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Modelling habitat suitability for the Capercaillie *Tetrao urogallus* in the national parks Bavarian Forest and Šumava

Miriam Teuscher[1*], Roland Brandl[1], Sascha Rösner[1,5], Luděk Bufka[2,3], Tomáš Lorenc[2], Bernhard Förster[4], Torsten Hothorn[5] and Jörg Müller[6]

[*] Corresponding Author

[1] AG Tierökologie, Fachbereich Biologie, Philipps-Universität Marburg, Karl-von-Frisch-Straße 8, 35032 Marburg, Deutschland
E-Mail: miriam.teuscher@gmx.de

[2] Verwaltung des Nationalparks und des Landschaftsschutzgebiets Šumava, Sušická 399, 341 92, Kašperské Hory, Tschechien

[3] Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamycka 1176, CZ-16521 Prague, Czech Republic

[4] Lehrstuhl für Strategie und Management der Landschaftsentwicklung, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Deutschland

[5] Institut für Statistik, Ludwig-Maximilians-Universität München, Ludwigstraße 33, 80539 München, Deutschland

[6] Nationalparkverwaltung Bayerischer Wald, Freyunger Straße 2, 94481 Grafenau, Deutschland

Modellierung der Habitateignung für das Auerhuhn *Tetrao urogallus* für die Nationalparke Bayerischer Wald und Šumava

Das Auerhuhn *Tetrao urogallus* hat eine starke Bindung an alte und strukturreiche Wälder. Diese engen Habitatpräferenzen und umfangreichen Raumansprüche bedingen, dass viele europäische Populationen dieses „Waldhuhns" aufgrund von Veränderungen in der Waldstruktur, aufgrund von Habitatverlust, aber auch aufgrund der Stressbelastung durch zunehmende Freizeitaktivitäten des Menschen stark rückläufig sind. Im Nationalpark Bayerischer Wald und dem Nationalpark Šumava wird das Auerhuhnvorkommen seit längerem erfasst. Ergebnisse der Kartierung der Auerhuhnpopulation in den Jahren 1972–1974 zeigten, dass die Populationsgröße im Nationalpark Bayerischer Wald seit 1945 von 250 Individuen auf lediglich 60 Individuen abgesunken war. In den Jahren 1984/1985 waren nur noch 16 Individuen nachweisbar. Zwischen 1985 und 2000 wurden daher zur Stabilisierung der Populationen 1,376 Individuen ausgewildert. Nach der Grenzöffnung wurden zwischen der Tschechischen Republik und Deutschland Grenzwege angelegt. Weitere grenzüberschreitende Wanderwege sind in Planung. Für die Planung dieser Wege werden räumlich hoch aufgelöste Karten der Habitateignung für das Auerhuhn benötigt, um eine Wegeführung mit möglichst geringen Auswirkungen auf die noch bestehenden Auerhuhnbestände sicherzustellen. Das Ziel der vorliegenden Studie war daher, die Habitateignung des Böhmerwaldes für das Auerhuhn flächendeckend (Nationalparke Bayerischer Wald und Šumava) mit genügender Auflösung zu bestimmen. Dazu wurden die Auerhuhnnachweise von 2000 bis 2005 auf ein Rastersystem (50 ha Rasterfläche) zusammengefasst sowie die Habitateigenschaften dieser Raster aus einer Befliegung im Jahr 2003 ermittelt. Mittels einer neuen Methode für die Schätzung generalisierter additiver Modelle, konnten die Meereshöhe über NN, liegendes Totholz, Kahlschlagflächen und ein gewisser Anteil an jungem Nadelwald als wichtige Faktoren für das ganzjährige Vorkommen des Auerhuhns identifiziert werden. Im Winter (November bis März) sind Höhe über NN und liegendes Totholz mit Mischwaldverjüngung wichtig. Verschiedene Methoden zur Evaluierung der Modelle zeigen, dass das Vorkommen des Auerhuhns realistisch abgebildet wird. Dabei ist die aus den Habitatmodellen geschätzte Habitateignung für die meisten Raster im Winter geringer als für das gesamte Jahr. Erstaunlicherweise fallen bei einer Evaluierung mit unabhängigen Daten (Auerhuhnnachweise 2006–2010; Habitateigenschaften Befliegung 2008) die Leistungswerte der Modelle besser aus, als bei einer Evaluierung mit den Daten, die für die Berechnung der Modelle verwendet wurden (Auerhuhnnachweise 2000–2005; Befliegung 2003). Dieser Unterschied wird auf das Vorkommen ausgesetzter Individuen in ungeeigneten Habitaten sowie eine vergleichsweise systematische Erfassung im zweiten Zeitabschnitt zurückgeführt. Die grenzüberschreitenden Karten für die Habitateignung bieten zum ersten Mal eine Grundlage für eine Besucherlenkung in beiden Nationalparks.

Key words: Habitat model, habitat suitability, boosting, conservation, Tetraonidae.

Introduction

The Capercaillie has extensive spatial requirements and needs specialized habitats (Rolstad 1988, Storch 1995). Based on this specific habitat requirements it is regarded as an umbrella species and management decisions for improving the situation of this species may also serve the needs for all other organisms living in its habitats (Suter et al. 2002, Pakkala et al. 2003). In central Europe and Scandinavia the species occurs in old coniferous or mixed forests. The intermediate canopy cover of these forests allows for a rich layer of ground vegetation dominated by bilberry *Vaccinium myrtillus*, which is as a main food source in summer (Bollmann et al. 2005, Gjerde 1991, Storch 1993b, Rolstad 1988, Baines et al. 2004). Due to the increasing intensity of land use and forest management in central Europe, populations of the Capercaillie are nowadays small and only loosely connected or even completely isolated from each other (e.g. Rolstad & Wegge 1989, Klaus & Bergmann 1994, Kurki et al. 2000, Mollet et al. 2003). Consequently, populations of the Capercaillie are declining in most parts of central Europe.

The Capercaillie population in the Bavarian Forest National Park declined from – 250 individuals around 1945 to 60 individuals between 1972 and 1974 (Scherzinger 2003). In 1984/1985, only 16 birds remained. Due to this dramatic decrease of population size, a release program was established: In the Bavarian National Park 1,376 individuals were released between 1985 and 2000 (Scherzinger 2003). Since the fall of the iron curtain between Germany and the Czech Republic in the early 1990th, a number of trails crossing the border have been established and further trails are planned. However, trails may direct visitors to the core areas of the Capercaillie distribution increasing the stress on the population of this bird species. The management of both parks urgently needs information about the habitat suitability for Capercaillie covering both parks to direct the activities of visitors but also other management activities without negative impacts on this endangered species. Thus, the main objectives of our study were, firstly, to develop a map that visualizes habitat suitability for the Capercaillie across the Bavarian Forest and Šumava National Park with a grain that allows meaningful management

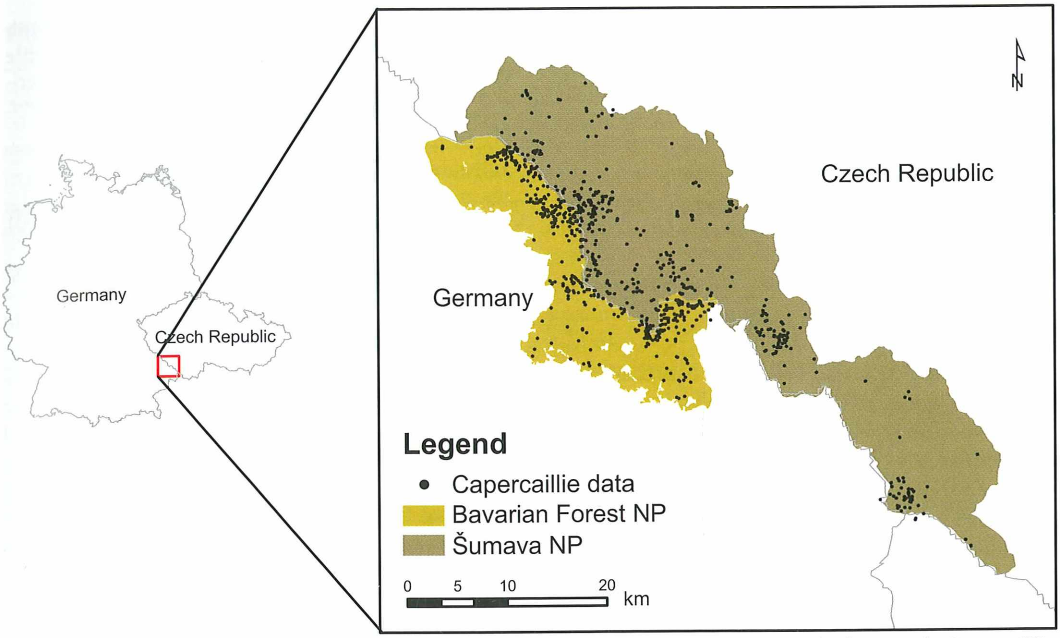

Fig. 1. Location of the study area in the Czech Republic (dark green) and Germany (light green). Capercaillie records from 2000 to 2005 are given as black dots. The two national parks comprise one of the largest forest landscapes in Central Europe (93,407 ha). – *Lage des Untersuchungsgebiets in der Tschechischen Republik (dunkelgrün) und Deutschland (hellgrün). Auerhuhn-Nachweise aus den Jahren 2000 bis 2005 sind als schwarze Punkte dargestellt. Beide Nationalparke umfassen mit einer Gesamtfläche von 93,407 ha eines der größten Waldgebiete Zentraleuropas.*

decisions. Secondly, we identified environmental variables that may affect the distribution of this species, and which may be used to predict the distribution in the future. To reach these two aims, we developed species distribution models covering the two national parks.

Material and Methods

Study area. The study was carried out in the Bohemian Forest within the area of the two national parks: the Bavarian Forest National Park, which is situated in south-eastern Germany and the adjacent Šumava National Park in the Czech Republic (Fig. 1). The former covers an area of 24,368 ha, the latter 69,039 ha.

Elevations range from 600 to 1,453 m a.s.l. On the Bavarian side, the total annual precipitation lies between 1,300 and 1,800 mm and the mean annual temperature ranges from 3.8°C to 8.4°C (Bässler 2004). The high montane forest (above an elevation of 1,100 – 1,200 m a.s.l.) is dominated by Norway Spruce *Picea abies*, with a small proportion of European Beech *Fagus sylvatica* and Mountain Ash *Sorbus aucuparia*. Below about 1,100 m spruce, beech and Silver Fir *Abies alba* prevail in the mixed montane forest (Walentowski et al. 2004). Snow cover is present at lower altitudes for about 100 days and at higher altitudes for almost 200 days of a year (Heurich & Neufanger 2005).

Habitat suitability models. To model habitat suitability we decided to use a grid system with a grid size of 50 ha. This grain is a compromise between the average home range size of the Capercaillie (550 ha, Storch 1995) and the spatial resolution needed for the park management. The grid was constructed on the basis of the Gauss-Krüger system. We used Capercaillie data from two time periods. Records from the years 2000–2005 for both national parks are non-systematic records of the presence of this species. These records include visual and acoustic observations, as well as records of nests, droppings, tracks and feathers. Rangers and scientists reporting all signs of Capercaillie occurrences are present year-round throughout the entire area of the national parks for various purposes (about 50 people on the German side).

Tab. 1. List of predictor variables used to develop and evaluate the models year-round 2003 and winter 2003 with their abbreviations, units, range and mean. Solar radiation and altitude were calculated from a SRTM (Shuttle Radar Topography Mission) – digital elevation model. All other environmental variables were derived from aerial photographs (see also Tab. 2). – *Umweltvariablen und deren Abkürzungen, Einheiten, Wertebereich sowie Mittelwert. Sonneneinstrahlung und Höhe wurden mithilfe eines digitalen Höhenmodells berechnet (siehe auch Tab. 2).*

Variable	Abbreviation	Unit	Range	Mean
longitude	X	m	4587121 - 4645811	4613901
latitude	Y	m	5399192 - 5451518	5428502
solar radiation from April to October	SoApOc	kWh	951 – 1293	1144
solar radiation from November to March	SoNoMa	kWh	120 – 354	236
build up area	blb	%	0 – 20	0.3
clear cut area	clc	%	0 – 33	1.2
coniferous stand - young	cnf_y	%	0 – 62	1.9
coniferous stand - medium	cnf_m	%	0 – 88	9.2
coniferous stand - old	cnf_o	%	0 – 99	34.9
deciduous stand - young	dcd_y	%	0 – 46	0.2
deciduous stand - medium	dcd_m	%	0 – 51	1.0
deciduous stand - old	dcd_o	%	0 – 96	7.1
lying dead wood	ldw	%	0 – 98	4.8
lying dead wood with coniferous regeneration	ldw_c	%	0 – 79	0.7
lying dead wood with deciduous regeneration	ldw_d	%	0 – 34	0.2
lying dead wood with mixed regeneration	ldw_m	%	0 – 74	0.8
meadows - cultivated	mdw_c	%	0 – 87	4.3
meadows - natural	mdw_n	%	0 – 70	3.2
meadows - wetlands	mdw_w	%	0 – 98	1.1
mixed stand - young	mxd_y	%	0 – 33	0.4
mixed stand - medium	mxd_m	%	0 – 71	1.3
mixed stand - old	mxd_o	%	0 – 89	12.1
roads	rds	%	0 -39	3.5
scrub pine	scp	%	0 – 71	0.9
standing dead wood	sdw	%	0 – 94	0.7
transition stands between forest, meadows and line vegetation	Trns	%	0 – 93	1.4
water bodies	wtr	%	0 – 79	1.1
altitude	altitude	m	595 – 1348	964
length of all marked hiking and biking trails	path length	m	0 – 7473	667

This coverage by observers justifies treating the data as presence-absence data. The data of the occurrence of Capercaillie from 2006–2010 are based on non-systematic records but also on a systematic sampling of droppings. For recording droppings, a team of 20 people covered the whole area of Capercaillie distribution in both national parks (2009–2010) and all 50 ha grids within the potential distribution of the species were visited during at least one excursion. For all records exact coordinates were available.

The total of 852 records between 2000 and 2005 and 1006 records between 2006 and 2010 were assigned to all 2,070 grid cells covering both parks. If there was at least one record of the species in a grid cell, the status of the cell was defined as "presence", otherwise as "absence". In a second step, only Capercaillie records from the winter (November–March, 325 in 2000–2005, 429 in 2006–2010) were assigned to the grid cells.

Environmental data were derived from a habitat map based on aerial photographs made during 2003 and 2008 (see Tab. 1). The map was intersected with the 50 ha grid system and coverage for each habitat type within each grid cell were calculated (in %). Mean values of elevation as well as solar radiation (for the periods from April to October and from November to March) were derived from a SRTM (Shuttle Radar Topography Mission) digital elevation model. Additionally, the lengths of marked hiking and biking trails for each grid cell were included in the set of variables. All in all, a set of 29 potential predictor variables was obtained for 2003 and 2008 (Tab. 1).

Two models were developed, one including the Capercaillie records throughout the year (model *year-round*) and one including only observations from winter (model *winter*, see also Tab. 2). For these models we used the data from 2000 to 2005 and within the text, figures and tables we refer to these models as *year-round* 2003 and *winter 2003*. For constructing the models and selecting variables, a new procedure described by Hothorn et al. (2011) was used. This procedure implements a component-wise functional gradient descent boosting algorithm for fitting a logistic additive model (Bühlmann & Hothorn 2007). The algorithm minimizes the negative log-likelihood function. The procedure starts with a constant model, computes residuals and then finds the regression model that best describes the residuals. This procedure is repeated. The stopping rule of iterations is determined via cross-validation (Bühlmann & Hothorn 2007). The final model is as complex as necessary but as parsimonious as possible (Hothorn et al. 2011). Subsequently, a stability selection procedure was performed (Meinshausen & Bühlmann 2010) and the variables that had a selection probability >50% in these calculations were regarded as being particular influential. In the present study we interpret the predicted probabilities of the occurrence of the Capercaillie as a measure of habitat suitability. Note that with our grain of 50 ha, several grids cover the home range of an individual. Therefore the presence/absence data do not indicate population size but the habitat use of the population.

For the evaluation of the models we used two basic approaches. First, we compared the predictions of the models *year-round 2003* and *winter 2003* with the actual records for 2000 to 2006 (internal evaluation; see Tab. 2). In a second step (further on labelled as *year-round 2008* and *winter 2008*) we plugged into the models the environmental data from 2008 and compared the predictions with the actual records from 2006 to 2010 (external evaluation; Tab. 2). These evaluations therefore use altogether independent data, nevertheless from the same region. For a visual evaluation of the models we present maps showing the predicted probabilities and we compare these probabilities with the actual records. For a more quantitative evaluation we inspected calibration plots (see Franklin 2009). These graphs plot predicted probabilities versus observed probabilities and provide thereby information whether the models are a fair representation of the distribution of the species). For a quantitative comparison of the model performances we calculated several metrics (Fielding & Bell 1997). Some of these metrics require transferring predicted probabilities into predicted presences and absences using a certain threshold. Furthermore, these measures of performance also depend on the prevalence of a species in an area (Fielding & Bell 1997, Manel et al. 2001). The simplest measure is the percentage of correctly classified cases (PCC). However, the costs of making an error in predicting the presence or absence of a species may be different and therefore we also present the sensitivity (proportion of correctly classified true positives) and specificity (proportion of correctly classified true negatives). We also give Cohen's kappa that describes the difference between the observed agreement and the agreement expected by chance. We estimated the threshold by specifying that for the predicted presences and absences the sensitivity should equal specificity. Numerous other criteria are possible (see Franklin 2009) and one has to tailor the criterion for each particular purpose. Although the criterion where false positives equal false negatives leads to inflated maps when transferring probabilities to predicted presences and absences, it ensures that we do not miss important areas. As a threshold-independent measure, the area under the curve (AUC) of the receiver-operating characteristic was used. AUC values vary between 0.5 and 1 and can be interpreted as the probability that for a randomly selected pair of presences and absences, the model will predict a higher score for the presences (Fielding & Bell 1997).

All statistical analyses were carried out with R v. 2.12.0 (R Development Core Team, 2010). Grid cells were computed with the 'RODBC' (Ripley & Lapsley 2010) and 'shapefiles' (Stabler 2006) packages. Boosting was done using the 'mboost' package (Bühlmann & Hothorn 2007, Hothorn et al. 2010). Values for assessing model performance were derived with the 'Presence-Absence' package (Freeman 2007).

Results

Between 2000 and 2005 the Capercaillie was recorded within 750 grid cells (prevalence 36.2%), and between 200 and 2010 in 268 grid cells (12.9%). In winter, the Capercaillie was recorded in 194 cells in 2000-2005, which corresponds to 9.3% of the study area. In 2006-2010 the species was recorded during winter in only 127 cells (6.1% of the study area). These data indicate a decrease of the area used by the Capercaillie population in the two national parks and a much more restricted distribution during winter.

The Capercaillie records of the time interval 2000-2005 and the environmental data for the year 2003 were used for the model *year-round 2003* (Tab. 2). The boosting procedure selected 18 environmental variables to predict occurrence of Capercaillie and their partial contributions are given in Fig. 2, which can be interpreted as a difference in log-odds ratios. Six variables were selected by the stability selection with a selection probability >50%. The probability of Capercaillie occurrence increased with altitude and with the amount of lying dead wood and lying dead wood with mixed regeneration, cleared areas as well as a small amount of young conifers. The fact that longitude also was selected by the stability criterion indicated

Tab. 2. List of models and corresponding data sets used to develop and evaluate the models. – *Modelle und Daten, die für die Entwicklung und Evaluierung dieser Modelle verwendet wurden.*

Model	Data	
	Predictor variables	Response variable
year-round 2003	Aerial photographs 2003	Capercaillie records 2000 to 2005 January to December (year-round)
external validation *year-round* 2008	Aerial photographs 2008	Capercaillie records 2006 to 2010 January to December (year-round)
winter 2003	Aerial photographs 2003	Capercaillie records 2000 to 2005 November to March (winter)
external validation *winter* 2008	Aerial photographs 2008	Capercaillie records 2006 to 2010 November to March (winter)

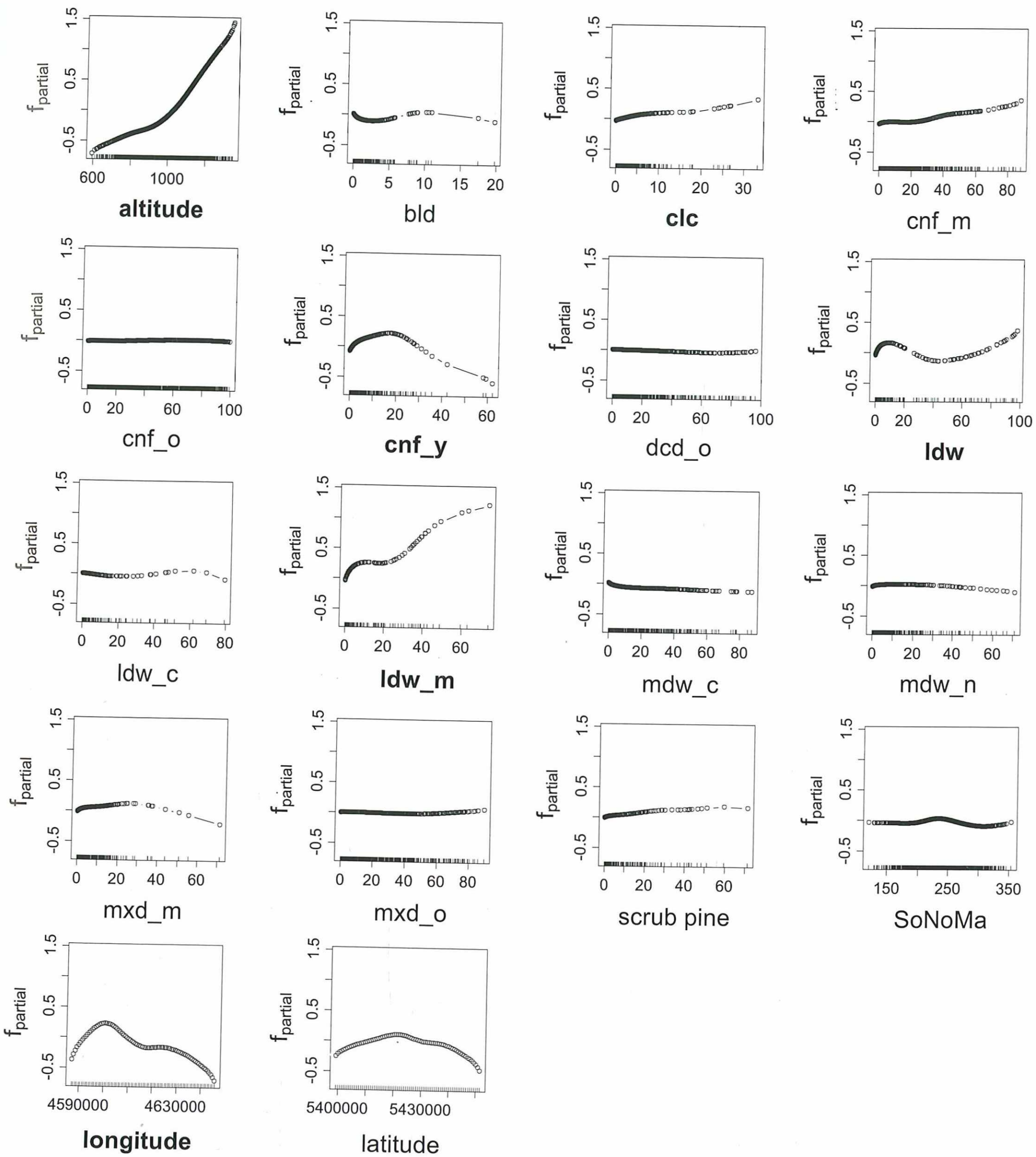

Fig. 2. Estimated partial effects of environmental variables (see Tab. 2) on Capercaillie presence/absence data collected from 2000 to 2005 in model *year-round 2003*. Variables selected by a stability selection with a selection probability >50% in bold. Partial effects can be interpreted as a difference in log-odds ratios. – *Geschätzte partielle Effekte der Umweltvariablen (siehe Tab. 2) auf Daten zum Vorkommen des Auerhuhns während des Zeitraums 2000–2005 im Modell „year-round 2003". Umweltvariablen, die bei der Stabilitätsüberprüfung mit einer Wahrscheinlichkeit >50% ausgewählt wurden, sind in Fettschrift dargestellt.*

that some variance in the data cannot be explained by the environmental variables at hand.

For predicting Capercaillie occurrence in winter with the model *winter 2003* (see Tab. 2), fewer variables are necessary than for the prediction of the bird's distribution in the model *year-round 2003*. The boosting procedure selected 16 variables and the stability criterion selected only three variables (partial contributions of the selected variables in Fig. 3). Capercaillie is

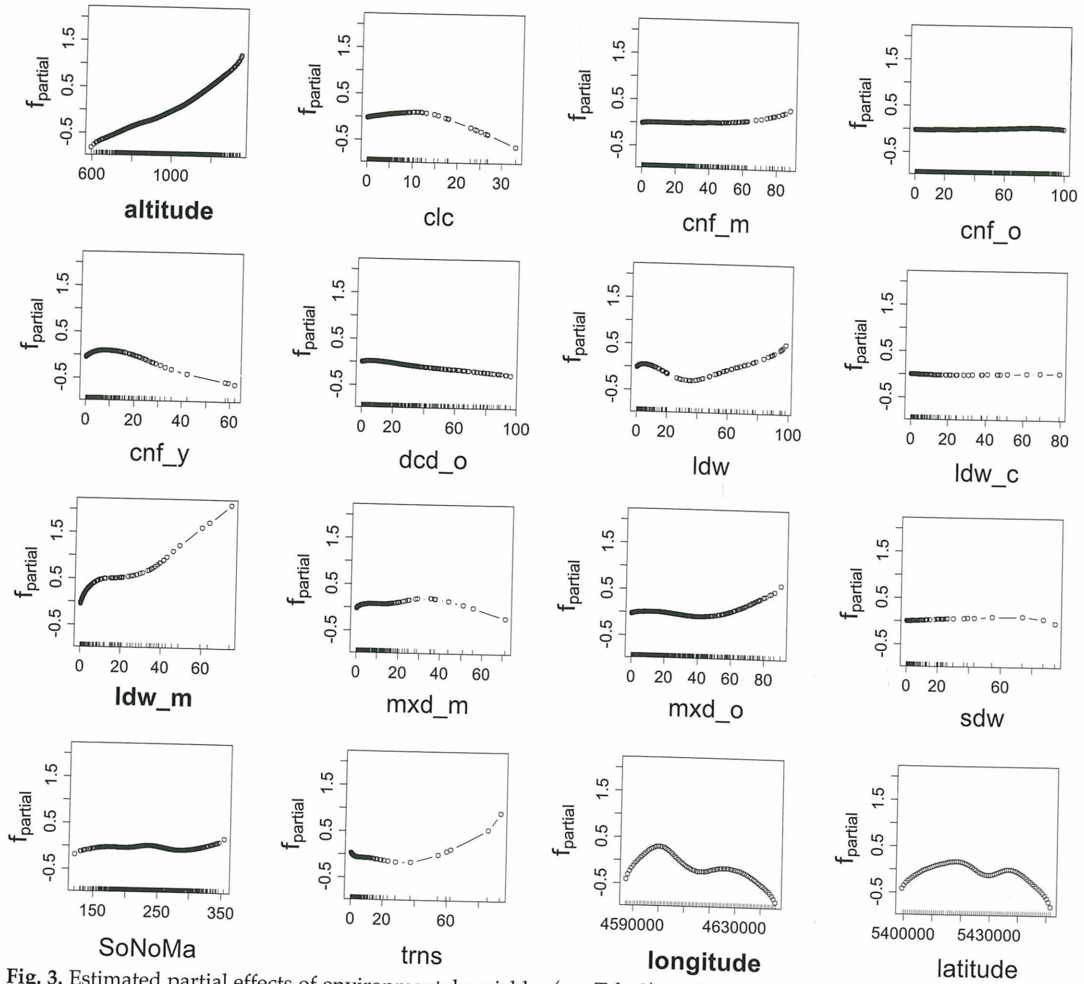

Fig. 3. Estimated partial effects of environmental variables (see Tab. 2) on Capercaillie presence/absence data collected from 2000 to 2005 in model *winter 2003*. Variables selected by a stability selection with a selection probability >50% in bold. Partial effects can be interpreted as a difference in log-odds ratios. – *Geschätzte partielle Effekte der Umweltvariablen (siehe Tab. 2) auf Daten zum Vorkommen des Auerhuhns während des Zeitraums 2000–2005) im Modell „winter 2003“. Umweltvariablen, die bei der Stabilitätsüberprüfung mit einer Wahrscheinlichkeit >50% ausgewählt wurden, sind in Fettschrift dargestellt.*

predicted to occur at high elevations, in open areas with lying dead wood with mixed regeneration (Fig. 3). Longitude was also selected by the stability criterion. Interestingly in both models the length of the trails in a grid had no influences on the occurrences of the Capercaillie.

A visual comparison of maps presenting the predicted probabilities calculated from the models and original records between indicated good performance of the models *year-round 2003* and *winter 2003*, although individuals were sometimes recorded in areas with low predicted probabilities (Fig. 4a, Fig. 5a). In all calibration plots the predicted probabilities of presences were very similar to the observed probabilities, irrespective of the data sets used (Fig. 6). This shows that our maps of the habitat suitability are a good representation of the real occurrences (see also Fig. 4, 5).

All internal and external evaluations of the two models showed good performance judged by the AUC-metric (Tab. 3). The external evaluations showed even a better performance than the internal evaluation, which is somewhat surprising. We estimated the threshold using the criterion sensitivity = specificity (Fig. 7) and

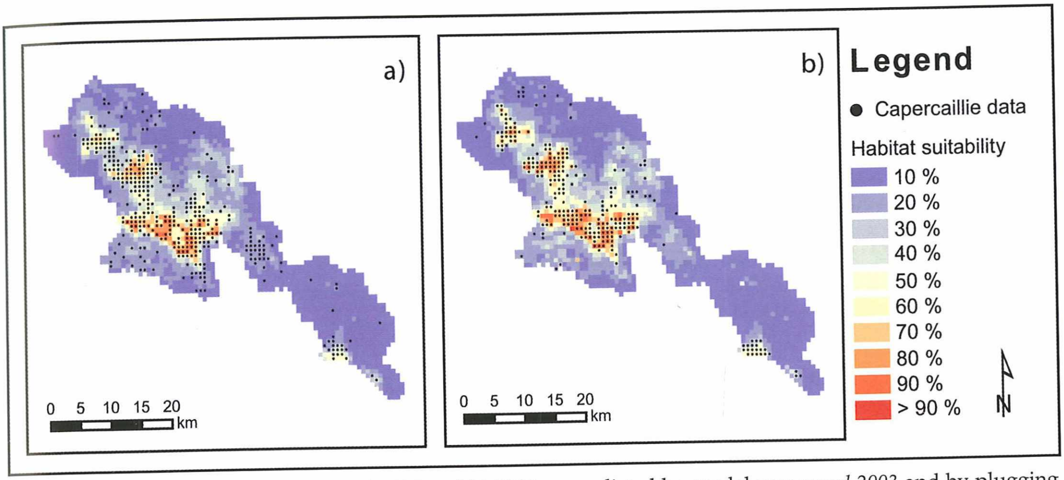

Fig. 4. Maps of habitat suitability for a) 2003 and b) 2008 as predicted by model *year-round 2003* and by plugging the environmental data from 2008 into that model. Black dots indicated the grids with field records of Capercaillie. – *Habitateignungskarten im Jahr a) 2003 und b) 2008, basierend auf dem Modell „year-round 2003" sowie bei der Benutzung der Umweltdaten von 2008 mit Modell „year-round 2003". Quadranten mit einem Nachweis für das Vorkommen des Auerhuhns sind durch schwarze Punkte gekennzeichnet.*

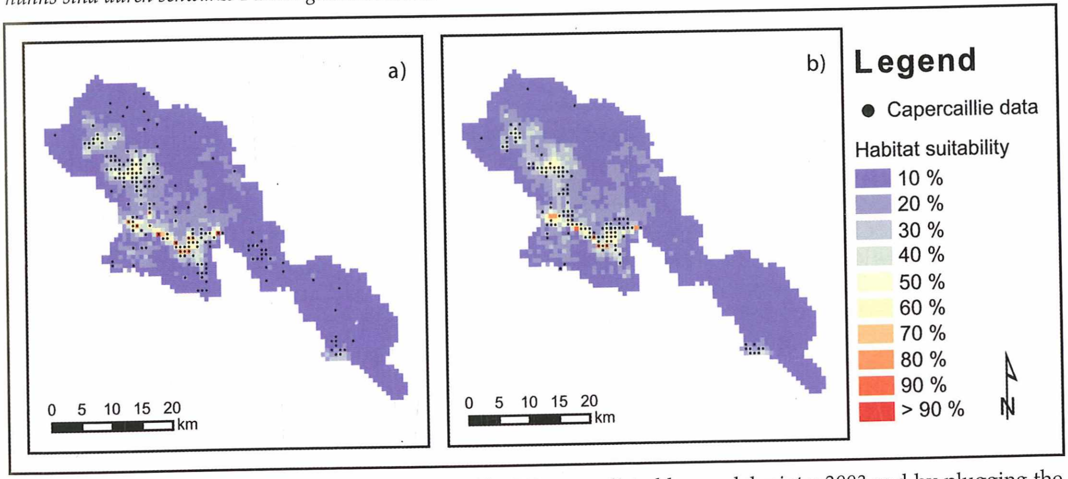

Fig. 5. Maps of habitat suitability for a) 2003 and b) 2008 as predicted by model *winter 2003* and by plugging the environmental data from 2008 into that model. Black dots indicated the grids with field records of Capercaillie. – *Habitateignungskarten im Jahr a) 2003 und b) 2008, basierend auf dem Modell „winter 2003" sowie bei der Benutzung der Umweltdaten von 2008 mit Modell „winter 2003". Quadranten mit einem Nachweis für das Vorkommen des Auerhuhns sind durch schwarze Punkte gekennzeichnet.*

used this thresholds to calculate the metrics. In all cases the model showed good performances and similar to the AUC-metric the models performed better during the external evaluation than during the internal evaluation (Tab. 3).

Discussion

Both models, *year-round 2003* and model *winter 2003*, showed an acceptable performance (Hosmer & Lemeshow 2000) and calibration plots indicated that the predicted probabilities are a fair representation of the occurrence of the Capercaillie across the two parks. The maps presented in Fig. 4 and 5 are therefore a good representation of the real habitat use in the field. Surprisingly, the external validation indicated a better performance than the internal evaluation. Indeed, between 2000 and 2005 Capercaillie distribution was much more widespread, with sev-

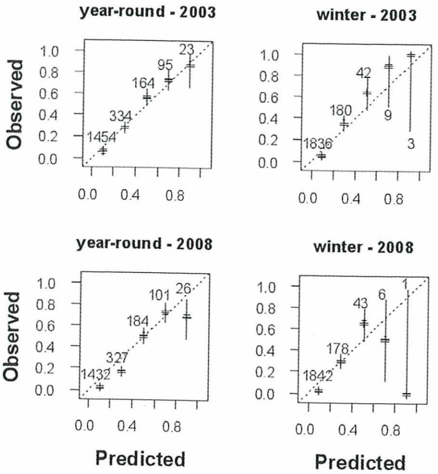

Fig. 6. Calibration plot with predicted versus observed values for the models *year-round 2003* and *winter 2003* as well as for evaluations of these models in *year-round 2008* and *winter 2008* (see Tab. 2). Note the good agreement between predicted and observed probabilities: all values scatter around the bisector. Above the symbols (with confidence interval) we present also the number of grids used to calculate the mean predicted and observed probabilities for each bin. – *Kalibrierungs-Plot mit den vorhergesagten gegenüber den beobachteten Vorkommenswahrscheinlichkeiten für die Modelle „year-round 2003" und „winter 2003" sowie den Evaluierungen dieser Modelle in „year-round 2008" und „winter 2008" (siehe Tabelle 2). Man beachte die gute Übereinstimmung zwischen beobachteten und geschätzten Wahrscheinlichkeiten: Alle Werte liegen um die 1:1-Linie. Die Werte über den Symbolen (mit Vertrauensbereich) geben die Zahl an Rastern an, die für jede Schätzung zusammengefasst wurden.*

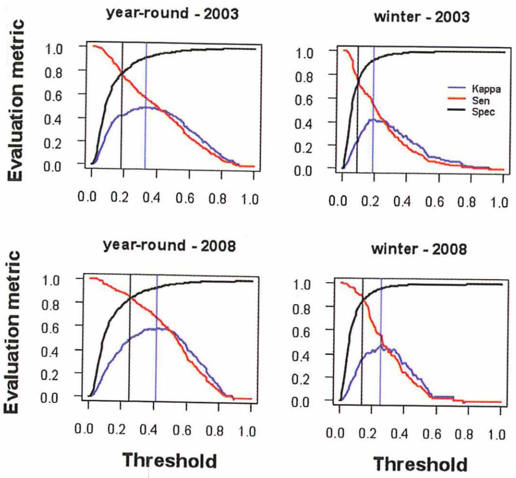

Fig. 7. Relationships of several criteria to evaluate the models (Kappa, sensitivity and specificity) from the threshold. The vertical lines show the maximum of Kappa (blue) and the crossing-point of sensitivity and specifity (black). Note the different thresholds when using as a criterion Kappa or sensitivity and specifity. The plots for 2008 are independent (external) evaluations of the models (see Tab. 2). – *Abhängigkeit einiger Kriterien für Modellgüte vom Bruchpunkt, ab dem ein Raster als besetzt eingestuft wird. Man beachte, dass sich je nach Kriterium (Maximum Kappa oder bei Sensitivität = Spezifität) unterschiedliche Bruchpunkte ergeben (vertikale Linien: Maximum Kappa – blau; Sensitivität = Spezifität – schwarz). Die Diagramme für 2008 sind unabhängige Evaluierungen der Modelle (siehe auch Tab. 2).*

eral records at lower altitudes and in grids with low habitat suitabilities as predicted by our model (Fig. 4a). The Capercaillie was even recorded close to human settlements. In general one expects that the performance of models decreases when applied to an independent data set (see Graf et al. 2006). However, the data from the period 2006 to 2010 were still from the same area as the model was calibrated for and hence may not be regarded as "truly" independent. Furthermore, between 1985 and 2000 birds were released at lower altitudes in the hope that they would re-colonize these areas (Scherzinger 2003). Since the end of the release program in 2000, the number of records throughout the area decreased considerably (Fig. 8, Fig. 4 b, Bufka 2011) and the occurrence of birds at lower altitudes also decreased. However, Capercaillie was distributed down to the Danube River one hundred years ago (Scherzinger 2003). Obviously, habitat has already changed in these areas before the release program. Finally, we want to note that the data of the occurrences of the bird used for the external evaluations in *year-round 2008* and *winter 2008* are in part based on a systematic sampling program leading to a more reliable data basis.

The variables selected by model *year-round 2003* agree with the known habitat requirements of the Capercaillie. Altitude had the highest selection probability using the stability selection approach. In Europe, the Capercaillie is mainly restricted to forests of the upper slopes of mountain ranges. It occurs at an elevation above 700 m in the Black Forest (Braunisch et al. 2008), 1,000 - 2,200 m in the Alps (Graf et al. 2005), in Cantabria at 1,200 - 1,600 m and in the Pyrenees at 1,700 - 2,000 m a.s.l. (Storch 2001). In Central

Tab. 3. Performance of th models *year-round* and *winter* using four different metrics: PCC = proportion of correctly classified cases, sensitivity = proportion of correctly classified true positives, specifity = proportion of correctly classified true negatives, Kappa = Cohen's kappa, AUC = area under the receiver operating curve. The internal model evaluation uses the same data as used for building the model (see also Tab. 2). For evaluation of PCC, sensitivity and specifity we estimated the metrics for the threshold where specifity ≈ sensitivity (see Fig. 7). Note that the AUC-value is independent of the threshold. Standard errors of the metrics in brackets. – *Leistungswerte der Modelle „year-round" und „winter": PCC = Anteil richtig klassifizierter Fälle, Sensitivity = Anteil richtig klassifizierter Vorkommen, Specifity = Anteil richtig klassifizierter Raster ohne Nachweis des Auerhuhns, Kappa = Cohen's kappa, AUC = Flächen unter der „receiver operating curve". Bei der internen Modell-Evaluation werden dieselben Daten verwendet, die auch für die Schätzung des Modells genutzt wurden (siehe auch Tab. 2). Für jede Evaluierung von PCC, Sensitivity und Specifity wurde der optimale Schwellenwert (Threshold) für die Klassifizierung der Raster geschätzt (Kriterium: Specifity ≈ Sensitivity; Fig. 7). Der AUC-Wert ist unabhängig von diesem Schwellenwert. In Klammern Standardfehler der Leistungswerte.*

Model	Evaluation	Threshold	PCC	Sensitivity	Specifity	Kappa	AUC
year-round 2003	intern	0.18	0.777 (0.00915)	0.768 (0.0218)	0.778 (0.0101)	0.421 (0.0213)	0.861 (0.0102)
year-round 2008	extern	0.25	0.838 (0.00909)	0.843 (0.0222)	0.837 (0.00869)	0.487 (0.0230)	0.909 (0.00966)
winter 2003	intern	0.09	0.724 (0.00983)	0.747 (0.0312)	0.721 (0.0104)	0.224 (0.0197)	0.835 (0.0154)
Winter 2008	extern	0.14	0.853 (0.00778)	0.866 (0.0303)	0.852 (0.00805)	0.360 (0.0267)	0.914 (0.0128)

Europe, the Capercaillie is regarded as a relict species, living "on the edge": Cold climatic conditions, large continuous forests, and low human disturbance are characteristics of its habitat. In Central Europe these conditions are only found in mountainous regions (Braunisch et al. 2008). Note that altitude does not only affect species distribution directly: Altitude is also a surrogate for temperature and rainfall that also influence distribution of species (Elith & Leathwick 2009). But as noted above, Capercaillie occurred in the investigated regions also at low altitudes several decades ago. We offer two explanations for this. Firstly, populations at lower altitudes were sink populations which survived only due to dispersal from the core areas and

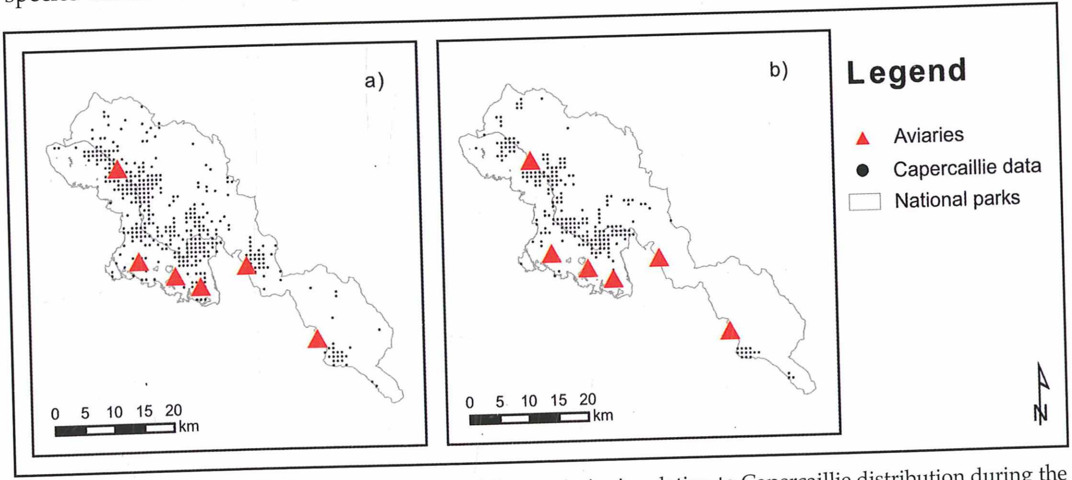

Fig. 8. Locations where Capercaillies were released from aviaries in relation to Capercaillie distribution during the period 2000–2005 (a) and 2006–2010 (b). After release birds (the program ended 2000) were still present close to the locations of the aviaries and the overall distribution was widespread. This pattern disappeared during the period 2006 to 2010. – *Lage der Auswilderungsvolieren innerhalb des Untersuchungsgebiets im Vergleich zu den Auerhuhn-Nachweisen in den Jahren 2000–2005 (a) und 2006–2010 (b). Kurz nach der Freilassung (bis 2000) konnten die Auerhühner noch nahe den Freilassungsstationen beobachtet werden und die gesamte Verbreitung war sehr ausgedehnt. In 2006–2010 ist dieses Muster nicht mehr erkennbar.*

Fig. 9. A dense field-layer, lying dead wood and a small amount of young conifers are important habitat factors for the occurrence of the Capercaillie. – *Dichter Unterwuchs, Totholz und ein kleiner Anteil an jungen Koniferen sind wichtige Habitatcharakteristika für das Vorkommen von Auerhühnern.* Foto: Sascha Rösner

during that time the population in the core area was large enough to produce a sufficient number of dispersers. Secondly, habitat suitability of forests at lower altitudes has decreased due to forest management or other processes.

Contrary to the general believe that the Capercaillie needs old forests, our models as well as published studies found that the species regularly uses small clear-cuts and patches of young successional stages of coniferous forests (Rolstad 1988, Storch 2001, Graf et al. 2007, Graf & Bollmann 2008). These young stages following the sapling phases seem to provide sufficient amount of invertebrates as well as bilberry (Lakka & Kouki 2009). Bilberry is the summer food for adults (Storch 2001) as well as shelter from avian predators (Storch 1993a, Wegge et al. 2005). Furthermore the amount of invertebrates is positively correlated with bilberry cover (Lakka & Kouki 2009). These insects are an important food source for chicks. Selås (2000) therefore found a positive relationship between bilberry production and winter survival. However, dense stands of saplings have a low biomass of epigaeic invertebrates, which are an important food for Capercaillie chicks (Wegge et al. 2005, Lakka & Kouki 2009). To conclude, our models show that even somewhat open areas provide suitable habitats for the Capercaillie (Fig. 9). Bark beetle infestation and the cyclone Cyril destroyed much of the mature coniferous forests along the mountain ridge on the Bavarian side of the study area (Fig. 9). On a long run, such disturbances may even promote the populations of the Capercaillie.

According to our models, the occurrence of Capercaillie increases with the amount of coniferous forest of middle age. Conifer needles are an important, nevertheless low-energy food source for the bird, especially in winter (Rolstad 1988, Scherzinger 2009). The amount of scrub pine *Pinus mugo* also positively influenced Capercaillie occurrence. The nutritional value of pine species exceeds the nutritional value of spruce and fir by 20% (Thiel et al. 2011).

The harsh winter conditions in the Bavarian Forest and the Šumava National Park demand special adaptations of species surviving these

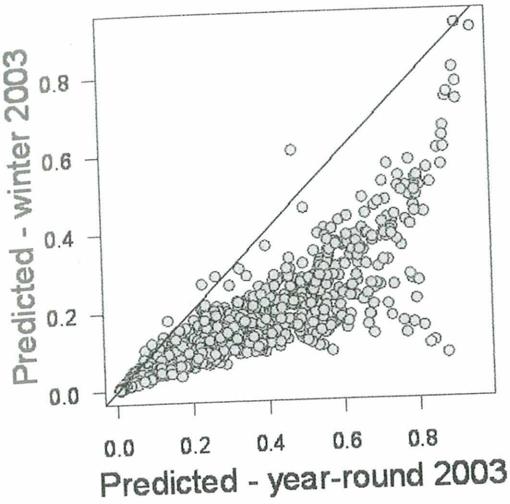

Fig. 10. Plot of predicted habitat suitability for the model *winter 2003* versus *year-round 2003*. Note that for almost all grids the habitat suitability is lower during winter compared during the estimates for the whole year. The line indicates the bisector. – *Das Diagramm zeigt die geschätzte Habitateignung für das Modell „winter 2003" im Vergleich zum Modell „year-round 2003". Man beachte, dass die Habitateignung der meisten Raster im Winter geringer ist als für das gesamte Jahr.*

winters. In winter, the major constraint is the lack of high-energy food and the Capercaillie has to rely on needles of conifers. Additionally, the time available for foraging is limited due to the short day. Therefore, in order to maintain a positive energy budget, birds must minimize their energy expenditure. We therefore expected that in winter the Capercaillie need to select different habitats than during year-round and therefore parameters selected by our models should have differed between the models *year-round 2003* and *winter 2003*. However, the model for the winter distribution was much simpler and only few variables were selected by the stability criterion. Plotting the habitat suitability of grids based on the model *year-round 2003* versus the suitability during *winter 2003* shows that both measures of habitat suitability are correlated. Nevertheless the model *winter 2003* predicted for most grids much lower probabilities than the model *year-round 2003* (Fig. 10). This indicates that in general the areas of both national parks provide harsh conditions during winter also leading to a more restricted distribution during this season (compare also Fig. 4a and 5a as well as Fig. 4b and 5b). Thiel et al. (2007) report-

Fig. 11. Capercaillie mainly feed on conifer needles, here: Norway spruce *Picea abies*, in the winter season. – *Das Auerhuhn ernährt sich im Winter überwiegend von Koniferennadeln, hier: Fichte* Picea abies. Foto: Michael Göggelmann

ed that during winter the Capercaillie prefer to roost in large trees in open forest stands close to forest edges. Single trees in open areas provide a good overview of the area and allow to spot approaching predators. In the Bavarian Forest one finds such single standing trees also within areas with a large amount of lying dead wood. Moreover, logs of dead wood lying upon each other may establish favourable microclimatic conditions even for snow burrows (Scherzinger, personal communication). Furthermore, the bird species needs to seek for shelter from wind behind lying logs or root plates to prevent heat loss. On root plates, the Capercaillie also finds grit, which is needed to digest the conifer needles (Storch 2001, Fig. 11).

Finally, we want to comment on the finding that in our models the length of hiking trails are not important for modelling the habitat suitability of the Capercaillie. However, existing trails are not necessarily a good proxy for the number of visitor. Most visitors concentrate on a few trails, many trails are only rarely used or even only seasonal open. Therefore, future investigations have to include the number of people using the trails and, furthermore, one needs to investigate the actual stress on the bird populations (for an example using Capercaillie see Thiel et al. 2011). Recent methods to measure stress hormones may be a good indicator of the actual stress (for a review see Sheriff et al. 2011) and such investigations are presently underway.

Our models provide reliable information of the predicted probabilities for the occurrences of the Capercaillie across the two national parks with a resolution of 50 ha. We interpret areas with a high predicted probability as core areas with suitable habitats for this enigmatic species. Furthermore, the interpretation of the variables selected by the model is consistent with the knowledge on habitat selection of the Capercaillie that accumulated during the last decades. These maps will form the basis for informed management decisions even across the borders between the two national parks.

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Abstract

The Capercaillie *Tetrao urogallus* relies on structurally rich forests and therefore functions as an umbrella species for plants and animals associated with old-growth conifer forests. Populations in Central Europe are declining due to changes in forest structure, habitat loss and increased stress due to human outdoor activities. The aim of this study was to analyse habitat suitability for the Capercaillie in the Bohemian Forest (comprising the Bavarian Forest and the Šumava National Park). Using a new method to build generalized additive models, we identified altitude, lying dead wood, clear cut areas and small amounts of young coniferous forest as important factors for the Capercaillie occurrence throughout the year. In winter, only altitude and lying dead wood with mixed regeneration were important. Calibration plots indicated that the calculated occurrence probabilities are a good representation of actual occurrences. Furthermore, our models showed a good performance when evaluated by the AUC-metric. Theses models provide for the first time detailed cross-boundary maps for management decisions (e.g. for new hiking trails), which are not in conflict with the conservation of the Capercaillie.

Modelace příhodnosti stanoviště tetřeva hlušce Tetrao urogallus v Národních parcích Bayerischer Wald a Šumava

Tetřev je kvůli své silné vazbě k bohatě strukturovaným lesům považován za reprezentativního zástupce mnoha druhů starých a bohatě strukturovaných jehličnatých lesů. Tyto úzké stanovištní preference a plošně rozsáhlé stanovištní nároky tohoto druhu ptáka mají za důsledek vysokou závislost na dynamice vývoje lesa. Středoevropské populace tohoto druhu se silně snižují, a to zejména díky ztrátě příhodných stanovišť, změn v struktuře lesa a zvýšenému stresovému zatíženív důsledku volnočasových aktivit člověka. V Národním parku Bavorský les se systematicky mapuje výskyt tetřeva od roku 1971. Výsledky tohoto mapování v letech 1972-1974 ukazují, že velikost populace se od roku 1945 (– 250 jedinců) snížila na pouhých 60 jedinců. V letech 1984/1985 zbylo jen 16 jedinců, poté byl zahájen program aktivního odchovu a vypouštění. Mezi lety 1985 a 2000 bylo v Národních parcích Bavorský les a Šumava vypuštěno

do volné přírody 1376 jedinců (Scherzinger, 2003). V rámci otevírání hranic mezi Českou republikou a Německem byly otevřeny nové přeshraniční turistické stezky a otevření dalších je plánováno. Proto je zapotřebí získat prostorové informace o vysokém rozlišení týkající se vhodnosti stanoviště pro tetřeva, aby bylo možné usměrnit pohyb návštěv zjištění níků za vyloučení negativního vlivu na populaci tetřeva. Cílem předkládané studie proto bylo detailní zjištění příhodnosti stanovišť pro tetřeva na celé ploše Národních parků Bavorský les a Šumava. Za tímto účelem byly shrnuty data o rozšíření tetřeva do rastrového systému (velikost čtverce 50 ha) a vlastnosti stanoviště v tomto systému zjištěny z leteckého snímkování z roku 2003. Pomocí nové metody k odhadnutí aditivního modelu GAM (generalized additiv boosting modell) byly identifikovány nadmořská výška, ležící mrtvé dřevo, plochy holosečí a malý podíl mladého jehličnatého lesa jako důležité faktory pro celoroční výskyt tetřeva. V zimě jsou rozhodujícími faktory nadmořská výška a ležící dřevo s zmlazením smíšeného lesa. Přitom je vhodnost stanoviště v zimě odhadovaná podle těchto modelů pro většinu čtverců v zásadě nižší než po celý zbytek roku. Překvapivé je, že při vyhodnocení s nezávislými soubory dat (pozorování tetřevů 2006-2010, vhodnost stanovišť podle leteckého snímkování 2008) jsou výsledky těchto modelů lepší, než při vyhodnocení s soubory dat, které byly pro výpočet modelů použity (pozorování tetřevů 2000-2005, vhodnost stanovišť podle leteckého snímkování 2003). Tento rozdíl je možné vysvětlit náhodným výskytem vysazenými tetřevy v nevhodných stanovištích stejně jako systematičtějším sběrem dat v druhém období sledování. Přeshraničně vypočítané mapy vhodnosti stanovišť tak poprvé nabízejí podklad k usměrnění návštěvníků v obou Národních parcích.

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Miriam Teuscher, Jg. 1985; M.Sc., Studium an den Universitäten Marburg und Bergen (Norwegen), seit März 2011 im Büro für Faunistik und Landschaftsökologie für die Erstellung ornithologischer Fachgutachten zuständig, ehrenamtliche Tätigkeit für den Mellumrat e.V. (Wat- und Wasservogelzählungen, floristische und faunistische Kartierungen, Umweltbildung) sowie den Verein Jordsand und die Vogelwarte Radolfzell (Mithilfe bei der Vogelberingung), Mitglied der Deutschen Ornithologen-Gesellschaft und des Mellumrat e.V.

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