	0.875	0.923	0.958	0.520	0.583	0.746	0.872

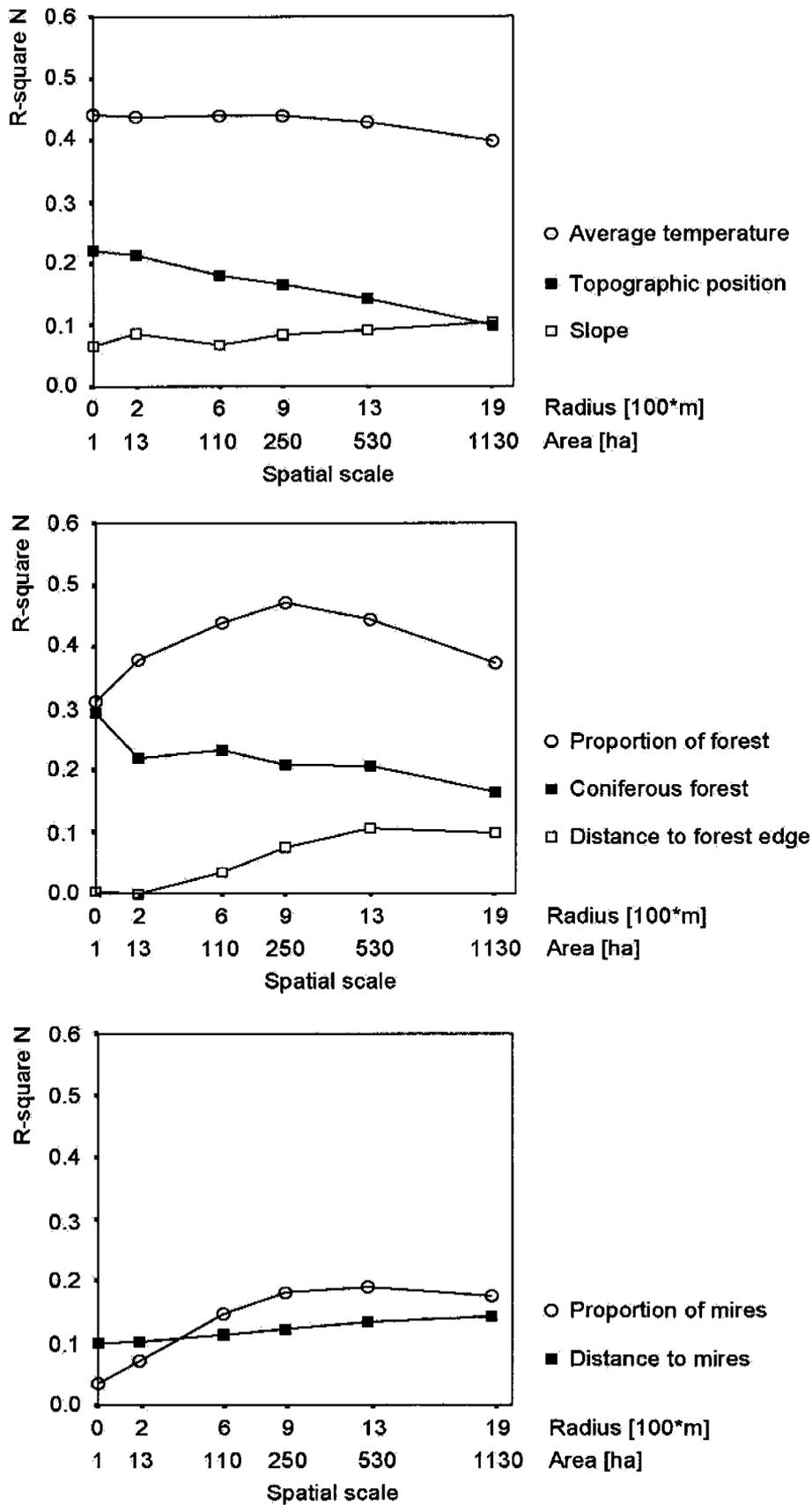


Figure 2: Accuracy of single variables across spatial scales.

Within the group of the single-scale models, where all variables were included at the same spatial scale, we found predictive power to be highest at the intermediate scales (113 ha and 253 ha; Table 2), with the model at a scale of 253 ha (radius 900 m) performing best ($R^2_N = 0.781$, $K_{0.5} = 0.839$, $AUC = 0.957$). The multi-scale model that included every variable at its best scale attained a similar accuracy ($R^2_N = 0.778$, $K_{0.5} = 0.845$, $AUC = 0.958$) as the best single-scale model (Figure 3). In the validation on the independent dataset from the Jura Mountains, the multi-scale model classified best when the same threshold value (0.5) was used as in the model calibration ($K_{0.5} = 0.520$; compared to $0.323 < K_{0.5} < 0.436$ of the single-scale models). At the optimized threshold value, the two single-scale models working at the smallest spatial scales performed best ($K_{opt} = 0.623$, and 0.617 , respectively).

The same variable set had been used for the calibration of the multi- and single-scale models. From this set, all single-scale and multi-scale models retained almost the same combination of variables. Those variables were “average temperature”, “proportion of forest”, “topographic position”, “slope” and “proportion of mires and wet forest” (Table 3). Most models retained the squared terms of “average temperature” and “slope”, indicating a unimodal response to capercaillie presence-absence. In the multi-scale model, “coniferous forest” was retained as an additional variable. Model coefficients and LOWESS curves describing the response of capercaillie to the variables retained by the multi-scale model are given in Appendix II.

The models not only differ in their accuracy, but also in the proportion and distribution of predicted presence area when applied on the study area (Figure 4). The mean proportion of predicted presence area of the single-scale models ranges from 18.0 percent (scale0) to 23.5 percent (scale19). The mean patch size increases from 38.4 ha (scale0) to 2050.1 ha (scale19). The multi-scale model, in which we included all variables at the best-explaining scale, shows intermediate values (proportion of presence area: 19.6 percent, mean patch size: 240.9 ha).

Sensitivity test of presence/absence definition

One could argue that our models have high accuracy values because we included a buffer zone of 1000 m between presence and absence cells, and thus many grid cells with intermediate suitability were excluded from the validation. To test the degree to which the buffer size influences model accuracy, we decreased buffer size stepwise (1000 m, 750 m, and 500 m) and thereby allowed more absence cells near capercaillie presence in the validation data set. The accuracy of the multi-scale model decreased with decreasing buffer size, yet remained on a high level: buffer of 1000 m ($K_{0.5} = 0.845$, $AUC = 0.958$), 750 m ($K_{0.5} = 0.777$, $AUC = 0.940$), 500 m ($K_{0.5} = 0.727$, $AUC = 0.934$). Decreasing model accuracy resulted from the decreasing positive predictive power (0.892, 0.813, 0.761), which means that there will be more grid cells that are wrongly classified as “presence”. An analogous decrease of model accuracy and positive predictive power was found for the single-scale models (data not shown).

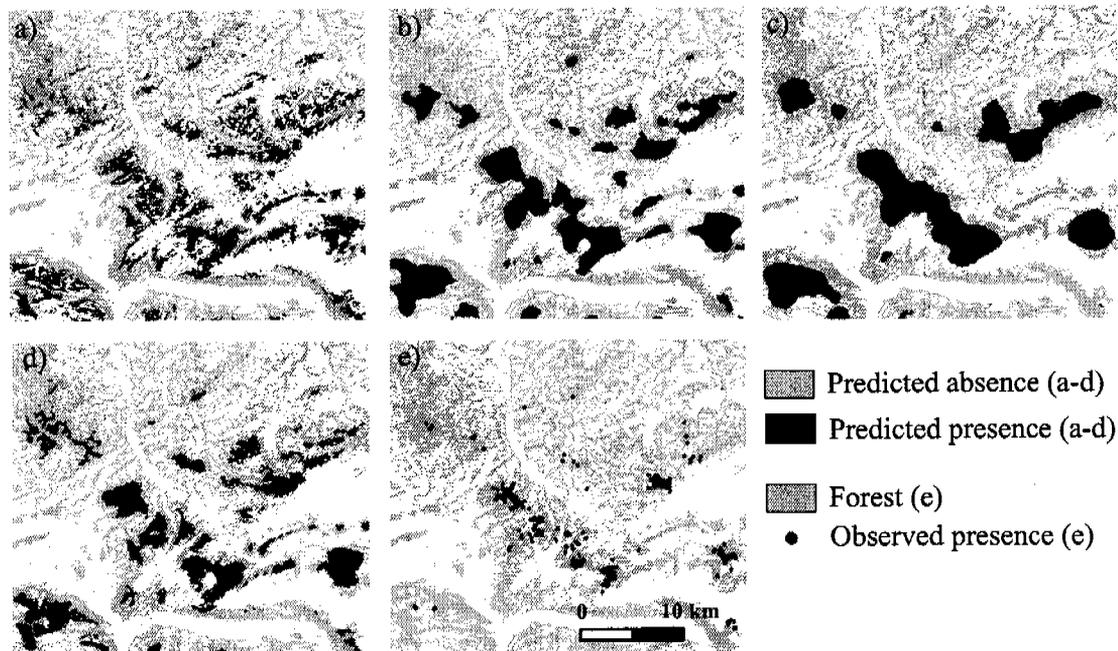


Figure 4: Distribution of predicted presence areas for different models (a–d) and observed presence (e); a) scale0: window size 1 ha, b) scale9: window size 253 ha, c) scale19: window size 1129 ha, d) multi-scale model, e) observed presence.

Spatial autocorrelation of residuals

Only weak spatial autocorrelation was found in the residuals of the multivariate models at the two largest scales. Moran's I was significantly different from zero in the residuals of the models at 529 ha (Moran's I = 0.048, $p < 0.050$) and 1129 ha (Moran's I = 0.081, $p < 0.001$). The residuals of the multi-scale model showed no significant spatial correlation (Moran's I = 0.012, $p = 0.202$). Given the weak spatial dependence of the residuals at the level of the first neighbor, we did not perceive a need to calculate correlograms and to further investigate spatial autocorrelation.

Discussion

The present study confirms other findings that species respond to ecological parameters at particular spatial scales. Based on our results, we will consider three main issues: First, we discuss the significance of scale for capercaillie occurrence in mountain landscapes and compare the single-scale with the multi-scale approach. Second, we address the high prediction success of the multivariate models. Third, we discuss the implications of the habitat parameters identified by the models as being important at the landscape scale.

Spatial scale

Spatial scale matters when habitat selection by capercaillie is studied. By comparing a number of single-scale models, we found the best grain size to be about 250 ha for habitat models for capercaillie. The value of 250 ha is equivalent to the size of a small annual home range (Rolstad et al. 1988; Storch 1995). Most studies of home range size use minimum convex polygons, i.e. a method that tends to overestimate the area actually used by the birds. Thus, our results support the suggestion that habitat selection of space-demanding large vertebrates may be dominated by factors operating at the home-range scale and above (Carroll et al. 1999).

Optimizing the spatial scale for each variable and calculating an optimized, multi-scale model proved to be a promising approach. Some variables explained species occurrence better at small scales, while others did better at large scales. This is in agreement with our hypothesis that the capercaillie responds to its environment at different spatial scales at the same time. Similar scale dependence of single habitat variables was found for reptiles (Fischer et al. 2004) or the bald eagle (*Haliaeetus leucocephalus*), another space-demanding bird species (Thompson and McGarigal 2002). In our case, the multi-scale model performed equally well as the best single-scale models when tested on independent data from the calibration area. However, the multi-scale model proved to be superior in the test on independent data from another, different area. Thus, the multi-scale approach seems to capture the species-habitat relationship in a more mechanistic way that leads to greater model generality. Consequently, we recommend that variables in multivariate habitat distribution models should be included at different spatial scales.

The models at the various spatial scales differ in accuracy, but all models reach good accuracy values ($Kappa > 0.7$). However, the resolution of predicted presence areas (Figure 4) depends on the spatial scale of the model. According to the objectives of a particular analysis, we might find different spatial scales to be the most appropriate ones. For instance, when aiming at identifying potentially suitable forest patches, we will probably use a model developed at a relatively small scale. For studying the distribution and connectivity of populations or providing a basis for meta-population modeling, a large-scale model would possibly be more appropriate. Additionally, model accuracy strongly depends on the scale and coding of the

response variable (Cushman and McGarigal 2004). In our study, however, the scale of the presence-absence data was kept constant.

Predictive ability of the models

Model predictions were quite good. We attribute this to two reasons: First, habitat preferences of capercaillie are specialized also at the landscape scale, so that a few of the common landscape-scale variables are capable of predicting capercaillie occurrence to a large extent. Second, our definition of presence and absence is probably bound to produce (relatively) good model predictions and must be considered in detail. In order to avoid false observed absences in the calibration and validation data-set, we applied a buffer of one kilometer around the presence points. This buffer led to “tolerant” habitat models that predict a high probability of capercaillie presence for almost all areas with capercaillie observations. Because we included a buffer around the observed presence cells, most observed absence cells were also classified correctly. By reducing the buffer in the validation process, the rate of false positives is increasing while the number of false negatives is remaining low. Still, the overall model accuracy remains high. Thus, we conclude that our approach is quite robust.

Variables selected by the models

Our results confirm that a small set of landscape-scale variables can explain capercaillie presence-absence to a considerable extent. They also support the conclusion of Storch (Storch 2002) that factors operating at the landscape scale could explain the variance of capercaillie occurrence that was not explained by small-scale habitat preferences.

Only few variables explain capercaillie occurrence in our models: proportion of forest, average temperature, topography, slope and proportion of mires and wet forests. Capercaillie preferably occur in large and well-connected forest tracts (Storch 1995; Kurki et al. 2000). This general finding is confirmed by the high significance of the variable “proportion of forest” in our models and concretized by the best scale of a small home range (250 ha) that we could detect for this variable. As expected, average temperature accounted for much of the explained variance in the multivariate models, since capercaillie in Switzerland (and most other parts of Central Europe) is restricted to a range of altitude starting at 800 m and extending to the upper tree line at 1600 – 2200 m a.s.l. This altitudinal range in Central Europe offers similar climate and similar coniferous forest vegetation as the boreal climate zone where optimal habitats for capercaillie are spread over large areas. Influence of topography on capercaillie habitat use has already been found in Central European populations (Storch 2002; Suchant 2002). Our results confirm that capercaillie prefer gentle slopes to precipitous topography. Additionally, capercaillie records are made more often on mountain ridges or upper slopes than in toe slopes or valley bottoms.

Some variables did not enter in our multivariate models but may nevertheless have an influence on capercaillie distribution. Some variables (e.g. road density, distance to

settlements) are highly significant in the univariate models ($R^2_N = 0.184$, $R^2_N = 0.129$, respectively), but they do not enter in the multivariate models. This is due to our strict criteria of including or excluding a variable in the multivariate models, which we applied in order to keep the models simple for the comparison between the different spatial scales. We allowed only a low level of collinearity (Spearman's $\rho < 0.5$) between two variables. Additionally, we used a significance level of 0.05 for retaining a variable in a model, whereas other authors have argued for a threshold of 0.1 (Schröder 2000) or even 0.2 (Hosmer and Lemeshow 1989; Menard 2002). Thus, we possibly excluded some variables from the analysis that, in reality, have an influence on capercaillie occurrence.

Our habitat models do not contain any information on small-scale habitat quality such as forest structure, cover of field layer, or cover of bilberry *Vaccinium myrtillus*. They can thus be regarded as simulating potential capercaillie habitat. This is supported by the fact that most predicted-presence areas without actual capercaillie records have indeed had capercaillie a few decades ago (Mollet et al. 2003). Therefore, areas with predicted presence may have been abandoned by capercaillie because of reasons operating at smaller spatial scales. For instance, forest structure may have become unsuitable or the areas may be disturbed frequently because of human activities (recreation, hunting, etc.). These considerations are relevant when we apply our models in practice: areas with suitable landscape structure (predicted presence) but presently without capercaillie could possibly be populated again if forest structure was improved and human disturbance was reduced.

Conclusions

Our multivariate models at the landscape scale predict capercaillie occurrence to a large extent and add significant insights in capercaillie habitat relationships at larger scales. The multi-scale approach is promising because it led to precise and at the same time general models and produced plausible distribution maps with an intermediate degree of detail. These maps can be used directly for large-scale conservation planning and as a basis for spatially explicit meta-population modeling.

Nevertheless, more detailed analyses of predictor variables are necessary to better understand the processes in habitat selection of capercaillie at large spatial scales. Do species-habitat relationships vary between different regions and to what extent? How does the coding of the response variable (presence-absence of capercaillie) influence the model prediction? Such questions should be addressed by comparing our "general" models with regional models calibrated in sub-regions of the study area.

In spite of the classification success of our large-scale models, considerable attention has to be paid to small-scale habitat quality. For instance, we need to know more about the requirements of capercaillie regarding the amount and spatial arrangement of suitable

habitats. Combining our large-scale approach with data describing habitat quality at the scale of forest stands would allow us to develop effective tools for capercaillie conservation.

Acknowledgements

We thank Niklaus E. Zimmermann, Curtis H. Flather and two anonymous reviewers for comments on the manuscript. Financial support for this publication was provided by the Swiss National Science Foundation (SNF) and the Swiss Federal Agency for the Environment, Forest and Landscape (BUWAL). The Swiss Ornithological Institute, the “Centre de conservation de la faune et de la nature” of the canton of Vaud and several local grouse experts provided large datasets on capercaillie occurrence.

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Paper II

On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions

Submitted as:

Roland F. Graf^{1,2}, Kurt Bollmann¹, Werner Suter¹, Harald Bugmann². On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. *Ecography*

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Abstract

Predictive habitat distribution models are normally assumed to sacrifice generality for precision and reality. Nevertheless, such models are often applied to predict the distribution of a species outside the area for which the model has been calibrated.

We investigated how the spatial extent of the data used for calibration influences the performance of habitat distribution models applied on independent data. Using a multi-scale logistic regression approach we developed three separate models for capercaillie *Tetrao urogallus* in the Swiss Alps: one for the northern Pre-Alps, one for the eastern Central Alps, and one with pooled data from both regions. The three models were validated with data from both regions and from the Jura Mountains, a mountain range outside the Alps. We used Cohen's Kappa and the area under the curve (AUC) of receiver operating characteristic (ROC) plots as accuracy measures.

The regional models performed well in the region where they had been calibrated but poorly to moderately well in the other two regions. The model built with pooled data of the Pre-Alps and Alps classified almost as well in the two regions as the regional models, and even better in the Jura Mountains. Large-scale habitat models often contain surrogate predictor variables that may differ between regions in how they are associated with the occurrence of the species.

Habitat models built with data from one region can thus fail to predict where the species occurs in another region. For predicting the distribution of a species in areas with sparse data, we recommend building general models with data from different regions.

Introduction

Predictive habitat distribution models have become an established instrument for describing species-habitat relationships (Guisan & Zimmermann 2000; Rushton et al. 2004). This development has been furthered by new powerful statistical techniques, increasing availability of data on species distribution and land use, and new computer tools for efficiently working with them (Guisan & Zimmermann 2000). Statistical models often contain surrogate (or indirect) variables to predict the occurrence of a species and therefore it is generally assumed that they sacrifice generality for precision and reality (Sharpe 1990). Nevertheless, the results are often assumed to apply elsewhere, e.g. for predicting potential habitats or the distribution of a species in areas with sparse data on the species presence (e.g., Mladenoff & Sickley 1998; Mace et al. 1999; Vernier et al. 2002). In addition, many studies of species-habitat relationships are performed at a small number of sites located in the same geographical area (Whittingham et al. 2003). Even when data are collected from a large range of geographical locations, the results are often pooled into one data set (e.g., Carroll et al. 1999; Corsi et al. 1999), without investigating regional differences.

Habitat models aimed at predicting species distributions have to be evaluated carefully. For studies carried out in homogenous regions, Fielding and Bell (Fielding & Bell 1997) recommended a data-partitioning technique such as k-fold partitioning or jack-knife cross-validation. However, such approaches remain weak in assessing model credibility and applicability because they do not evaluate the model outside of its calibration range (Guisan & Zimmermann 2000). The most appropriate way of evaluating predictive habitat models would be to apply them on independent data sets from geographically distinct regions (Manel et al. 1999; Guisan & Zimmermann 2000). However, this has been done rarely across a range of separated areas (e.g., Fielding & Haworth 1995; Rodriguez & Andren 1999; Morris et al. 2001; Zabel et al. 2003), because often no equivalent evaluation data are available.

The capercaillie (*Tetrao urogallus*, Tetraonidae, Aves), a large forest grouse species, has specialized habitat preferences (e.g., Schroth 1992; Sjöberg 1996) and extensive spatial requirements (Storch 1995), making it highly susceptible to habitat and landscape changes. Capercaillie populations are declining throughout most of their central European range (e.g., Klaus et al. 1986; Storch 2000a), as loss and fragmentation of suitable habitats have split populations into smaller units loosely connected or even completely isolated. This is especially true in Switzerland, where the remaining population of 900 – 1000 adult individuals (Mollet et al. 2003) faces a high risk to become extinct due to environmental, demographic, and genetic processes.

At the forest stand scale, the habitat requirements of capercaillie have been studied intensively throughout its distribution range in Europe (Klaus et al. 1985; Leclercq 1987; Gjerde 1991; Picozzi et al. 1992; Schroth 1992; Storch 1993; Sjöberg 1996). Some habitat features are common to most of the capercaillie regions. Capercaillie requires open-structured coniferous or mixed forest (Klaus et al. 1986) with a lush field layer (Picozzi et al. 1992; Schroth 1992; Storch 1994; Sjöberg 1996) ideally dominated by bilberry (*Vaccinium myrtillus*, Klaus et al. 1985; Rolstad 1988; Schroth 1992; Storch 1993; Baines et al. 2004).

Conservation actions at the forest stand scale based on the large knowledge regarding small-scale habitat preferences have not been able to slow down the population decline. Therefore, remedy is now sought on larger spatial scales. Telemetry studies in Scandinavia and in Central Europe have revealed that spatial requirements of capercaillie are extensive (Wegge & Larsen 1987; Storch 1995). Further, they have shown that capercaillie populations are also sensitive to the spatial configuration of preferred habitats and to forest fragmentation (Rolstad & Wegge 1989; Wegge et al. 1992). Recent work has affirmed that capercaillie populations are strongly driven by landscape-scale processes (Storch 1997; Kurki et al. 2000). These processes, however, have only partly been addressed in predictive habitat modelling designed for large spatial scales. The habitat models for capercaillie at the landscape scale that are presently available do not include spatial variables (Storch 2002), or do not address spatial scale explicitly (Sachot et al. 2003) or do not include several spatial scales in a single statistical model (Suchant 2002). Thus, uncovering larger-scale habitat relationships is an important research need in those regions where the species is endangered (Storch 2000b), and analyses should be conducted at multiple scales (Keppie & Kierstead 2003).

In this study, we investigated how the data used for model calibration influence (i) the set of variables retained by the habitat models and (ii) the performance of habitat models on independent evaluation data (generality). We developed separate habitat models for capercaillie for two regions that differ strongly in terms of climate, landscape structure and land use. These regional models were compared with a model built with pooled data from both regions. To assess the precision and generality of all the models, we evaluated them using (1) data from the two regions, (2) pooled data from both regions, and (3) data from a third, geographically distinct region.

Methods

Study area and capercaillie distribution

After several decades of continuous decline, the distribution of capercaillie in Switzerland is now much fragmented. However, capercaillie still occurs in three mountain regions: Jura, Prealps, and eastern Central Alps (Fig. 1). These regions differ in terms of climate, topography and geology, forest distribution and human land use. The eastern Central Alps (600 – 3500 m above sea level) have a continental climate with a relatively low precipitation rate (800 – 2000 mm/year), cold winters but warm and dry summers. Under these conditions, upper natural tree-line is located at an altitude of about 2300 m above sea level. Large contiguous and mostly conifer-dominated forests spread along the valley slopes. Generally, human population density and tourist pressure are low, except for some areas that are used very intensively for winter and summer sport activities.

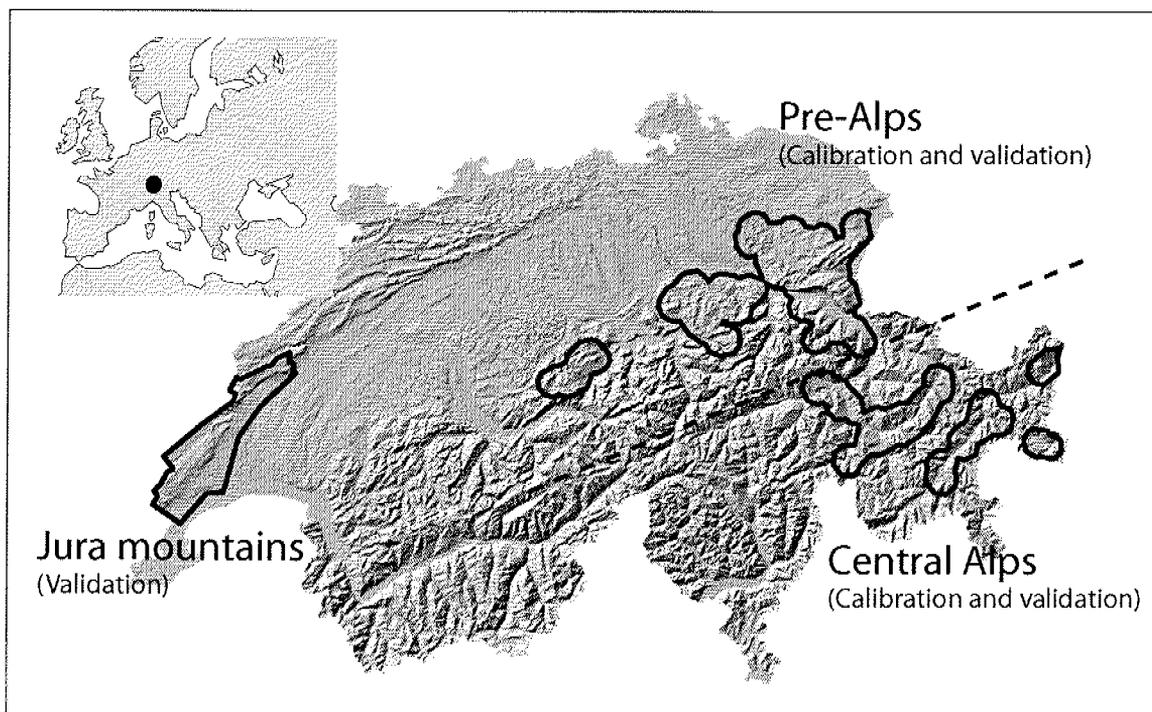


Figure 1: Map of Switzerland with the three study regions and their use for modeling. The dashed line separates the regions of the Northern Pre-Alps and the Eastern Central Alps. The three study regions do not represent the whole capercaillie distribution in Switzerland.

In the northern Pre-Alps (400 – 2800 m above sea level), a more atlantic climate with cold-temperate winters and wet summer months limits the upper tree-line to about 2000 m above sea level. High precipitation (2000 – 3000 mm/year) and often impervious soils have led to the development of many mires allowed to develop. In their surrounding, forest stands are naturally open and diversely structured. They thus have little commercial value but are favoured by capercaillie and other woodland grouse species. The northern Pre-Alps have been altered strongly by farming practices that depend mostly on livestock, and this has created a

patchy pattern of forest and pasture over large areas. The northern Pre-Alps are within a half day's drive of the major Swiss cities, and thus are frequently used for recreation activities, which are assumed to lower the survival and the reproduction of the sensitive bird species.

The Jura Mountains (800 km², 400 – 1700 m above sea level) are a calcareous mountain range in the north-western part of Switzerland, geographically separated from the Pre-Alps and the Alps by the plateau (width of 30 – 40 km). They have an atlantic climate similar to that of the Pre-Alps (average precipitation 2000 mm/year) but are, in contrast to the other two regions, characterized by gentle slopes and larger, contiguous forest areas.

In our study, we used data from parts of the eastern Central Alps (1700 km², lat. 47° – 46°50' N, long. 9°30' – 10°30' E) and from the northern Pre-Alps (2800 km², lat. 46°45' – 47°25' N, long. 8° – 9°30' E) for calibration and evaluation of habitat models, whereas data from the Jura Mountains (800 km², lat. 46°20' – 46°55' N, long. 6°10' – 6°45' E) were used for evaluation purposes only (Fig. 1).

Capercaillie distribution data originated from our own fieldwork and from several regional inventories. They include sightings and indirect evidence of capercaillie presence (faeces, feathers, footprints, etc.). The records stem mainly from late winter and spring surveys but were supplemented with all available data (records by game wardens, ornithologists, foresters, etc.) from throughout the year.

As habitat relationships of rare species tend to be better explained by presence-absence data than by abundance data (Cushman & McGarigal 2004) we used only presence-absence data. Presence-absence data were processed in grid format with a cell size of 1 ha, which equals the resolution of most environmental data used for the present paper. We defined cells as "presence" if they contained at least one capercaillie record. Not all presence cells were used in the analyses, as their clumped distribution could have led to autocorrelation problems. Therefore, we reduced the number of presence cells, so that the minimum distance between any two presence cells was at least 500 m.

Between presence and absence cells, we applied a minimum distance of 1 km (cf. Graf et al. in press). This leads to a minimum buffer area of about 3 km² around all observations, an area that equals about the size of the home range of a capercaillie individual. Home range size in telemetry studies ranged from 1 km² (only summer home range, Rolstad et al. 1988) up to 5.5 km² (annual home range, Storch 1995). Using this minimum distance between presence and absence cells, we also avoid that actual presence cells (where no record was obtained) are erroneously classified as absence.

Thus, absence cells used in the analysis are a randomly selected subset of cells with a minimum distance of 1 km to the nearest presence cell, a minimum distance of 500 m to the nearest absence cell and a maximum distance of 5 km to the nearest presence cell. The last

rule ensured that only those areas were included that are located within a realistic dispersal distance from actual capercaillie populations (Storch & Segelbacher 2000; Segelbacher et al. 2003). By doing so, we implicitly assume habitat suitability to be the reason for the absence of capercaillie, not large-scale population effects.

Environmental variables

There was one important constraint in the type of variables we could use for model building: data had to be consistently available for large areas. In practice, this meant that we could use only data available in national data-sets, which excluded data on composition and structure of forest stands. We eventually selected a set of 28 environmental parameters as independent variables (Table 1). The variables express aspects of topography, climate, habitat and human disturbance. All variables have been reported in the literature as having explanatory value for distribution or population dynamics of capercaillie.

As parameters representing different aspects of topography, we used altitude, slope (steepness), and topographic position. Topographic position is a measure to express the relative exposure of a location compared to the surrounding terrain. Positive values express ridges, hilltops and exposed sites, negative values stand for depressions, gullies, valleys or toe slopes (cf. Graf et al. in press).

Local climate is an important factor affecting reproduction of capercaillie, with dry and warm weather in early summer reducing chick mortality (Moss et al. 2001; Summers et al. 2004). We used average temperature and potential direct solar radiation as parameters to characterize the climate (cf. Graf et al. in press). Instead of using aspect as in many other studies (e.g., Suchant 2002; Sachot et al. 2003), we used potential direct solar radiation, a more direct predictor to represent local climate. To calculate this variable from the DEM, we applied the method developed by Kumar et al. (Kumar et al. 1997), which incorporates topographic shading effects.

Spatial vegetation patterns are a crucial factor influencing population density, home range size, mortality and reproductive success of capercaillie (Wegge & Rolstad 1986; Storch 1994, 1995; Kurki et al. 2000; Baines et al. 2004). Thus, we included variables describing the distribution of forest area, forest type, distance of a site to forest edge and forest edge density, abundance of and distance to mires. The variables "proportion of forest", "forest edge density" and "distance to forest edge" stem from a grid data set (1 = forest, 0 = not forest; cell size 20 m) derived from thematic pixel maps (PK25 © 2004, SWISSTOPO, DV033594; scale of 1:25'000). Cells were defined as forest edge when either the focal cell was forest and at least one of the surrounding cells was not forest, or the focal cell was not forest and at least one surrounding cell was forest. The dataset "forest type" (WMG25, BFS GEOSTAT) was derived from satellite images (Landsat-5, Thematic Mapper) by an automated classification procedure (cf. Graf et al. in press). "Forest type" is available in four different categories:

conifer forest (Cat. 1), conifer-dominated mixed forest (Cat. 2), deciduous-dominated mixed forest (Cat. 3), and deciduous forest (Cat. 4). In the variable “proportion of mires and wet forest”, we combined data from the two inventories of mires and fens (Swiss Federal Research Institute WSL) with data denoting the wet areas from the vector25 dataset (Vector25 © 2004, SWISSTOPO, DV033594). The categories included are mires in open land, mires with bushes, mires in closed forests and mires in open forests. The original vectorized data were converted into grids with 20 m cell size. The values in the final 100 m (1 ha) grid represent the number of 20 m cells defined as moor, swamp or any other wetland.

Disturbances by tourism and leisure activities are generally assumed to negatively affect capercaillie populations (Storch 2000a). Possible disturbance by human activities was expressed through the presence and proximity of roads, alpine ski runs and settlements. The vector25 dataset (Vector25 © 2004, SWISSTOPO, DV033594) provides six different categories of roads. We combined categories one to four into “motorable roads”, categories five and six into “non-motorable trails”. In the variable “settlements”, all cells defined as settlements (area statistics 1992/97, BFS GEOSTAT) were included for the calculation of an index of settlement density. In “distance to settlements”, we only included clusters of grid cells with built-up areas of at least four hectares (small village). Thus, single houses with low or almost no disturbance effect were ignored for calculating the distance to settlements.

Farmland in the neighbourhood of suitable habitats is supposed to negatively affect the reproductive success of woodland grouse species because it promotes high abundances of generalist predators (Kurki et al. 2000). We distinguished between seasonally used areas (alpine meadows and pastures) and farmland used during the whole vegetation period (meadows, pastures, arable fields, horticultural areas, orchards, and vineyards; area statistics 1992/97, BFS GEOSTAT).

We prepared all independent variables in grid format with a cell size of one hectare. With a moving window analysis (ARC/INFO 8.3), we calculated the mean, sum or majority values for a circular neighborhood of each grid cell for each environmental variable. The window size was increased stepwise from 1 ha up to just over 1100 ha, which is about twice the size of a mean home range (Storch 1995). We included 10 window sizes, hereafter called “spatial scales” (the radius [100*m] of the circular analysis window is given in parentheses): 1 (0), 5 (1), 13 (2), 29 (3), 49 (4), 81 (5), 113 (6), 253 (9), 529 (13), and 1129 ha (19). The uneven numbers result from the moving window algorithm that works with entire grid cells.

Table 1: *Environmental variables.*

Variable description	Abbreviation	Unit (Range)	Dropped because of correlation with ($r_s > 0.7$)		
			Pooled data	Pre-Alps	Alps
Altitude	DEM	m	TAVE	TAVE	TAVE
Slope	SLOPE	degrees			
Topographic position	TOP	unitless			
Potential direct solar radiation in Average temperature (June)	SDIR TAVE	kJ/day °C *100			
Proportion of forest	PFOR	%*4 (0–25)			
Density of forest edges	FE	%*4 (0–25)			
Distance to forest edge	DFE	m	FE		FE
Forest type	FT	4 categories			
Conifer forest ratio	CFR	Index (0–1)		TAVE	
Proportion of conifer forest	CF	%*6.25 (0–16)	PFOR	PFOR	PFOR
Coniferous forest	FTC	0/1			
Deciduous forest	FTD	0/1		FTC	
Proportion of mires and wet forests	MIRE	%*4 (0–25)			
Distance to mires and wet forests	DMIRE	m	MIRE	MIRE	
Total density of roads and trails	RO	m/ha	ROD	TAVE	
Density of motorable roads	ROD	m/ha		TAVE	
Distance to roads and trails	DRO	m		TAVE	
Distance to motorable roads	DROD	m	ROD		TAVE
Distance to alpine ski runs	DSKI	m			
Density of settlements	SETTL	0/1		TAVE	
Distance to settlements	DSETTL	m			
Distance to farmland used all year	DAGRY	m	TAVE	DSETTL	
Distance to farmland used seasonally	DAGRS	m	AGS	DSETTL	
Distance to farmland	DAGR	m		PFOR	
Proportion of farmland	AG	%*4 (0–25)	PFOR	PFOR	PFOR
Proportion of farmland used all year	AGY	%*4 (0–25)	TAVE	TAVE	
Proportion of farmland used seasonally	AGS	%*4 (0–25)			

Statistical modelling

Modelling procedure

First, we calculated univariate models for all predictor variables on each spatial scale. For every predictor variable, we chose the scale of the model with the highest explained variance (Graf et al. in press). The univariate models gave us information on the response and predictive power of each predictor variable (Table 2). For the variables slope, proportion of forest edges, distance to forest edges, density of motorable roads, and distance to motorable roads we chose smaller spatial scales than the one with the highest explained variance, because in these cases, the variables are increasingly correlated with others as spatial scale increases. High explained variance may then occur because the variable is highly correlated with another biologically more significant variable. Using such variables can lead to implausible results and interpretations.

Second, we developed multivariate models for the Alps and Pre-Alps separately ($N = 222$; $N_{\text{Pres}} = 83$, $N_{\text{Abs}} = 139$) and for the pooled data from both regions ($N = 444$; $N_{\text{Pres}} = 166$, $N_{\text{Abs}} = 278$). All three models were then evaluated using independent data from the Pre-Alps ($N=144$), the Alps ($N=144$), from both regions ($N=288$) and from the spatially distinct Jura Mountains ($N = 500$; $N_{\text{Pres}} = 200$, $N_{\text{Abs}} = 300$). The different size of the presence and absence sample was actively chosen to account for the larger variance in the absence data.

Logistic regression

Logistic regression (Manly et al. 2002; Menard 2002) was applied for all habitat modelling using the software SPSS 11.0. Following Hosmer & Lemeshow (2000), we used a binomial error distribution and a logit link function. In all multivariate models, we applied both stepwise backward and stepwise forward procedures to find robust models (Menard 2002). Most species modelling studies use a threshold probability of 0.05 for the decision of keeping or omitting a predictor variable (Pearce & Ferrier 2000). As a number of authors have suggested that this may be too stringent (e.g., Hosmer & Lemeshow 2000) we use a threshold of 0.1. In all modelling, we included untransformed variables, as normality is not required and error terms are allowed to have non-Gaussian distributions (Guisan & Zimmermann 2000). By plotting the frequency distribution of the predictor variables for both presence and absence cells, we searched for the type of response. In the case of a unimodal response, the squared predictor variables were also included in the analyses.

Multicollinearity of independent variables can cause problems in logistic regression models (Menard 2002). Fielding & Haworth (Fielding & Haworth 1995) suggested that a correlation higher than 0.7 may be critical. If a bivariate correlation exceeded this value, we omitted the variable with no (or less) direct influence on capercaillie populations from the analysis (Table 1). In the case of equal biological relevance of two variables, we kept the variable that explained better in the univariate models. Additionally, the algebraic sign of the coefficient of

a variable had to be the same in the multivariate model as in the univariate model, and it had to be biologically plausible. Otherwise, the variable was omitted.

Calibration and validation

For assessing the model fit, we used R-square Nagelkerke (1991), which is a measure of the variance in the dependent variable that is explained by the independent variables. For evaluating the models, we used measures based on a confusion matrix (Fielding & Bell 1997; Boyce et al. 2002). A confusion matrix contains the predicted and observed presences and absences based on a fitted model. From this matrix, a number of different accuracy measures can be derived. We use the correct classification rate (CCR) and Kappa-statistics (Monserud & Leemans 1992). Kappa measures the actual agreement minus the agreement expected by chance and can take values between 0 (no agreement) and 1 (perfect agreement). We used Kappa both at a threshold of 0.5 (Kappa_05) and at the optimized threshold (Kappa_opt). If a model is applied in an area with poor knowledge on the species' distribution, the threshold can not be optimized. Therefore, we considered the accuracy at the threshold for which the model was calibrated (normally 0.5) to be a particularly important measure. The problems with the fixed threshold can be avoided by using a threshold-independent measure of model accuracy. We use the area under the ROC-function (AUC, Deleo 1993), which is assumed to be an important index because it provides a single measure of overall accuracy that is not dependent upon a particular threshold (Fielding & Bell 1997; Boyce et al. 2002; McPherson et al. 2004). AUC varies between 0 and 1. A value of 0.8 for the AUC means that for 80 % of the time a random selection from the presence cells will have a score greater than a random selection from the absence cells.

Results

Univariate analysis

The explained variance of all variables differs among the spatial scales. We defined the "best" scale as the scale where a variable explained the highest amount of the variance in capercaillie presence-absence (cf. Graf et al. in press). Some variables, such as "proportion of forest" (PFOR) and "average temperature" (TAVE), show a similar scale dependence in the different regions although their explanatory power is on a different level (Figure 2). Other variables, however, performed quite differently in the Pre-Alps and in the Alps: they include topographic position (TOP), slope (SLOPE), density of motorable roads (ROD), proportion of mires (MIRE) and density of forest edges (FE, Figure 2). The algebraic sign of the coefficient of "density of forest edges" (FE) is different in the two regions (Table 2). All these differences give weight to our decision to analyze the two regions separately.

A considerable number of variables have a high predictive power in the univariate models ($R^2_N > 0.3$; Table 2): altitude (DEM), topographic position (TOP, Alps), average temperature (TAVE), proportion of forest (PFOR), forest type (FT), proportion of motorable roads (ROD),

density of settlements (SETTL, Pre-Alps), distance to farmland (DAGR, Pre-Alps) and proportion of farmland (AGR). However, some of these high R-squares probably have no biological meaning but are simply due to correlations with other, biologically more meaningful parameters (e.g., altitude with average temperature, proportion of farmland with proportion of forest).

Multivariate analysis

All three models (Pre-Alps, Alps, Pooled data) explain a large amount of the variance of the presence-absence pattern ($R^2_N > 0.74$ and $CCR_{05} > 89\%$; cf. Table 3). They also show a good agreement with independent data from the same region for which they were calibrated ($Kappa_{05} > 0.78$, $Kappa_{opt} > 0.85$, $CCR_{05} > 89\%$, $AUC > 0.89$). However, the regional models (Pre-Alps, Alps) performed poorly or moderately in the other region ($Kappa_{05} < 0.32$) and moderately in the Jura Mountains ($Kappa_{05} < 0.43$). The model calibrated with the pooled data from both regions classified very well on set-aside data from the Pre-Alps ($Kappa_{05} = 0.82$), and the Alps ($Kappa_{05} = 0.73$) and performed clearly better in the Jura Mountains ($Kappa_{05} = 0.52$) than the regional models.

Two predictor variables were selected by all three models: Average temperature (TAVE) and proportion of forest (PFOR, Table 4). These two variables also explain much of the variance of capercaillie occurrence in the univariate analyses (Table 2). The model developed with the pooled data also contains the squared average temperature (TAVE²) and thereby simulates a unimodal response of temperature to capercaillie occurrence. The variables "slope" (SLOPE) and "density of forest edges" (FE) are selected by the multivariate models although they explain only little variance in the univariate models. The density of forest edges (FE) is selected by both regional models, although with a positive Beta-value in the Pre-Alps and a negative Beta-value in the Alps. Thus, the models suggest that capercaillie preferably occur near forest edges in the Pre-Alps whereas they seem to avoid forest edges in the eastern Central Alps. As expected from the univariate analysis, the proportion of mires (MIRE) is only significant in the model for the Pre-Alps. Model coefficients and LOWESS curves describing the response of capercaillie to the variables selected by the models are given in Appendix III.

Table 2: Univariate logistic regression models; scale of analysis (Radius [$m*1/100$] of moving window); explained variance expressed by R-square Nagelkerke (R^2_N); type of response to capercaillie occurrence, i.e. positive (pos), negative (neg), unimodal or categorical (cat).

Variable	Pooled data			Pre-Alps			Alps		
	Scale	R^2_N	Response	Scale	R^2_N	Response	Scale	R^2_N	Response
DEM	9	0.361	unimodal	0	0.549	unimodal	9	0.247	unimodal
SLOPE	1	0.087	unimodal	1	0.064	unimodal	1	0.119	unimodal
TOP	0	0.239	unimodal	0	0.087	pos	3	0.429	unimodal
SDIR	0	0.027	unimodal	0	0.014	unimodal	0	0.040	unimodal
TAVE	9	0.410	unimodal	0	0.577	unimodal	9	0.282	unimodal
PFOR	9	0.516	pos	9	0.426	pos	5	0.701	pos
FE	0	0.017	neg	3	0.045	pos	0	0.122	neg
DFE	0	0.021	pos	13	0.063	neg	0	0.082	pos
FT	1	0.336	cat	1	0.456	cat	0	0.332	cat
CFR	1	0.291	pos	9	0.544	pos	5	0.369	pos
CF	6	0.469	pos	9	0.577	pos	5	0.607	pos
FTC	0	0.230	pos	6	0.374	pos	0	0.266	pos
FTD	9	0.175	neg	9	0.350	neg	0	0.040	neg
MIRE	9	0.127	pos	9	0.288	pos	1	0.023	neg
DMIRE	19	0.078	unimodal	19	0.288	unimodal	19	0.059	pos
RO	6	0.074	neg	6	0.303	neg	1	0.011	neg
ROD	6	0.152	neg	6	0.306	neg	4	0.058	neg
DRO	6	0.001	neg	6	0.147	pos	6	0.036	neg
DROD	0	0.012	pos	0	0.122	pos	19	0.028	neg
DSKI	9	0.056	unimodal	5	0.049	unimodal	9	0.074	unimodal
SETTL	6	0.264	neg	13	0.528	neg	5	0.198	neg
DSETTL	0	0.038	pos	0	0.201	pos	19	0.022	pos
DAGRY	0	0.112	pos	0	0.415	pos	19	0.005	pos
DAGRS	0	0.068	neg	19	0.268	neg	0	0.001	neg
DAGR	0	0.106	pos	9	0.354	pos	0	0.093	pos
AG	4	0.340	neg	9	0.420	neg	4	0.469	neg
AGY	5	0.423	neg	6	0.614	neg	3	0.297	neg
AGS	1	0.006	neg	19	0.283	pos	2	0.158	neg

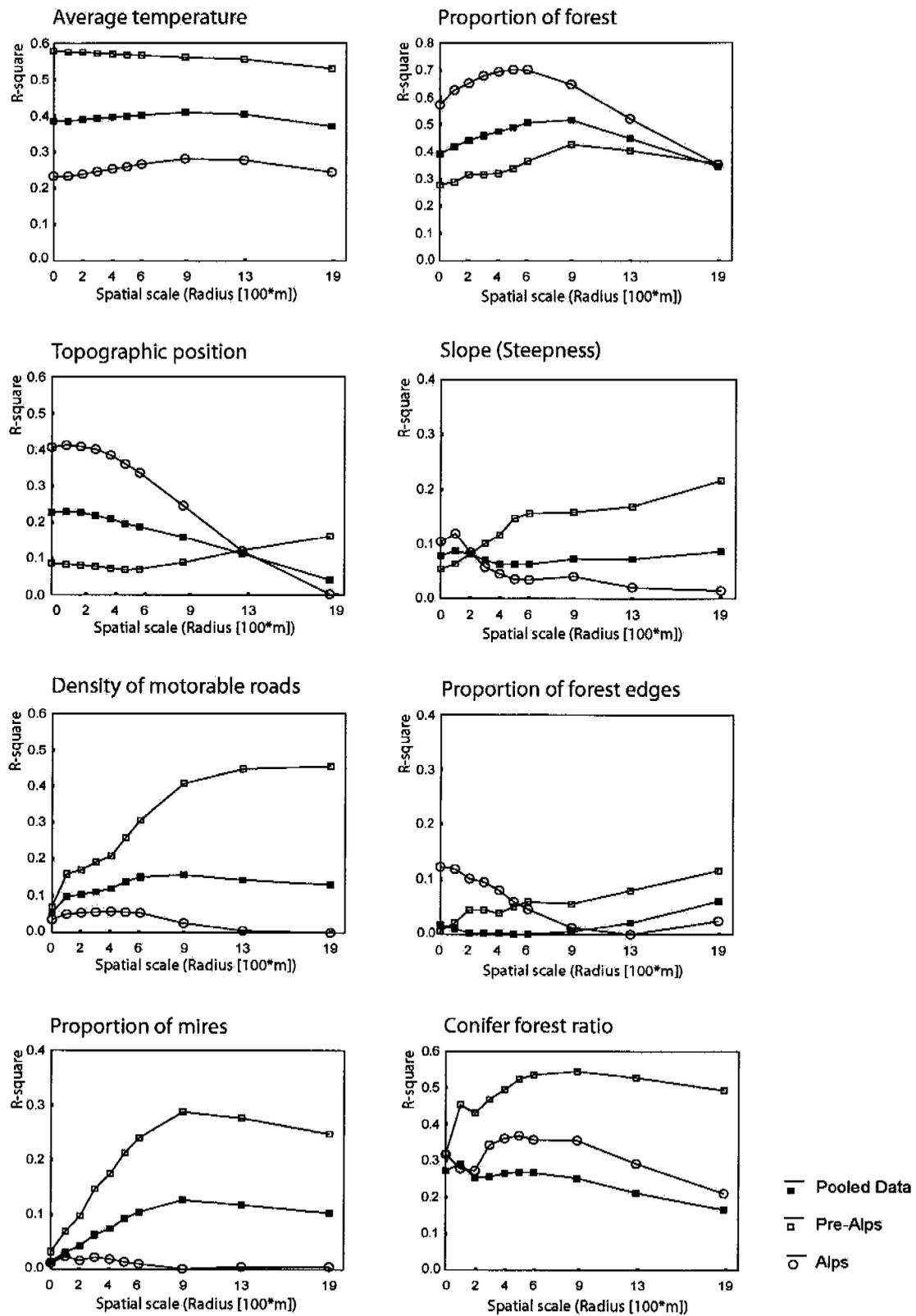


Figure 2: Explained variance (*R-square Nagelkerke*) of univariate models as a function of spatial scale for a set of selected predictor variables.

Table 3: Accuracy of multivariate habitat distribution models built with pooled data (HSM_Pooled), with data from the Pre-Alps (HSM_Pre-Alps) and with data from the Alps (HSM_Alps); sample size in calibration data set (N_{calib}), R-square Nagelkerke (R^2_N), Kappa at a threshold of 0.5 (Kappa_05), Kappa at optimized threshold (Kappa_opt), Correct classification rate at a threshold of 0.5 (CCR_05), Area under the ROC-curve (AUC).

Model	N_calib	Model Calibration	
		R^2_N	CCR_05
HSM_Pooled	444	0.74	89.41
HSM_Pre-Alps	222	0.80	89.64
HSM_Alps	222	0.85	92.34

Validation on Prealps and Alps (N=288)				
Model	Kappa_05	Kappa_opt	CCR_05	AUC
HSM_Pooled	0.78	0.85	0.89	0.93
HSM_Pre-Alps	0.56	0.75	0.77	0.90
HSM_Alps	0.47	0.62	0.75	0.88

Validation on Prealps (N=144)				
Model	Kappa_05	Kappa_opt	CCR_05	AUC
HSM_Pooled	0.82	0.85	0.91	0.92
HSM_Pre-Alps	0.87	0.89	0.94	0.93
HSM_Alps	0.20	0.64	0.58	0.82

Validation on Alps (N=144)				
Model	Kappa_05	Kappa_opt	CCR_05	AUC
HSM_Pooled	0.73	0.86	0.87	0.95
HSM_Pre-Alps	0.32	0.82	0.61	0.92
HSM_Alps	0.82	0.86	0.92	0.98

Validation on Jura Mountains (N=500)				
Model	Kappa_05	Kappa_opt	CCR_05	AUC
HSM_Pooled	0.52	0.66	0.75	0.90
HSM_Pre-Alps	0.43	0.58	0.69	0.89
HSM_Alps	0.42	0.43	0.72	0.80

Table 4: Variables selected by multivariate models with their “best explaining” scale (Scale; Radius of circular analysis window [$m \cdot 0.01$]); type of response, i.e. positive (pos), negative (neg) or unimodal; level of significance (***: p -value < 0.001 , **: $0.01 > p > 0.001$, *: $0.1 > p > 0.01$)

Variable	HSM_Pooled			HSM_Pre-Alps			HSM_Alps		
	Scale	Response	Sig.	Scale	Response	Sig.	Scale	Response	Sig.
TAVE	9	unimodal	***						
TAVE ²	9	unimodal	***	0	neg	***	9	neg	***
PFOR	9	pos	***	9	pos	***	5	pos	***
TOP	0	pos	***				3	pos	***
SLOPE	1	neg	***	1	neg	*			
ROD	6	neg	**						
FE				3	pos	*	0	neg	*
MIRE				9	pos	*			

Discussion

Model precision versus generality

Habitat distribution models often have limited predictive success when applied to other regions (Fielding & Haworth 1995; Corsi et al. 1999; Guisan & Zimmermann 2000; Lawler & Edwards 2002). The aim of this study was to explore the generality of habitat distribution models for capercaillie using data from three extensive mountainous areas. We found that models calibrated from regional data had limited predictive success outside the calibration area but that a model that used pooled data from two regions was more successful. Though not surprising, it is still noteworthy that two reasons may be responsible for the differences in model performance. First, if species-habitat relationships are influenced by regional conditions, generality of a model will be higher with increasing variation in the data used for calibration (see Dettmers et al. 2002). Models were successful in predicting species distribution away from the calibration area if the new area was ecologically similar with respect to the predictor variables (Rodriguez & Andren 1999; Morris et al. 2001; Whittingham et al. 2003). Second, generality of a model depends on the degree to which the predictor variables have direct ecological significance, as opposed to being surrogate variables (Guisan & Zimmermann 2000).

Variables selected for the models

Generality versus regional singularity are also reflected in the variables selected by the models. The two variables selected by all three models (average temperature, proportion of forest) are in agreement with findings from beyond the Swiss distribution range. That capercaillie needs large and well-connected forests is documented both for Central Europe

(Storch 1995) and Scandinavia (Kurki et al. 2000; Linden et al. 2000). Capercaillie also mainly occurs in the temperature zone that allows coniferous forests to grow naturally (Klaus et al. 1986).

Only a few studies, mainly from Central Europe, discuss the role of topography in habitat use of capercaillie (Eiberle 1976; Schroth 1992; Suchant 2002). Slope (steepness) was selected both in the regional model of the Pre-Alps and in the model built with the pooled data. This confirms our impression from field work that capercaillie avoid steep slopes, a fact that is known also from other Central European habitats (e.g., Suchant 2002). In our study, topographic position was selected in the model built with pooled data and in the regional model of the Alps. Capercaillie thus avoid valley bottoms and preferably inhabit ridges and upper slopes. This could be explained (1) by ridges and upper slopes having better habitat quality or (2) by predator-avoidance behaviour. Capercaillie disturbed by predators or humans tend to escape downhill (own observations), where they need habitat suitable for landing, hiding, and from where they can safely walk back.

The peculiarities of the regions are represented in the models by two variables defining habitat quality: proportion of mires and proportion of forest edges. In the Pre-Alps, mires are an important landscape element for capercaillie. In the neighbourhood of mires, forests are on average more open and more diversely structured than elsewhere. They are often dominated by mountain pine (*Pinus mugo*), which are particularly suitable trees for lekking and feeding in winter (e.g., Schroth 1992). Additionally, the field layer near mires often contains high amounts of bilberry and other ericaceous shrubs, which are important for capercaillie, especially for hens with chicks (Stuen & Spidsø 1988; Storch 1993, 1994; Picozzi et al. 1999). Density of forest edges was a positive predictor in the Pre-Alps and negative in the Alps. Whether capercaillie do use a forest edge or not depends on the use or vegetation type of the adjacent land. In the Pre-Alps, contiguous forests are often interspersed with mires, a combination providing inner edges and preferred habitat as described earlier in this paragraph. In the Alps, however, forest edges are usually outer edges to pastures and meadows or to the upper tree line. Here, the field layer is often poor due to cattle-grazing, and such edge areas may allow higher densities of generalist predators than do mires (see Kurki & Linden 1995). Additionally, forests in the Alps are generally more open than forests in the Pre-Alps (Brassel & Brändli 1999). Thus, we expect optimal habitats for capercaillie within contiguous forests to be more frequent in the Alps than in the Pre-Alps. In the Pre-Alps, capercaillie often find open structures only at the forest edges.

Disturbances by human activities are often mentioned as an important factor affecting capercaillie populations in Central Europe (Storch 2000b), although scientific evidence is rare (Raety 1979; Leclercq 1987). We used the density of motorable roads as an indirect measure of the frequency of human disturbance. This variable was selected in the model built with the pooled data. One would have expected it to enter in the model of the Pre-Alps as well because

the corresponding univariate model explains much of the variance ($R^2_{N=0.306}$). However, in the Pre-Alps, we had to exclude the density of motorable roads because it was strongly correlated with average temperature ($r_s=0.746$). This correlation is not surprising as settlements are most often located in the valley bottoms and are surrounded by areas with a high road density. Still, the density of motorable roads probably has an influence on capercaillie occurrence. In the alpine part this variable explained only little variance. This supports the belief of those forest managers who assert that roads by themselves, i.e. as a landscape element, have no impact on capercaillie populations, whereas the consequences of the roads being used (disturbance) are clearly negative. As the human population density is much higher in the Pre-Alps than in the Alps, roads in the Pre-Alps are probably used more frequently for recreation activities than the roads in the Alps.

Causality versus correlation

From a mechanistic point of view, it is desirable to predict the distribution of a species on the basis of ecological parameters that are believed to be the causal (direct) driving forces for their distribution and abundance (Guisan & Zimmermann 2000). In our case, the collinearity between variables increases with the spatial scale of the analysis. In the data used for modelling, several variables were highly correlated (especially in the Pre-Alps; Table 1). This made it difficult to detect whether a variable has direct ecological significance or whether it is just correlated with another predictor variable that influences capercaillie distribution more directly. Very often, both variables probably influence species occurrence to some degree. One drawback of using such indirect parameters is that a model can only be applied within a limited geographical extent without significant errors (Guisan & Zimmermann 2000). Thus, the best solution would be to include more direct predictor variables such as data on forest structure. As such data are very often not (yet) available over large areas with full coverage, it is important to investigate the power and limitations of large-scale habitat distribution models that are at least partly based on indirect predictor variables.

Conclusions

The results of this study support earlier warnings that caution is required when habitat models are applied in other geographical regions. We found that the importance of predictor variables varied between different regions in the Swiss Alps. This was especially prevalent in variables that may influence capercaillie occurrence only indirectly. Indirect variables can be problematic in that they reduce the applicability of the model to larger geographical extents (Guisan & Zimmermann 2000; Gibson et al. 2004). Predictor variables may to some degree also reflect regional peculiarities, particularly when they express very specific landscape ecological features, e.g. the density of forest edges in our study. Applying models can thus lead to poor predictions if the area where the model is applied differs from the calibration area. We circumvented these problems by building a habitat model with data pooled from two regions that were different with respect to climate, topography, forest distribution patterns and

tree species composition. This approach produced a model with higher generality without losing much precision when applied in the individual regions. Our model therefore meets the prerequisites for predictive models to be useful as conservation and management tools. We recommend using our pooling approach with other animal species and habitats to test for its general usefulness.

Acknowledgements

This study received financial support from the Swiss National Science Foundation (SNF) and the Swiss Federal Agency for the Environment, Forest and Landscape (BUWAL). The Swiss Ornithological Institute, the "Centre de conservation de la faune et de la nature" of the canton of Vaud and several local grouse experts provided us large data-sets on capercaillie occurrence.

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Paper III

Forest and landscape structure as predictors of capercaillie occurrence at the forest stand and home range scales

Submitted as:

Roland F. Graf^{1,2}, Kurt Bollmann¹, Werner Suter¹, Harald Bugmann². Forest and landscape structure as predictors of capercaillie occurrence at the forest stand and home range scales. *Ecological Applications*.

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Abstract

Whereas wildlife ecologists studying species-habitat relationships have traditionally focused on small spatial scales, new techniques of remote sensing and GIS now allow researchers to study large-scale habitat selection. Such studies most often rely on correlative species-habitat relationships and thus may be of little value for understanding the processes governing occurrence patterns of a species. Therefore, habitat factors with direct influence on species populations should ideally be included in large-scale studies.

Capercaillie is a large, endangered forest grouse species with narrow habitat preferences and large spatial requirements, making it a model organism of both theoretical and practical interest. In two Swiss regions, we investigated capercaillie habitat relationships at the forest stand and home-range scale. Forest structure was assessed from aerial photographs in 52 study plots of 5 km² each and for two points in time, 1960 and 2000. Plots belonged to one of three categories denoting the observed population trend (stable, declining, extinct). At the scale of grid cells (stands) within the plots, we used presence-absence data to build predictive habitat models with logistic regression.

At the stand scale, models based on variables relating to forest structure alone explained the occurrence of capercaillie only partly. Landscape variables improved the models significantly. At the home-range scale, the area predicted as presence by the models and forest structure variables such as the proportion of open or multistoried forest differed significantly between the plot categories. Changes in forest structure between 1960 and 2000 were not large enough to be detected with our coarse assessment method.

We conclude that small-scale forest structure has limited power to predict capercaillie occurrence in forest stands, but it explains well at the home-range scale. Including landscape structure variables improves predictions at the forest stand scale significantly. Thus, multi-scale approaches are necessary for better understanding species-habitat relationships. Our results can serve as guidelines for practitioners who wish to manage their forests so as to maintain viable capercaillie populations.

Introduction

The role of scale in ecology has been discussed extensively over the past three decades and is now widely recognized as being of vital importance for understanding ecological processes (Wiens 1989; Levin 1992). As several scales are usually involved in species-habitat interactions of one species, habitat analyses should adopt multi-scale approaches for better understanding patterns of species occurrences (Addicott et al. 1987; Bissonette 1997; Storch 1997). The fast progress in remote sensing, GIS and statistical analysis tools initiated a large number of multi-scale studies (Fuhlendorf et al. 2002; Lawler & Edwards 2002; Thompson & McGarigal 2002; Zabel et al. 2003; Fischer et al. 2004; Graf et al. in press). These studies often use low resolution data gained from remote sensing (e.g., Mladenoff & Sickley 1998; Gibson et al. 2004) and thus are facing the problem of having to work with indirect or surrogate variables (Bissonette 1997). However, for the efficient conservation and management of endangered species, it would be desirable to know more about the requirements of a species regarding the distribution of suitable habitat at the scales of individual home ranges or local populations. Thus, larger-scale approaches should include habitat predictors with a direct influence on the species' populations (e.g. Thompson & McGarigal 2002). Yet, if important habitat features have to be assessed for animals with large home ranges, this would require huge personal and financial resources. Therefore, habitat suitability models at intermediate scales preferably are based on variables that can be measured easily over large areas with high resolution, e.g., from remote sensing data.

Aerial photographs are a prime data source for assessing the structure of and changes in forests and landscapes (D'Aoust et al. 2004; Holder 2004); they can also be used to investigate present and past habitat quality (Kadmon & Harari-Kremer 1999; Roland et al. 2000; McGrath et al. 2003; Lofvenhaft et al. 2004; Marchand & Litvaitis 2004; Plante et al. 2004). Even specific habitat features such as the presence of spruce snags (Butler & Schlaepfer

2004) or stand characteristics indicating lichen diversity (Ask & Nilsson 2004) can be quantified from color infrared aerial photographs. Automatic assessment of detailed forest structure variables for large areas can be expected to be operational soon based on laser-scanning data (e.g. Maltamo et al. 2004). However, if the past development of forest and landscape structure is of interest, black-and-white aerial photographs of intermediate resolution are the only available data (in some regions dating back to the beginning of the 20th century, cf. Barbezat & Jacot 1998).

Capercaillie is a large forest grouse species with specialized habitat preferences and extensive spatial requirements (Rolstad et al. 1988; Storch 1995), thus making it highly susceptible to habitat and landscape changes. Capercaillie populations are declining in most of their central European range (Storch 2000), as loss and fragmentation of suitable habitats have split populations into smaller units that are connected loosely or even isolated completely. In Switzerland, capercaillie faces a high extinction risk as only some 900 – 1000 individuals remain in highly fragmented populations (Mollet et al. 2003). It is assumed that landscape-wide changes in forest structure resulting in loss and deterioration of suitable habitats is a major cause for this decline (e.g., Klaus 1991).

Many studies at the local scale have elucidated habitat requirements of capercaillie. Important habitat features for the central European and Scandinavian populations are intermediate canopy cover (Gjerde 1991; Storch 1993b; Suchant 2002) and rich ground vegetation cover (e.g. Klaus et al. 1985; Picozzi et al. 1992; Sjöberg 1996; Bollmann et al. submitted) ideally dominated by bilberry (Eiberle 1976; Schroth 1992; Storch 1993a). Telemetry studies revealed the extensive spatial requirements of capercaillie (e.g., Rolstad et al. 1988; Storch 1995) and showed that populations are sensitive to macrohabitat alterations such as forest fragmentation or the spatial arrangement of favorable habitat (Rolstad & Wegge 1987, 1989). In detail, habitat quality increases with the proportion of old-growth forest, and with it the number of lekking males increases while home range size decreases (Wegge & Rolstad 1986; Storch 1995).

Recent population studies on capercaillie ecology indicate that reproductive success is at least partly explained by landscape factors operating at a scale that is an order of magnitude larger ($\sim 100 \text{ km}^2$) than the area used by a grouse individual (a few km^2 , Kurki et al. 2000). In recent years, GIS-based analyses of aerial photographs and spatially explicit landscape models have become powerful instruments to study the influence of the quantity, quality, and distribution of grouse habitat at different scales (Niemuth & Boyce 1995; Kurki et al. 2000; Fuhlendorf et al. 2002; Graf et al. in press). Still, for the efficient conservation of grouse species, habitat analyses at multiple spatial scales are necessary, especially in regions where the species is endangered (Storch 2002; Keppie & Kierstead 2003).

The goal of this study was to investigate capercaillie habitat relationships at the two scales of forest stands and home ranges. In particular, we analyzed the power and limitation of forest

structure variables for predicting capercaillie occurrence at the two scales and compared their predictive power with that of a set of landscape variables. Also, we tried to relate the observed capercaillie decline to forest and landscape structure changes relevant for capercaillie habitat suitability over the past forty years.

Methods

Study area

Capercaillie in Switzerland is split into four independent meta-populations across three mountain regions: the Jura mountains, the northern Pre-Alps, and the eastern Central Alps (Mollet et al. 2003). In this study, we used data from the northern Pre-Alps and the eastern Central Alps (Fig. 1). These two geographic regions differ significantly in terms of climate, topography and geology, forest distribution and human land use. The climate of the eastern Central Alps (600 – 3500 m asl.) is continental with relatively low precipitation rate (800 – 2000 mm/year), cold winters but warm and dry summers. Large contiguous and mostly conifer-dominated forests spread along the valley slopes, and natural tree line is at c. 2300 m asl. Generally, human population density and impact by tourism are low, except for some centers with both summer and winter tourism.

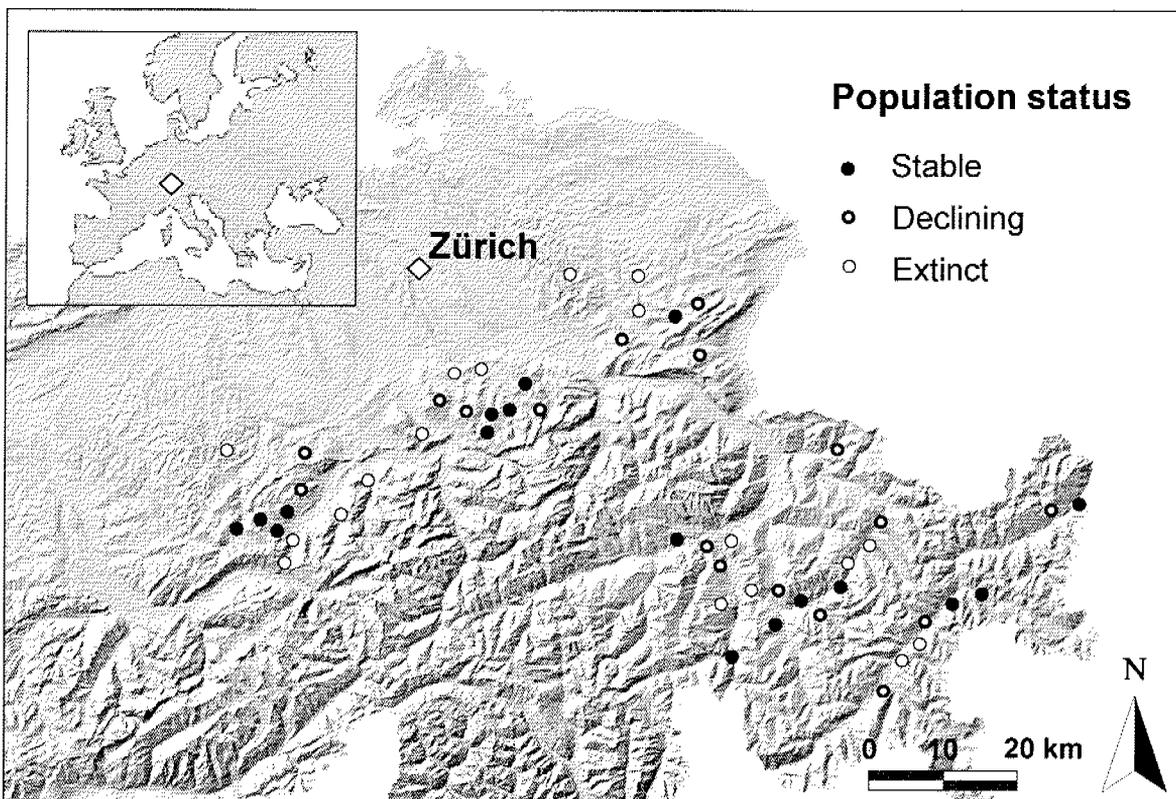


Figure 1. Fifty-two study plots of 5 km² each; they belong to the three plot categories “stable”, “declining” and “extinct”.

In the northern Pre-Alps (400 – 2800 m asl.), the climate is more atlantic with cold-temperate winters and wet summer months confining upper tree-line to about 2000 m asl. Because of the high precipitation (2000–3000 mm/year), forests are interspersed with mires where impervious soils and topography allow. Here, forest stands are naturally open and diversely structured with low timber value. Such areas are favored by capercaillie and other woodland grouse species. Northern Pre-Alpine landscapes have been altered by livestock farming for a long time, and today there is a patchy pattern of forest and pasture over large areas. The northern Pre-Alps are within half a day's drive of major Swiss cities and thus frequently used for recreation, probably affecting the survival rate and reproductive success of capercaillie.

Study plots and species data

We used 52 study plots (circles) of 5 km² each for the analyses at the home range scale. The locations of the study plots were chosen by a 2-step procedure: First, we used the three national capercaillie surveys (1971, 1985, 2001, Mollet et al. 2003) to classify areas with a high forest cover (more than 50% within 5 km²) by their population status as “stable”, “declining” or “extinct”. We then randomly selected the locations of 52 study plots so that (1) plots were located at minimum distances of 1.3 km (radius of study plots; edge-to-edge distance) from each other and (2) the three plot categories as well as the two regions (Pre-Alps and Alps) were sampled equally. Of the 52 plots, 28 are located in the Pre-Alps (category “stable”: 9 plots, “declining”: 8 plots, “extinct”: 11 plots) and 24 in the Alps (“stable”: 8, “declining”: 9, “extinct”: 7; Fig. 1).

Capercaillie do not necessarily use the entire area of a study plot. Therefore, we assumed that those parts of the study plots with actual capercaillie observations are used regularly by capercaillie, and that the other parts are, if at all, used only temporarily by the species. Thus, areas with capercaillie observations are assumed to be suitable habitat. On the contrary, areas without observations cannot a priori be assumed to be unsuitable, but they on average are probably less appropriate for the species.

We used a comprehensive set of observation data from different sources (own field surveys, records of game wardens and local experts, cf. Appendix I) to identify presence and absence areas within the plots (Fig. 2) as a basis for calibrating the regression models. The observation data were converted to a grid with a cell size of 20 m. From these grid cells, we extracted a sample of 296 cells from the Pre-Alps (presence: 146, absence: 150, respectively) and 180 from the Central Alps (presence: 90, absence: 90, respectively). Presence cells were sampled randomly, but there had to be a minimum distance of 150 m between presence cells. Absence cells were chosen randomly from a 250 m net, but there had to be a minimum distance of 250 m between presence and absence cells.

As our capercaillie occurrence data stem mostly from winter surveys, our results will primarily apply to winter habitat selection. In the Pre-Alps, we have good evidence that the

winter ranges provide also preferred summer habitat (unpublished data; Hess, Rudmann, pers. comm.). For the Central Alps, however, such information is not available, and we have to assume that winter and summer ranges differ to some degree, as observed in other parts of the capercaillie distribution range (Rolstad & Wegge 1989; Storch 1995). At the scale of entire study plots (5 km²), we assumed that we included both winter and summer ranges.

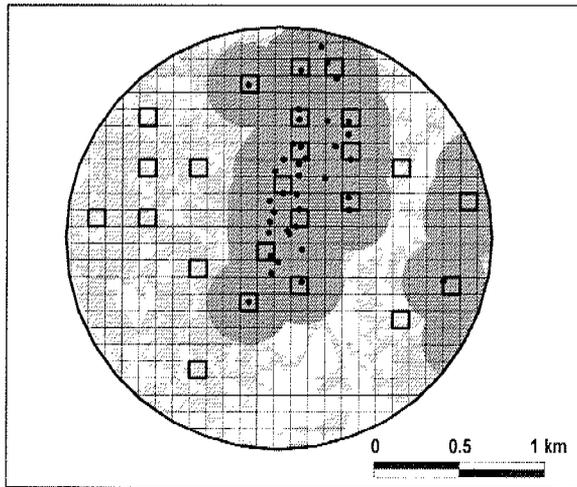


Figure 2. Coding of presence-absence within study plots; here shown on the basis of a 1 ha-grid for better illustration (in the analysis, a grid with a cell size of 400 m² was used; see methods; black points: capercaillie observations, dark grey area: buffer of 250 m around observations, light grey: forested areas without capercaillie observations; grid cells outside the buffer area are defined as "absence". The subset of cells used in the analyses is highlighted in bold.

Assessing forest structure from aerial photographs

Forest structure variables were assessed from black-and-white aerial photographs with a ground resolution of 65 cm (aerial photographs © swisstopo, DVO033373). The most recent and the historical aerial photographs were of identical quality, and therefore they allowed us to compare forest structure between the two time steps, 1960 and 2000. The images were ortho-rectified by monoplotted in Erdas Imagine 8.6 using a digital elevation model with 25 m resolution as vertical reference file (DEM; DHM25 © 2004, swisstopo, DVO033594). For the most recent images, we had image orientation parameters so that ortho-rectification of the images was very exact (\pm 5 meters). The historical images were then ortho-rectified on the basis of pass-points identified from the most recent ortho-images.

A standardized manual interpretation procedure was developed to assess forest structure variables from the ortho-rectified aerial photographs. Polygons with uniform forest stands or clearings (gaps) were delineated (digitized) in ArcView3.2a in compliance with a specified set of rules: (1) fixed view-scale at 1:5'000, (2) minimum size of forest patches of 0.25 ha. A set of structure variables was then estimated for each forested polygon. We trained patch delineation and forest structure assessment in test areas and verified first results in the field.

We chose variables that are known to be important for capercaillie habitat quality and that are visible in aerial photographs: succession state, overall canopy cover, tree cover, understorey cover, vertical structure, and horizontal structure (Table 1). Most of these variables are identical to or have been adapted from variables assessed in the Swiss National Forest Inventory (NFI, Brassel & Lischke 2001).

Table 1. Description of forest structure variables stemming from aerial photographs.

Variable description	Abbreviation	Unit (range)	Dropped because of correlation with ($r_s > 0.7$)	
			Pre-Alps	Alps
Total canopy cover; 1: open area, 2: canopy cover of 1–10 %, 3: 10–25 %, 4: 25–50 %, 5: 50–75 %, 6: 75–90 %, 7: 90–100 %	CC	Cat (1–7)	CC100	CC100
Mean of total canopy cover within a 100m-circle around the center of the grid cell	CC100	%		
Canopy cover of tree layer; 1: open area, 2: canopy cover of 1–10 %, 3: 10–25 %, 4: 25–50 %, 5: 50–75 %, 6: 75–90 %, 7: 90–100 %	CCT	Cat (1–7)	CC100	CC100
Mean of tree cover within a 100m-circle around the center of the grid cell	CCT100	%	CC100	CC100
Canopy cover of understorey; 1: open area, 2: canopy cover of 1–10 %, 3: 10–25 %, 4: 25–50 %, 5: 50–75 %, 6: 75–90 %, 7: 90–100 %	CCU	Cat (1–7)		
Mean of understorey cover within a 100m-circle around the center of the grid cell	CCU100	%		
Succession state; 1: young-growth stand, 2: pole stand, 3: old-growth, 4: mixed	SS	Cat (1–4)		
Horizontal stand structure; 1: no clusters, 2: open clusters, 3: dense clusters	HS	Cat (1–3)	CC100	CC100
Sum of clustered forests (HS >1) within a 100m-circle around the center of the grid cell	HS100	ha	CC100	CC100
Vertical stand structure; 1: uniform, 2: two-layered, 3: multi-layered	VS	Cat (1–3)	VS100	
Sum of multistoried forests (VS >1) within a 100m-circle around the center of the grid cell	VS100	ha		
Proportion of forest edges; proportion of forest edges to open area	FE100	m		
Variation of canopy cover; number of different canopy cover categories occurring within a 100m-circle around the center of the grid cells.	CCV100	index		
Variation of succession state; number of different succession state categories occurring within a 100m-circle around the center of the grid cells.	SSV100	index		FE100

The manual interpretation of aerial photographs encompasses the problem of accuracy and reproducibility of the data. We tested the quality of our data with two approaches: First, we assessed forest structure variables in the field (ground-truthing) in 179 patches from four study plots (two each in Pre-Alps and Alps). It should be borne in mind that field estimates are not necessarily more reliable than the aerial photograph interpretation (exception: succession state, regeneration cover). Estimates of succession state and horizontal structure were similar in field and remote sensing assessment (over 70% of the patches were classified identically, over 95% identical or in neighboring category). Vertical stand structure and overall canopy cover were also assessed successfully (50% of the patches classified identically, over 95% were assigned at least to the neighboring category), whereas the cover of the tree regeneration layer was difficult to estimate from aerial photographs (only about 40% of the polygons classified identically, about 80% assigned to neighboring category).

Second, parts of the data were assessed twice to measure the degree of reproducibility of the interpretation and to find potential biases in the estimation of the variables. In 82 quadratic cells of 0.25 km² (40 distributed over 10 study plots in the Pre-Alps, 42 within 12 study plots in the Alps) we repeated data assessment and compared mean values per cell between the two assessments using bivariate correlation (Pearson). With this method, we also tracked differences in the delineation of patches (which was not the case for ground-truthing). The distinction between forest and open area was most reliable (Pearson Correlation = 0.98), but also all the other variables attained a correlation of at least 0.80.

In the forest structure variables, we included both the values at the exact location of a grid cell and the mean values or sums from a circular analysis window with a radius of 100 m (chosen arbitrarily; Table 1). Thereby, we intended to better account for scale-dependent habitat relationships of capercaillie. For instance, dense forests with a poor field layer are usually assumed to be unsuitable for capercaillie (Schroth 1992; Storch 1993a; Suchant 2002). However, a dense group of trees surrounded by open forest or close to a gap or opening can provide shelter for capercaillie. Such mosaics are captured at least to a certain degree with the moving window approach.

Landscape-scale variables

To compare the predictive power of the forest structure variables described above with the power of large-scale predictors, we chose a set of landscape variables that are assumed to be relevant for capercaillie occurrence and had been used by us before (Table 2, Graf et al. in press, submitted). These variables were included in the analysis at different spatial scales by calculating the mean, sum or majority values for different moving windows from 1 to just over 1100 ha (ArcInfo 9.0, focal statistics). In this paper, we used the variables at the scales at which they were found to explain the occurrence of capercaillie best in univariate analyses (Graf et al., submitted), i.e. we chose the best explaining scale for every variable and for the

two regions (Pre-Alps, Alps) separately. Detailed descriptions of the variables were given in Graf et al. (in press).

Table 2. *Landscape-scale variables*

Variable description	Abbreviation	Unit (Range)	Dropped because of correlation with ($r_s > 0.7$)	
			Pre-Alps	Alps
Altitude	DEM	m	TAVE	TAVE
Slope	SLOPE	degrees		
Topographic position	TOP	unitless		
Potential direct solar radiation in April	SDIR	kJ/day		
Average temperature (June)	TAVE	°C *100		
Proportion of forest	PFOR	%*4 (0–25)		
Density of forest edges	FE	%*4 (0–25)		
Distance to forest edge	DFE	m		FE
Conifer forest ratio	CFR	Index (0–1)	TAVE	
Coniferous forest	FTC	0/1		
Deciduous forest	FTD	0/1	FTC	
Proportion of mires and wet forests	MIRE	%*4 (0–25)		
Density of motorable roads	ROD	m/ha	TAVE	
Distance to motorable roads	DROD	m		TAVE
Distance to alpine ski runs	DSKI	m		
Density of settlements	SETTL	0/1	TAVE	
Distance to settlements	DSETTL	m		
Distance to farmland	DAGR	m	PFOR	
Proportion of farmland	AG	%*4 (0–25)	PFOR	PFOR

Statistical analyses

At the scale of entire study plots, we compared means or sums of variables between the plot categories “stable”, “declining” and “extinct”. To identify significant differences, we applied non-parametric test statistics, i.e. Kruskal-Wallis H for differences between the three plot categories and Mann-Whitney U-test for differences between presence (stable and declining) and absence (extinct).

At the cell scale, we explored all variables separately by plotting frequency distributions. We searched for differences between presence and absence and between the two regions (Pre-Alps, Alps) and for potential unimodal responses between capercaillie occurrence and the predictor variables. Then we calculated pairwise correlations (Spearman’s Rho) between all

variables and for the two regions separately. All significance tests and correlations were performed in SPSS 11.0.

These exploratory analyses at the cell scale were used as a basis for regression modeling (see below). Four habitat suitability models were developed: we built separate models with data from the Pre-Alps and the Alps, and included either variables of only forest structure or variables of both forest and landscape structure. All four models were then applied to the entire study plots for the time step of 2000. Grid cells predicted as presence were identified as having a predicted probability of capercaillie occurrence higher than 0.5. The proportion of grid cells predicted as presence was then compared between plot categories using Kruskal Wallis and Mann-Whitney tests. For the paired comparison of predicted presence between 1960 and 2000, we used Wilcoxon's signed-rank test (Sokal & Rohlf 1995). Only the models based on variables relating to forest structure alone were applied to the historical data, because some relevant variables of landscape structure were not available for the time step of 1960 (e.g., density of settlements).

Logistic regression

Logistic regression (Manly et al. 2002; Menard 2002) was applied for all habitat modeling using the software SPSS 11.0. Following Hosmer and Lemeshow (2000), we used a binomial error distribution and a logit link function. In all modeling, we included untransformed variables, as normality is not required and error terms are allowed to have non-Gaussian distributions (Guisan & Zimmermann 2000). By plotting the frequency distribution of the predictor variables for both presence and absence plots, we evaluated the type of response. In the case of a unimodal response, the squared predictor variables were included in the univariate and multivariate analyses as well (Guisan & Zimmermann 2000).

Variable selection

Four procedures helped us in deciding whether to include or exclude a predictor variable in the multivariate regression models. First, in pairs of highly correlated variables (Spearman's rank correlation higher than 0.7, Fielding & Haworth 1995), we excluded the one with no (or less) direct influence on capercaillie populations judged on biological grounds (Tables 1 and 2). Second, the algebraic sign of the coefficient of a variable had to be ecologically plausible. Otherwise, the variable was omitted. Third, in the stepwise model building procedure we used a threshold of $P < 0.1$ for the decision of keeping or dropping a predictor variable. For comparing the fit of different models, we used the Akaike Information Criterion AIC (Boyce et al. 2002; Rushton et al. 2004) that identifies the model accounting for the most variation with the fewest variables. Fourth, if the variables selected in the final models were not consistent with the results from hierarchical partitioning (see below), we calculated new models including the variables with the highest proportion of independently and jointly explained variance.

Hierarchical partitioning

To improve the variable selection in the multivariate regression models, we applied hierarchical partitioning (cf. Mac Nally 2000; Heikkinen et al. 2004). This method considers all possible models in a multiple regression setting to identify the most likely causal variables (Mac Nally 2000). This involves the computation of the increase in the fit of all models with a particular variable compared to the equivalent model without that variable. The “explanatory” power of a variable is thus segregated into independent effects, I, and effects caused jointly with other variables, J. Unimodal responses to predictor variables can not be captured with hierarchical partitioning (Heikkinen et al. 2004), so that some variables were used in the multivariate models although they explained only little variation in hierarchical partitioning (e.g., average temperature in the model for the Alps). We applied hierarchical partitioning using the R-package “hier.part” (<http://cran.r-project.org/doc/packages/hier.part.pdf>). As only twelve variables can be investigated in one calculation, we adopted a stepwise approach in those cases where more than twelve variables had to be considered: we divided the variables into two groups, ran the hierarchical partitioning for the two groups separately, and ran the calculation again for those twelve variables with the highest independently explained variance.

Model evaluation

For evaluating the models, we used measures based on a confusion matrix (Fielding & Bell 1997; Guisan & Zimmermann 2000; Boyce et al. 2002). A confusion matrix contains the predicted and observed presences and absences based on a fitted model. From this matrix, a large number of measures can be derived. We use the correct classification rate (CCR) and Kappa statistics (Monserud & Leemans 1992). Kappa measures the actual agreement minus the agreement expected by chance; it takes values between 0 and 1 (0.00–0.05 = no agreement, 0.05–0.20 = very poor, 0.20–0.40 = poor, 0.40–0.55 = moderate, 0.55–0.70 = good, 0.70–0.85 = very good, 0.85–0.99 = excellent, 0.99–1 = perfect agreement). We used Kappa both at a threshold of 0.5 ($Kappa_{0.5}$) and at the optimized threshold ($Kappa_{opt}$). To determine the optimized threshold, we calculated Kappa for all possible threshold values from 0.01 to 0.99. Because all these measures depend on a particular threshold, we also use the Receiver Operating Characteristic (ROC, Deleo 1993). The area under the ROC function (AUC) is usually taken to be an important index because it provides a single measure of overall accuracy that is not dependent upon a particular threshold (Fielding & Bell 1997; Boyce et al. 2002). AUC can take values between 0 and 1. A value of 0.8 for the AUC, for example, means that for 80 % of the time a random selection from the positive group will have a score greater than a random selection from the negative group.

We evaluated all four habitat models with three different approaches. First, model performance on the data used for calibration was tested (internal evaluation). Second, we parted the calibration data set randomly into 10 equal subsets and calculated AUC separately for each subset (10-fold cross-validation). In the results, we give mean and standard deviation

of AUC for all models (AUC_{Mean} , SD). Further, the two models calibrated with data from the Pre-Alps were tested on data from the Alps and, inversely, the two Alpine models on data from the Pre-Alps (independent validation).

Results

Plot scale

We investigated several variables that are known from the literature to influence capercaillie habitat selection at the forest stand scale at the scale of an average home range (study plots of 5 km²). We calculated mean or sum values for the plots and compared means between plot categories (Fig. 3). The two regions of the Pre-Alps and Central Alps were analyzed separately because they were found to differ considerably with respect to several important variables.

The mean forested area per 5-km² plot was 340 ha in the Pre-Alps and 373 ha in the Central Alps. In the Pre-Alps, forest area did not differ between plot categories (Kruskal-Wallis, $H = 0.45$, $p = 0.800$), but in the Alps the plots of the category "stable" had the highest and those of the category "extinct" the lowest proportions of forest area ($H = 14.05$, $p = 0.001$; Fig. 3). Forest edge length was higher in the Pre-Alps than in the Alps (44.6 km and 25.7 km, respectively; Mann-Whitney, $U = 80$, $p < 0.001$). In the Pre-Alps, forest edge length was higher in plots with capercaillie (cat. 1 and 2) than in plots without capercaillie (cat. 3; $U = 49.00$, $p = 0.036$).

The proportion of multi-layered forest was lower in the Pre-Alps than in the Alps (188 ha and 285 ha, respectively; $U = 151$, $p = 0.001$). In both regions, however, plots with capercaillie contained more multi-layered forest than plots without capercaillie, with the category "stable" showing the highest values (Pre-Alps: $H = 8.90$, $p = 0.012$; Alps: $H = 13.86$, $p = 0.001$). The proportion of old-growth forest in relation to overall forest area did not differ between plot categories in both regions. In the Alps, however, the absolute amount of old-growth forest differed significantly between plot categories ($H = 7.98$, $p = 0.019$), with highest values in the category "stable".

Generally, mean canopy cover was higher in the Pre-Alps than in the Alps (80.0% and 70.9%, respectively; $U = 134$, $p < 0.001$). In the Pre-Alps, the canopy was less dense in the capercaillie presence plots than in plots without capercaillie, and lowest values occurred in the category "stable" ($H = 11.08$, $p = 0.004$), whereas no differences between plot categories were found in the Alps ($H = 0.97$, $p = 0.616$). As a consequence, in the Pre-Alps the proportion of open forest (canopy cover between 25 and 75%) was higher in plots with capercaillie than in the plot category "extinct" ($U = 10$, $p < 0.001$). The same results were found with absolute values in the Alps ($U = 25$, $p = 0.028$), whereas no differences between plot categories were found when the ratio of open forest to total forest area was considered ($U = 51$, $p = 0.589$).

Similarly, in the Pre-Alps patches of open forest were better connected in capercaillie plots than in plots where capercaillie was absent ($U = 10$, $p < 0.001$).

The density of motorable roads was higher in plots without capercaillie than in the capercaillie plots in the Pre-Alps ($U = 23$, $p = 0.001$). In the Alps, no such pattern could be found.

Scale of grid cells within plots

By means of hierarchical partitioning, we identified those variables that most likely had the strongest effect on capercaillie occurrence. Thus, we were looking for those variables with the highest proportion of independently or jointly explained variance. Different variables were important in the two regions, and the total amount of explained variation was higher for variables describing landscape structure than forest structure (Table 3). In the Pre-Alps, the three best explaining variables related to forest structure were total canopy cover at the 100 m-scale, variation of canopy cover and multistoried forests (Table 3a), whereas regarding landscape structure, they are average temperature, proportion of settlements and proportion of mires (Table 3b). In the Alps, variation of canopy cover, density of forest edges, and multistoried forests on the one hand and proportion of forest, topographic position and proportion of farmland on the other hand explained best (see also Appendix IV).

The multivariate models built with only forest structure variables explained capercaillie occurrence moderately well (Table 4). In the Pre-Alps, the model contained variables of forest structure such as total canopy cover at the 100 m-scale and its squared term and multistoried forests (Table 5a). The variation of canopy cover indicates that borders between different forest patches increase habitat suitability. The model built with data from the Alps contained three variables defining features that are avoided by capercaillie: Young stands, variation of canopy cover and forest edges. These habitat relationships found for the Pre-Alps and the Alps, respectively, are contradictory to some degree. Consequently, both regional models (built with data from Pre-Alps and Alps, separately) failed to predict capercaillie occurrence in the other area (AUC = 0.39, AUC = 0.46, respectively; see Table 4 for other accuracy measures).

Including landscape variables increased model performance significantly (increase of AUC by 0.14 in the Pre-Alps and by 0.15 in the Alps, respectively). In contrast to the models with only forest structure variables, these models showed at least some degree of generality (AUC = 0.70, AUC = 0.67, respectively). The variables selected by these models are partly identical to those included in the forest structure models and some landscape variables that proved to be important in the hierarchical partitioning (Table 3, Table 5b, Appendix IV). A similar set of landscape variables also explained capercaillie occurrence with a different definition of presence-absence as presented in Graf et al. (Graf et al. submitted).

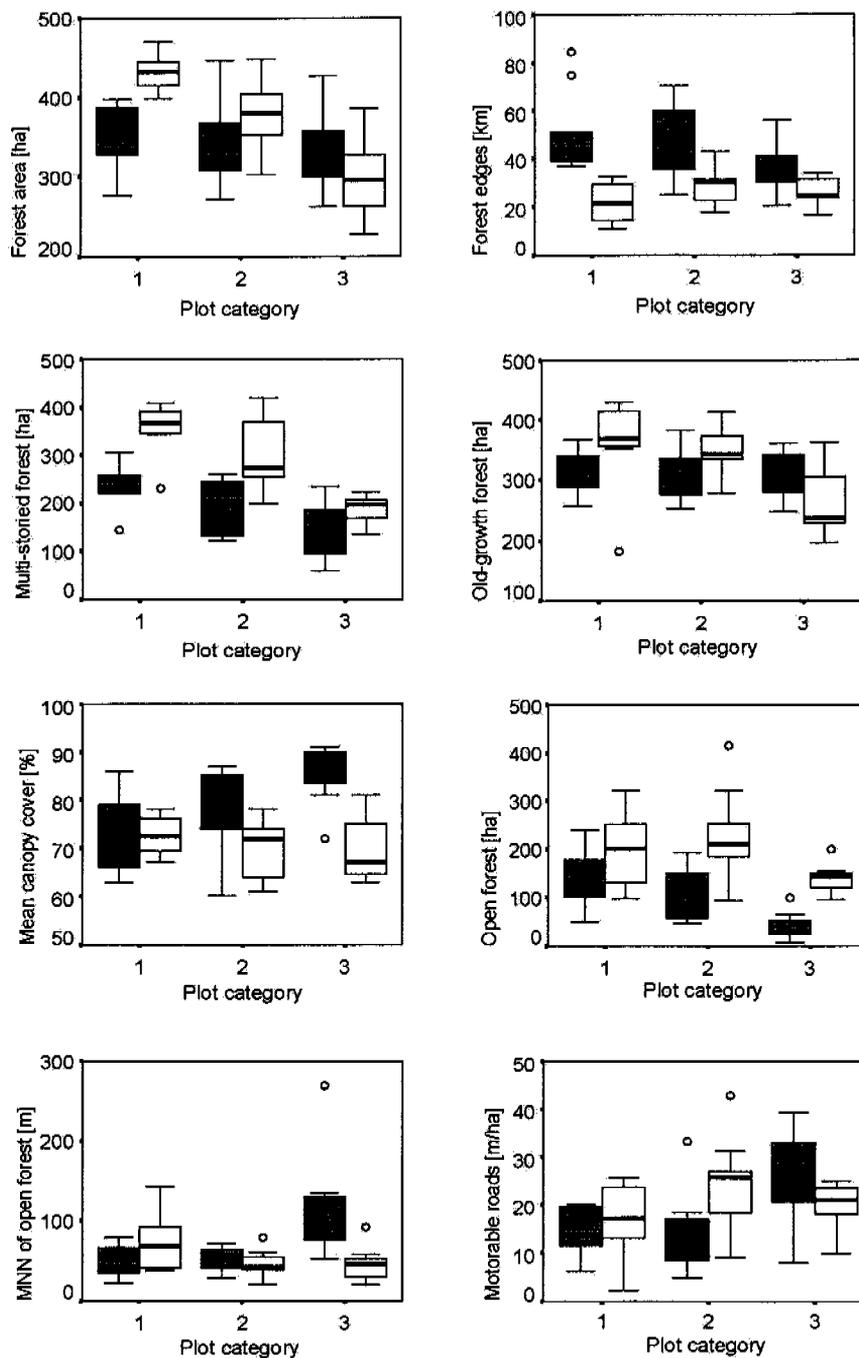


Figure 3. Comparison of means or sum values per plot category; plot categories represent different population trends, i.e. stable (plot category 1), declining (plot category 2), and extinct (plot category 3). Separate clusters for Pre-Alps (dark grey) and Alps (white).

Table 3. Hierarchical partitioning for the Pre-Alps and the Alps; independent part (I) and joint part (J) of the explained variance for different sets of variables.

Pre-Alps			Alps		
a) Forest structure variables					
Variable	I	J	Variable	I	J
SS	0.67	-0.43	SS	1.11	3.77
CC	2.96	7.76	CC	0.37	0.00
CCU	0.79	-0.16	CCU	1.87	3.98
VS	1.89	3.80	VS	0.57	0.90
CC100	4.80	11.60	CC100	0.45	0.55
CCU100	0.70	-0.56	CCU100	0.61	1.62
SSV100	1.00	0.25	SSV100	2.55	8.83
CCV100	7.44	14.51	CCV100	4.08	11.64
FE100	1.50	2.17	FE100	3.87	11.05
VS100	4.46	9.09	VS100	2.44	3.69
b) Landscape variables					
Variable	I	J	Variable	I	J
TAVE	12.33	37.23	SLOPE	6.20	5.34
SLOPE	4.67	13.77	TOP	15.01	12.90
TOP	5.30	10.91	SDIR	3.36	2.59
SDIR	2.67	6.19	CFR	2.85	6.70
PFOR	1.21	-1.03	SETTL	4.38	4.22
FTC	3.18	10.37	AG	8.36	8.59
CFR	4.11	12.11	TAVE	2.82	1.09
MIRE	6.89	17.97	PFOR	23.81	20.57
DAGR	1.52	-0.13			
SETTL	9.35	24.44			
ROD	2.49	5.71			
c) Forest and landscape variables					
Variable	I	J	Variable	I	J
CC	1.92	8.80	CCU	6.17	-0.32
CC100	2.99	13.41	SSV100	6.69	4.69
CCV100	8.20	13.75	CCV100	7.57	8.16
VS100	3.11	10.44	FE100	7.38	7.54
TAVE	13.51	36.05	VS100	5.68	0.46
SLOPE	5.52	12.92	SLOPE	7.58	3.95
TOP	5.54	10.67	TOP	11.63	16.28
CFR	3.98	12.23	SDIR	5.79	0.16
SETTL	10.26	23.54	SETTL	7.14	1.46
MIRE	11.57	13.29	AG	9.01	7.93
			TAVE	3.56	0.35
			PFOR	11.65	32.74

Table 4. Accuracy of the four multivariate models; model built with data from Pre-Alps based on variables relating to forest structure only (PA_FS), model for Pre-Alps with forest and landscape variables (PA_FLS), model for Alps with forest structure variables (A_FS), model for Alps with forest and landscape variables (A_FLS).

Model	Model fitting		Performance on calibration data			
	AIC	R ² _N	Kappa ₀₅	Kappa _{opt}	CCR ₀₅	AUC
PA_FS	330.011	0.351	0.473	0.480	0.736	0.794
PA_FLS	229.855	0.656	0.669	0.682	0.834	0.922
A_FS	194.721	0.350	0.478	0.500	0.739	0.800
A_FLS	114.214	0.764	0.789	0.800	0.894	0.954

	Cross-validation (10-fold)		Validation on Pre-Alps/ Alps			
	AUC _{Mean}	SD	Kappa ₀₅	Kappa _{opt}	CCR ₀₅	AUC
PA_FS	0.779	0.084	-0.167	0.111	0.417	0.378
PA_FLS	0.904	0.042	0.033	0.267	0.517	0.678
A_FS	0.798	0.079	-0.036	0.004	0.486	0.456
A_FLS	0.942	0.043	0.171	0.308	0.588	0.669

Table 5. Predictor variables selected by the models for different regions and with different variable sets; response type and significance of variables.

a) Forest structure					
Pre-Alps (PA_FS)			Alps (A_FS)		
Variable	Response	Sign.	Variable	Response	Sign.
CC100	pos	<0.001	CCU	neg	0.002
CC100 ²	neg	<0.001	CCV100	neg	0.057
CCV100	pos	<0.001	VS100	pos	0.01
VS100	pos	0.01	FE100	neg	0.027

b) Forest and landscape structure					
Pre-Alps (PA_FLS)			Alps (A_FLS)		
Variable	Response	Sign.	Variable	Response	Sign.
CC100	pos	<0.001	CCU	neg	0.002
CC100 ²	neg	0.001	CCV100	neg	0.003
CCV100	pos	0.001	TAVE	pos	0.037
TAVE	pos	0.001	TAVE ²	neg	0.024
TAVE ²	neg	0.001	TOP	pos	<0.001
TOP	pos	<0.001	SLOPE	neg	0.033
SLOPE	neg	0.038	PFOR	pos	0.002
MIRE	pos	0.003	SETTL	neg	0.053
SETTL	neg	0.001			

Application of models to every grid cell in the study plots

All four models were applied to every grid cell in the study plots. The area predicted as presence by the models (threshold $P > 0.5$) was then determined per plot and the averages were compared between the plot categories. We recorded a higher average proportion of cells with predicted presence in plots with capercaillie than in the plots without capercaillie (Fig. 4). In the Pre-Alps, the proportion of forest area predicted as presence was highest in the plot category “stable” (model with forest structure: 59.1 %, model with forest and landscape structure: 56.6 %, respectively), intermediate in the category “declining” (49.6 % and 41.4 %, respectively) and lowest in the plots without capercaillie (21.7 % and 12.1 %, respectively). The difference was highly significant (Kruskal-Wallis, in both cases $p < 0.001$). In the Alps, the plot categories “stable” (59.8 % and 63.3 %, respectively) and “declining” (69.3 % and 57.6 %, respectively) had similar proportions, whereas the plot category “extinct” had the lowest proportions (36.2 % and 3.9 %). The differences between capercaillie plots (“stable” and “declining”) and plots without capercaillie were significant only for the model with forest and landscape structure variables (Mann-Whitney, $U = 30$, $p < 0.063$; $U = 9$, $p = 0.001$, respectively).

Historical changes

All forest structure variables were also assessed for the time of 1960. With a few exceptions, we detected no significant changes between the two points in time. Forest area has increased by 4.2 % (SD = 6.8) in the Pre-Alps and by 6.0 % (SD = 9.142) in the Alps. The density of forest edges has decreased slightly in the Pre-Alps and in the Alps.

The strongest changes were found in human infrastructure. The density of motorable roads increased from 7.8 m/ha (SD = 7.0) to 19.1 m/ha (SD = 10.0) in the Pre-Alps (increase of 11.3 m/ha) and from 12.2 m/ha (SD = 6.7) to 22.2 m/ha (SD = 11.5) in the Alps (increase of 10.1 m/ha; Fig. 5). In the Pre-Alps, the increase was highest in the plots where capercaillie went extinct in the past decades (13.1 m/ha).

The habitat models developed at the scale of grid cells were applied to the data of 1960. The amount and distribution of grid cells predicted as presence did not change significantly between the two time steps with one exception. In the plot category “stable” in the Alps, the amount of grid cells predicted as presence was higher in 1960 than 2000 (Wilcoxon, $p = 0.012$; cf. Figures 4a and 4c).

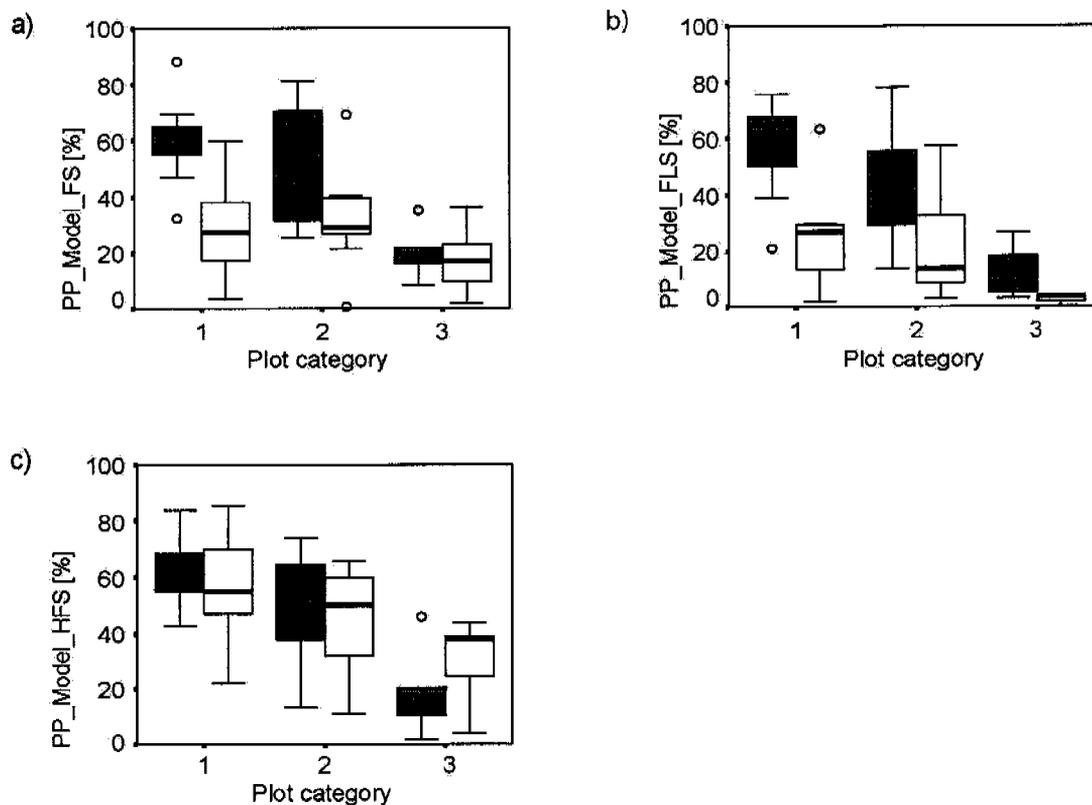


Figure 4. Proportion of predicted presence cells per plot; a) models with forest structure variables only (PP_Model_FS), b) models for forest and landscape structure variables (PP_Model_FLS); c) models with historical forest structure variables (PP_Model_HFS). Plot categories represent different population trends, i.e. stable (plot category 1), declining (plot category 2), and extinct (plot category 3). Separate clusters for Pre-Alps (dark grey) and Alps (white).

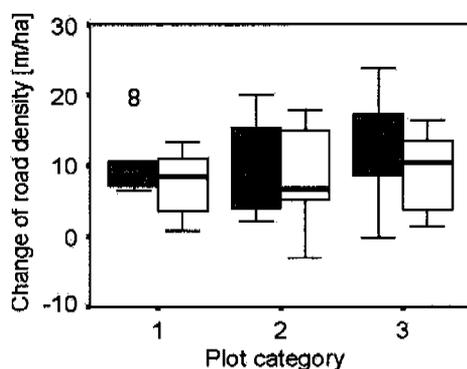


Figure 5. Change of motorable forestry roads [m/ha] between 1960 and 2000; positive values mean an increase, negative values a decrease. Plot categories represent different population trends, i.e. stable (plot category 1), declining (plot category 2), and extinct (plot category 3). Separate clusters for Pre-Alps (dark grey) and Alps (white).

Discussion

We investigated habitat relationships of capercaillie at two different levels, i.e. the scale of an annual home range and the scale of forest stands that may be used by an individual in the course of a day. We structure the discussion into three major sections: First, we discuss the explanatory power of variables at the scale of study plots that have the size of an annual home range. Second, the power and limitations of models built with presence-absence data at the grid cell scale within the study plots are assessed. Third, we discuss the question of the different capercaillie-habitat relationships in the two study regions. Finally, we evaluate the forest and landscape structure changes detected between 1960 and 2000.

Scale of home ranges

At the scale of average home ranges (plot scale), clear differences in variables relating to forest structure occurred between the plot categories representing capercaillie population trends. Variables such as the proportion of open forest, the proportion of multistoried forest and mean canopy cover differed significantly between plot categories. The variables we found to explain at the home range scale are known to influence capercaillie habitat selection at the forest stand scale: open forest or an intermediate canopy cover have been reported as important features for Scandinavian (e.g., Gjerde 1991; Sjöberg 1996) and central European habitats (Storch 2002; Suchant 2002; Bollmann et al. submitted). A preference for multistoried forests as found here has been emphasized in older work (Eiberle 1976; Scherzinger 1976) and has been confirmed recently (Suter et al. 2002; Bollmann et al. submitted). This relationship, however, may reflect a preference for open forests that usually are characterized by multiple layers, whereas dense, unsuitable forest stands mostly show a uniform vertical structure (Suchant 2002). In boreal-type old-growth forests, however, the tree layer need not be multistoried (Gjerde 1991; Moss & Picozzi 1994).

The density of forest edges was a positive predictor for capercaillie occurrence in the Pre-Alps but not in the Alps. This result is in agreement with our earlier results at a larger spatial scale with different coding of presence-absence (Graf et al. submitted). In central European habitats, forest edges are found to be preferably used by capercaillie when they provide warm and sunny places that have a rich field layer and high insect abundance (e.g. Müller 1974; Stein 1974). Such areas are found at boundaries of mires or at edges to clear-cut or wind-throw areas and are often used by hens with chicks. However, forest edges to open land, especially to farmland, may allow higher densities of generalist predators that decrease the reproductive success of grouse species (Kurki & Linden 1995; Kurki et al. 2000).

Scale of forest stands

At the scale of forest stands (grid cell of 400 m²) within home ranges, forest structure variables explained winter occurrence of capercaillie only partly, whereas landscape variables used in earlier work at larger scales improved the performance of the habitat models significantly. Strong differences arose between the two study regions, so that we discuss the

results separately. In the Pre-Alps, canopy cover, variation of canopy cover and the proportion of multi-layered forest explained capercaillie occurrence best. The preference for an intermediate canopy cover has been reported many times before (e.g., De Franceschi & Bottazzo 1991; Gjerde 1991; Storch 2002; Suchant 2002). The possible effect of diversely structured stands has been discussed above, whereas the role of boundaries within forests is difficult to evaluate because different measuring methods are used. Most often, a high density of boundaries within forests is seen as a positive habitat feature (De Franceschi & Bottazzo 1991; Schroth 1992), especially in areas where forests are generally dense and uniform due to intensive forestry (Suchant 2002).

The only variable that was common to the models of both regions was the proportion of multistoried stands. In the Alps, all other variables describe habitat features that are avoided by capercaillie. These included young stands and, in contrast to the Pre-Alps, a negative relation with density of within-forest boundaries and forest edges. Surprisingly, canopy cover had no predictive power here. We attribute this to the generally open forest stands, so that large proportions of potential capercaillie habitat occur in those parts of the Alps where the species is actually absent (cf. Aberg et al. 2000). Here, other factors must be important for capercaillie habitat selection. Such factors can be identified at smaller spatial scales using more detailed forest structure data (e.g., solitary trees, Bollmann et al. submitted). Also, landscape variables increased the performance of the habitat models significantly (see below).

Independent of the study region, forest structure variables as identified from aerial photographs can only partly explain winter occurrence of capercaillie. Reasons for this limitation may be that we lack information about cover and plant species composition of the field layer, tree species composition and detailed stand structure (e.g., Rolstad 1988; Schroth 1992; Storch 1993a). Additionally, to a certain extent capercaillie may use habitats that would be classified as unsuitable by experts (Storch 1997). Also, our coding of presence-absence has to be viewed critically here. In the Pre-Alps, we had large data sets of capercaillie observations stemming from different sources and from different years. Thus, we may have lumped different habitat uses over time. For large parts of the eastern Central Alps, however, the observational data stem from our own field survey so that every location was sampled only once in spring. Therefore, especially in the Alps, an unknown proportion of our "absence" cells may actually be used at least temporarily by capercaillie. In spite of these constraints, the proportion of grid cells predicted as presence (based on the habitat models with forest structure variables only) is significantly higher in plots with capercaillie than in plots where capercaillie have disappeared.

Landscape variables explained much of the variation in capercaillie occurrence. This is in accordance with Storch (2002) who inferred from her results that landscape variables probably accounted for much of the unexplained variation. In our case, important variables were average temperature, topographic position, slope and density of settlements for both

regions, variables that had proved to be good predictors in earlier work with another larger-scale coding of presence-absence (Graf et al. in press, submitted). Regionally important variables were the proportion of mires and wet forest in the Pre-Alps and the proportion of forest in the Alps. The models with forest structure and landscape variables showed at least a moderate degree of generality when applied to the other region.

Regional differences

Species-habitat relationships can differ markedly between ecologically different regions (Collins 1983). Thanks to our cross-regional approach, we were able to track such differences. If we had selected Pre-alpine study areas only, our results would have been largely in agreement with most other studies from central European habitats (e.g., Schroth 1992; Storch 2002; Suchant 2002). However, our results at the forest stand scale and also at the home range scale for the central Alps reveal that environmental conditions and capercaillie-habitat relationships are different. This is supported at the forest stand scale by a field study by Bollmann et al. (submitted) and at larger spatial scales by Graf et al. (submitted). In spite of the differences, at larger spatial scales capercaillie occurrence can be predicted well in both regions with one single habitat model if the model is calibrated with pooled data from both regions (Graf et al. in press, submitted).

Historical changes

We were not able to detect significant forest structure changes over the past forty years. Perhaps, our method was too coarse to detect the changes that had happened in Swiss forests. The increase of canopy cover reported in the second Swiss National Forest Inventory (Brassel & Brändli 1999) gives weight to this assumption. Also, important changes may have happened at very small spatial scales that went unnoticed by our approach. For instance, the field layer may have changed towards less suitable species composition, a less favorable structure or lower insect availability. Furthermore, the most pronounced changes responsible for the recent large-scale population decline probably happened before 1960 (Fritsche 2004), so that we missed them with our analysis. Capercaillie as a long-lived species may react with a considerable temporal delay to habitat changes. Areas with a certain pattern of forest stands may still be occupied by capercaillie although they provide less suitable habitat than preferred by or required for a viable population. This time lag may be another reason why we were unable to identify the changes that are responsible for the decline of capercaillie.

Besides these constraints, factors other than forest structure changes may have caused the population decline of capercaillie. Partly, this development may be explained by the increase of motorable roads as identified over the past forty years. At least in the Pre-Alps, where most forestry roads are used regularly for recreation activities, we found a negative relation between capercaillie occurrence and road density. In the literature, increase of predator densities (e.g., Klaus 1991; Storch 2000), increase of human disturbances (e.g., Zeitler & Glänzer 1998) and climate change (e.g., Moss et al. 2001) are often stated as other factors that

may be responsible for the decline. Unfortunately, we were unable to assess these factors in our study.

Conclusions

Home ranges of capercaillie encompass suitable and unsuitable forest stands. Within their home ranges, capercaillie use forest stands in a non-random manner, but they spend a certain amount of time in unsuitable habitats (Storch 1997). Consequently, habitat models at the forest stand scale built with forest structure variables can only partly explain capercaillie occurrence (cf. Storch 2002; Bollmann et al. submitted). However, a home range has to contain a certain minimum amount of suitable habitats (forest with an intermediate canopy cover). This is mirrored in our analyses at the plot scale by the clear differences between plot categories with respect to the proportion of suitable forest area.

As expected earlier (Storch 2002), landscape variables explain a considerable part of the variation in capercaillie occurrence and thus increase the predictive power of habitat models. This has several implications for forest management and species conservation efforts. First, conservation actions have to be planned and coordinated at sufficiently large scales. Spatially explicit conservation action plans based on landscape-scale habitat models can identify priority areas where conservation actions should be taken to be most effective (Graf et al. 2004). Second, landscape structure has always changed, and the rate of change is increasing under the influence of various human demands for natural resources (With 2004). Future research should therefore focus on dynamic landscape models for simulating the development of potential capercaillie habitats under different scenarios. This would allow us to identify i) actual capercaillie areas that are developing towards unsuitability, but also ii) new potential areas that are presently not occupied.

Quantitative recommendations regarding the preferred mosaic of suitable forest stands would be appreciated by resource managers. As a rule of thumb, Storch (1999) suggested that a forest mosaic containing one third of optimal, suitable and unsuitable habitat, respectively, should be appropriate for capercaillie. Our results support this rule of thumb. However, it would be problematic to derive fixed threshold values of proportions of suitable habitat that must be available in a forest to ensure the viability of the local capercaillie population (cf. Fahrig 2001). In most cases, our study plots cover only a small part of the area that is used by a local population (sub-population). Here, it is important to consider how a study plot or forest parcel is embedded within the landscape and within the (meta) population to which a plot/ parcel belongs (cf. Paper IV). Thus, our results suggest that multi-scale approaches are necessary to disentangle the complex species habitat relationships, and that conservation programs will be most effective only if they consider the whole set of relevant scales.

Acknowledgements

This study received financial support from the Swiss National Science Foundation (SNF) and the Swiss Federal Agency for the Environment, Forests and Landscape (SAEFL). The Swiss Ornithological Institute and several local grouse experts provided to us large data-sets on capercaillie occurrence.

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Paper IV

Assessing the roles of patch area, isolation, and connectivity for predicting capercaillie occurrence in the Alps

To be submitted as:

Kurt Bollmann¹, Roland F. Graf^{1,2}, Werner Suter¹. Assessing the roles of patch area, isolation, and connectivity for predicting capercaillie occurrence in the Alps.

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Abstract

According to the metapopulation theory, the long-term persistence of a species depends on the number, size and spatial configuration of suitable habitat patches. Habitat loss and fragmentation reduce the viability of a regional population. We investigated the patch occupancy pattern of the threatened capercaillie (*Tetrao urogallus*) in the Alps. The study area comprises 12'752 km² of Pre-Alpine and Alpine landscape and 3'429 km² of potentially suitable forest habitat. The population system consists of a network of local populations inhabiting discrete patches. We confirmed the existence of a local population for 55% of the patches. Logistic regression analysis revealed that the probability of a patch being occupied increased with its size and increasing longitude, and decreased with increasing distance to the next occupied patch. Patch area was the most important predictor for patch occupancy. Occupied patches varied considerably in size from 54 to 4'960 ha and were significantly larger than unoccupied patches. The median nearest-neighbour distances were 1'040 m and 2'986 m for occupied and unoccupied patches, respectively. We assume source-sink metapopulation dynamics for capercaillie at the regional scale in the Alps that are influenced by a long-term decline at the large scale. We discuss our findings within the context of metapopulation theory and conclude that the conservation of several large core populations is most crucial for the persistence of the species at the regional scale.

Introduction

The loss and fragmentation of suitable habitat are among the most serious environmental threats for the long-term survival of animal species worldwide (Soulé 1986; Edwards et al. 1994; Laurance & Bierregaard 1997). Negative effects associated with fragmentation include habitat loss, smaller patch sizes, increasing isolation from other habitat patches, discrete distribution of populations, and edge effects (Franklin & Forman 1987; Wiens 1989; Sherrocks & Swingland 1990; Gilpin & Hanski 1991; Andrén 1994; Schmiegelow & Mönkkönen 2002). Responses of species to habitat loss and fragmentation often involve thresholds (Hanski 1998) due to non-linear relationships between habitat availability and the occurrence of a species (Fahrig 2002). Thus, the effect of landscape structure on species persistence is a key question in conservation biology (Fahrig & Merriam 1994). As fragmentation and isolation continue to increase, it is crucially important for both basic and applied ecology to quantify the patch occupancy patterns and population dynamics of threatened species (Hanski 1994a).

The increasing probability of occurrence of a species in patches with increasing area and with decreasing isolation can be derived directly from the theories of island biogeography (MacArthur & Wilson 1967) and metapopulation ecology (Hanski 1994a, 1999). The former deals with the occupation probability of patches (islands) of a certain area varying in distance from the mainland. The latter describes the dynamics of regional (meta)populations that are divided into small (sub)populations living in suitable habitat patches linked by dispersal and embedded in a uniform matrix of unsuitable habitat (Hanski 1991; Harrison 1991; Hanski 1994b).

Empirical testing of these theories requires extensive datasets including descriptions of local dynamics and demographic data. Conservation biology has to develop instruments, concepts and guidelines for the applied work in reasonable time, but the discipline lacks the resources to compile all the data needed for a full metapopulation analysis. Consequently, relatively simple but robust population models have been developed that, with a reasonably small set of input variables, may adequately predict patch occupancy by a species (Hanski 1998).

Stochastic patch occupancy models (SPOM) (Hanski 1994b; Day & Possingham 1995; Ovaskainen & Hanski 2004) are one basic type of such models. They derive the presence of local populations from a single snapshot of presence-absence data in a habitat patch matrix based on the number, size and spatial configuration of the patches (Hanski 1994b; Moilanen 1999; Fleishman et al. 2002). In SPOMs, datasets, descriptions and parameterisations of local patch dynamics and population turnover are not essential, but extinction processes are assumed to depend on the structure of the landscape alone (Ovaskainen & Hanski 2004). However, the extinction rates of local populations can be altered dramatically by metapopulation processes resulting, among others, from the increasing fragmentation of habitat (Saunders et al. 1991; Hanski 1994a; Carlson 2000). Therefore, besides patch area,

measures of connectivity are often used as surrogates for the extinction probability of a local populations. Three categories can be distinguished (Moilanen & Nieminen 2002): 1) the distance to the nearest neighbour, 2) buffer measures that consider the areas of all occupied patches within a limited neighbourhood of the focal patch, and 3) incidence function measures (Hanski 1994b) that take into account the areas of and distances to all occupied patches within the study area.

For many wildlife species, guidelines for management and conservation have to be developed based on field survey and GIS data as the only data sources. This also applies for capercaillie in Switzerland. The capercaillie is a forest grouse species with large home ranges. In central Europe, it is restricted to mountainous areas where coniferous forests dominate with an intermediate canopy cover and a well-developed field layer. Like in most countries of central Europe, the capercaillie suffered a long-term population decline in Switzerland due to changes in forest use causing the loss and fragmentation of suitable habitat (Mollet et al. 2003). As a consequence, the species' distribution pattern has become discontinuous and patchy. Because capercaillie is assumed to occur in meta-populations in central Europe (Storch & Segelbacher 2000; Segelbacher & Storch 2002), the current distribution patterns may render the capercaillie especially vulnerable. With only 450–500 adult males left, the Swiss population is likely to have reached a critical population size. Thus, the capercaillie is red-listed in Switzerland (Storch 2000; Keller et al. 2001) and was declared a priority bird for species action plans (Bollmann et al. 2002). An essential prerequisite of such an Action Plan are scientific criteria to define spatially explicit priority areas for conservation that consider the requirements of viable metapopulations.

Graf et al. (in press) developed landscape-scale habitat models for capercaillie in the Swiss Alps. Based on this work, we investigated patch occupancy of Alpine capercaillie as a function of the configuration of discrete habitat patches. In the present paper, we (i) analyse the current configuration of habitat patches for capercaillie in the Swiss Alps, (ii) examine the relationship between patch area, isolation, connectivity, and geographic position and patch occupancy by capercaillie, and (iii) investigate the sensitivity of the model to variation in significant predictors of patch occupancy. Finally, we discuss our results in the context of metapopulation theory and draw conclusions for the conservation of viable regional populations.

Methods

Study area and patch selection

In Switzerland, capercaillie is restricted to five regions with isolated populations (Mollet et al. 2003) (Figure 1). Region 1 holds the Jura population, regions 2, 3 and 4a the Pre-Alpine populations, and regions 4b and 5 the Alpine populations. Our study area corresponds to the capercaillie regions 3, 4a, 4b and 5 (Mollet et al. 2003), comprising the central and eastern Pre-Alps and the eastern Central Alps. With this selection, the study area holds about 80% of the national population, and represents the ecological gradient inhabited by the species along the cross section of the Swiss Alps. Since region 1 belongs to a different biogeographical region separated from the Alps by the plateau (Gonseth et al. 2001), it was not considered in our study. Region 2 represents the western Pre-Alps but actually holds only a relict population of capercaillie (Mollet et al. 2003) and would have provided a very bad effort-return ratio. Table 1 summarises landscape metrics of the study area and potential capercaillie habitat, respectively. The study area comprises 12'752 km² of Alpine landscape, typically zoned into farmland, forests, alpine pastures and mountain chains. 27 % (3429 km²) of the area is estimated to be potential capercaillie habitat (i.e., forest area above 800 m a.s.l.).

In the study area, forests below 1300 m are mainly mixed deciduous, whereas above 1300 m a.s.l. they consist of Norway spruce (*Picea abies*), silver fir (*Abies alba*) and mountain pine (*Pinus mugo*). Tree line elevation varies with aspect and regional climate. It is normally found at 1800 m a.s.l. in the Pre-Alps but up to 2300 m a.s.l. in the central Alps (Steiger 1994).

We used the multi-scale habitat suitability model of Graf et al. (in press) to identify the configuration of discrete habitat patches for the analyses. Thus, each patch is a fraction of the total capercaillie habitat separated from other patches by unsuitable habitat (matrix). We first fitted multi-scale logistic regression models with presence-absence data of capercaillie from our own field studies (2000–2003) and from several regional inventories. A set of 30 environmental variables was used as explanatory variables. Variable descriptions, the modeling procedure and predictions are given in Graf et al. (in press). All data were processed in grid format with a cell size of 1 ha. Thereafter, the model was applied in GIS for all of Switzerland resulting in a grid with probability values between 1 (presence) and 0 (absence). By using a threshold of 0.8, the data were transformed into a boolean grid with predicted presence and absence. Then, we calculated the neighborhood sum for each grid cell for a circular window of 81 ha (radius of 500 m) and defined presence cells as having a minimum of 25 % predicted presence within the analysis window. This resulted in a new presence-absence map at a larger spatial scale with discrete habitat patches embedded in a matrix of predicted absence. To calculate a suitability index for each patch independent of its size, we calculated the average predicted presence based on the predictions for each grid cell of a patch.

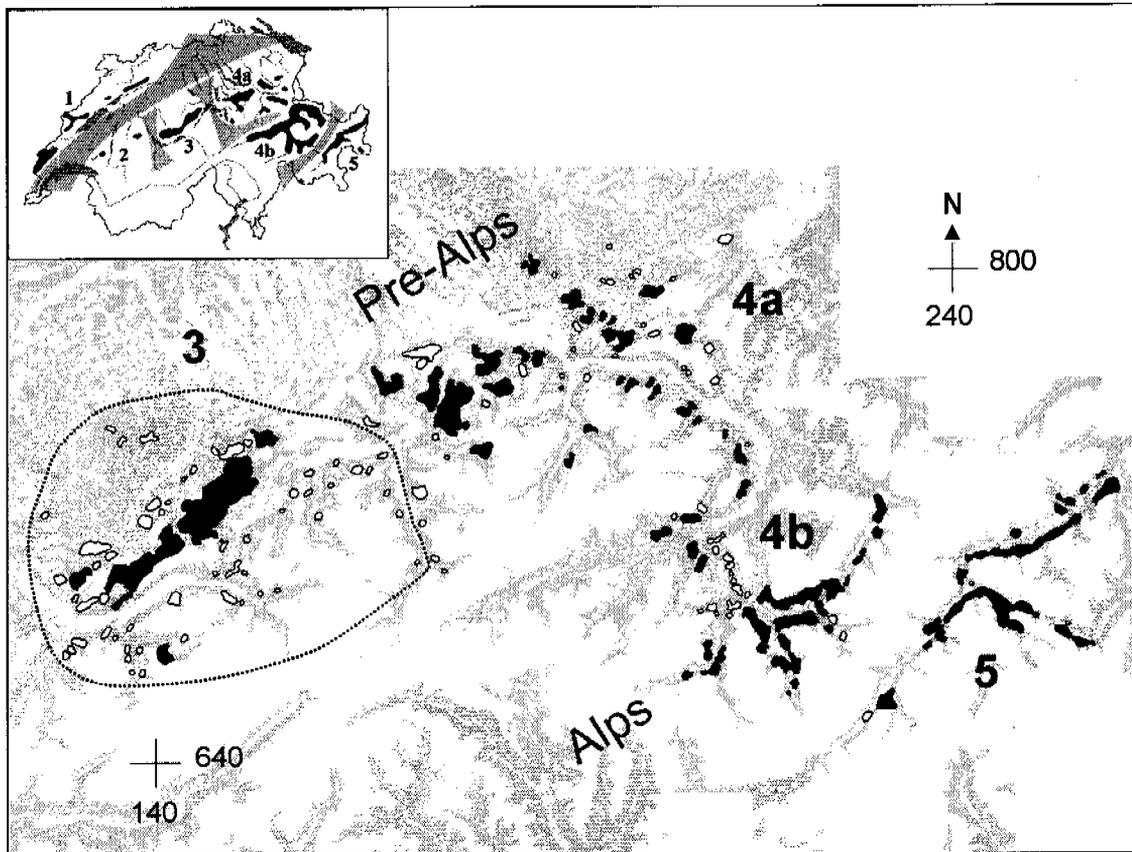


Figure 1. Study area and configuration of patch occupancy by capercaillie: black – occupied patches, white – unoccupied patches, grey – forest area. The independent validation region 3 is indicated by a stippled line. The northwest and southeast portions of the study area belong to the Pre-Alpine and Alpine mountain ranges respectively. Inset: Distribution of capercaillie in Switzerland (dark shading). Barriers dividing capercaillie range into five isolated populations are indicated with light shading (Figure from Mollet et al. 2003).

Only patches with an area of at least 50 ha were considered for the analyses because 50–100 ha of suitable habitat are considered to be the minimum area for supporting the species' habitat requirements (Storch 1999; Suchant 2002). A total of 174 patches met this criterion within the study area. Of these patches, 124 were used for model calibration, the other 60 patches were used for model validation.

Capercaillie surveys and patch status

Patch status was determined as presence (1 – occupied) or absence (0 – unoccupied) of a local population within a patch. We defined a local population as a group of individuals living in the same habitat patch that were assumed to interact with each other (Hanski & Simberloff 1997). We defined a patch as occupied if (1) it contained at least one survey record of capercaillie between 2000 and 2003, and (2) the patch was additionally confirmed by the respective regional inventory as holding a local population. Unpublished regional inventories exist in the cantons of Glarus, Graubünden, and St. Gallen (see also Appendix I). Data on

patch status were obtained from our own capercaillie surveys in the cantons of Glarus, Graubünden, Luzern, Obwalden, St. Gallen, and Zürich between 2000 and 2003.

The capercaillie is strongly sedentary, and the decline of the distribution area has been observed to progress from the periphery to the core of regional populations (Nievergelt & Hess 1984). We stratified the study area and applied a systematic plot sampling (Ratti & Garton 1994). For that purpose, we focused our survey efforts on those areas for which capercaillie presence had been reported in at least one of the national surveys of 1971 (Glutz von Blotzheim 1973) and 1985 (Marti 1986). This procedure was adequate because in the meantime no successful (re)colonisation events of unoccupied patches have been observed by wildlife wardens and ornithologists in the Alps. Our field surveys covered the formerly occupied forests by a systematic search for indirect and direct evidence of capercaillie presence. Hereby, we concentrated the search on key elements of capercaillie winter habitat: feeding and roosting trees, rest sites, low-branched trees, lek areas, internal forest edges, etc. This approach is adequate because the birds select only a few structural and nutritional home range components of suitable forest habitat during winter (Klaus et al. 1989; Storch 2001). Therefore, the probability is small that we failed to detect the species where it actually was present, and we feel that our determinations of current patch status are reasonably reliable.

Capercaillie records include sightings and indirect evidence of capercaillie presence (mainly faeces, feathers, and footprints) between January and May. Because capercaillie concentrate their activities near the leks in winter/spring (Wegge & Rolstad 1986; Storch 1995), evidence of capercaillie presence may be interpreted as representing the core area of a local population. Regional inventories and data of the third national capercaillie inventory (Mollet et al. 2003) were used to validate our own data base or to complete it for the areas where we had done no field work (canton of Schwyz, parts of the cantons of Berne, Glarus and Lucerne). Some valleys of regions 4b (Prättigau, Schanfigg, Surselva) and 5 (Bergell, Puschlav) were excluded from the analyses of patch occupancy because (1) they had not been covered with our own field surveys at all, and (2) the only available data to assess capercaillie status for a patch (occupied vs. unoccupied) were of inferior quality. Thus, these areas were not directly comparable to the other regions.

Independent variables

A small set of predictor variables was used to parameterize the model: one parameter for habitat availability, two parameters each for habitat connectivity (or its reverse, isolation) and geographic position, and one parameter for altitude. All of them are continuous and were derived from GIS (with ArcView 3.3). Habitat availability was approximated by the area A_i of the focal patch i . Minimum distance d_{ij} of a focal patch i to the nearest-neighbour population j and connectivity S_i were used as correlates for the isolation of a patch. The former is the simplest connectivity measure widely used in literature (Moilanen & Nieminen 2002). S_i is a buffer connectivity measure of the type of concentric isolation metrics (Hanski 1994b) that

accounts for all area of occupied patches within a limited neighbourhood of the focal patch i equally, i.e. with no effect of distance. We used edge-to-edge distances for both connectivity measures. The buffer radius used in this study was 5 km. Dispersal capabilities of 5–6 km for juvenile birds and 1–2 km for adults have been reported in several studies throughout the species range (reviewed in Storch & Segelbacher 2000). Exceptional long-distance dispersal may occur and has been reported from Scandinavia, but we did not account for it here.

The geographic metrics X and Y correspond to the longitude and the latitude of the patch centre. They, together with altitude, were included to identify patterns of patch occupancy within the Alps that may reflect large-scale processes unrelated to regional patch configuration.

Statistical analysis

Stepwise multiple logistic regression (Sjögren-Gulve & Ray 1996; Hosmer & Lemeshow 2000) was used to model patch status in the study area. We selected the models that provided the best fit for patch occupancy using the software SPSS 11.0. The dependent variable was presence/absence of capercaillie; independent variables were patch size A_i , nearest-neighbour distance to the next occupied patch d_{ij} , connectivity S_i , longitude X and latitude Y , and altitude. Following Hosmer & Lemeshow (2000), we used a binomial error distribution and a logit link function. Predictor variables were kept or omitted with a critical significance level of $P = 0.05$. We included untransformed variables in the modelling because normality is not required, and error terms are allowed to have non-Gaussian distribution (Guisan & Zimmermann 2000). Both stepwise backward and stepwise forward selection procedures were used to find robust models.

Models were calibrated and evaluated by a combined dataset from the Pre-Alps and the Alps including the surveyed areas of regions 4a, 4b and 5 ($N = 114$; $N_0 = 51$; $N_1 = 63$). Further, we tested the best model with a data set from the capercaillie region 3 that is supposed to be spatially independent from the calibration area (Mollet et al. 2003). Due to a biased prevalence measure for this region (0.08) we reduced the number of non-occupied patches by a random function so that the validation measures could be judged objectively. We used the R-square by Nagelkerke (R^2_N , Nagelkerke 1991) to assess the model fit. The models were validated with measures derived from a confusion matrix (e.g. Fielding & Bell 1997, Boyce et al. 2002): correct classification rate (CCR), Kappa at the threshold of 0.5 ($K_{0.5}$) and at the optimised threshold (K_{opt}) (Monserud & Leemans 1992). As a threshold-independent measure of overall accuracy, the AUC is also presented (Fielding & Bell 1997; Boyce et al. 2002).

Results

Of the study area of 12'752 km², 3'429 km² were classified as potential capercaillie habitat (forest area above 800 m a.s.l.), but only 572 km² were predicted presence area (16.7 % of the potential suitable habitat, 4.5 % of the study area) (Table 1). The relative figures varied among the different regions. The percentage of predicted presence per entire area of a region ranged from 13.6 % (region 4a) to 23.6 % (region 5). Due to the method of patch determination and the smoothing process, the total area covered by the patches of region 3, 4 and 5 (n = 226) was considerably larger than the predicted presence area and amounted to 1'187 km² (34.6 % of potential capercaillie habitat).

Table 1. Landscape metrics for the different capercaillie regions (Mollet et al. 2003) and the species' potential habitat in the central and eastern Alps of Switzerland. WT800: forest area above 800 m asl., PP_08: predicted presence area with threshold 0.8 (for methods see Graf et al. in press).

Region	Area [km ²]	WT800 [km ²]	WT800 [%]	PP_08 [km ²]	PP_08 [%]
3	3'431	1'059	30.9	166	15.7
4a	3'833	979	25.5	133	13.6
4b	3'812	1'005	26.4	182	18.1
5	1'676	386	23.0	91	23.6
Total	12'752	3'429	26.9	572	16.7

Patch configuration and composition

Patches of the patch occupancy analysis varied considerably in size, linear isolation, and connectivity (Figure 1). Patches were generally quite small, with a median area of 243 ha and a median nearest-neighbor distance of 1608 m (Table 2). For 55 % (n = 63) of the patches covering an area of 543 km², the presence of a local population could be verified. The percentage of occupied patches was higher in the Alps (64.9%) than in the Pre-Alps (45.6%) (Chi-square test: Chi-square = 4.293, p = 0.038). Occupied and unoccupied patches differed significantly with respect to A_i, d_{ij}, and S_i (Mann-Whitney U-test: Z = -6.614, d.f. = 1, p < 0.001; Z = -4.611, d.f. = 1, p < 0.001; Z = -3.633, d.f. = 1, p < 0.001, respectively). The smallest patch inhabited by capercaillie was 54 ha in size, the largest 4'960 ha. Thus, the median area of unoccupied patches (117 ha) lay within the size range of patches that were inhabited by a local population. Nearest-neighbor distance did not exceed 10.1 km for occupied patches, but had a maximum of 16.5 km for unoccupied patches. The average connectivity of occupied patches was about twice as high as that of unoccupied patches.

Eight of 114 patches accounted for 50 % of the occupied area. The likelihood of a patch being occupied increased with patch size (Figure 2). The area-isolation plot shows a good discrimination of occupied and unoccupied patches (Figure 3). 82.5 % of the occupied patches

were located above the 0.5 line of incidence, and the respective figure for unoccupied patches was 21.6 %. Average patch suitability (average predicted presence of all grid cells in the patch) differed significantly between patch status ($Z = -3.502$, $p < 0.001$, d.f. = 1). We determined values of 0.434 and 0.343 for occupied and unoccupied patches, respectively. Mainly the large patches contributed to this result, because occupied and unoccupied patches smaller than 250 ha (52 % of all patches) did not differ in average patch suitability. 75 % of the occupied patches were characterized by an average patch suitability that was below the 90% percentile of the data range of unoccupied patches.

Table 2. Metrics for capercaillie habitat patches with different status. Independent variables: A_i = area of patch i , d_{ij} = nearest-neighbor distance to the next occupied patch j , S_i = connectivity with a buffer of 5 km.

	Min	Max	Average	SE	Median
All patches (114):					
A_i [ha]	50	4960	558	80	243
d_{ij} [m]	112	16'467	2'822	293	1'608
S_i [ha]	0	5'160	942	89	734
Occupied patches (63):					
A_i [ha]	54	4'960	862	131	504
d_{ij} [m]	112	10'092	1'772	251	1'040
S_i [ha]	0	5'160	1'216	136	1'002
Unoccupied patches (51):					
A_i [ha]	50	1'345	181	28	117
d_{ij} [m]	440	16'467	4'120	525	2'986
S_i [ha]	0	2'033	603	89	505

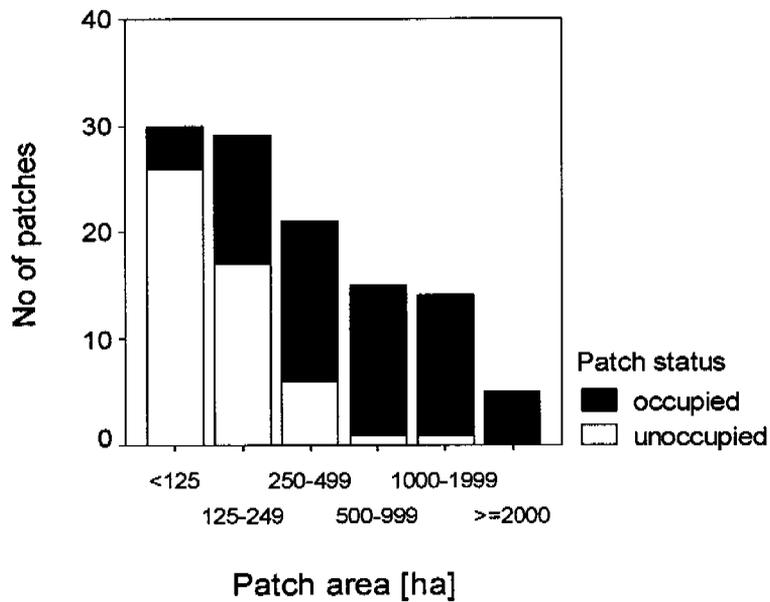


Figure 2. Absolute numbers of occupied and unoccupied patches for six size categories.

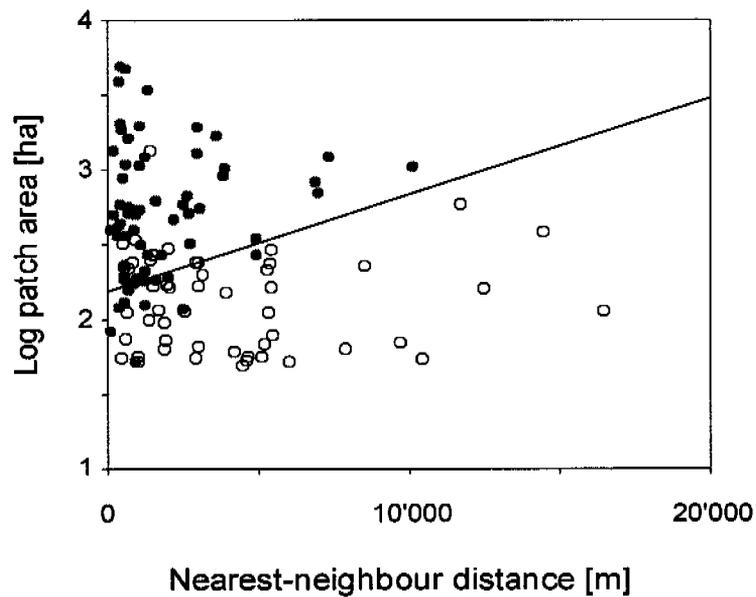


Figure 3. Area-isolation plot showing occupied (solid) and unoccupied (open) habitat patches for Alpine capercaillie. The line represents the 50% probability of occupancy from the logistic regression equation. The predicted probability of patch occupancy is greater than 0.5 above the line, below the line it is less than 0.5.

Factors affecting patch occupancy

In the univariate logistic regressions, five out of six variables were significant (Table 3). The variables with the highest predictive power were A_i , d_{ij} and S_i , with an R^2_N of 0.440, 0.200 and 0.154, respectively. The magnitude of the effects of the significant variables on patch occupancy is shown by the odds ratio (Table 3).

To calibrate the stepwise multiple regression model, we had to omit the variable altitude due to its high inter-correlation with X and Y (Spearman rank correlation: $r_s > 0.78$). Three of the remaining five variables were retained in the final, combined model. Patch occupancy increased with patch area and longitude, and decreased with increasing distance to the next occupied patch (Table 4). Connectivity and latitude did not significantly contribute to the combined model.

The regional models for the subdivided datasets of the Pre-Alps and the Alps selected the same variables with the same responses (Table 4). In the Alpine model, d_{ij} was only weakly significant.

Table 3. Results of univariate logistic regressions of six independent variables and the dichotomous variable patch status (0 = unoccupied, 1 = occupied). A_i = area of patch i , d_{ij} = nearest-neighbour distance to the next occupied patch j , S_i = connectivity with a buffer of 5 km, X = longitude, Y = latitude, Alt = altitude.

Variable	Response	R^2_N	CCR	P =	Odds ratio
A_i	pos	0.440	0.772	0.000	14.556
d_{ij}	neg	0.200	0.667	0.000	4.552
S_i	pos	0.154	0.632	0.001	2.834
X	pos	0.116	0.588	0.003	1.897
Y	neg	0.035	0.553	0.084	---
Alt	pos	0.110	0.579	0.003	1.766

Table 4. Predictor variables selected by the different models with their type of response and significance levels.

Models	N =	Predictor variables	Response	P =
Pre-Alps–Alps	114	A_i	pos	< 0.001
		d_{ij}	neg	0.011
		X	pos	0.011
Pre-Alps	57	A_i	pos	0.003
		d_{ij}	neg	0.028
		X	pos	0.042
Alps	57	A_i	pos	0.002
		d_{ij}	neg	0.056
		X	pos	0.036

Model evaluation and sensitivity of predictor variables

The Wald Chi-square for the model was significant ($P < 0.001$). 82.5% of the patches were correctly classified by the model. Generally, the combined model as well as the regional (Pre-Alpine, Alpine) models performed well on the data from the calibration area. They had R^2_N above 0.6, and good to very good values of performance (Table 5). The respective numbers for the dataset of the independent validation area indicated a very good performance too (Table 5).

The sensitivity of the final model for the predicted probability of patch occupancy to differences in the variables A_i and d_{ij} is shown in Figure 4. Patch occupancy was very sensitive to A_i , and moderately sensitive to d_{ij} . For a d_{ij} of 1'000 m, the model predicted patch occupancy of 1.0 for patches greater than 900 ha. This number increased to about 1'200 ha for a d_{ij} of 10'000 m. To the contrary, a 10-fold increase in patch area strikingly increased the probability of patch occupation, especially between 500 and 5'000 ha.

Table 5. Accuracy measures of the logistic regression models of different regions for patch occupancy by capercaillie.

Model	Model fitting		Test in calibration region			
	N	R^2_N	K_05	K_opt	CCR_05	AUC
Pre-Alps–Alps	114	0.632	0.645	0.685	0.825	0.925
Pre-Alps	57	0.637	0.679	0.755	0.679	0.932
Alps	57	0.682	0.641	0.685	0.842	0.842
Validation on independent region						
Pre-Alps–Alps			0.571	0.727	0.800	0.920

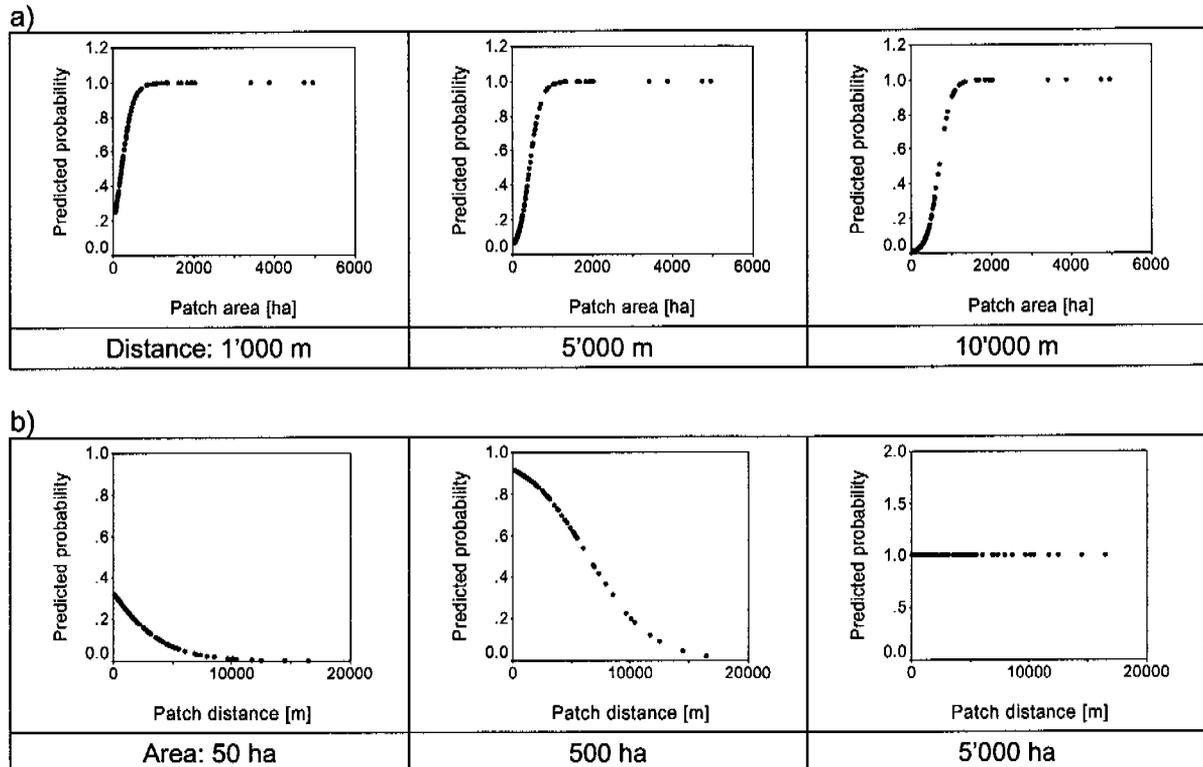


Figure 4. Sensitivity of the final model for patch occupancy in relation to variation in (a) nearest-neighbour distance to the next occupied patch, and (b) patch area. X-coordinate was held constant at the median for patches of the study area (749'484) (Swiss coordinate system) for all analyses.

Discussion

The capercaillie population of the Swiss Alps is distributed within a network of habitat patches with a median size of only 243 ha but a large range from 50 to 4'960 ha. The predicted presence area and the total patch area represented only 16.7 % and 34.6 % of the potentially suitable habitat (forest area above 800 m a.s.l.) in the study area. According to Andrén (1994) and Hanski (1994b), we would expect the effects of patch area and isolation to be pronounced for patch occupancy under these circumstances.

Patch area and patch occupancy

We were able to confirm the significance of patch area and isolation for the incidence of patch occupancy with our data: the probability that a patch was occupied increased with its size and decreased with patch isolation. Suitable unoccupied patches were significantly smaller than and significantly farther away from the nearest occupied patches that represent a potential source of colonists. Accordingly, patch configuration is a good predictor of capercaillie patch occupancy in the Alps, and patch area was the most important predictor of patch occupancy. A strong relationship between patch area and patch occupancy has also been demonstrated for invertebrates (Kindvall & Ahlén 1992; Hanski 1994b), amphibians (Sjögren 1991; Bradford

et al. 2003), birds (McGarigal & McComb 1995; Deng & Zheng 2004) and mammals (Verbeylen et al. 2003). The “area-and-isolation paradigm” (Hanski 1998) has been demonstrated for different groups of organisms (e.g. Smith 1980; Verboom et al. 1991; Hanski & Thomas 1994; Lindenmayer et al. 1999). The significance of patch area and isolation as predictors for patch occupancy was not only robust in the combined model but also in the regional models. The sensitivity analysis revealed that for patches with an area below the threshold of 900–1200 ha (dependent on d_{ij}), mean predicted probabilities of occupancy decreased sharply with patch size. Accordingly, a patch size above a threshold of about 1000 ha is the major requirement for a patch to be occupied. As long as this condition is fulfilled, other variables are much less important. Recent studies revealed that population dynamics of capercaillie were influenced considerably by the pattern of forest vs. open land and habitat connectivity at a scale that is much larger than an average home range (Kurki et al. 2000; Storch 2003). Average annual home ranges for males and females amount to about 550 ha in central Europe (Storch 1995). This figure is remarkably close to the median area of occupied patches (504 ha). However, a direct comparison of these figures is difficult because patch extension and area do not determine a spatially explicit habitat block (e.g. forest) with sharp edges to the adjacent habitat type (open land). Rather, our patches were determined by a habitat model and represent suitable capercaillie habitat within larger forest blocks (Graf et al. in press). Consequently, a local capercaillie population is not restricted exclusively to its patch, as the potential area of habitat consists of the patch itself plus the surrounding forests that may at least temporarily suit the demands of individual birds (see Figure 1).

There are several lines of empirical evidence from other species that population size increases with patch area (e.g. see Hanski 1999). Based on our results that patch geometry, particularly patch area and isolation, was associated significantly with patch occupancy, we suggest a positive correlation between population size of Alpine capercaillie and patch area. Consequently, we expect that the probability of population extinction decreases with increasing patch area. Independently of their size, small patches in the vicinity of large occupied patches may enjoy a rescue effect (Brown & Kodric-Brown 1977; Hanski & Gyllenberg 1993) because immigration from nearby large populations may reduce extinction risk in these small populations (Hanski 1998).

Patch area also reflects the amount of suitable habitat, an equivalent for average patch suitability. The significance of patch suitability or quality for predicting patch occupancy has been confirmed for other species as well (Hanski 1991; Harrison & Taylor 1997; see also Moilanen & Hanski 1998; Dennis & Eales 1999; Fleishman et al. 2002). Additionally, we found higher average patch suitability for occupied patches compared to unoccupied ones, and the largest patches contributed strongly to this result. We interpret this as a consequence of an edge effect (Murcia 1995), because (i) the most suitable habitat conditions for capercaillie may occur only in patches above a certain area threshold, and (ii) the highest numbers of predicted presence are concentrated mostly in the core of a single patch, where detrimental

factors such as human disturbance and predation by generalist species are least likely to occur. In our study, the core of a patch corresponded largely to the interior of a forest block. Storch (2003) also assumed that for the predation risk of capercaillie decreased from the forest edge to the forest interior.

Isolation measures

Our study supports the hypothesis that the probability of patch occupancy is related to patch isolation. Nearest-neighbour distance was a significant predictor in the overall and the Pre-Alpine patch occupancy models, but it was less important in the Alpine model. This may be a consequence of (i) the type of measurement, as d_{ij} was calculated as Euclidian distance, and (ii) the topographic differences between the Pre-Alps and the Alps. Nearest-neighbour distance represents a realistic dispersal measure for structural connectivity of the large majority of capercaillie patches in the Pre-Alps. Here, adjacent patches may be reached in a direct flight by dispersing birds because mountain ranges only locally form barriers that have to be flown around. Thus, the colonisation rate of patches is expected to decrease with increasing degree of isolation, especially because the matrix often consists of unsuitable forests or open land. In the Alps, however, the coniferous forests of neighbouring valleys are typically separated by high mountain ranges exceeding the timber line. Accordingly, dispersing individuals are forced to fly along the main valley slopes to move to neighbouring patches. Nevertheless, dispersal might be less costly and more frequent in the Alps than in the Pre-Alps because the large majority of local capercaillie populations can be found in continuous forest belts, and dispersing individuals do not or only infrequently have to leave the main habitat to reach distant patches. Such a linear forest patch system might also support stepwise dispersal events resulting in long distance dispersal that exceeds the empirically demonstrated dispersal distances of 5–10 km (Storch & Segelbacher 2000). As most of the nearest-neighbour distances in our patch system were less than 5–10 km, we can expect a certain degree of individual exchange among patches as well as the chance of recolonization of unoccupied patches. This view is also supported by Segelbacher and Storch (2002), who found only moderate genetic structuring of Alpine capercaillie and suppose a still high degree of connectivity among populations. Consequently, a cost-distance measure (Chardon et al. 2003; Opdam et al. 2003) that incorporates landscape permeability would probably represent a better functional isolation measure (Adriaensen et al. 2003) for capercaillie in the Alpine region than the simple nearest-neighbour distance.

Our study does not support the hypothesis that patch occupancy is influenced significantly by connectivity as measured by S_i . Buffer measures are generally considered to be superior to nearest-neighbour measures (Vos & Stumpel 1996; Moilanen & Nieminen 2002), especially for terrestrial metapopulations. However, our model was insensitive to S_i even when we increased the buffer radius from 5 to 10 km. We thus assume d_{ij} to be a superior measure of isolation for capercaillie metapopulations in fragmented or topographically strongly structured landscapes, and S_i to be a biologically more adequate measure for example in the continuous,

boreal distribution range of the species. We did not perceive a need to include the incidence function measures of Hanski (1994b) into our analysis because (i) they would be correlated strongly with S_i and (ii) the incidence function measures account for the area of all occupied patches with no distance threshold.

One geographic metric (longitude) also influenced patch occupancy. We assume this relationship to be directly associated with the distribution range of the species. The average altitude of the study area increases from NW to SE, i.e. from the Pre-Alps to the Alps. Consequently, the average altitude of patches in the Alpine valleys is higher. These patches often include the upper zone of the forest belt close to the tree line. Since these forests generally grow less dense and more often show a canopy cover of the preferred intermediate type (Graf et al. in prep.), it is not surprising that we found a higher amount of occupied patches (64.9% vs. 45.6%) in the southeastern portion of the study area. Patch occupancy showed a positive response to altitude in the univariate logistic regression. Simultaneously, the characteristics of the climate shift from maritime to more continental conditions with increasing longitude. Since climatic conditions, especially the amount and distribution of rainfall during the breeding season, influence the reproductive success of capercaillie (Schröder et al. 1982; Klaus et al. 1989), and hens generally rear more chicks in years with less rain days in June (Moss 1985; Moss et al. 2001), the continental climate of the southeastern portion of the study area may allow a higher recruitment rate compared with the Pre-Alpine portion that is more exposed to substantial summer precipitation. Consequently, the carrying capacity of Alpine forests for capercaillie may increase with increasing longitude due to the harsher growing conditions for forests at higher altitudes and the more favourable breeding conditions for the grouse species.

Source-sink distribution

With 55 % of patches occupied and a large variability in patch area, our data suggest that the Pre-Alpine-Alpine capercaillie population represents a source-sink distribution (Hanski et al. 1993; Hanski & Simberloff 1997), as it meets several of the criteria proposed by Hanski (Hanski 1999): First, the probability of occupied patches increased with patch size. Second, we found a 100-fold difference in the sizes of the smallest and largest patches. Third, seven percent of the patches accounted for 50 % of the occupied area. The largest patches are likely to hold source populations in times of good environmental conditions, thus supporting high recruitment rates and low adult mortality. Third, we reported 51 (45 %) unoccupied patches with an equivalent of 93 km² (15 %) unused habitat potential. As the smaller half of all patches did not differ in average patch suitability, the different status (occupied vs. unoccupied) of small patches may reflect the higher probability of local extinction and recolonization of small patches (cf. Fritz 1979) as well as a higher degree of stochasticity. Although large differences in patch size exist, we do not think capercaillie follows a mainland-island metapopulation because several small patches in the close vicinity of large patches were not occupied, whereas others were. However, we can not principally exclude a

non-equilibrium metapopulation (Harrison 1991; Hanski & Simberloff 1997) because our analysis is based on a single survey. Local patch abandonment might occur as an effect of the species' overall large-scale decline (Rolstad 1991). Such a range contraction has been documented for capercaillie in Switzerland, and it is assumed to be a consequence of habitat change and fragmentation in the 20th century (Mollet et al. 2003). Much of the former suitable forest stands deteriorated as a consequence of changing forest use and management in Switzerland. However, Fritsche (2004) showed that the loss of preferred forest stand types between 1932 and 1999 may only partially explain the range contraction and decrease in the number of capercaillie. Accordingly, we suggest that non-equilibrium metapopulation dynamics as the sole cause for the observed patterns is quite unlikely, because in such a situation we would expect relatively few and mainly the large patches to be occupied, rather than the majority of patches.

We conclude that the incidence of patch occupancy by capercaillie in the Swiss Alps can be explained by an intermediate type of metapopulation that combines source-sink dynamics on a regional scale with a non-equilibrium long-term process at the national scale. The distinction between the two types is difficult as it depends on both the timescale (Harrison 1991) and the spatial scale being considered. Based on their genetic analyses, Segelbacher and Storch (2002) concluded that the Alpine capercaillie population is organised as a metapopulation with core-edge dynamics. Our results also suggest that large and healthy core populations with high survival and recruitment rates promoting the source-sink process may benefit core populations to stay viable and are most crucial for the species' persistence on the regional scale. We assume the extinction-recolonization dynamics of a classic metapopulation to be of lesser importance for the Alpine capercaillie populations because their persistence may be relatively unaffected by the population turnover of small patches.

Conclusions

Our patch occupancy model is a useful approximation for the distribution and configuration of local capercaillie populations in the Alps. Patch area and patch isolation are the dominant predictors for patch occupancy. Our results allowed us to determine spatial thresholds (minimum patch area, maximum nearest-neighbour distance) for the identification of priority areas for species conservation at the large scale (see also Graf et al. 2004). Nevertheless, our patch-matrix model does not consider the landscape structure of the matrix and its consequences for dispersal between patches, although inter-patch movement is one of the fundamental characteristics of metapopulation dynamics (Wiens 1997). The incorporation of cost-distance measures of patch connectivity and cohesion would certainly improve our understanding of patch occupancy of capercaillie in the Alps.

Considering the large range of the area of occupied and unoccupied patches, further attention needs to be given to the habitat suitability within single patches. The amount and spatial

distribution of suitable habitat within each patch may cause different probabilities of occupation by a local population. Our decision tools for capercaillie management could be improved if we succeed to combine the patch occupancy model with an analysis of habitat suitability at the scale of each single patch.

Acknowledgements

We thank the cantonal authorities for permission to conduct the capercaillie surveys and to supplement our data with the cantonal inventories. Pierre Mollet from the Swiss Ornithological Institute as well as Ruedi Hess, Franz Rudmann and Bruno Badilatti provided datasets on capercaillie occurrence to our disposal. We acknowledge Ueli Rehsteiner and Dominik Thiel for assistance in the field. We are grateful to Harald Bugmann for useful comments on the manuscript. This study was supported by the Swiss Agency for the Environment, Forests and Landscape (SAEFL) and the Swiss National Science Foundation (SNF: grant number 3100-065199).

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Paper V

Using a multi-scale model for identifying priority areas in capercaillie (*Tetrao urogallus*) conservation

Published as:

Graf, R.F.^{1,2}, Bollmann, K.¹, Suter, W.¹, and Bugmann, H.², 2004. Using a multi-scale model for identifying priority areas in capercaillie (*Tetrao urogallus*) conservation. In Smithers R. (ed), Proceedings of the 12th annual IALE(UK) conference "Landscape ecology of trees and forests". Pages 84–90. Cirencester, UK.

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Abstract

The capercaillie (*Tetrao urogallus*) is a forest grouse species with large spatial requirements and narrow habitat preferences. A large amount of research and conservation efforts, at mostly small spatial scales, could not slow down the decline of capercaillie in Central Europe. Apparently, many population processes operate at larger scales than usually considered, and require large-scale and multi-scale analyses to understand them.

We developed a multivariate habitat suitability model for capercaillie in the Swiss Prealps and Alps. This model, in which we included variables expressed at different spatial scales, can explain capercaillie occurrence with a high degree of precision. Because it predicts almost all occupied areas as presence and identifies ecologically similar areas, it can be interpreted as simulating potential capercaillie habitat. As such, it is an important tool in the national Capercaillie Species Action Plan and helps to strengthen capercaillie populations more efficiently.

Introduction

The role of scale in ecology has been discussed extensively over the past three decades and is now widely recognised as being of vital importance for understanding ecological processes (Wiens, 1989; Levin, 1992). Although there has been much research exploring and confirming the scale dependence of species-habitat relationships (Fuhlendorf et al., 2002; Lawler and Edwards, 2002; Thompson and McGarigal, 2002), many investigations are still conducted at arbitrary and often small spatial scales. This, however, can lead to wrong conclusions about the importance of different habitat factors and thus to less efficient tools in conservation practice.

The capercaillie (*Tetrao urogallus*, Tetraonidae, Aves) is a charismatic forest grouse species with narrow habitat preferences (e.g. Schroth, 1992; Sjöberg, 1996) and large spatial requirements (Rolstad et al., 1988; Storch, 1995). This makes it highly susceptible to habitat and landscape changes. Capercaillie populations are declining in most of their central European range (Klaus et al., 1986; Storch, 2000) as habitat loss and fragmentation have resulted in small populations with different degrees of connectivity or isolation. In Switzerland, the remaining population of 900 – 1000 individuals (Mollet et al., 2003) faces a high extinction risk.

In capercaillie, most research as well as conservation measures have hitherto focused on small spatial scales (e.g. Klaus et al., 1985; Schroth, 1992). These efforts did little to stop the ongoing decline of the grouse species. Recent work mainly in Scandinavia has shown that capercaillie populations are in fact substantially driven by processes operating on the landscape-scale (Rolstad and Wegge, 1989; Helle et al., 1994; Kurki et al., 2000; Storch, 2002). Presently available habitat models at the landscape scale do not address spatial scale explicitly (Sachot et al., 2003) or do not include different spatial scales in a single model (Storch, 2002; Suchant, 2002). Thus, larger-scale habitat relationships are still insufficiently known in those regions where the species is endangered (Storch, 2000). Analyses should be conducted at multiple scales (Keppie and Kierstead, 2003).

We analyzed species-habitat relationships of capercaillie on different landscape scales in the Swiss Prealps and Alps. We hypothesized that the predictive power of single variables would vary among the spatial scales. Therefore, we calculated univariate models for all variables on several spatial scales and thus identified the optimal scale for every variable. This information was used to calculate a multivariate model where all variables were entered on their optimal scale.

Methods

Based on our own field records and additional data sets (from regional recorders and the Swiss Ornithological Institute, cf. Appendix I), we allocated presence/absence information to a boolean grid covering the Swiss Prealps and Alps (Graf et al. submitted). A set of environmental data available area-wide for the whole of Switzerland was used as independent variables. All data were processed in a GIS (ARC/INFO 8.3) as grids with a cell size of 1 ha. With a moving window analysis, we calculated neighbourhood means for different circular areas for every variable. Circular area was increased stepwise from 5 ha up to 1100 ha, which is about two times the size of the bird's home range (Storch, 1995).

In a first step, we calculated univariate logistic regression models (in SPSS, Menard, 2002) for each variable on every spatial scale (Graf et al. submitted). By comparing the explained variance of all these models, we defined the optimal scale for every predictor variable as the one with the highest amount of variability explained; in other words, we searched for the scale at which the variable best explained the spatial pattern of presence-absence in capercaillie. In a second step, we calculated a multivariate logistic regression model (stepwise backwards) where we entered every variable on its optimal scale. If two variables were highly correlated (Spearman's $\rho > 0.7$, Hosmer and Lemeshow, 1989), we omitted the one that we felt had less biological significance. The resulting multi-scale model was validated on data from the region that had provided the data for model calibration and on independent data from a separate area. To measure accuracy, we used Kappa-statistics (Monserud and Leemans, 1992) and calculated the area under the ROC-function (AUC; Fielding and Bell, 1997).

By applying the model equation in a GIS (ARC/INFO 8.3) we produced a grid-based map of predicted probability of capercaillie occurrence (1 = Presence, 0 = Absence). The grid cells were then reclassified according to an accurate threshold value (0.5). The result was a boolean map representing predicted presence and absence areas (Figure 1a).

Results and Discussion

The variables tested univariately performed best at scales ranging from 1 – 530 ha (Table 1). Some variables were almost indifferent to the spatial scale of analysis (e.g. average temperature), others did best at small scales (e.g. index of topography, slope) and some variables have the highest predictive power at large scales (e.g. proportion of forest, proportion of moors). All variables were then used at their optimal scale for building a multivariate, multi-scale model.

The multi-scale model performed excellently when tested in the region that had provided the data for model calibration ($Kappa_{opt} = 0.89$, $AUC = 0.96$). The validation of the model on data from the independent area of the Jura Mountains ($Kappa_{opt} = 0.60$, $AUC = 0.88$) indicates that the model has a high degree of generality and could also be applied elsewhere. Two very

important variables in the model are included at a large spatial scale (proportion of forest, proportion of moors; Table 1). They account for the large spatial requirements of capercaillie (average home range ca. 500 ha; Storch, 1995). By containing several variables at the 1-ha-scale, the model identifies the areas that are suitable with respect to local topography and forest type.

As the multi-scale model predicts presence for almost all occupied areas and ecologically similar zones (Figure 1), it can be interpreted simulating potential capercaillie habitat. In fact, the predicted presence areas are to a large degree identical with the areas that were occupied by capercaillie in the past decades (1950 – 1970), when the populations were about twice as large as today (Mollet et al., 2003). As we had to rely on environmental data-sets that were available area-wide, the predictive power of our models is limited. Predicted presence areas that did not hold capercaillie may have been abandoned because of other reasons working on smaller scales. For instance, forest structure may be locally unsuitable or human activities may cause frequent disturbances.

Table 1. Variables included in the multivariate logistic regression model; Scale: spatial scale at which a variable was included; Beta-value: coefficients from the regression equation; P-value: significance of single variables; ²⁾ squared variable included because of a unimodal response.

Variable	Scale [ha]	Beta-value	P-value
Proportion of forest	250	0.39483	< 0.001
Proportion of moors	530	0.55717	< 0.001
Slope	13	- 0.00174	< 0.001
Average temperature	1	0.03458	< 0.001
Average temperature ²	1	- 0.00001	< 0.001
Index of topography	1	0.00586	< 0.001
Cost distance to large rivers	1	0.00003	0.001
Forest type coniferous	1	0.72786	0.029

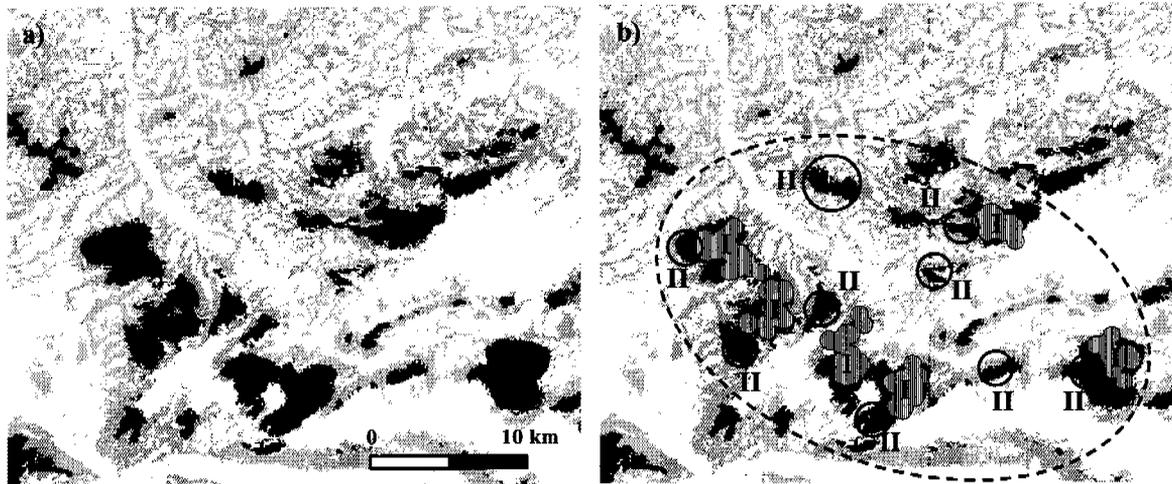


Figure 1. Distribution of predicted presence areas for the multi-scale model (a) and priority setting in the Species Action Plan (b); light grey: forest areas; dark grey: predicted presence, streaked: actual populations (within a focus area), I: Priority I (actual presence), IIa: Priority II (close to presence), IIb: Priority II (stepping stone), III: Priority III (potential expanding areas).

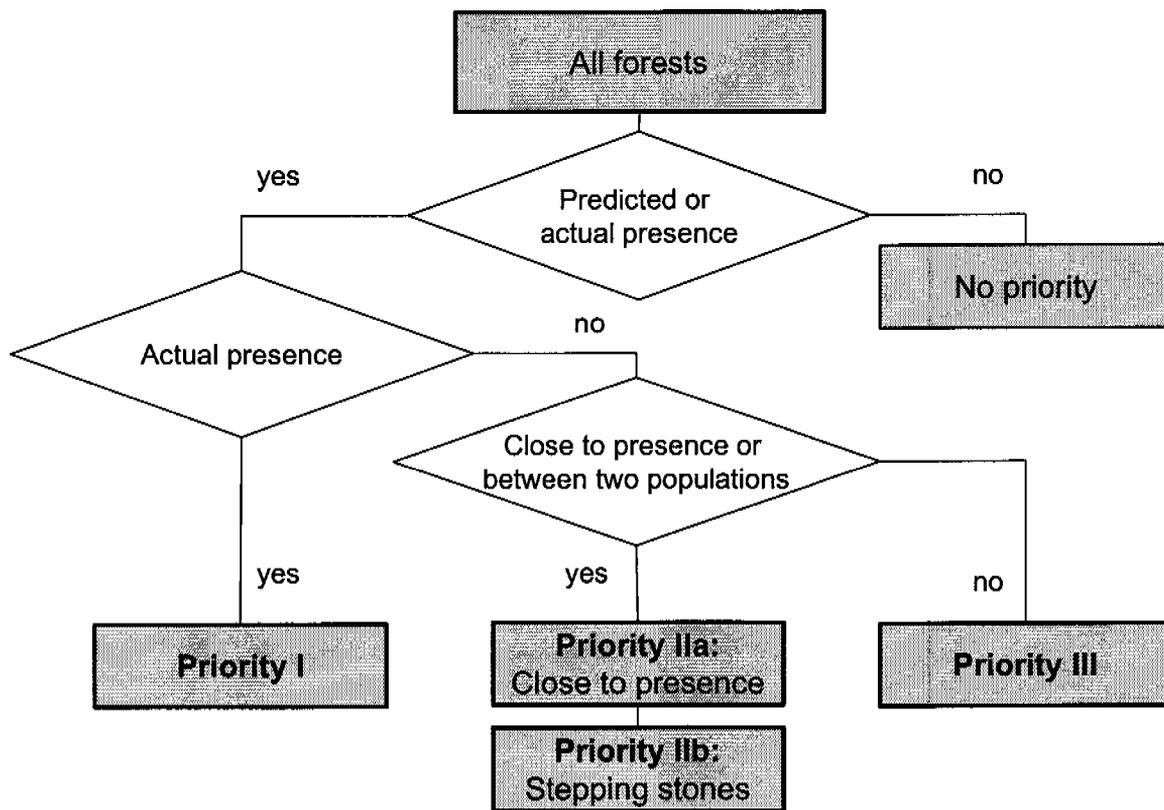


Figure 2. Priority setting in the Species Action Plan.

Implications for conservation

In combination with the inventory of the actual populations, our model provides a basis for the national Species Action Plan. It allows us to define priority areas for conservation measures in a spatially explicit way (Figure 1b, Figure 2). The areas with actual populations (Priority I) are crucial for the conservation of the species. They are the fragmented remnants (metapopulation) of a formerly much larger and contiguous distribution and are often inhabited by only few individuals. In this situation, every small population can be essential for the survival of the metapopulation system (Segelbacher, 2002). Thus, all presence areas have to be conserved by all means.

In the long term, it should be possible to restore capercaillie populations in the Swiss Prealps to a viable level, if the actual distribution can be enlarged, better connected and if abundance can be increased. This can most probably be attained in areas with suitable landscape ecological characteristics that are close to extant populations (Priority IIa). Some areas with predicted presence but actually without capercaillie can act as linkages between existing subpopulations (Priority IIb), if they are situated at reasonable distances. Such “stepping-stones” can significantly increase the viability of the whole capercaillie metapopulation (Segelbacher, 2002).

Until only a few decades ago, additional areas were occupied by capercaillie (Mollet et al., 2003). At present, these areas are not likely to be colonised again soon and can not act as stepping stones because they are situated peripherally (Priority III). However, if we are able to increase the Swiss capercaillie population onto a sustainable level, these areas will eventually be populated again.

In all priority categories, the same conservation measures are necessary to strengthen the capercaillie populations: habitat improvement and reduction of human disturbance. However, conservation measures should be brought forward in areas of priority I and II. Forest structure has to be improved for capercaillie where the stands are presently too dense and uniform. At least two thirds of the forested area should provide an open and diverse forest structure with a lush field layer. Wherever possible, measures to improve the habitat should be included in the normal forestry practice. Suitable habitats for hens with chicks need special attention, because in most cases, summer habitat is supposed to be more limited than winter habitat (Storch, 1999). Open and diversely-structured forests should be furthered also in regions with lower priority (Priority III). Because capercaillie has proven to be a suitable umbrella species (Suter et al., 2002) a large number of rare mountain birds with similar habitat requirements will benefit from conservation actions in favour of this single forest grouse species. Additionally, disturbance by human activities should be minimised. At least in areas with actual populations, tourists (hikers, snow shoe hikers, etc.) should be advised to stay on the trails and forestry roads have to be closed for private traffic.

Our habitat suitability model provides a tool for decision-making in the planning of conservation measures on a large scale. However, additional information with smaller resolution is needed for planning conservation actions in detail (Storch, 1997). For instance, to optimize the measures to improve habitat in a certain area we need information about actual stand structure and tree species composition, cover of field layer, soil characteristics and potential natural vegetation. Information about existing or planned forest reserves should also be included in the planning process. In such areas, it can be much more promising to implement conservation measures than in areas with regular management mainly focussing on wood production.

By combining the potential habitat map with data on the actual capercaillie distribution, forest structure and site characteristics, an effective instrument for the spatially explicit planning of conservation measures in favour of this threatened species can be developed. In fact, our potential habitat map will promptly be included in the national Species Action Plan that will be completed in 2004.

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Synthesis

The main goal of this thesis was to identify important factors of landscape and forest structure affecting capercaillie occurrence. To reach this goal, I analyzed capercaillie habitat at several spatial scales using statistical model approaches. In this synthesis chapter, I discuss issues of methodology, habitat ecology and conservation, structured into three sections:

- (1) methodological aspects, including scale issues, spatial autocorrelation and the question of dealing with either direct or surrogate predictors
- (2) habitat ecology of capercaillie, including new insights on large-scale requirements and differences between geographic regions
- (3) implications of these results for conservation.

Methodological aspects

Scale of independent variables

To date, capercaillie research has focused mostly on capercaillie-habitat relationships at one or few selected spatial scales, such as the forest stand (daily habitat use), stand mosaics (annual home range), or landscapes (population, e.g., Storch 1997). In our analyses, we moved stepwise across all these scales from 1 ha up to 1100 ha using the same analysis design (Papers I and II). What can we learn from this approach that involved assembling a large amount of data and dealing with a complex data structure? First, we accounted for the fact that every variable may influence species occurrence at one or several particular scales. In fact, the scales at which capercaillie occurrence was explained best differed strongly between the predictor variables. Second, the multi-scale approach produced a better habitat model than the one we had identified with a single-scale approach at one arbitrarily chosen scale. Third, depending on the primary aim of an analysis, the optimal scale at which to build a model may differ. In our case, the model at the smallest scale detected every grid-cell that might be potentially suitable for the species, and this may be useful for identifying the exact locations for taking conservation actions. On the contrary, the model at the largest scale produced a coarse pattern of discrete patches of potential presence that might serve as spatially explicit input data for population viability analyses (Paper I).

Coding of dependent variable

The coding of species data can significantly influence the outcome of a habitat analysis (e.g., Cushman & McGarigal 2004). It is important to adapt the coding of the dependent variable to the species' biology and to the questions to be answered by an analysis. Two aspects of the coding of the capercaillie data are important in our analyses, i.e. the chosen resolution of presence-absence and the decision whether to use presence-absence or abundance data.

In papers I and II, we used a coarse definition for identifying presence and absence cells. This was in agreement with our aim to identify those factors that drive the large-scale pattern of capercaillie occurrence. In paper III, we aimed at identifying suitable forest stands within the study plots, and thus used a finer coding of presence-absence data. Such differences in the scale of the coding of the dependent variable have a strong influence on the habitat models and therefore on the inferences drawn from the analyses.

There are two major reasons why we used presence-absence and not abundance data. First, we would perhaps have used abundance data if they had been available or measurable in sufficient quality. However, counting the rare and cryptic capercaillie in Central European habitats is difficult and requires high financial and personal resources (Klaus et al. 1986). Still, even if perfect abundance data had been available for large areas, it would have remained problematic to assign abundances and, thus, densities to grid cells or to study plots. In contrast, assessing capercaillie presence-absence for grid cells by using direct observations and indirect evidence (feaces, feathers, footprints) is much more reliable and much less expensive. Second, Cushman and McGarigal (2004) found that habitat relationships of infrequently recorded species tend to be better explained by presence-absence data than by abundance data, while the opposite is true for common species. As capercaillie in the Swiss Alps is obviously rare and hard to observe (Mollet et al. 2003), our decision to work with presence-absence data was justified.

Temporal scale

Predictive habitat distribution models rely on the assumption that the occurrence of the investigated species is in equilibrium with its environment. This assumption is hardly met in the occurrence pattern of long-lived species such as the capercaillie. Such species do not react instantly to habitat changes, but rather with a time lag that depends on the species' longevity and its ability to reproduce in small populations with low densities. Thus, areas that no longer provide enough suitable habitat to sustain a viable population may still be occupied by the species for several years, maybe even for decades. Such situations may produce an "extinction debt" (Hanski & Ovaskainen 2002), such that the status of (meta-) populations may not be predicted well by current landscape patterns (With 2004). Also, this may explain partly why we did not find a strong change of forest structure over the past forty years when capercaillie populations in Switzerland experienced a strong decline. Perhaps we missed the most important changes because they had happened earlier. Another hypothesis is that the relevant changes happened at smaller spatial scales, so that they were not detected with our coarse method.

Spatial autocorrelation

Spatial autocorrelation, formerly perceived as an annoying phenomenon in statistical analyses, can be introduced explicitly into ecological models (Legendre 1993). For instance, the spatial dependence of a species' occurrence can be included in autologistic regression

models, and such models have proven to fit better than “normal” logistic regression approaches (e.g., Augustin et al. 1996). Nevertheless, we did not include spatial autocorrelation in our habitat models, but chose our sample design so as to ensure independence of the observations. We then ran post hoc tests for detecting problematic spatial dependences of model residuals (Papers I, II, and III). There is one important reason that made us do so. Our aim was to build “pure” habitat suitability models identifying all grid cells that were potentially suitable for capercaillie, independent of capercaillie occurrence patterns in the neighborhood. The resulting maps were then used for further analyses which now considered spatial autocorrelation of capercaillie presence. First, our models were overlaid with the actual capercaillie occurrences and then used to identify and classify areas with priority for capercaillie conservation (Paper V). Second, we identified discrete patches of predicted presence from the habitat models and characterized them with respect to their size, juxtaposition and connectivity (Paper IV). In the future, these same patches may be used as a spatially explicit basis for dynamic population models. Thus, we planned to include spatial autocorrelation in our approach, not at the stage of modeling habitat suitability but afterwards for characterizing and classifying potentially suitable habitat patches. By introducing spatial dependence of the response variable in model calibration, our models might have fitted better. However, we would probably have missed patches of potential capercaillie habitat that are presently not occupied but that may be important for the long-term persistence of the species.

Direct versus indirect predictors

Large-scale approaches normally use large empirical data sets as input data for statistical models, and thus the models are likely to predict the realized (ecological) niche of the species (cf. Guisan & Zimmermann 2000). The same holds true for our approach, thus probably limiting the applicability of our models under changing environmental conditions. In particular, we have to assume that some of our large-scale variables probably are indirect (surrogate) predictors for capercaillie occurrence. This means that they have no direct influence on the species, but were in our study area and at the time of the investigation, correlated with one or several factors that actually drive capercaillie populations or occurrence patterns, but for which no data are available. In our case, habitat models built with landscape variables predicted capercaillie occurrence well and proved to be good instruments for large-scale planning of conservation actions. However, we have to be aware of the limitations of such models. For instance, the models may only be used within a certain geographic range (cf. Papers II and III), and inferences from the models have to account for the spatial resolution used for model calibration. Also, the application of the model in changing environmental situations is limited, because the correlations of surrogate predictor variables with species occurrence are likely to change over time.

However, it is difficult and probably impossible with statistical models to reliably assess whether a predictor affects the habitat selection of a species directly or indirectly. As wildlife ecologists have traditionally focused on small spatial scales, there is still widespread belief

that small-scale habitat features affect patterns of species occurrence more directly than do landscape variables. We assume that at least some landscape variables affect capercaillie habitat use as directly as do many small-scale habitat variables, although at different scales (see below).

New insights in the habitat ecology of capercaillie

The traditional view of capercaillie as a sedentary bird with a small home range has recently been corrected by telemetry studies and landscape analyses revealing the large spatial requirements of capercaillie. For the first time, we have analyzed capercaillie habitat with a major focus on landscape ecology involving a set of spatial scales and statistical model approaches. Unlike many previous studies, we had large data sets of capercaillie occurrence, included ecologically differing regions, and tested most of our models on independent data from spatially separated regions. These analyses provided new insights in the large-scale habitat requirements of capercaillie important for the use of predictive habitat distribution models for the conservation of endangered species.

Landscape versus forest structure variables

There is good evidence that both small-scale and landscape-scale characteristics of the habitat are significant predictors of capercaillie occurrence and abundance. But what is the relative importance of the two scales? Small-scale habitat features are generally perceived as having a major influence on capercaillie populations. However, at the scale of forest stands, small-scale habitat features (forest structure, food availability) explain the variation in capercaillie occurrence in Central Europe only partly (Paper III, Storch 2002; Bollmann et al. submitted). In our case, two major reasons may have caused this low predictive power. First, forest structure assessed from aerial photographs, such as canopy cover or successional state, expresses the relevant habitat features only to a certain degree. Other important variables for habitat selection of capercaillie, such as the cover of the field layer or of bilberry can be assessed only with field work. Consequently, they cannot be assessed over large areas unless unlimited financial and personal resources were available. Second, results from telemetry studies (Storch 1997) revealed that individual home ranges may include a certain amount of unsuitable habitats, i.e. that capercaillie individuals spend a certain amount of time in unsuitable habitats. Thus, it is likely that our presence data sets encompass capercaillie observations in unfavorable habitat, thus decreasing model fit.

Does small-scale habitat structure explain large-scale patterns of capercaillie habitat use? Storch (2002) used aggregated habitat suitability index (HSI) scores to predict capercaillie occurrence and abundance at different spatial scales. These models predicted capercaillie occurrence best at the smallest scales, and their performance deteriorated with increasing scale. Differences in capercaillie abundance between study areas could not be explained by the mean HSI scores. The proportion of unexplained variance may have been reduced to some

degree if spatial variables had been used instead of averaging plot-sample data. We used at least coarse spatial estimates of forest structure to explain capercaillie occurrence at the scale of entire home ranges (Paper III). Forest structure differed significantly between occupied and abandoned plots, in spite of our limited data resolution. Thus, we speculate that having spatial information on small-scale habitat features for large areas would improve habitat models significantly. Air-borne laser scanning methods may soon provide area-wide data sets of detailed forest structure variables such as canopy cover and vertical stand structure (L. Mathys, personal communication) and thus may offer new possibilities for large-scale habitat studies.

Our results demonstrate the high power of landscape ecological variables for predicting coarse occurrence patterns of capercaillie. Generally, a few landscape characteristics explain most of the variation in capercaillie occurrence: large forests at elevated topographic position with temperature conditions allowing only coniferous trees to dominate the stands. These results are in agreement with those from other regions. The relation between the size of a forest patch and the probability of capercaillie occupancy has been investigated both in Central European and Scandinavian landscapes (Rolstad et al. 1987; Storch 1997). Characteristics of topography, temperature and tree species composition are typical predictors in Central European landscapes, where the remaining capercaillie populations live in conifer-dominated forests at higher elevations (e.g., Suchant 2002; Segelbacher et al. 2003).

Landscape-scale edge effects may help to explain why capercaillie populations locally decline or become extinct without any noticeable change in forest structure (Storch 2003). However, we found that capercaillie occurrence responded to edges in different ways between regions (Papers II and III). In the Pre-Alps, capercaillie occurrence was positively related with the density of forest edges. This result may be explained by the interspersion of forests with mires providing forest edges that exhibit favorable conditions for hens with chicks. Possible negative effects of forest-farmland edges may have been outweighed by the positive influence of mires. Also, forests in the Pre-Alps are generally dense so that edges become important habitat features as they provide a rich field layer with high food supply. In the Alps, where forests are generally more open, capercaillie appear to avoid forest edges and prefer the core areas of large forests. This may be due to the different landscape structure without mires but with farmland, settlements and mountains surrounding rather compact forest blocks. Farmland and recreation activities may produce higher densities of generalist predators that also penetrate at some distance into forest areas for foraging. The core areas of forests – and therefore large, contiguous forests – are less affected by increased predator densities than small forest fragments (cf. Storch 1997; Kurki et al. 2000). Thus, effects of forest edge on capercaillie populations should depend on the characteristics of the open land, of the habitat quality of the forest and on the scale at which the response of capercaillie to habitat characteristics is investigated.

Regional differences

As discussed above, marked differences in the habitat relationships of capercaillie can be found between regions. In our case, we identified regional differences with respect to the importance of landscape and forest structure variables and forest edge effects (Papers II and III). This confirms the importance of comparative studies between regions and makes our cross-regional approach particularly valuable. Comparing capercaillie-habitat relationships of several ecologically differing regions can help to identify the causal factors affecting capercaillie populations at the relevant spatial scales. Further, regionally different patterns may raise new research questions and new hypotheses on capercaillie-habitat relationships.

Implications for capercaillie conservation

From landscape ecology to conservation practice

Conservation measures to halt the overall decline of capercaillie have rarely succeeded, probably because they were local in scope and neglected population processes operating at the landscape scale (Storch 2002). Capercaillie does not care about ownership borders or territories of cantons and countries. Therefore, capercaillie conservation must be coordinated over large areas. This is especially difficult in a country with a fine-grained mosaic of forest parcels with different owners as found in Switzerland. Large-scale habitat models as presented in this thesis can help authorities to apply standardized criteria for spatially explicit priority setting for efficient conservation. At the stage when a large-scale concept (e.g. National Species Action Plan) is elaborated and widely accepted by stake-holders, small-scale habitat quality becomes important for the planning of conservation actions in the field. Detailed knowledge on the present habitat quality and the habitat potential of a certain area is needed to decide whether or not to take certain management actions at specific locations. Thus, as proposed earlier (e.g., Suchant 2002; Storch 2003), conservation programs for endangered species must rely on a multi-scale habitat concept in order to be most effective.

Is capercaillie prone to extinction in Central Europe due to global warming?

Critical voices say that capercaillie in Central Europe is prone to extinction due to global warming. They expect deciduous trees to dominate in the future where conifer stands are stocking today, leading to a serious loss of suitable habitat for capercaillie and other species typical of boreal-type coniferous forests. However, in some regions large areas of potential habitat for capercaillie are currently covered with farmland that is seasonally used as pastures. In a preliminary analysis, we identified a large amount of potential habitat outside the presently forested areas (Appendix II, Figure 3). If pastures are given up in these areas, forests will grow and the amount of suitable capercaillie habitat will increase, which may lead to larger populations. Consequently, human land-use has to be considered when we aim at predicting the future of an endangered species, because human land-use in this part of the globe is changing fast and affects forest and landscape structure strongly.

Changes of human land-use or of climatic conditions will affect small- and large-scale structure of forests and landscapes and the effects will occur on large areas. Therefore, the consequences of such changes for the persistence of a target species or an animal community cannot be investigated with field experiments or estimated from past experience. Dynamic modeling may offer tools to deal with such problems. For instance, by combining statistic habitat models with dynamic landscape and metapopulation models, the persistence probability of a species can be estimated for different future scenarios (e.g., Akcakaya et al. 2004). In our case, combining our habitat models with a dynamic landscape model would allow us to make quantitative predictions on how different political and management strategies would influence the amount of capercaillie habitat. This knowledge will probably help conservationists to decide between different strategies.

Which scenario will come true is – among other factors – depending on the value of the target species for the stake holders. Capercaillie is more than just “yet another endangered species” that needs to be furthered and protected. Capercaillie has fascinated people since a long time, as expressed by its still high value for hunters, its use in advertising for tourism or beer brands. Recently, capercaillie has been used as surrogate species by nature conservationists in the sense of an indicator, flagship or umbrella species (e.g., Suter et al. 2002; Storch & Bissonette 2003; Bollmann et al. 2004). These characteristics may influence the sensitivity of stakeholders for species conservation and their management decisions. Thus, the persistence of capercaillie populations in Central Europe will probably depend less on climate change but rather on human land use and on the will of stakeholders to conserve viable capercaillie populations and the entire animal community of boreal-type mountain forests.

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Appendix I: Capercaillie data

Methods used for capercaillie census

As many other forest-dwelling species capercaillie occurrence and abundance are difficult to assess. The choice of the appropriate method depends on the aim of an investigation and on regional peculiarities such as topography or population density of capercaillie. Direct census methods include lek-counts in late winter, surveys along transects or systematic flushing of birds by humans or with dogs. Lek-counts are widely applied in both central European and Scandinavian habitats (Klaus et al. 1986; Rolstad & Wegge 1987; Picozzi et al. 1992). In Finland, forests were crossed on triangular transects and flushed birds were counted (Helle & Lindström 1991). Capercaillie abundance and reproductive success were assessed by counting birds flushed by several observers crossing forest tracts on parallel transects (Leclercq 1987) or by searching for adult birds and hens with chicks using trained dogs (e.g., Baines et al. 2004). Indirect census methods use any evidence of capercaillie presence that can be found in the field to assess capercaillie occurrence (e.g., Bollmann et al. submitted) or to get a relative measure of abundance (e.g., Gjerde 1991). Field evidences of capercaillie presence comprise faeces, feathers, footprints, sand-bath places, etc. and occasional direct observations (Eiberle 1974; Schroth 1992). Methods based on indirect evidences were mostly applied on raster cells or study plots (e.g., Schroth 1992; Storch 2002; Sachot et al. 2003) or by “scanning” larger plots or entire forest parcels (e.g., Klaus et al. 1985; Hess 1997; Graf 2000). Recently, populations have been estimated with genetic methods that identified unique genotypes from DNA extracted from faeces and feathers (Debrunner 2004).

Sources of species data used in this project

In this thesis, we used presence-absence instead of abundance data for several reasons that are discussed earlier (Synthesis/ Coding of dependent variable). We used all available data stemming from both direct and indirect assessments of capercaillie to build presence-absence data at different spatial scales (cf. Paper I, Paper III, Paper IV). In the following paragraph, we add information about the various origins of the capercaillie data and on the applied census methods.

Data from capercaillie project at WSL

In the capercaillie project, we stratified the whole study area and applied a systematic plot sampling (Ratti & Garton 1994). First, we identified those areas, for which capercaillie presence had been reported in one of the national surveys of 1971 (Glutz von Blotzheim 1973) and 1985 (Marti 1986). Since then, wildlife wardens and ornithologists have not observed any (re)colonization events in the Swiss Alps. Second, we searched all formerly occupied areas systematically for direct and indirect evidences of capercaillie presence. Hereby, we focused our search on key elements of capercaillie habitat, such as roosting or feeding trees, rest sites, low-branched trees, internal forest edges, etc. (cf. Klaus et al. 1986;

Schroth 1992; Storch 1993; Bollmann et al. submitted). As capercaillie populations were assessed reliably well in some areas (see below), we concentrated our effort on areas with less data.

National inventories

The data used in the national capercaillie inventories originated from direct counting of displaying males at leks and from stratified plot sampling of indirect evidences. Additionally, different observers, such as ornithologists, hunters and foresters contributed data to the inventories. As a result, data quality was not homogenous over all regions. We used the data of the three inventories of 1971 (Glutz von Blotzheim 1973), 1985 (Marti 1986) and 2001 (Mollet et al. 2003) to stratify our entire study area into smaller units with three different population trends, i.e. "stable", "declining" and "extinct" (cf. Paper III).

Regional inventories

In some parts of the capercaillie regions, regional inventories of high quality were available. In the regions 4a and 4b, a similar method of plot sampling was used as described above. Such inventories were available for the cantons of Schwyz (Hess 1997), Zug (Graf 2000) and for the canton of St.Gall (Rudmann 2001). In the canton of Grison, locations of capercaillie observations and indirect evidence were collected from wildlife wardens and synthesized in maps of capercaillie occurrence (Amt für Jagd und Fischerei Graubünden 2001). Together with our own field data, these inventories were used to define presence-absence in Papers I, III and IV. In the canton of Vaud, capercaillie occurrence was derived from various sources, such as lek-counts, evidence from plot sampling and occasional capercaillie records (Dändliker et al. 1996). The data from the canton of Vaud were used to validate the models built in the Papers I and II.

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Appendix II: additional information regarding Paper I

More detailed information on model results regarding Paper I and additional analyses are given in this chapter. First, we add detailed descriptions of the multi-scale and the best-explaining single-scale model (Table 1) and illustrate the type of response of capercaillie to important predictor variables (Figure 1). Second, the proportion and distribution of potential capercaillie habitat (predicted-presence by the multi-scale model) within the 5 Swiss capercaillie regions is analyzed (Figure 2, Table 2). Further, we quantify predicted-presence areas that are currently not forested (Figure 3, Table 3). Such areas might develop towards forest due to land-use change and thus might provide suitable capercaillie habitat in the future.

Table 1. Detailed description of the two most important models of Paper II, i.e. the multi-scale model (Multi-scale) and the best-explaining single-scale model found at the scale of 253 ha (Scale9); coefficient of variables in the model equation (B), standard error of B (SE), Wald statistic (Wald), significance of predictor variables (Sig), estimated odds ratio (Exp(B)).

Model Multi-scale						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
PFOR	253	0.37586	0.035	113.565	0.000	1.456
TAVE	1	0.04044	0.009	19.449	0.000	1.041
TAVE ²	1	-0.00002	0.000	26.440	0.000	1.000
TOP	1	0.00714	0.002	19.522	0.000	1.007
SLOPE ²	13	-0.00161	0.000	18.325	0.000	0.998
MIRE	529	0.55622	0.107	26.836	0.000	1.744
FTC	1	0.68988	0.324	4.543	0.033	1.993
Constant		-21.44556	4.667	21.118	0.000	0.000
Model Scale9						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
PFOR	253	0.43811	0.038	136.247	0.000	1.550
TAVE	253	0.04708	0.009	25.195	0.000	1.048
TAVE ²	253	-0.00003	0.000	33.979	0.000	1.000
TOP	253	0.01515	0.003	26.826	0.000	1.015
SLOPE	253	0.48059	0.152	9.995	0.002	1.617
SLOPE ²	253	-0.01248	0.003	14.237	0.000	0.988
MIRE	253	0.61030	0.117	27.390	0.000	1.841
Constant	253	-29.59788	5.066	34.139	0.000	0.000

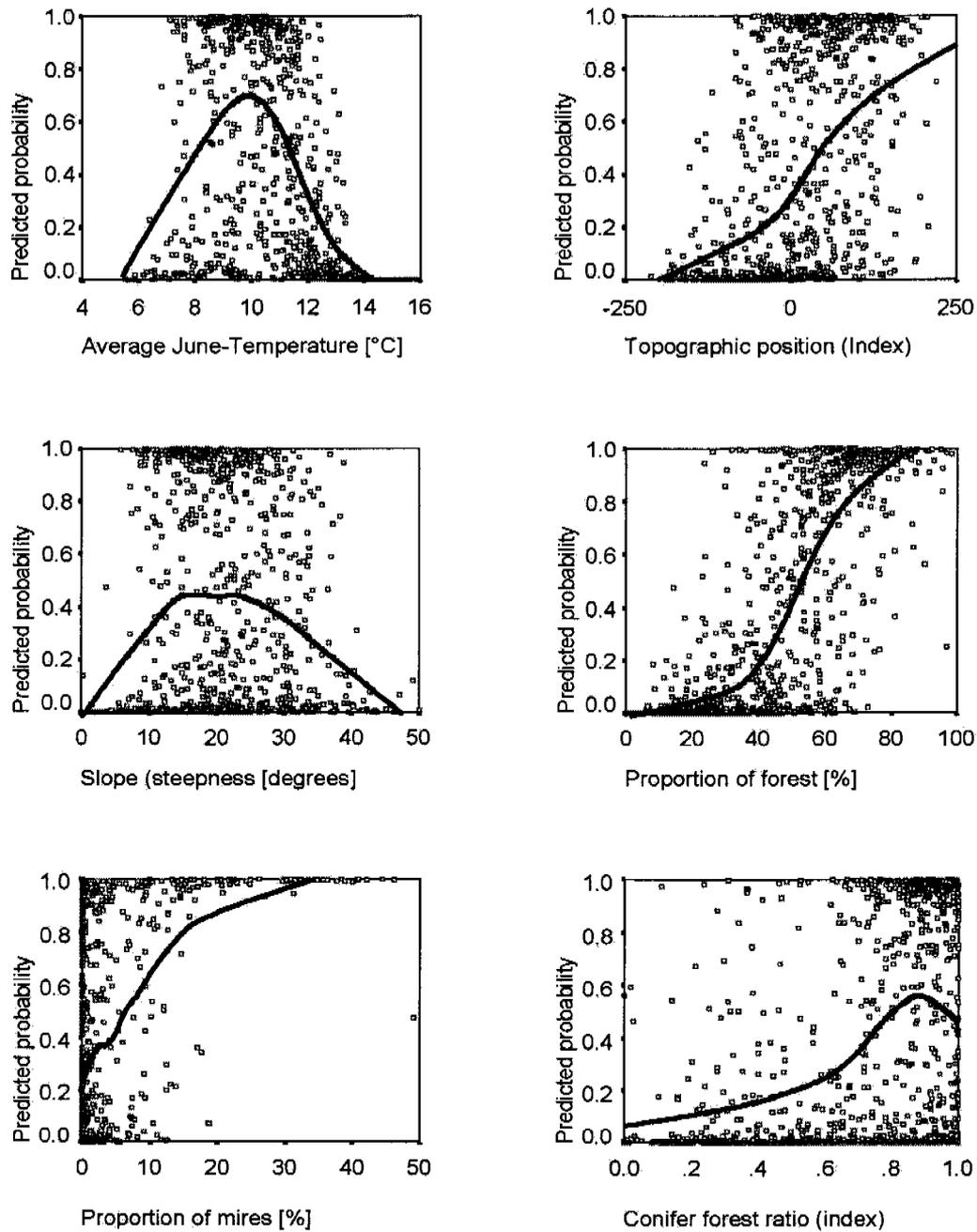


Figure 1. The variables selected by the multi-scale model presented in Paper I are plotted against the probability for capercaillie presence predicted by the model. Response curves fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

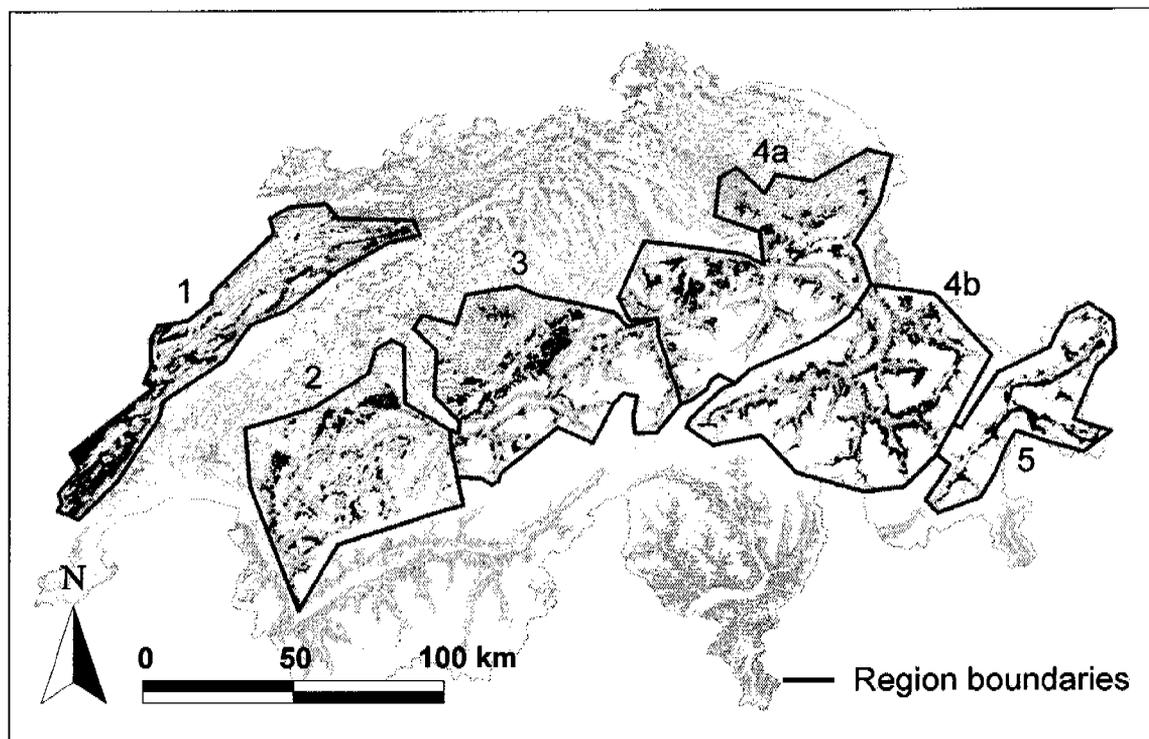


Figure 2. Distribution of potential capercaillie habitat (black) in the five Swiss capercaillie regions; potential habitat is defined as areas predicted as presence by the multi-scale model from Paper I (threshold 0.5); additional forest areas are predicted as absence (Probability < 0.5; light grey).

Table 2. Amount and distribution of potential capercaillie habitat within the Swiss capercaillie regions. Landscape metrics were calculated with PatchAnalyst (metrics based on FRAGSTATS) in ArcView3.2a. Total area per region (Area), forest area above 800 m asl. (WT800), predicted-presence area with a threshold of 0.5 as absolute values and as percentages of forest area above 800 m asl. (PP_05), analogous values for a threshold of 0.8 (PP_08), number of predicted-presence patches (NUMP_05), mean patch size (MPS_05) and mean nearest neighbor of each patch within a region (MNN_05).

Region	Area [km ²]	WT800 [km ²]	PP_05 [km ²]	PP_05 %	PP_08 [km ²]	PP_08 %	NUMP_05	MPS_05 [ha]	MNN_05 [m]
1	2400.69	972.18	426.21	43.84	259.84	26.73	445.00	95.78	224.80
2	3154.39	916.66	209.83	22.89	104.03	11.35	608.00	34.51	237.96
3	3431.12	1059.35	278.77	26.32	166.13	15.68	645.00	43.22	251.47
4a	3833.31	979.42	266.71	27.23	132.88	13.57	650.00	41.03	244.48
4b	3811.83	1005.00	387.09	38.52	182.13	18.12	514.00	75.31	197.73
5	1675.48	386.36	179.20	46.38	91.35	23.64	112.00	160.00	261.68

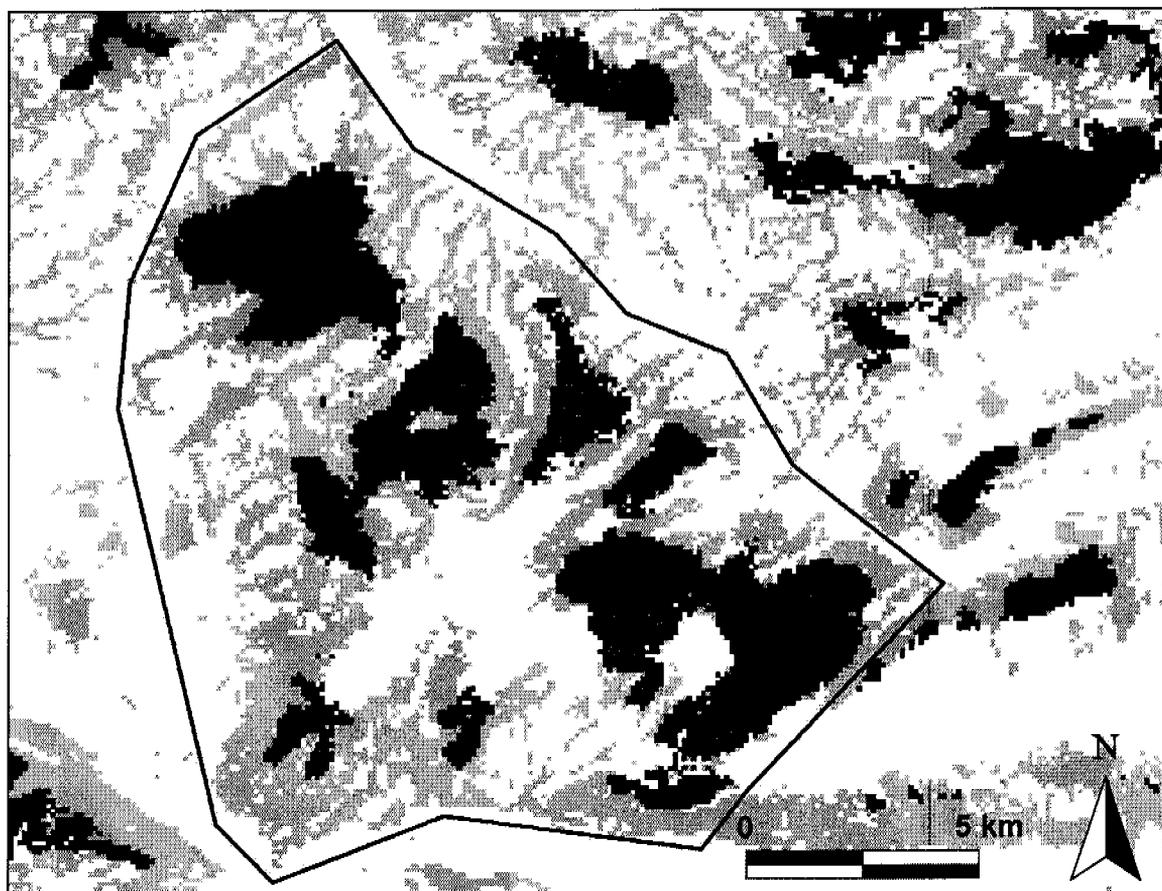


Figure 3. Distribution of potential capercaillie habitat in forested (dark grey) and presently open areas (black) in a well-defined area in the Swiss Pre-Alps (latitude 47°10'N, longitude 9°10' E). Potential habitat is defined as areas predicted as presence by the multi-scale model from Paper I (threshold 0.5); additional forest areas predicted as absence (Probability < 0.5; light grey). A considerable proportion of potential capercaillie habitat is presently used as farmland, mostly as pastures. These areas might develop towards forest due to land-use change and thus might provide suitable capercaillie habitat in the future.

Table 3. Absolute figures of potential capercaillie habitat in forested and open areas and proportions of the entire study area.

	Area [ha]	Area [%]
Entire study area	19817	100
Forested area	9176	46
Potential habitat	5306	27
Potential habitat within forest	3647	18
Potential habitat in open land	1659	9

Appendix III: details on models presented in Paper II

More detailed information on model results regarding Paper II are given in this appendix chapter. First, we add detailed descriptions of the three models built with data from the Pre-Alps, the Alps and with pooled data for both regions (Table 4). Second, we illustrate the type of response of capercaillie to important predictor variables for the two regional models for the Pre-Alps and the Alps (Figures 4 and 5).

Table 4. Detailed description of the three models built with pooled data and with data from the Pre-Alps and Alps, respectively; coefficient of variables in the model equation (B), standard error of B (SE), Wald statistic (Wald), significance of predictor variables (Sig), estimated odds ratio (Exp(B)).

Model with pooled data from both regions						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
SLOPE	5	-0.07312	0.020	13.895	0.000	0.929
TOP	1	0.00833	0.002	15.267	0.000	1.008
TAVE	253	0.05358	0.012	21.220	0.000	1.055
PFOR	253	0.37226	0.044	70.389	0.000	1.451
ROD	110	-0.04397	0.013	10.853	0.001	0.957
TAVE ²	253	-0.00003	0.000	24.798	0.000	1.000
Constant		-26.78261	5.900	20.603	0.000	0.000
Model with data from Pre-Alps						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
SLOPE	5	-0.07730	0.033	5.483	0.019	0.926
PFOR	253	0.48211	0.084	32.734	0.000	1.619
FE	29	0.17170	0.088	3.767	0.052	1.187
TAVE	1	-0.00001	0.000	28.343	0.000	1.000
MIRE	253	0.55490	0.289	3.683	0.055	1.742
Constant		3.10660	1.843	2.840	0.092	22.345
Model with data from Alps						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
TOP	29	0.01672	0.005	11.171	0.001	1.017
PFOR	81	0.59183	0.103	33.024	0.000	1.807
FE	1	-0.07780	0.044	3.116	0.078	0.925
TAVE ²	253	0.00000	0.000	20.275	0.000	1.000
Constant		-5.43854	1.475	13.594	0.000	0.004

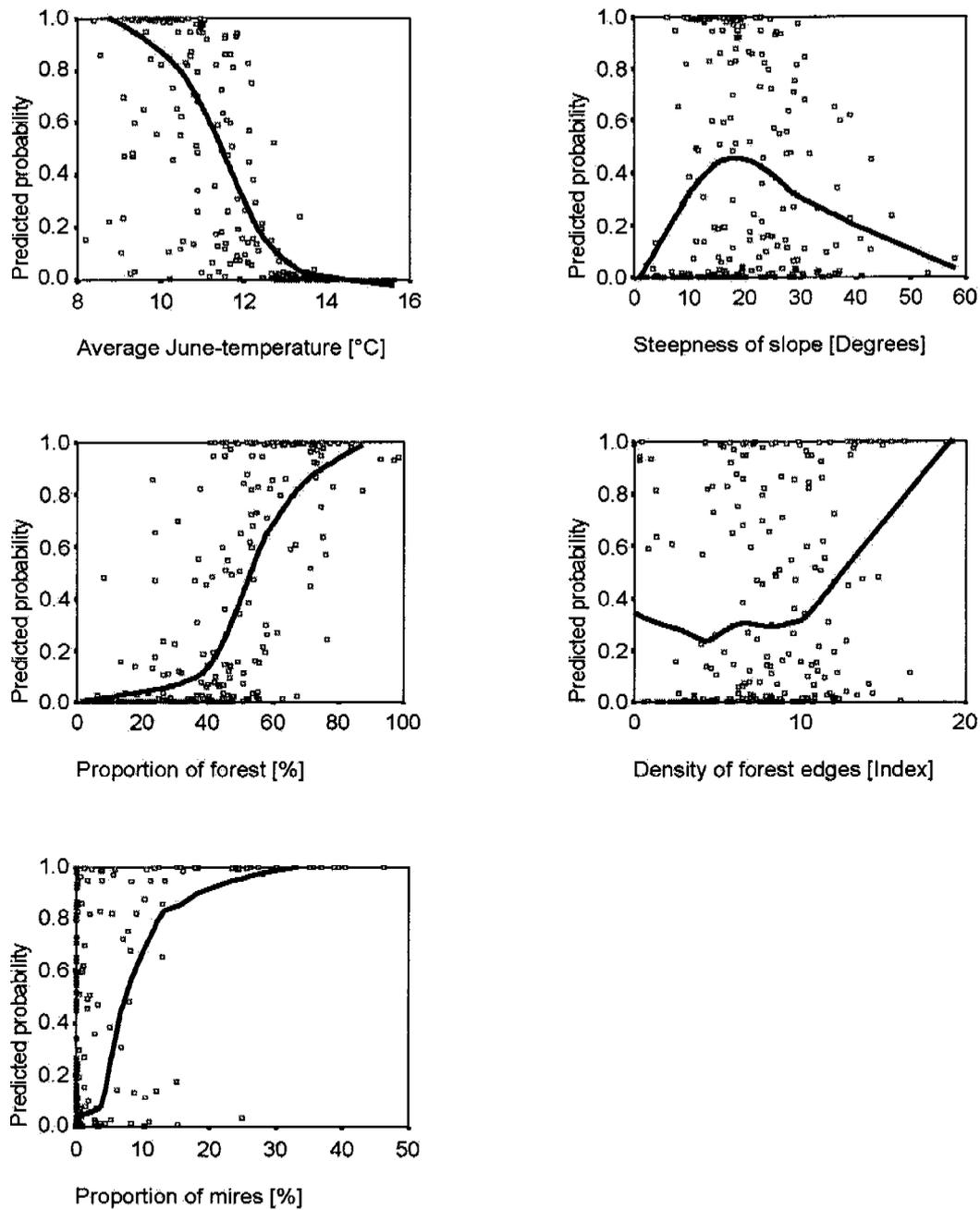


Figure 4. Response curves for Paper II/ Pre-Alps. The variables selected by the model built with data from the Pre-Alps are plotted against the probability for capercaillie presence predicted by the model. Response curves are fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

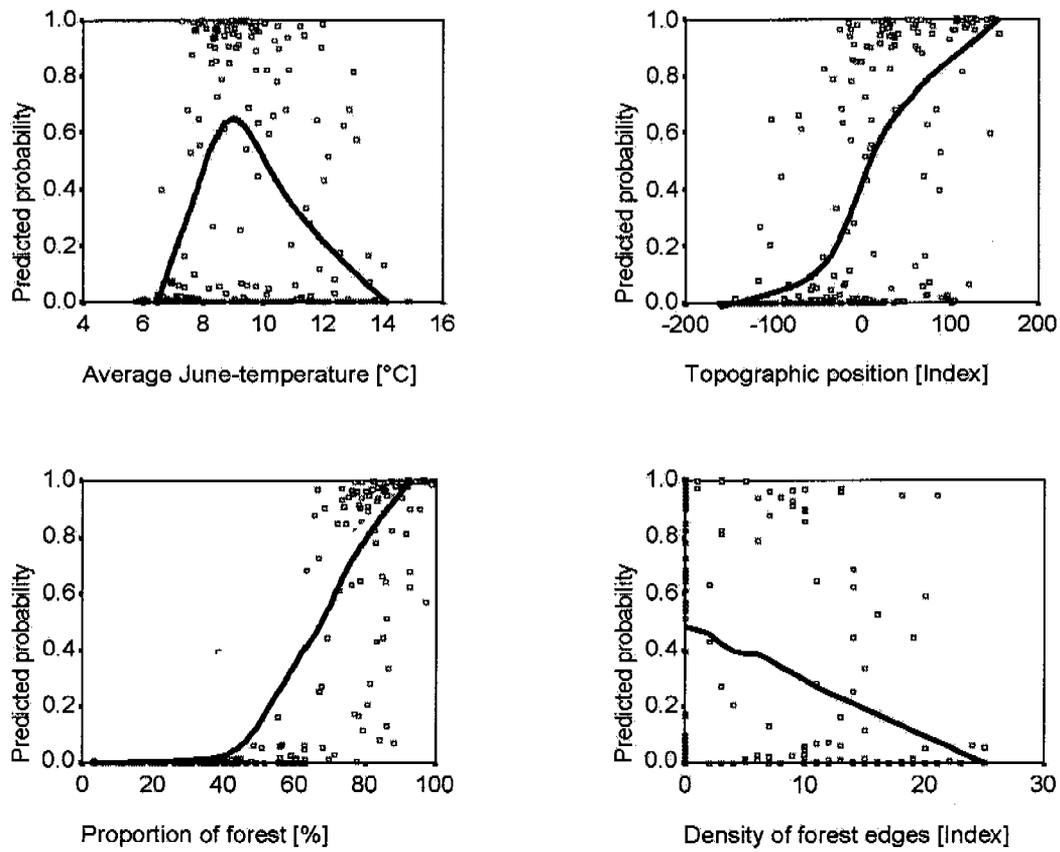


Figure 5. Response curves for Paper II/ Alps. The variables selected by the model built with data from the Alps are plotted against the probability for capercaillie presence predicted by the model. Response curves are fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

Appendix IV: details on models presented in paper III

Here, we add more detailed information on model results regarding Paper III. First, detailed descriptions of the four models presented in Paper III are given (Table 6).

Table 6. Detailed description of the four models presented in paper III: model for Pre-Alps with forest structure variables (FA_FS), Pre-Alps with forest and landscape structure variables (FA_FLS), Alps with forest structure variables (A_FS), and Alps with forest and landscape structure variables (A_FLS); coefficient of variables in the model equation (B), standard error of B (SE), Wald statistic (Wald), significance of predictor variables (Sig), estimated odds ratio (Exp(B)).

Model PA_FS						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
CC100	3.14	0.40173	0.111	13.158	0.000	1.494
CC100 ²	3.14	-0.00293	0.001	15.287	0.000	0.997
CCV100	3.14	0.63274	0.145	18.930	0.000	1.883
VS100	3.14	1.16937	0.457	6.548	0.010	3.220
Constant	3.14	-16.95500	4.141	16.767	0.000	0.000
Model PA_FLS						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
CC100	3.14	0.50139	0.143	12.291	0.000	1.651
CC100 ²	3.14	-0.00334	0.001	12.027	0.001	0.997
CCV100	3.14	0.60101	0.180	11.129	0.001	1.824
SETTL	529.00	-159.22698	48.275	10.879	0.001	0.000
MIRE	253.00	0.26545	0.090	8.780	0.003	1.304
TAVE	1.00	0.13577	0.042	10.557	0.001	1.145
TAVE ²	1.00	-0.00006	0.000	10.989	0.001	1.000
TOP	1.00	0.01355	0.003	18.591	0.000	1.014
SLOPE	5.00	-0.05680	0.027	4.290	0.038	0.945
Constant		-90.56557	22.249	16.569	0.000	0.000
Model A_FS						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
CCU	0.04	-0.13055	0.042	9.492	0.002	0.878
VS100	3.14	2.33004	0.905	6.629	0.010	10.278
CCV100	3.14	-0.47362	0.249	3.623	0.057	0.623
FE100	3.14	-119.13187	53.993	4.868	0.027	0.000
Constant		-2.39653	1.841	1.695	0.193	0.091
Model A_FLS						
Variable	Scale [ha]	B	S.E.	Wald	Sig.	Exp(B)
CCU	0.04	-0.19986	0.063	9.992	0.002	0.819
CCV100	3.14	-0.93264	0.318	8.592	0.003	0.394
SLOPE	5.00	-0.07304	0.034	4.571	0.033	0.930
TOP	49.00	0.02070	0.006	14.062	0.000	1.021
SETTL	81.00	-50.93702	26.332	3.742	0.053	0.000
PFOR	81.00	0.34080	0.110	9.665	0.002	1.406
TAVE	1.00	0.04518	0.022	4.351	0.037	1.046
TAVE ²	1.00	-0.00002	0.000	5.107	0.024	1.000
Constant		-22.55198	10.259	4.833	0.028	0.000

Second, we illustrate the type of response of capercaillie to important predictor variables for the four different models presented in Paper III (Figures 6, 7, 8 and 9).

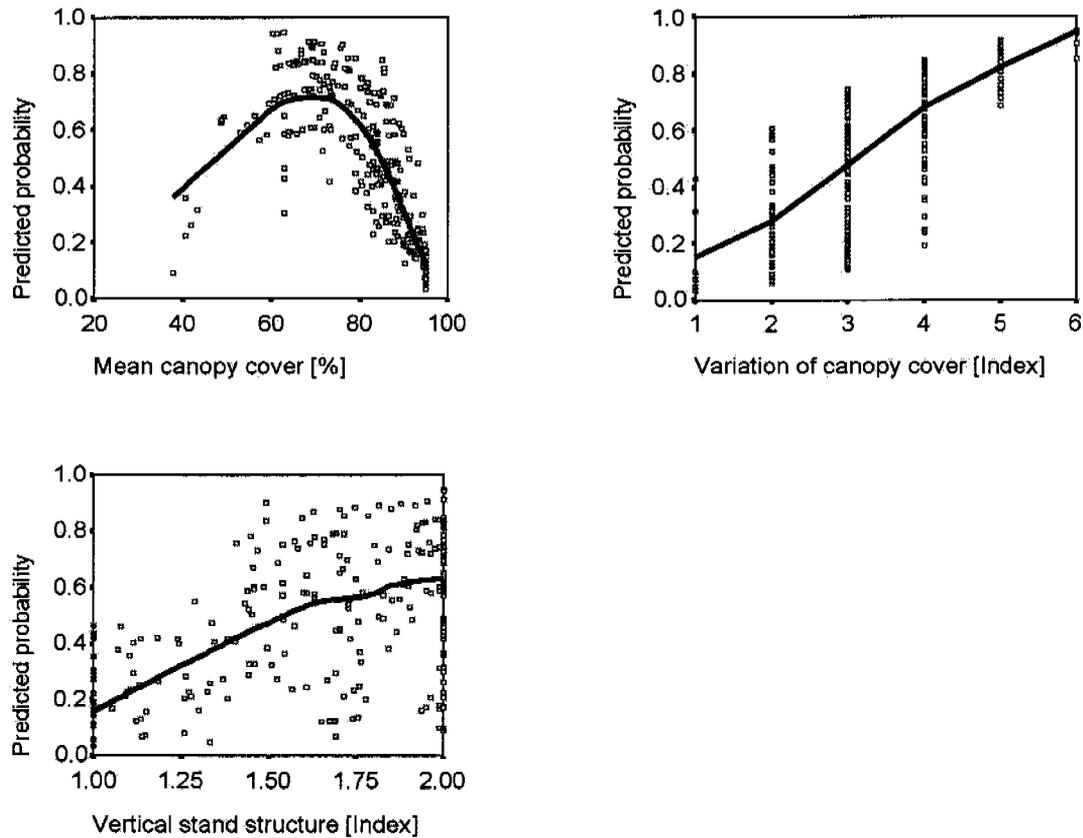


Figure 6. Response curves for Paper III/ Forest structure/ Pre-Alps. The variables selected by the model built with forest structure variables only and with data from the Pre-Alps are plotted against the probability for capercaillie presence predicted by the model. Response curves are fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

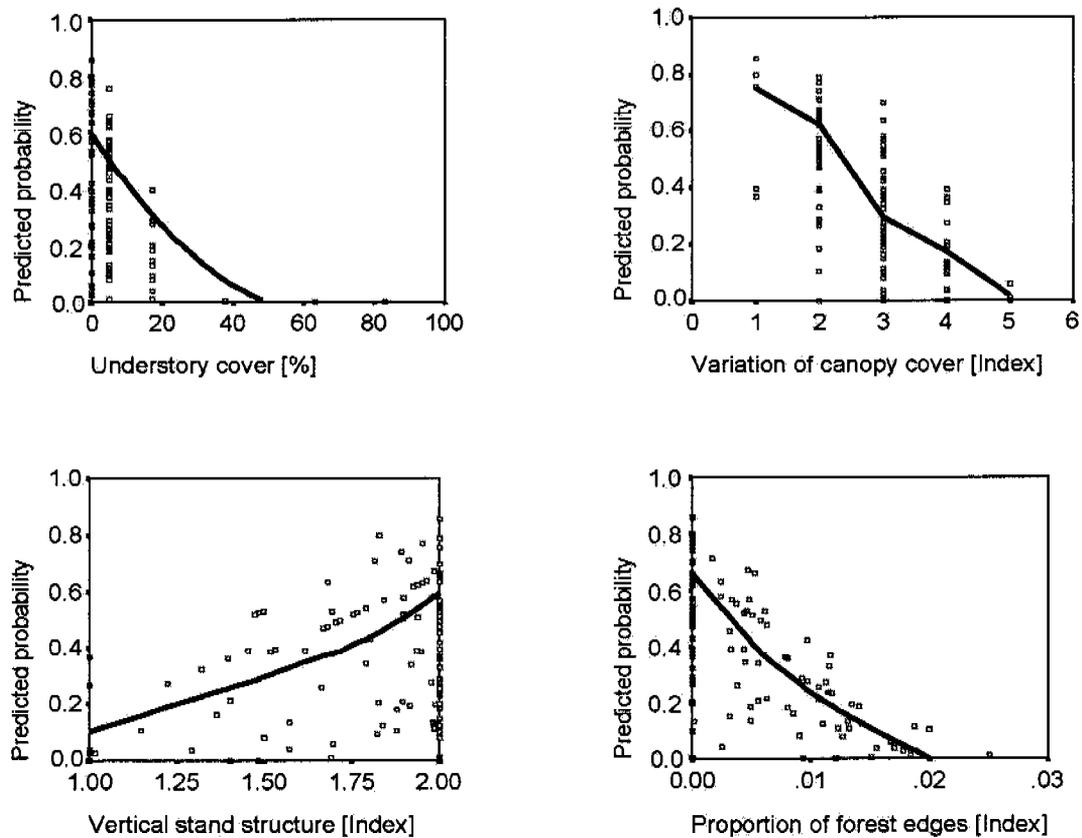


Figure 7. Response curves for Paper III/ Forest structure/ Alps. The variables selected by the model built with forest structure variables only and with data from the Alps are plotted against the probability for capercaillie presence predicted by the model. Response curves are fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

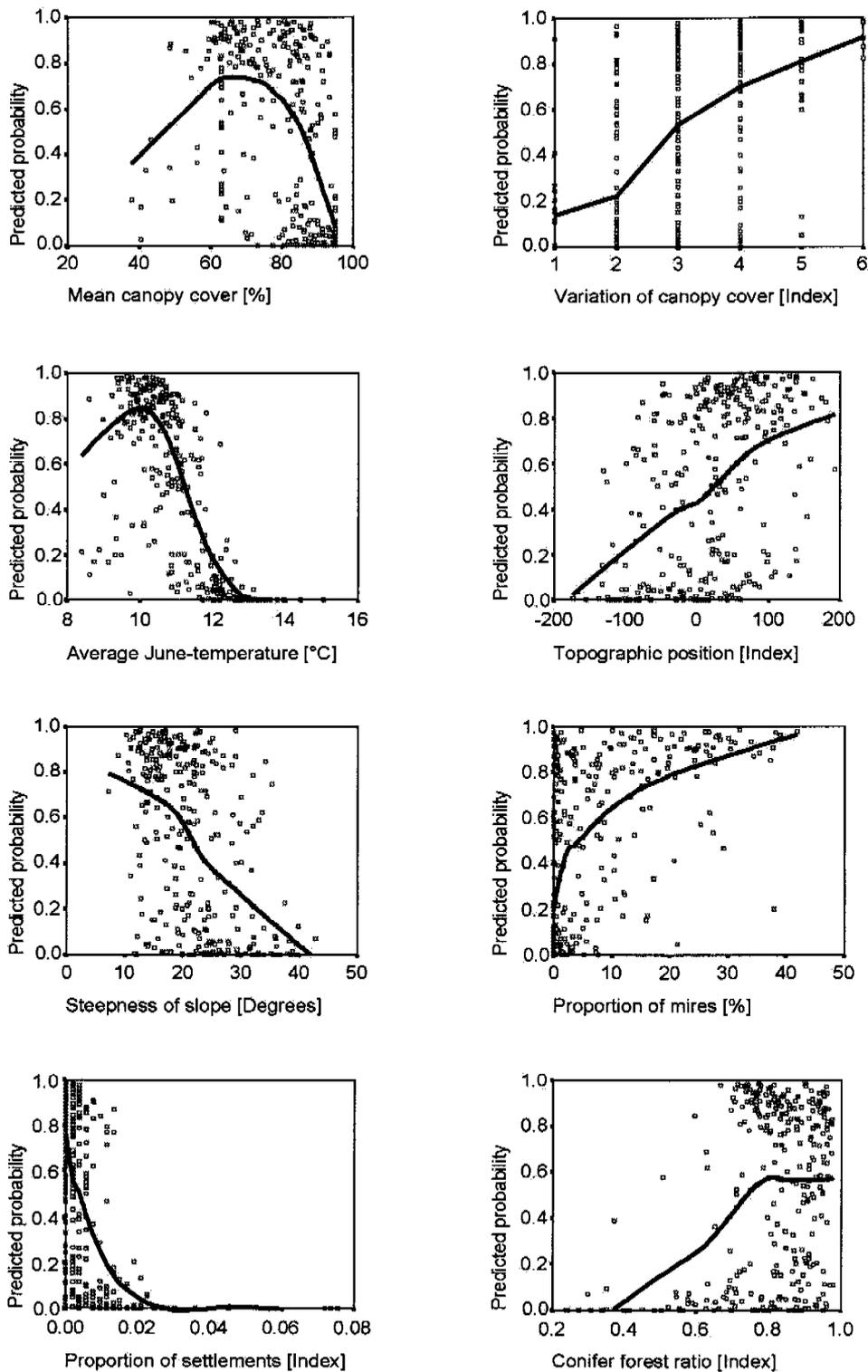


Figure 8. Response curves for Paper III/ Forest and landscape structure/ Pre-Alps. The variables selected by the model built with forest and landscape structure variables using data from the Pre-Alps are plotted against the probability for capercaillie presence predicted by the model. Response curves are fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

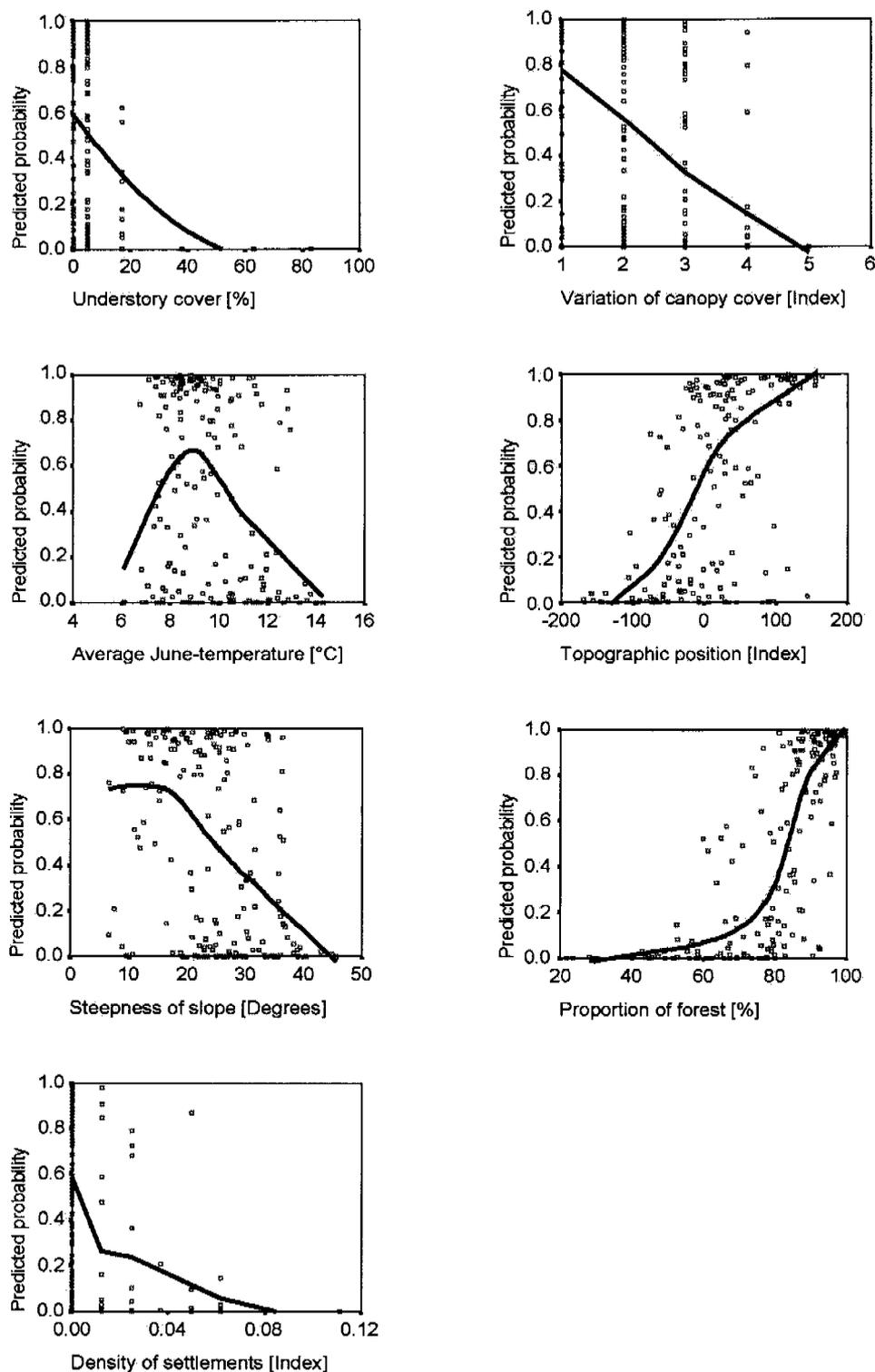


Figure 9. Response curves for Paper III/ Forest and landscape structure/ Alps. The variables selected by the model built with forest and landscape structure variables using data from the Alps are plotted against the probability for capercaillie presence predicted by the model. Response curves are fitted with a locally weighted least-squares method (LOWESS, SPSS11.0.1).

Acknowledgements

First of all, I would like to thank Prof. Dr. Harald Bugmann (ETH, advisor), Dr. Werner Suter (WSL, co-advisor) and Dr. Kurt Bollmann (WSL, co-advisor) for all their support during the last three years. During many short and long discussions they broadened my knowledge in conservation biology, landscape ecology and ecological modeling and helped me to take strategic decisions. Their critical reading and commenting of several manuscripts was highly appreciated. Special thanks go to Kurt Bollmann, my office mate, for countless discussions about scientific and other issues and for helping me to find my motivation again after difficult moments.

I am indebted to Prof. Dr. Ilse Storch for acting as external examiner of my thesis.

Many thanks go to the entire team of the research program "Forest-Wildlife-Cultural Landscape" WWK for their manifold support during my thesis. They enriched my time at the WSL by sharing ideas and comments in many stimulating discussions during coffee breaks, lunch, and group seminars or helped me solve methodological problems or with data assessment.

I would like to thank all members of the group of Forest ecology of ETH. The coffee breaks and social hours were good opportunities to discuss about the daily problems and pleasures of Ph.D. students or post docs.

I am grateful to Dr. Helene Wagner, Dr. Peter J. Weisberg, Dr. Lorenz Fahse and Dr. Andreas Huth for supervising my first steps in the fields of applied landscape ecology and ecological modeling. In two courses they instructed at ETH, they stimulated my curiosity for new scientific fields and increased my motivation for the thesis and for planning my further research career.

I am indebted to the whole community of grouse adepts of Switzerland and Central Europe. The regular meetings at different locations with different people were excellent opportunities to profit from interesting presentations, field excursions and numerous discussions and to improve my knowledge of grouse ecology and conservation. I always returned to WSL with new motivation and new ideas.

My gratitude goes to all people at WSL who helped me in many ways during the past four years. They supported me by providing equipment, software, and methodological knowledge, and by sharing ideas and comments in many stimulating discussions during coffee breaks, lunch, and institute seminars.

The Swiss Ornithological Institute, the “Centre de conservation de la faune et de la nature” of the canton of Vaud and several local grouse experts provided us large data-sets on capercaillie occurrence in the Alps, Pre-Alps and Jura Mountains.

This study received financial support from the Swiss National Science Foundation SNF (Grant Number 3100-065199), the Swiss Federal Research Institute WSL, the Swiss Agency for the Environment, Forests and Landscape SAEFL, and the Swiss Federal Institute of Technology ETH Zürich.

Special thanks go Marion Schmid for her love, patience and manifold support during the past four years.

I am grateful to my parents, who gave me the possibility to create and cultivate set-aside areas and to cut wood when I needed to get rid of the held-back physical energy that gathered in my body during long days in the office. Also, they made my studies possible.

Curriculum Vitae

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