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# Winter habitat selection and conservation of Hazel Grouse (*Bonasa bonasia*) in mountain forests

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**Abstract** The Hazel Grouse (*Bonasa bonasia*) has suffered from habitat loss due to changes in forestry practices in many regions of Europe. The widespread conversion of structurally heterogeneous to uniform, single-layered stands has caused many of its populations to decline. The trend in multi-functional forestry towards more dynamic processes and natural rejuvenation offers a unique opportunity to restore many habitats of Hazel Grouse in core areas of its actual distribution. As the Alps represent a stronghold of Hazel Grouse distribution in Central Europe, we aimed to determine the species–habitat relationship in mountain forests. We assessed the distribution and characteristics of Hazel Grouse habitat in a forest reserve of the Swiss Alps. Abiotic, structural and vegetation characteristics were investigated at the small scale, and abiotic and forest inventory data at the large scale. We compared the habitat characteristics of used and unused forest stands with a raster system consisting of bird presence and absence cells by applying a logistic regression. Hazel Grouse preferred stands with high proportions of tall rowans, forest edges, and a dense shrub layer at the small scale. Rowans had the strongest influence on Hazel Grouse occurrence. At the large scale, Hazel Grouse preferred forests with large proportions of alder and a diverse mosaic of canopy closure and stand structure. For 44% of the study area, the large-scale model predicted a probability of Hazel Grouse occurrence of more than 0.5. Our data supports the recommendation that the availability of suitable habitat for Hazel Grouse can be increased by natural reforestation of tree-fall gaps and stands with bark beetle infestation, as well as by enhancing the proportion of old-growth stands. Both measures will augment the shrub cover and number of rowan trees, two essential habitat and food resources for Hazel Grouse in mountain forests.

**Keywords** Alps · *Bonasa bonasia* · Food plants · Habitat suitability model · Multi-species management · Switzerland

## Introduction

Mountain ecosystems are generally regarded as hotspots of biodiversity and priority regions for conservation (Körner and Spehn 2002; Körner 2004). In particular, mountain forests cover one quarter of the mountainous areas of the world. In Central Europe, these forests provide habitats for a multitude of species, and may function as important source of colonizers for the surrounding lowland areas. This is reflected in the present distribution of several habitat specialists, like the Hazel Grouse (*Bonasa bonasia*). Aside from some isolated occurrences in lower mountain ranges, its Central European distribution is largely restricted to the Alpine region (e.g., Bergmann et al. 1996; Klaus et al. 2003; Klaus and Bergmann 2004). Thus, the conservation of forest habitats in the Alps contributes significantly to the viability of Hazel Grouse and other habitat specialists or threatened species at the large scale. This also applies to Switzerland, where forests are the largest near-natural habitat and they are a stronghold of

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biodiversity (Bollmann et al. 2009; Scheidegger et al. 2010). They cover 31% of the country's territory (Brändli 2010) and provide habitats for around 20,000 species (Meyer and Debrot 1989). Half of all breeding bird species in Switzerland use forests for breeding and feeding (Keller and Zbinden 2001).

During the last century, forest policies and changes in forest use have resulted in a shift towards even-aged high forests (Schönenberger 2001). For economic reasons, forestry harvesting has decreased significantly in Switzerland, while the standing stock of wood has permanently increased (Brändli 2000; Wildi and Wohlgemuth 2007). Compared to natural forests, young serial stages with pioneer tree species and old-growth stands with gaps are underrepresented in semi-natural and even sustainable managed forests (Bollmann et al. 2009). In general, there is a specific deficit in structural richness and heterogeneity. Consequently, habitat specialists of open and heterogeneous forests with warm microclimatic conditions, e.g., "coppice with standard," have become rare (Scherzinger 1996). They are often threatened and of conservational concern.

The Hazel Grouse *Bonasa bonasia* is a striking example of a species that suffers from changes in forest management and a trend towards uniform stands. The species has lost most of its former distribution in the lowland of western and Central Europe (Scherzinger 1976; Hagemeijer and Blair 1997; Burfield and van Bommel 2004). Whereas the species is still common and widespread in Asia, the Hazel Grouse is endangered throughout Europe (Swenson and Danielsen 1991; Storch 2000), listed in Appendix 1 of the European Birds Directive (2009/147/EC), and classified as a vulnerable species that is a priority for conservation in Switzerland (Keller et al. 2001; Bollmann et al. 2002). Over the course of decades, lowland habitats in Switzerland became unsuitable and fragmented due to forest succession and changes in forest use (Zbinden and Blattner 1998). Thus, the Hazel Grouse is now restricted to mountain forests, where small-scale changes in site conditions and natural disturbances support stand heterogeneity, and forest practices have not inhibited the development of light-demanding food species of the genera *Sorbus*, *Betula*, *Salix*, *Corylus*, *Crataegus*, *Alnus*, *Populus*, *Rosa*, and *Rubus* (Blattner 1998). These have been removed selectively, as they represented unwelcome competitors to the target tree species in forestry (Blattner 1998; Lieser 2003). However, the buds and catkins of these wood genera represent important elements of the winter food of Hazel Grouse.

An upwards shift in the realized niche towards mountain ecosystems has also been documented for other habitat specialists that suffer from changes in habitat use, deterioration or intensification in lowland areas: Black Grouse

*Tetrao tetrix* (Ludwig et al. 2008), Whinchat *Saxicola rubetra* (Müller et al. 2005; Horch et al. 2008), and Tree Pipit *Anthus trivialis* (Marti 2004). Thus, the Alps are a stronghold of the remaining population of these bird species in Central Europe, but at the same time they probably represent the edge of the fundamental ecological niche for these birds rather than their optimal niche. As a consequence, population densities are generally low, because food resources and time for breeding are limited at higher altitudes due to short vegetation periods. The Hazel Grouse is a poor disperser (Swenson 1991; Åberg et al. 1995; but see also Montadert and Léonard 2006), and a recolonization of remote lowland habitats cannot be expected in the near future (Pulliam 2000). Thus, the populations in the Alps must be conserved to ensure that this species does not suffer from regional extinction.

Since habitat loss and deterioration are considered the most important threat to biological diversity (European Environment Agency 1998; IUCN 2008), the accurate analysis of species–habitat relationships is indispensable for animal conservation. Habitat selection refers to a hierarchical process of behavioral responses which may result in the disproportionate use of habitats that influence the survival and fitness of individuals (Hutto 1985; Block and Brennan 1993). The selected habitat can be assessed by comparing used with unused habitats (Jones 2001). Such a comparison can be achieved with habitat models that formalize the relationship between a species and environmental factors (Morrison et al. 1998; Scott et al. 2002). Holloway et al. (2003) recommended that such information should be used to develop species action plans. They are especially valuable if they utilize small- and large-scale analyses to predict the distribution and abundance of a species (Mazerolle and Villard 1999; Storch 2002; Graf et al. 2007).

The Hazel Grouse is a territorial forest bird species with specific habitat and food requirements. It populates early seral stages of forests with their transient pioneer communities that result from natural disturbances such as fires, snow breaks, avalanches, or storms (Scherzinger 1976). Small rejuvenation areas embedded in old-growth forests and the proximity of water courses and mires are also suitable as Hazel Grouse habitats (Swenson 1995; Sachot et al. 2003). The habitat requirements of Hazel Grouse have been investigated in several studies in boreal and temperate forests of Fennoscandia, Asia and Central Europe (e.g., Eiberle and Koch 1975; Wiesner et al. 1977; Koch 1978; Zbinden 1979; Klaus 1991; Kämpfer-Lauenstein 1997; Sachot et al. 2003; Åberg et al. 2003; Mulhauser 2003; Mathys et al. 2006; Rhim 2006; Müller et al. 2009). Central European studies have mainly focused on low mountain ranges rather than the higher areas of the Alps.

Forest reserves have become a valuable and effective tool for supporting natural dynamics and managing forests so as to favor threatened species and the overall biodiversity of a biogeographic region (Bollmann et al. 2009). The forest reserve of Amden in the higher mountain and subalpine zone of the Swiss Pre-Alps is a representative example. The reserve was established in the year 2006 with the aim to extend and enhance the habitat and its quality for the local Capercaillie (*Tetrao urogallus*) population (Ehrbar 2006). Population abundance and preferred habitat variables have been investigated and described by Bollmann et al. (2005), Friedrich (2006), Imhof (2007), and Lanz and Bollmann (2008). As Capercaillie is known to be an umbrella species (Suter et al. 2002), other specialized, co-occurring bird species of semi-open and well-structured forest stands of mountain forests should benefit from habitat measures intended for Capercaillie (Bollmann et al. 2004; Bollmann 2006). This guild includes the Hazel Grouse, for which Switzerland has special international responsibility (Keller and Bollmann 2001). Both species of forest grouse, Capercaillie and Hazel Grouse occur in the forest reserve. With the overall goal being to develop an appropriate reserve management that includes the habitat requirements of both species, we intended to obtain knowledge on the distribution and habitat use of the elusive Hazel Grouse.

The aim of this study was to quantify the habitat requirements of Hazel Grouse in an Alpine area. For this purpose, we (1) assessed the distribution of the species in late winter by noninvasive transect surveys, (2) measured habitat variables at two spatial scales, (3) compared used habitat with unused habitat, and (4) developed a predictive habitat model for Hazel Grouse across the entire study area.

## Methods

The study was conducted in the special forest reserve of Amden (47°10′N, 9°13′E) in the Pre-Alps of the canton of St. Gallen, Switzerland. This reserve comprises the large contiguous woodland on both sides of the watershed of the rivers Linth and Thur. The forest reserve has an area of 1,772 ha, of which 975 ha are documented to be forest (Ehrbar 2006). Average annual precipitation amounts to 1,930 mm. The phytosociological map of the forest stands reports 253 different units, including transitions and tessellations. This large number of stand units is the result of a high variability in site conditions, especially in geology and soil types. The altitude of the forest reserve ranges between 1,041 m and 1,800 m a.s.l. This range corresponds to the phytosociological altitudinal belts "montane," "upper montane," and "subalpine." Fir (*Abies alba*)–beech

(*Fagus silvatica*) and fir–spruce (*Picea abies*) stands dominate the forest reserve and cover 83% of the forest area (Ehrbar et al. 2010). The reserve is characterized by a heterogeneous mosaic of forests and mires with large and small fens (Brülisauer 2006). The study area covered the eastern part of the reserve, with its two main directions being southwest and northeast. The study area had a surface area of 6.14 km$^2$ and consisted of a regular grid with 393 raster cells. Each cell had a quadratic extent of 125 m × 125 m and covered an area of 1.56 ha. This area corresponds to the average size of a stand unit (1.46 ha) in the forest reserve.

Data were collected between March 27th and May 27th, 2007. Territorial activity and pair bonding is pronounced during this time of the year, which climatically corresponds to late winter in the study area. This period is also most suitable for detecting indirect evidence of the species (e.g., droppings), because the area is completely covered with snow. The ongoing snow-melting process accumulates signs of the species' habitat use from the whole winter season. Accordingly, our data represent habitat use in winter, a season when abundance and distribution of winter food significantly characterize the realized ecological niche of the species (Swenson 1995).

### Species data

The grid raster was used to systematically document the number and distribution of indirect evidence of Hazel Grouse. We applied a transect survey method that standardized the effort for every raster cell. Therein, we followed a curved transect line from the basement to the highest elevated border of each raster cell using a GPS (Haicom 303S CF) (Fig. 1). The shape and length (300 m) of the transect line and the respective area of 0.9 ha (58% of the cell's size) guaranteed that all major habitat and vegetation types of a cell were covered by the survey.

Indirect evidence such as droppings, feathers, footprints and snow caves was thoroughly searched for on the transect line and within a 15 m wide band on both sides of the line. Droppings accounted for more than 90% of the species data. Most of the droppings and traces are generally found in the proximity of food plants of Hazel Grouse (Kaiser et al. 2003; M. Blattner, pers. commun.; R. Hess, pers. commun.) and below small coniferous trees, which are often used as sleeping and resting sites (Kaiser et al. 2003). The positions of the species' signs of habitat use were recorded with the GPS receiver on a handheld computer (hp iPAQ hx2100 with ArcPad, version 7.0.1). If less than a quarter of a raster cell could be inspected due to topographic constraints, the raster cell was excluded from the analysis. Otherwise, we followed the transect line as long as possible. We cannot exclude a certain bias in the
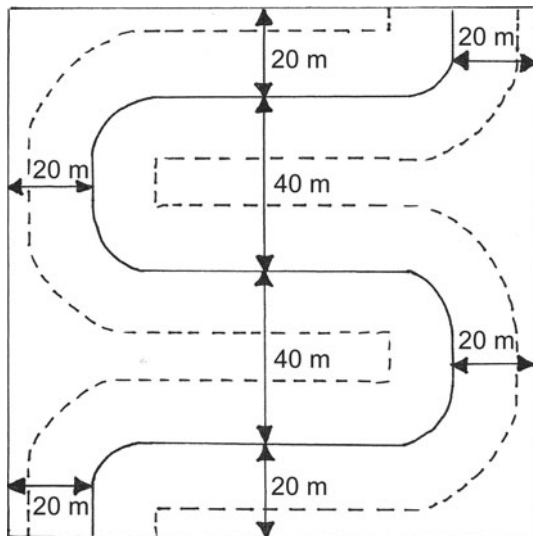
**Fig. 1** Schematic illustration of the shape and dimension of the transect line that was used to search for indirect evidence of Hazel Grouse occurrence in each grid cell (125 m × 125 m). *Arrows* denote line-specific buffer distances of the survey area

detectability of Hazel Grouse signs during the field period because the snow-melting process accelerated at the end of the season. However, we judge this effect as negligible, as the plant development is delayed at this altitude and the ground vegetation did not hide the droppings during the last phase of the field season.

All 63 raster cells that contained indirect evidence of Hazel Grouse presence were defined as presence cells. Among the remaining raster cells, we selected 65 random points by considering the main stratification of the habitat. Thus, cells with a random point, hereafter referred to as "absence cells," were proportionally distributed over the three main forest types (fir–beech forest, fir–spruce forest, remaining forest types) and the two main aspects of the study area. Each absence cell contained only one random point, so as to reduce autocorrelation among absence cells. This stratified random design guaranteed that the habitat variable of the absence cells represented the range and diversity of habitat conditions in the study area.

Habitat data

Habitat data were collected at two spatial scales. We aimed to represent both preferences of Hazel Grouse when exploiting a territory and compositional needs of the species in a territory. We recorded 29 habitat variables in plots of 25 m × 25 m (625 m$^2$) for the small-scale analysis (Table 1). According to Bollmann et al. (2005), a minimal plot area of 500 m$^2$ is needed to assess stand structure in mountain forests. Habitat variables were recorded in presence and absence plots. The first detected evidence of

Hazel Grouse in a raster cell was used as the center of the presence plot, whereas the random points were used as the centers of the absence plots. The set of variables consisted of climatic, topographic, structural and compositional variables. Variables were assigned to the tree (≥5 m), shrub (≥0.5 m, <5 m), and field (<0.5 m) layers to characterize the texture of the stands. We also included important food plants of the Hazel Grouse (Koch 1978; Zbinden 1979; Glutz von Blotzheim 1981; Jacob 1988; Klaus 1991; Bergmann et al. 1996; Zbinden and Blattner 1998; Hess, pers. commun.). Twenty-six out of the 29 variables were directly assessed in the field. The "structure" and "food plant" variables of the herb layer (Zbinden 1979; Bernard-Laurent and Magnani 1994) were recorded after snowmelt in all plots. The variable "altitude" was derived from a digital terrain model (dtm) with a resolution of 25 m × 25 m [dtm25; DHM25$^©$ 2004 swisstopo (DV033492)]. We used "temperature" and "solar radiation" as proxies for the local climate. Temperature was interpolated from the national network of meteorological stations using long-term monthly means (March–May) and the dtm25 according to Zimmermann and Kienast (1999) and Zimmermann and Roberts (2001). Solar radiation was calculated from the dtm25 using the method of Kumar et al. (1997), which considers topographic shading effects.

At the large scale, habitat assessment was conducted for the entire raster cell (125 m × 125 m). We used forest stand data of the forest inventory of the canton of St. Gallen (unpublished data) for this analysis. The inventory includes spatially explicit forest data for each stand. We adopted 15 variables with potential importance to Hazel Grouse (Table 2). Since forest stands varied in surface and shape, the variables were calculated in proportion to their occurrence in each raster cell. We also derived new variables from the forest stand data, such as the number of different stand structures per raster cell, the number of different canopy closures, the number of different seral stages, and the number of forest stand units, as well as the inter-stand edge length.

Model building and evaluation

We used Hazel Grouse presence/absence data as a response variable and habitat data at the small and large scale as predictor variables to build models with logistic regression (general linear model with binomial errors and logit function: Harrell 2001; Quinn and Keough 2002). A separate analysis was conducted for both scales, because variables from different scales should not be analyzed together (Morrison et al. 1998). Statistical analyses were performed in the statistical environment R, version 2.5.0 (R Development Core Team 2008), complemented by the package Design (version 2.0–12; Harrel 2001).

**Table 1** Variables that were used to characterize the habitat plots (25 m × 25 m) for the small-scale analysis

| Variable | Definition |
|---|---|
| Temperature | Monthly mean of average temperature (1961–1990) in °C (Zimmermann and Kienast 1999; Zimmermann and Roberts 2001) |
| Solar radiation | Monthly global potential shortwave radiation kJ/day = monthly potential diffuse shortwave radiation (Kumar et al. 1997) + monthly potential direct shortwave radiation (Kumar et al. 1997) |
| Slope | Slope in ° |
| Altitude | In m a.s.l., derived from dtm25 |
| Forest edge | Total length of boundary between forest and gaps/clearances in m |
| Gaps | Number of gaps in a plot with a surface ≥ 10% of plot area |
| Area of gaps | Area of gaps in a plot estimated in 10% steps |
| Brooks | Total length of brooks in m |
| Basal–branched trees | Total edge length of basal-branched coniferous trees in m |
| Lying deadwood | Total length of lying deadwood in m (length and height ≥ 0.5 m) |
| Deciduous trees | Number of deciduous trees ≥ 5 m |
| Small deciduous trees and bushes | Number of deciduous trees and bushes (height: ≥0.5 m, <5 m) |
| Coniferous trees | Number of coniferous trees ≥ 5 m |
| Small coniferous trees | Number of coniferous trees (≥0.5 m, <5 m) |
| Stand structure | Stand structure in four categories: |
|  | 1 = one-layered |
|  | 2 = two-layered |
|  | 3 = three-layered |
|  | 4 = multi-layered |
| Stem distribution | Stem distribution in four categories: |
|  | 1 = crowded [defined as canopy closures 1 and 2 of the LFI (Keller 2005)] |
|  | 2 = normal [=canopy closures 3 of the LFI (Keller 2005)] |
|  | 3 = spare [=canopy closures 4 and 5 of the LFI (Keller 2005)] |
|  | 4 = grouped [=canopy closures 6 and 7 of the LFI (Keller 2005)] |
| Canopy cover | Area covered by crowns, estimated in 10% steps (Keller 2005) |
| Shrub cover | Area covered by shrub layer (≥0.5 m, <5 m), estimated in 10% steps |
| Herb cover | Area covered by herb layer, estimated in 10% steps |
| Herbage/fern cover | Area covered by herbage or fern, estimated in 10% steps |
| Tall rowans | Number of rowans (*Sorbus aucuparia*) > 5 m |
| Medium rowans | Number of rowans 1–5 m |
| Small rowans | Number of rowans < 1 m |
| Tall beeches | Number of beeches (*Fagus sylvatica*) > 5 m |
| Small beeches | Number of beeches (≥0.5 m, <5 m) |
| Alders | Number of alders (*Alnus* sp.) |
| Willows | Number of willows (*Salix* sp.) |
| *Vaccinium*-shrub cover | Area covered by shrubs of the genus *Vaccinium*, estimated in 10% steps |
| Bilberry cover | Area covered by bilberry (*Vaccinium myrtillus*) alone, estimated in 10% steps |

*dtm25*, digital terrain model with a resolution of 25 × 25 m; *LFI*, Swiss National Forest Inventory

We first explored the relationship between Hazel Grouse response and each predictor variable separately. In the case of a unimodal response, we also included the squared term of the predictor variable. The variable set was reduced in three steps because a large variable set risks overfitting the model and consequently loses generality and interpretability (Schröder and Reineking 2004a). In a first step, we studied bivariate correlations, because multi-collinearity of independent variables can cause problems in logistic regression models (Hosmer and Lemeshow 2000). Fielding and Haworth (1995) suggested that a correlation of higher than 0.7 is critical. In cases with correlations $r_S > 0.7$ (Spearman/Pearson rank correlation), the variable with the least biological

**Table 2** Variables that were used for the large-scale analysis (raster cells of 125 m × 125 m)

| Variable | Definition |
|---|---|
| Temperature | Monthly mean of average temperature (1961–1990) in °C (Zimmermann and Kienast 1999; Zimmermann and Roberts 2001) |
| Solar radiation | Monthly gobal potential shortwave radiation kJ/day (monthly avg) = monthly potential diffuse shortwave radiation (sdif, Kumar et al. 1997) + monthly potential direct shortwave radiation (sdir, Kumar et al. 1997) |
| Slope | Slope in ° (slp25_d8) based on D8 algorithm. Processing description: ArcInfo: slp25_d8 = slope (dtm25) |
| Altitude | In m a.s.l., derived from dtm25 |
| Number of different stand structures | Number of different stand structures. Stand structure values: clearance, one-layered = stand structure 1 of the LFI (Keller 2005) and multilayered = stand structures 2–4 of the LFI (Keller 2005) |
| Number of different seral stages | Number of different seral stages (Keller 2005) |
| Number of different canopy closures | Number of different canopy closures (Keller 2005) |
| Number of forest stand units | Number of forest stand units (Keller 2005) |
| Non-forest proportion | Proportion of gaps in % |
| Canopy cover | Area covered by crowns, estimated in 10% steps (Keller 2005) |
| Coniferous trees | Cover of coniferous trees, estimated in 10% steps |
| Inter-stand edge length | Total length of boundaries between stands in m |
| Brooks | Total length of brooks in m, digitalized from a 1:25,000 map |
| Beech | Proportion of beeches, estimated in 10% steps |
| Alder | Proportion of alders, estimated in 10% steps |
| Rowan | Proportion of rowans, estimated in 10% steps |

*dtm25*, digital terrain model with a resolution of 25 × 25 m

explanatory potential was excluded from further analysis. In a second step, univariate models were calculated for all predictor variables, as recommended by Hosmer and Lemeshow (2000). Based on logistic regressions of univariate models, nonsignificant variables ($P > 0.05$) were excluded from further analysis (Hosmer and Lemeshow 2000). In a third step, the full model that contained all significant univariate variables was reduced stepwise backwards based on Akaike's information criterion (AIC; Akaike 1974). We excluded variables with $P > 0.05$. Finally, means and standard errors of all variables which significantly contributed to the model were calculated for Hazel Grouse presence and absence plots and cells, respectively.

We evaluated the models with the procedure "validate," implemented in the R package Design (version 2.0–12; Harrel 2001). We applied bootstrapping ($N = 1000$) as a method because we lacked a separate validation sample, and calculated the corrected indices of $R^2$ and the threshold-independent area under the receiver operating curve, AUC (Fielding and Bell 1997). AUC is considered to be an important index because it provides a single measure of accuracy that does not dependent upon a particular threshold (Fielding and Bell 1997; Boyce et al. 2002). The AUC assesses the discriminative power of a model (Fielding and

Bell 1997). The value of the AUC lies between 0.5 and 1.0. If the value is 0.5, the scores for two groups do not differ, while a score of 1.0 indicates no overlap in the distributions of the group scores. Bootstrapping corrects for overoptimism (Guisan and Zimmermann 2000; Schröder and Reineking 2004b).

Additionally, we used accuracy measures based on a confusion matrix (Guisan and Zimmermann 2000). A confusion matrix contrasts the predicted with the observed presences and absences based on a fitted and classified model. A large number of different measures can be derived from this matrix. We report the correct classification rate (CCR) and Cohen's kappa (Cohen 1960) at a threshold of 0.5, as recommended in Reineking and Schröder (2004). Cohen's kappa measures the actual agreement minus the agreement expected by chance; it takes values between 0 and 1.

Habitat suitability map

A predictive habitat model for the entire study area was calculated with the forest stand data. Predicted values were illustrated in GIS (ArcGIS 9.2) using the back-transformed logistic regression equation of the model from the large-scale habitat analysis.

## Results

### Habitat analysis at the small scale

Thirteen habitat variables were significant ($P < 0.05$) in the univariate analyses and were thus subjected to further analysis (Table 3). The number of tall rowans and the total area of shrub cover each yielded high explanatory power, with $R^2 > 0.3$. The abundance of tall rowans had the strongest influence on Hazel Grouse occurrence. The variables "shrub cover", "stand structure", "basal branched trees", and "medium rowans" explained a relatively high proportion of the model's variance (all $R^2 > 0.19$).

The best multivariate model obtained from stepwise backward reduction and selection by AIC retained five of the 13 predictor variables entered: forest edge, shrub cover, tall rowans, temperature, and bilberry cover (Table 3). The first four variables significantly contributed to the model. Forest edge, shrub cover, tall rowans and bilberry cover influenced Hazel Grouse occurrence positively. Tall rowans had the strongest effect. On average $1.44 \pm 0.37$ (SE) tall rowans were found in the presence plots, compared to only $0.03 \pm 0.02$ in the absence plots. The respective figures for shrub cover were $17.87 \pm 2.55\%$ in the presence plots and $3.49 \pm 1.02\%$ in the absence plots. The length of forest edges was higher in presence plots ($37.33 \pm 3.05$ m) than in absence plots ($23.6 \pm 2.59$ m). Temperature showed a strong negative relationship to Hazel Grouse occurrence. In the presence plots, the mean temperature from March to May was lower ($2.47 \pm 0.07$°C) than in the absence plots ($2.70 \pm 0.09$°C). Even though bilberry cover was not a significant factor, it was retained in the model and was nearly twice as high in the presence plots ($40.25 \pm 4.09\%$) than in the absence plots ($23.65 \pm 3.30\%$). The habitat model showed an $R^2$ of 0.58, and the evaluation of the GLM resulted in an AUC of 0.90. The correct classification rate and kappa at the cut-off level of 0.50 were very good and reached values of 0.88 and 0.76, respectively.

### Habitat analysis at the large scale

Five predictor variables contributed significantly ($P < 0.05$) to Hazel Grouse occurrence in univariate models at the large scale (Table 4). The variables showed relatively low explanatory power ($0.07 \leq R^2 \leq 0.11$); this was highest for the number of different canopy closures and the proportion of alder.

Four predictor variables contributed significantly to the multivariate model: number of different stand structures, number of different canopy closures, proportion of alder, and temperature squared (Table 4). The first three variables had a positive relationship with Hazel Grouse occurrence. There were more different stand structures ($2.63 \pm 0.06$) in the presence cells than in the absence cells ($2.38 \pm 0.08$). The number of different canopy closures was higher in the presence than in the absence cells ($3.87 \pm 0.12$ vs. $3.31 \pm 0.11$). The respective figures for the mean proportion of alder were $1.42 \pm 0.47\%$ and $0.16 \pm 0.09\%$. Temperature squared had a negative relationship with Hazel Grouse occurrence. Thus, temperature squared was lower in presence cells ($6.55 \pm 0.38$°C$^2$) than in absence cells ($7.91 \pm 0.50$°C$^2$). The predictor variables explained 22% of the variance in Hazel Grouse occurrence. The accuracy measures were $\text{AUC} = 0.74$, $\text{CCR}_{0.5} = 0.68$, and $\kappa_{0.5} = 0.37$.

**Table 3** Results of the small-scale habitat analysis. We report the significant variables and their regression coefficients $\beta$, their $P$ values, and their $R^2$ values from univariate analysis and the results of the multivariate logistic regression

| Variables | Univariate models | | | Multivariate model | | |
|---|---|---|---|---|---|---|
| | $\beta$ | $P$ | $R^2$ | $\beta$ | SE | $P$ |
| Intercept | | | | −0.200 | 1.355 | 0.883 |
| Forest edge | 0.028 | 0.001 | 0.117 | 0.036 | 0.013 | 0.006 |
| Tall rowans (>5 m) | 2.272 | 0.002 | 0.327 | 1.975 | 0.813 | 0.015 |
| Shrub cover | 0.108 | <0.001 | 0.309 | 0.101 | 0.026 | <0.001 |
| Bilberry cover | 0.019 | 0.003 | 0.100 | 0.017 | 0.010 | 0.079 |
| Temperature | −0.006 | 0.048 | 0.043 | −1.177 | 0.500 | 0.019 |
| Basal branched trees | 0.075 | <0.001 | 0.193 | | | |
| Medium rowans (1–5 m) | 0.173 | 0.004 | 0.169 | | | |
| Herbage/fern cover | −0.023 | 0.003 | 0.102 | | | |
| Slope | 0.049 | 0.010 | 0.074 | | | |
| Slope$^2$ | 0.001 | 0.040 | 0.048 | | | |
| Temperature$^2$ | −0.113 | 0.035 | 0.050 | | | |
| (Canopy cover)$^2$ | $-1.419 \times 10^{-4}$ | 0.044 | 0.045 | | | |
| Stand structure | 0.739 | <0.001 | 0.219 | | | |

**Table 4** Significant variables and regression coefficients $\beta$, $P$-values, and $R^2$ values of univariate analysis and the results from the multivariate logistic regression model of the large-scale habitat analysis

| Variables | Univariate models | | | Multivariate model | | |
|---|---|---|---|---|---|---|
| | $\beta$ | $P$ | $R^2$ | $\beta$ | SE | $P$ |
| Intercept | | | | −3.404 | 1.339 | 0.011 |
| Number of different stand structures | 0.844 | 0.012 | 0.068 | 0.923 | 0.389 | 0.018 |
| Temperature$^2$ | −0.110 | 0.036 | 0.048 | −0.134 | 0.064 | 0.035 |
| Number of different canopy closures | 0.653 | 0.002 | 0.112 | 0.498 | 0.223 | 0.025 |
| Proportion of alder | 0.398 | 0.043 | 0.101 | 0.461 | 0.230 | 0.045 |
| Number of different stands | 0.184 | 0.035 | 0.049 | | | |

## Habitat suitability map

Based on the variable equation for the large-scale analysis, we calibrated a predictive habitat suitability model for the entire study area. A habitat suitability of >0.5 was predicted for 44% of the study area. We illustrated the results of the model by considering five equal classes of habitat suitability (Fig. 2). Fifteen percent of the study area had a very low suitability (smaller than 0.2). Suitability values of between 0.2 and 0.4 were found in 27% of the study area. Raster cells with intermediate suitability (0.4–0.6) were most common in the study area (29%). In 22% of the study area, habitat suitability amounted to 0.6–0.8. Only 7% of the study area provided highly suitable habitat conditions with values of greater than 0.8.

## Discussion

Today, Alpine habitats are a major stronghold of Hazel Grouse populations in Central Europe (Klaus et al. 2003). However, our study indicates that the dominance of coniferous forest and the limited time for breeding may limit the amount of suitable habitat and the population density in higher mountainous areas. This assessment is supported by our large-scale habitat suitability model. Only 44% of the study area was predicted to have a habitat suitability of >0.5. Moreover, the proportion of high-quality habitat (>0.8) was less than 10%. Thus, most of the study area seems to be of intermediate or low habitat quality, only providing the territorial resources for 5–8 males (Schäublin 2007). These figures correspond to our general impression that forest stands at early seral stages represent a low proportion of the study area, and are interspersed within large areas of mature, single-layer stands. Unfortunately, we were not able to test our model with an independent data set. However, we estimate that our study area is representative of the living conditions of Hazel Grouse in spruce-dominated forests of the Alps. Thus, we conclude that habitat quality could be improved in the study area and many parts of the Alps by adopting forestry measures that aim to increase the carrying capacity
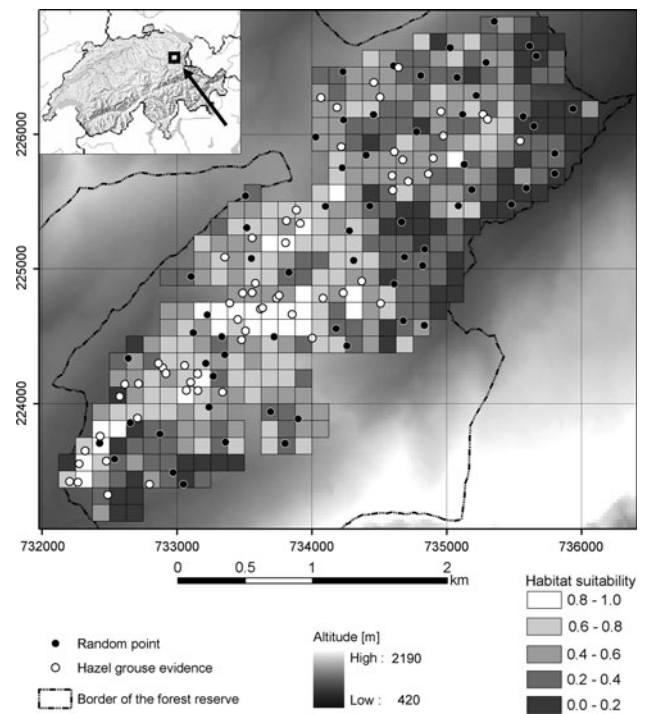


**Fig. 2** Location and map of the study area in Switzerland, including the 393 grid cells that were classified into five equal classes of habitat suitability

of Hazel Grouse. Below, we discuss the essential elements of Hazel Grouse habitat, the limitations of our models, and the differences between the small- and large-scale models. We also recommend measures for habitat and multi-species management if the Hazel Grouse is found to be syntopic with Capercaillie.

### Essential elements of Hazel Grouse habitat in mountain forests

In this study, we confirm that the Hazel Grouse is a distinct habitat and food specialist (Bergmann et al. 1996). The structural diversity of the understory and the minimal availability and accessibility of food plants mainly influenced the occurrence of the species in our study area.

A well-developed understorey with deciduous softwood vegetation is essential to optimize the food and energy budget of Hazel Grouse in conifer-dominated regions with winter-cold climates.

The presence of tall rowans, dense shrub cover, and a high density of forest edges significantly increased the probability of Hazel Grouse occurrence at the small scale. A well-developed shrub layer also proved to be an important key element of Hazel Grouse habitat in recent studies in the Jura Mountains (Sachot et al. 2003; Mathys et al. 2006), as well as in other regions of Europe (Wiesner et al. 1977; Bernard-Laurent and Magnani 1994; Klaus 1995; Swenson 1995; Zeiler 1998; Müller et al. 2009). Shrubs provide feeding, resting, and sleeping sites with protection against predators due to greatly reduced visibility. As a well-developed understory with pioneer wood vegetation is a characteristic of young seral stages, natural rejuvenation in gaps after windfalls, insect calamities or avalanches can enlarge the area of Hazel Grouse habitat in a mountain forest.

Tall rowans are crucial elements for Hazel Grouse in mountain habitats (Koch 1978; Zbinden 1979; Jacob 1988; Bernard-Laurent and Magnani 1994; Müller et al. 2009), and an absence of rowans seems to limit the occurrence of Hazel Grouse in spruce-dominated forests during a period of extensive snow cover (Koch 1978; Klaus 1991, 1995). Hibernal alimentation can be restricted to rowan buds and berries when other elements are not or are only sparsely available and accessible. Koch (1978) found that tall rowans were used as a food source during days with deep snow, whereas small rowans were only frequented when snow cover was low. In general, tall rowans may be preferred because they have more branches and thus provide more cover and more buds and berries than smaller ones.

Forest edge ecotones are characteristic elements of Hazel Grouse habitats (Wiesner et al. 1977; Zbinden 1979; Bernard-Laurent and Magnani 1994; De Francesci 1994; Mathys et al. 2006). Along the transition areas between forest stands and, openings and open land, site conditions (sunlight, temperature) change over short distances. Consequently, forest edges are rich in structural elements and in species diversity (Glutz von Blotzheim 1981; Swenson 1995; Flückiger and Duelli 1997). Our finding that forest edge density positively influenced Hazel Grouse occurrence reflects this species' contrasting habitat requirements with regard to food and protective cover against predators at the small scale.

Structural heterogeneity positively influences bird diversity in general (Thiollay 1990), and it supported Hazel Grouse occurrence at the large scale in our model. The numbers of different stand structures and canopy closures were significant predictors. Both variables are useful indices of structural diversity, a major predictor of Hazel Grouse occurrence in the Bavarian Forest (Müller et al. 2009). Forests that vary in stand structure show a heterogeneous mosaic of one-layered and multi-layered stands, and thus provide lots of edges. Forest areas that vary in their degree of canopy closure differ in the pattern of sunlight and microclimatic conditions at the ground. This promotes well-developed ground vegetation and shrub cover, with pioneer trees offering nutritious buds and fruits to Hazel Grouse and other bird species (Blake and Hoppes 1986; Bergmann et al. 1996; Fuller 2000).

## Model comparison and limitations

Five and four variables made significant contributions to the small- and large-scale multivariate models, respectively. The small-scale model that used data at the plot level undoubtedly had a better accuracy than the large-scale model that was calibrated with stand data from the cantonal forest inventory. This is a clear hint that the Hazel Grouse reacts more to local variables such as shrub cover and availability of berries than to stand variables that mainly indicate forest composition and heterogeneity. Thus, fine-grained habitat variables better reflect the habitat requirements of the species, at least in winter. Consistent with results from Capercaillie studies (Bollmann et al. 2005), we propose to complement forest inventories with small-scale habitat predictors of forest grouse species. Therefore, area-wide forest inventories would become a useful tool for monitoring habitat suitability at the landscape and thus metapopulation scale.

One group of such predictor variables concerns the cover and composition of the field layer. These variables are important indicators of habitat quality for Capercaillie and Hazel grouse (Klaus et al. 1986; Bergmann et al. 1996). Since we surveyed Hazel Grouse during winter, we assessed the ground vegetation variables only after snow melt. Therefore, the ground vegetation could only indirectly influence the habitat use of our study species during the period of snow cover. This may be why the $P$ value of bilberry cover was 0.08 in the multivariate model but significantly differed between the used and unused plots. The changing ratio of snow cover during the fieldwork could have further influenced this result.

We did not expect alder to be a significant predictor in our large-scale model. *Alnus glutinosa* is an important food plant in boreal forests during winter (Swenson 1993; Bergmann et al. 1996; Jansson et al. 2004), but we are not aware of any report of mountain habitats in Central Europe where alder occurs in the diet of Hazel Grouse. In the Pre-Alps, *A. glutinosa* is restricted to areas at altitudes of less than 1200 m. Consequently, *A. viridis* and *A. incana* occurred in our study area. We do not have any evidence that these species directly influenced the habitat use of

Hazel Grouse. Further, we suppose that the variable "alder" is an indicator of important habitat elements like brook, rejuvenation gap, and forest edge. Areas next to these elements are often characterized by a well-developed understory and a good abundance of rowans. If rowans constituted less than 10% of the forest stands in our study area, it did not appear in the large-scale dataset, and so could not directly contribute to the respective model.

Temperature proved to have a negative influence on Hazel Grouse occurrence in the study area. We assume that this result is linked to the advantageous conditions of cooler sites and higher reaches, because they provide deeper and drier snow for snow caves in winter. However, we do not have data to test this hypothesis, and cannot exclude an artifact. Thus, the resolution of the variable "temperature" does not match very well to those of other predictor variables at the small and large scales. Temperature was interpolated from data provided by a net of meteorological stations outside the study area with a dtm. Thus, temperature does not represent the fine-grained temperature differences in presence and absence plots.

## Implications for conservation and multi-species management

Our results generally confirm those of other studies and highlight the importance of structured forest stands with a well-developed understory as habitat for Hazel Grouse. Special attention should be paid to the result that a few scattered rowan trees can already meet the winter food requirements and enable the survival of Hazel Grouse in conifer-dominated mountain forests. In our study, we found an average density of 23 rowans taller than 5 m per hectare in used stands. However, such a threshold does not necessarily indicate that these stands are of outstanding quality, because habitat quality depends on the availability of alternative stands or resources (Arthur et al. 1996). Further investigations must show how the density of tall rowan trees correlates with demographic and fitness parameters of Hazel Grouse.

We recommend a well-developed shrub cover, high edge density, interspersed rowan trees, and preferably good bilberry cover as general goals for habitat management focusing on Hazel Grouse. To maintain and facilitate these elements, shrubs and deciduous tree species of the genera *Sorbus*, *Salix*, *Betula*, *Alnus*, *Sambucus*, *Corylus*, and *Populus* should not be removed during thinning operations in coniferous forests, as has been common until recently (Blattner 1998; Lieser 2003). In particular, rowan trees should be conserved. They are the essential factor in winter, when snow inhibits access to bilberry (Eiberle and Koch 1975). Gaps resulting from natural disturbances such

as windfalls, avalanches, snow breaks, or insect calamities should be left to natural succession and rejuvenation. Structural elements typical of natural succession can also be created and supported by human-induced forestry measures, like selective group cutting of mature trees. Stands with interspersed gaps increase the amount of forest edges and improve the quality of Hazel Grouse habitat through a high supply of food plants. The growth of rowan and bilberry is stimulated by exposure to sunlight in small openings. Special attention should also be paid to linear habitats on both sides of brooks. These habitats are characterized by dynamic processes at the small scale and support the growth of pioneer tree species such as willow, alder and rowan. At the large scale, a diverse mosaic of forests stands varying in canopy closure and stand structure can additionally improve habitat quality. Since Hazel Grouse rapidly responds to changes in habitat quality, positive results can be expected after time periods of only 10–20 years (Klaus 1991, 1995; Bergmann et al. 1996).

National parks, nature and forest reserves are delineated to meet specific conservation goals, and are often hotspots of species richness. The syntopic occurrence of several species of conservational concern and the need for an optimal cost–benefit ratio in such areas necessitates multi-species habitat management. This also applies to our study area, which has been identified as a regional hotspot for Capercaillie conservation (Bollmann 2006; Ehrbar et al. 2010). In contrast to the Hazel Grouse, which prefers moderately dense shrub cover, Capercaillie prefers habitats with low shrub cover. Average figures in used plots amounted to only 3.27% in the forest reserve of Amden (Imhof 2007). This finding corresponds with the results from the study of Sachot et al. (2003) in the Jura Mountains, where both grouse species also coexist and are of conservational concern. The authors recommend that the general matrix should be managed for Capercaillie. The contrasting habitat preferences should then be met by a mosaic of different habitat types for both Capercaillie and Hazel Grouse. Specifically, they propose a patchy distribution of young regeneration stages within an old successional matrix.

We support this general recommendation and stress the point that as well as the proportion of habitat required for each species, special attention should also be paid to the connectivity of habitat patches within the matrix of old-growth stands (Andrén et al. 1997). Capercaillie is a habitat specialist and is generally considered to prefer old-growth forests (Rolstad and Wegge 1987; Storch 2001). It has large area requirements, with home ranges of about 550 ha (Storch 1995). The Hazel Grouse, however, populates young seral stages (Bergmann et al. 1996) and occupies territories of between 8.3 ha (Wiesner et al. 1977) and 40 ha (Jansson et al. 2004). Next to gaps in old-growth

stands, young seral stages evolve at sites disturbed by natural events like windthrow, avalanches, insect calamities, fires, and erosion along steep slopes. Thus, suitable patches of Hazel Grouse habitat can arise suddenly and relatively quickly, whereas old-growth forest stands that provide suitable Capercaillie habitat evolve slowly and need to be continuous for a long time. Therefore, multi-species management for both forest grouse should be primarily directed towards Capercaillie. Old-growth stands with gaps should dominate the area, but should still provide enough space to integrate a mosaic of early seral stages. The topography of Alpine forests supports such a mosaic anyway due to abrupt changes in exposure, steepness, and soil condition. Because natural forest gaps occur only sporadically and rarely compared to forest management interventions, the availability of suitable Hazel Grouse habitat beside old-growth stands can be enhanced by adopting forestry measures between old-growth stands and along brooks, openings, and forest roads. The resulting mosaic, which will be dominated by old seral stages with intermediate canopy cover and gaps, and complemented by stands of young seral stages with rowan and willow and small groups of spruce trees, will support the coexistence of Capercaillie and Hazel Grouse in large contiguous forests.

Attention should also be paid to the matrix, which strongly influences the occurrence of Hazel Grouse in habitat fragments (Jansson et al. 2004). The separation of habitat patches by more than 2 km of intensively managed forest or more than 200 m of open land can have a highly isolating effect (Åberg et al. 1995). Therefore, we generally recommend that particular patches should not be segregated by more than these distances, although studies in the southeastern Alps have reported a higher dispersal potential for the species (Montadert and Léonard 2006). We instead propose that remote habitat patches should be connected via inner and outer forest edges in order to support the dispersal of individual Hazel Grouse between neighboring populations.

## Zusammenfassung

### Lebensraumnutzung des Haselhuhns im Winter und Maßnahmen zur Förderung der Art im Gebirgswald

Das Haselhuhn (*Bonasa bonasia*) hat in vielen Gebieten Europas starke Bestandrückgänge erlitten. Die forstliche Förderung des gleichförmigen und einschichtigen Hochwaldes in den letzten hundertfünfzig Jahren hat dazu geführt, dass sich die Qualität der Lebensräume dieser Art deutlich verschlechterte. Strukturreiche, vielfältige Waldbestände der frühen und späten Sukzesssionsphasen verschwanden vielerorts und verursachten die Bestandsrückgänge. Da die multifunktionelle Waldwirtschaft heute vermehrt dynamische Prozesse und Naturverjüngung unterstützt, eröffnet sich die einmalige Gelegenheit, den Lebensraum des Haselhuhns in den Kernbieten der aktuellen Verbreitung zu fördern. Weil die Alpen ein solches Kerngebiet in Mitteleuropa sind, haben wir uns zum Ziel gesetzt, die Lebensraumnutzung des Haselhuhns im Gebirgswald zu untersuchen und Schwellenwerte für die Lebensraumförderung zu bestimmen. Wir führten unsere Studie im Sonderwaldreservat Amden in den nordöstlichen Voralpen der Schweiz durch. In einem Gebiet von 6.14 km$^2$ mit einem Raster von 393 quadratischen Zellen von 125 m Seitenlänge taxierten wir im Winter die Spuren des Haselhuhns flächendeckend, erfassten die Lebensraumnutzung der Art und die Eigenschaften ihres Lebensraums. Dazu erhoben wir die standortökologischen, strukturellen und vegetationskundlichen Variablen auf der kleinen räumlichen Skala (25 × 25 m) und die standortökologischen und forstlichen Bestandsvariablen auf der grossen Skala (125 × 125 m). Wir verglichen die Eigenschaften von genutzten und ungenutzten Rasterzellen mittels logistischer Regression mit schrittweiser Rückwärtsselektion und dem Akaike Informationskriterium. Die Haselhühner bevorzugten Bestände mit einem hohen Anteil an Vogelbeerbäumen > 5 m (*Sorbus aucuparia*), inneren Randlinien und einer gut entwickelten Strauchschicht auf der kleinen Skala. Vogelbeerbäume mit einer Höhe > 5 m hatten den stärksten Einfluss auf die Vorkommenswahrscheinlichkeit des Haselhuhns und wiesen in genutzten Flächen eine mittlere Dichte von 23 Individuen pro ha auf. Waldbereiche, die sich aus Beständen mit unterschiedlichen Kronenschlüssen und Bestandsstrukturen zusammensetzten und einen hohen Anteil an Erlen (*Alnus* sp.) aufwiesen, wurden auf der grossen Skala bevorzugt. Ein Habitatmodell prognostizierte für 44% des Untersuchungsgebiets eine Vorkommenswahrscheinlichkeit für das Haselhuhn von mehr als 0.5. Der entsprechende Anteil für Werte > 0.8 war nur 7%. Unsere Resultate zeigen, dass der Anteil an nutzbarem Lebensraum für das Haselhuhn durch natürliche Waldverjüngung nach Windwurf, Borkenkäferbefall, Lawinen oder Holzschlag und durch einen höheren Anteil an biologisch alten Waldbeständen verbessert werden kann. Beide Massnahmen fördern den heterogenen Bestandsaufbau sowie die Mächtigkeit der Strauchschicht und die Häufigkeit der Vogelbeere — zwei wichtige Habitat- und Nahrungskomponenten für das Haselhuhn im Nadelbaum dominierten Gebirgswald.

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