

# Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications

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**Abstract** European Alpine landscapes are facing marked land-use changes. On the one hand, outdoor winter recreation is spreading, with ski infrastructure degrading fragile mountain habitats, and snowsports causing disturbance and stress to wildlife. On the other hand, the abandonment of traditional grazing practices on timberline grasslands is leading to their encroachment by shrubs and forest, which decreases habitat heterogeneity and negatively affects biodiversity. We used the black grouse, a declining key indicator species of the Alpine timberline ecosystem, to assess optimal breeding habitat characteristics, with the goal of providing guidelines for appropriate restoration. Using Mixed Effects Logistic Regression analyses, we compared habitat features both at visited and at pseudo-absence locations within individual home ranges in order to

determine the optimal habitat for males and females. Horizontal and vertical structural heterogeneity within all vegetation layers was the best predictor of occurrence for both sexes. In contrast, vegetation composition affected the presence of females, but not that of males. Females preferred a diverse, complex mosaic consisting of isolated mature coniferous trees and scattered small regenerating trees, associated with shrub cover (Ericaceae) and Alpine meadows (Nardion). Chick-rearing females furthermore avoided roads, forest tracks and walking paths. The optimal predicted proportions of habitat types obtained from the model provide guidelines for the restoration of timberline ecosystems through corrective forestry measures and/or adapted grazing practices. These measures are likely to also benefit other Alpine timberline biodiversity.

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Patrick Patthey and Natalina Signorell contributed equally to the study.

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## Introduction

In contrast to many lowland ecosystems, negative anthropogenic impacts on Alpine ecosystems are relatively new, but they have significantly increased over the past decades (Körner 2000). The constantly growing winter and summer tourism industry has resulted in an expansion of infrastructure, especially ski-lift installations, and an increasing human penetration into vulnerable, formerly relatively untouched ecosystems outside ski resorts (Arlettaz et al. 2007; Delgado et al. 2007). In addition, the progressive abandonment of traditional farming practices, such as extensive cattle grazing and meadow mowing, also threatens Alpine biodiversity (Maurer et al. 2006).

In mountainous regions, the effects of land-use changes on native flora and fauna are complex, variable in space and time (Körner 2000; Tasser et al. 2007) and remain poorly understood. Negative anthropogenic impacts on Alpine wildlife population dynamics may operate through changes in habitat quality caused by e.g. modifications of vegetation, or direct human disturbance (Watson and Moss 2004; Ingold 2005; Arlettaz et al. 2007; Patthey et al. 2008). The maintenance or restoration of high-quality habitats in semi-natural and anthropogenic landscapes is a key issue in conservation biology, as habitat quality is one of the main determinants of reproductive output and survival (Pärt 2001; Vickery et al. 2001).

In farmland ecosystems, spatial and temporal habitat heterogeneity, which operates at different scales, has been shown to be essential for biodiversity (Benton et al. 2003). The same probably holds true for Alpine grasslands, which have for long been heavily grazed by cattle and sheep. Among Alpine ecosystems, timberline habitats, which are situated at the interface between subalpine coniferous forests, adjacent dwarf shrub formations and alpine meadows, are a naturally diverse ecotone that harbours a high diversity of plant and animal species (Camarero and Gutiérrez 2002). Many of these species are specialised and therefore restricted to this ecotone (Sippola et al. 2002), rendering them especially vulnerable to habitat modifications. Timberline ecosystems are also the favourite areas for the development of snow sports such as skiing or snowshoeing. Compared to sites without ski infrastructure, ski runs and their surroundings feature lower plant productivity and species richness, reduced abundance and cover of woody plants, as well as diminished arthropod abundance and bird species diversity (Wipf et al. 2005; Rolando et al. 2007). Moreover, any increase of human disturbance within recreation areas may decrease individual fitness and, consequently, wildlife abundance (Watson and Moss 2004; Patthey et al. 2008).

Grouse species are viewed as indicators of ecosystem integrity (Storch 2007). The black grouse *Tetrao tetrix* L., an emblematic representative of the timberline fauna, is likely to play the role of an indicator species, if not of an umbrella species, for timberline ecosystems. Black grouse populations are declining in most Central European countries, especially in peripheral areas situated at species' distribution edge, including external Alpine massifs (Storch 2007). Habitat loss, degradation and/or fragmentation (Kurki et al. 2000; Storch 2007), climatic variation (Lindström et al. 1997; Zbinden and Salvioni 2004) and disturbance caused by human activities (Arlettaz et al. 2007; Patthey et al. 2008) are regarded as the main factors leading to population shrinkage. Reproductive success is the principal determinant of black grouse population dynamics, and is most likely to depend on weather variation (Zbinden and Salvioni 2004) and habitat quality (Ludwig et

al. 2008). Using radio-tracking, we investigated fine-grained habitat selection of black grouse in the Alps. Given the indicator, and presumed umbrella, functions of black grouse, and the role of reproductive success in determining population dynamics, we assumed that the habitat preferences shown by breeding females, compared to non-breeding females and males, would provide the essential information needed to define adequate habitat management measures, which, in turn, would promote overall biodiversity.

## Methods

### Study area

This study was conducted in the upper subalpine forests and the adjacent timberline at seven different sites in SW Switzerland (canton of Valais, 46°12' N; 7°20' E) and at two sites in N Italy close to the Swiss border (Piemonte, Verbania Province, 46°06' N; 8°18' E) between 1,400 and 2,300 m above sea level. In most study sites, the dominant tree species are larch *Larix decidua* and arolla pine *Pinus cembra*, but Norway spruce *Picea abies* is more common in the West. Dwarf shrubs (e.g. alpenrose *Rhododendron ferrugineum*, bilberry *Vaccinium myrtillus*, northern bilberry *Vaccinium uliginosum*, dwarf juniper *Juniperus communis nana*, heather *Calluna vulgaris*, bearberry *Arctostaphylos uva-ursi* and crowberry *Empetrum nigrum*) and grasses (e.g. matgrass *Nardus stricta*, *Calamagrostis villosa*) represent a characteristic fieldlayer in all areas (Signorell et al. 2010). The study areas are characterised by a subcontinental to continental climate, with warm, dry summers and cold, relatively wet winters (Reisigl and Keller 1999).

### Radio-locations and pseudo-absence points

Birds were captured from snow burrows between January and March in 2003–2006. We placed a 2×2.5-m mist-net stretched between 2- and 6-m long telescopic fishing rods on the snow surface above visually pre-located igloos and flushed the birds into the mesh while approaching closer to them (Marti 1985). Birds were also mist-netted at leks during April–June in the same years. They were tagged with neck-laced radio-transmitters with an activity sensor (12 and 15 g for females and males, respectively). In July and August, i.e. during the chick-rearing period, females were radio-located every day and males every second day for a period of 30 consecutive days. In every study area, radio-tracking, irrespective of sex or female breeding status, started on the day the first chicks hatched. Radio-locations were obtained by triangulation and homing-in onto the animal but without approaching closer than 10–15 m in order to avoid inadvertently flushing the grouse. We made



mature trees (>3 m height), small trees (<3 m), shrub, herbaceous, bare ground and rock habitat features. A virtual, 30-m long horizontal transect line centred on each point was set. Horizontal heterogeneity was considered to be high when corresponding to the maximum heterogeneity observable in our study area. Low and middle levels were assessed in the same way. The number of habitat features (low, 0–1 habitat features; middle, 2–4; high, >4) along the transect line were used to estimate vertical heterogeneity. Moreover, average habitat feature height (0–3, ascending), number of stumps and grazing activity (presence–absence) were also considered as structural predictors.

We hypothesized that the higher the vegetation heterogeneity the more likely would be the occurrence of black grouse, so horizontal and vertical heterogeneity were analysed as linear functions. The same held for stumps, since they are an indicator for richly structured habitats and high biodiversity (Humphrey et al. 2002). For vegetation height, however, we expected a quadratic relation with the occurrence of birds: if vegetation was low, it would increase predation risk, whereas if it were too tall, it could impede the mobility of the birds and the accessibility of ground-dwelling arthropods for young chicks (Signorell et al. 2010).

#### *Plant species cover*

The percentage cover of each plant species was estimated visually, within each vegetation layer to the nearest 1% for cover between 0% and 10% cover, and to the nearest 5% for cover greater than 10% (Online Resource 1). We included the linear and quadratic functions for all predictors, except for megaforbs (i.e. tall herb associations such as *Adenostylion* and *Filipendulion*), and rock cover, since they do not represent typical black grouse habitat features and are likely to be avoided (Klaus et al. 1990).

#### *Plant community cover*

Percentage cover of a given plant community was visually estimated as for plant species cover (Online Resource 1). Plant communities were classified according to Delarze et al. (1999), and included plants, as well as other ground cover information such as bare ground, rocks, screes, etc. The classification by Delarze et al. (1999) was applied to each vegetation layer. The linear and quadratic terms for all plant community predictors, except rocks and screes were included in the analysis.

#### *Topography*

Slope, southing (cosine of aspect) and easting (sinus of aspect) and convexity were used to describe the relief (Online Resource 1). Since these predictors affect the

microclimatic conditions and influence the vegetation, they may play a role in habitat selection.

#### *Human infrastructure and tourism*

We selected two predictors for human infrastructure and tourism, based on the presence–absence or Euclidean distance to the nearest infrastructure (road, forest track or walking trail). These predictors integrated human disturbance as well as vegetation modifications (Online Resource 1). We hypothesized that sites near human facilities are avoided, whilst site quality increases with the distance from human facilities.

#### *Food abundance*

Ants and grasshoppers (Ponce and Magnani 1988; Ponce 1992a) are considered to be crucial food sources for grouse chicks during their first weeks of life. We used the number of anthills as an estimate of ant abundance. Grasshopper abundance can be assumed to be already approximated through the estimation of alpine meadow cover (Signorell et al. 2010).

#### *Modelling and model selection process*

To enable the simultaneous analysis of habitat selection in all birds pooled together, we used Mixed Effects Logistic Regressions, with study sites, and individuals nested within study site, being treated as random effects. The predictors of occurrence were modelled as fixed effects. To identify which habitat descriptor best explained the occurrence of birds, and to avoid drawbacks inherent to stepwise regression (Whittingham et al. 2006), we applied an information theoretic approach (Burnham and Anderson 1998; Johnson and Omland 2004). We first excluded those predictors ( $n$  total=91) that occurred only marginally (e.g. *E. nigrum*, descriptor # 39, Online Resource 1) and the less biologically meaningful variables for each pair of correlated ( $r_s \geq |0.7|$ ) variables. For some predictors, the quadratic term was used in addition to the linear term in order to model possible curvilinear preferences. Variables expressing structural heterogeneity (vegetation structure) and variables within the habitat categories plant species cover and plant community cover were logically grouped into sub-categories according to the specific vegetation layer in which they occurred (Online Resource 1). The overall modelling and model selection procedure is shown in Fig. 1.

#### *Model selection within sub-categories*

First, we looked at single and combined contributions of the various habitat predictors within the sub-categories of the

three main categories, namely vegetation structure, species plant cover and plant community cover (up to six variables per sub-category, Online Resource 1). We then retained the best model for subsequent analyses.

#### *Model selection within categories*

Second, each of the variables from the best model for each of the categories (vegetation structure, plant species and plant community covers) were modelled singly, as well as in every possible combination of the variables retained within each sub-category. The model with the lowest Akaike's Information Criterion corrected for small sample sizes ( $AIC_C$ ) value was retained for further modelling. The variables within the categories topography, human infrastructure and tourism and food abundance were tested singly, as well as in combination. Again, the model with the lowest  $AIC_C$  value within each of these three categories was retained for further modelling.

#### *Combining plant species cover and plant community cover into vegetation composition*

Third, we grouped the categories plant cover and plant community cover, as they both describe the cover structure of the mapping locations. This new group was called vegetation composition. The model selection process was the same as that mentioned above.

#### *Best overall model*

Finally, the set of explanatory variables of the single best model obtained for each category was used to build a new set of candidate models, in order to select the best overall model. Model performance was estimated by using the Kappa statistic (Vaughan and Ormerod 2005). Model performance was considered poor when Kappa was lower than 0.4, good when Kappa was between 0.4 and 0.75 and excellent when Kappa was above 0.75 (Fielding and Bell 1997).

Our approach allowed the number of predictors to be reduced and the most likely explanatory predictors to be selected at each stage (e.g. Johnson et al. 2005). This also avoided testing all possible combinations of predictors, which would have dramatically inflated the number of candidate models. Candidate models (each combination of habitat predictor categories) were ranked based on Akaike's Information Criterion corrected for small sample sizes and Akaike weights ( $w_i$ ) (Burnham and Anderson 1998; Johnson and Omland 2004). The selection probability of a given habitat category was calculated as the sum of the  $AIC_C$  weights of those candidate models in which that category was included (Burnham and Anderson 1998). Finally, we used model averaging to calculate a general

model and to estimate coefficients and 95% confidence intervals (CI) for each habitat predictor by averaging the models that had  $\Delta AIC_C < 2$  compared to the best candidate model. Model performance was again estimated with the Kappa statistic (Vaughan and Ormerod 2005). All statistical analyses were performed using the software R 2.4.1 (lme4 and PresenceAbsence libraries, R Development Core Team 2006).

## Results

Thirty black grouse, distributed across nine study sites, were radio-tracked during the chick-rearing period. Our sample was biased towards males ( $n=15$ ) and unsuccessful breeding females ( $n=11$ ), compared to successful chick-rearing females ( $n=4$ ). Although 80% of the radio-tracked hens began incubation each year (2003–2006), only 28.6% of the incubating females successfully raised their chicks. Failures were due either to nest failure (62.5%) or chick mortality (37.5%) that occurred during the first 10 days of chicks' life. All unsuccessful females stayed within the perimeter of the study site after losing their brood. Home range sizes were between 9.8 and 18.5 ha (mean $\pm$ SD, 13.5 $\pm$ 3.6) for successful breeding females, 9.8–48.8 ha (18.1 $\pm$ 13.0) for unsuccessful breeding females and 4.0–80.0 ha (18.0 $\pm$ 19.2) for males.

#### Model selection

Among the set of candidate models, vegetation structure presented the most likely ecological correlation for black grouse occurrence, showing a selection probability of nearly 100% for all three bird classes (Table 1). Vegetation composition and human infrastructure and tourism were also likely predictors of the occurrence of unsuccessful and successful chick-rearing females (selection probability [ $AIC_C$  weights] $>77\%$ ), but not for males ( $<59\%$ ). The probability of linking topography with bird occurrence was high for males (83%) and low for females ( $<46\%$ ). Ant abundance, on the other hand, had a very low selection probability for all three bird classes (25% to 27%). The best candidate models ( $\Delta AIC_C < 2$ ) used to estimate the averaged model for each bird class all had good to very good predictive power (Kappa, 0.59–0.83).

#### Averaged occurrence models

Averaged models showed that female and male black grouse selected the most heterogeneous locations, mainly described as having horizontal and vertical heterogeneity of the different vegetation layers (Table 2). The probability of the presence of breeding females was higher when mean

**Table 1** Outcome of the model selection procedure performed for the habitat selection analysis, during the chick-rearing season, of 15 breeding females (four successful and 11 unsuccessful) and 15 black grouse males in the Swiss and Italian Alps

Vegetation structure	Vegetation composition	Topography	Human infrastructure and tourism	Food abundance	<i>k</i>	$\Delta_i$	$w_i$	Kappa
Successful breeding females								
x	x		x		32	0.00	0.430	0.81±0.04
x	x		x	x	33	2.19	0.144	
x	x	x	x		33	2.39	0.130	
x			x		21	3.34	0.081	
x					19	4.65	0.042	
x	x	x	x	x	34	4.71	0.041	
x		x	x		22	5.06	0.034	
x			x	x	22	5.66	0.025	
x		x			20	6.13	0.020	
1.000 <sup>a</sup>	0.766 <sup>a</sup>	0.248 <sup>a</sup>	0.896 <sup>a</sup>	0.246 <sup>a</sup>				
Unsuccessful breeding females								
X	X		X		58	0.00	0.402	0.78±0.02
X	X	x	X		59	0.81	0.268	0.77±0.02
X	X	x	X		60	2.34	0.125	
X	X		x	X	59	2.91	0.094	
x	x			x	57	4.99	0.033	
1.000 <sup>a</sup>	1.000 <sup>a</sup>	0.462 <sup>a</sup>	0.888 <sup>a</sup>	0.266 <sup>a</sup>				
Males								
X		X	X		28	0.00	0.328	0.59±0.04
X		X			27	0.33	0.279	0.59±0.04
X		X	X	X	29	2.09	0.116	
X		X		X	28	2.50	0.094	
X			X		27	3.03	0.072	
X			X		26	3.96	0.045	
1.000 <sup>a</sup>	0.017 <sup>a</sup>	0.826 <sup>a</sup>	0.585 <sup>a</sup>	0.258 <sup>a</sup>				

Only the best candidate models are presented (cumulative  $AIC_C$  weights <0.95) among all possible combinations of the five habitat categories (Fig. 1). Number of model parameters (*k*), differences in small sample unbiased Akaike's Information Criterion scores ( $\Delta_i$ ) and weights ( $w_i$ ), as well as Kappa statistic ( $\pm$ SD) for the models with a  $\Delta_i < 2$  are indicated

<sup>a</sup> Selection probability (see text for explanations)

grass height was low (1–10 cm), and decreased further with increasing grass height.

Variables describing vegetation composition were only retained in averaged models for successful and unsuccessful breeding females (Table 1). The averaged models for hens consisted of a complex assemblage of predictors. Although many predictors appeared in both models, there was no clear common link with bird occurrence for any of these fine-grained habitat predictors, except for the negative correlation with rocky habitats (Table 2, negative coefficients). To better understand the habitat composition correlating with bird occurrence, we used a reduced simple vegetation composition model that included shrubs, Alpine meadow and small and mature tree covers. We plotted predicted occurrence probability as a function of each vegetation cover by holding constant the other cover

predictors at their averaged values (Fig. 2). The probability of the occurrence of brood-rearing hens was higher with a small cover of alpine meadow (10–50%) mixed with small tree cover (20–60%), mature tree cover (10–50%) and a cover of shrubs (>50%). Unsuccessful breeding hens selected the same broad habitat as chick-rearing hens, except that they showed a preference for an even higher alpine meadow cover (>50%).

The probability of occurrence of successful and unsuccessful females was lower when tourism infrastructure (roads, forest tracks and walking trails) was present within a 30-m diameter circle (Table 2), and the occurrence of chick-rearing females was negatively correlated with proximity to roads (Table 2). Black grouse males have a tendency to select steeper sites (Table 2). Our ant abundance index was not correlated with any of our bird class occurrences (Table 2).

## Discussion

The present study demonstrates that both male and female black grouse show a high preference for patchy, heterogeneous microhabitats, consisting of a field layer of mixed shrubland, interspersed with alpine meadow, within a matrix dominated by both isolated mature and young, regenerating coniferous trees. Habitat heterogeneity has been shown to be a key element for sustaining high biodiversity in ecosystems in general (Benton et al. 2003; Hamer et al. 2003; Tews et al. 2004), particularly in Alpine timberline ecosystems (Dufour et al. 2006). Here, we have quantitatively established that vegetation heterogeneity in timberline ecotones is essential for the occurrence of black grouse, an emblematic element of the Alpine fauna. This indirectly confirms the presumption that black grouse may play the role of an umbrella species within timberline ecosystems, similar to that of the capercaillie *Tetrao urogallus* in subalpine woodland (Suter et al. 2002). Promoting optimal conditions for their survival would therefore be beneficial to Alpine biodiversity in general.

In contrast to males, females showed a preference for a specific vegetation composition pattern. These different selection patterns may be linked to sex and/or breeding status. The pronounced sexual dimorphism (body mass of hens, 960 g; cocks, 1,311 g; Marti and Pauli 1985) combined with a completely different plumage coloration (males, black and white; females, cryptic brown) may be related to different eco-physiological adaptations (body size) and/or anti-predator behaviour (cryptic plumage) (Wolf and Walsberg 2000; Signorell et al. 2010). Although eco-physiological adaptations mediated through plumage structure and coloration may be essential in mountainous ecosystems subjected to marked microclimatic variation, only black grouse cocks might afford a conspicuous dark, sun-capturing plumage because they feed twice a day, mostly at dusk and dawn, always remaining close to vegetation cover. In contrast, brood-rearing hens face the challenge of providing sufficient protein-rich food for their chicks throughout the entire day. Their best source of food comes in the form of invertebrates, which are most abundant and accessible in open meadow, where the concealment from predators is lowest (Signorell et al. 2010). Diverging sex-specific selection pressures in terms of optimal habitat selection constraints may explain these plumage differences, in addition to sexual-selection mechanisms.

A comparison of vegetation composition preferences of successful and unsuccessful breeding hens suggests that these two classes differ little in their habitat selection pattern. However, successful chick-rearing females appear to have a much narrower niche than unsuccessful breeding females, the former being typically restricted to a more specific range of open and semi-open vegetation cover.

This difference is best explained by the need to not only provide chicks with a good food supply, as mentioned above, but also to ensure adequate shelter, such as regenerating trees and dense shrubland, in order to decrease exposure to predators (Signorell et al. 2010). Broodless females feed mainly on plant material, and in the absence of chicks, they would thus have less specific requirements.

Our results suggest that hens avoided roads, forest tracks and walking paths. Roads may impair habitat quality directly, by degrading the vegetation, and indirectly through increased human disturbance. We do not know which of these factor(s) are linked to the occurrence of breeding females, but both factors could negatively affect reproductive success and, ultimately, black grouse density (Patthey et al. 2008).

We were unable to establish any association between the occurrence of chick-rearing females and the number of anthills. Either the index of ant abundance is too crude, or ants do not play such an important role for black grouse broods (Wegge and Kastdalen 2008). In effect, grasshoppers may be a more crucial resource for chicks in the Alps (Ponce 1992b; Signorell et al. 2010).

### Recommendations for the management of Alpine timberline habitats

Guidelines for an optimal chick-rearing matrix can be derived from our model projections concerning occurrence probability in relation to the most important environmental predictors. These guidelines may be applied where habitat composition and food resources are the same as in our study area, i.e. in the Internal Alps.

Ericaceae shrubland (mainly *R. ferrugineum* and *Vaccinium* spp., >50% cover) and alpine meadow (mainly *Nardion strictae* and *Festucion variae*, 10–50% cover) must constitute the field vegetation layer, combined with scattered small (<3 m) regenerating coniferous trees (spruce, larch and arolla pine, density ca. 30 individuals per hectare, 10–50% cover). All these should be interspersed so as to form a spatially diversified mosaic. The upper layer should consist of isolated mature trees (ca. 10 trees per hectare, 10–50% cover). These elements should be available regularly along the timberline belt. As the latter is on average 300 m broad, depending on slope steepness, we suggest ensuring a repetition of the mosaic at least every 400 m along the timberline. Such an area (12 ha) roughly corresponds to the average home range for a successful chick-rearing hen (13.5 ha in this study) and may thus constitute a good minimal reference area for restoration management.

Vegetation heterogeneity, which plays such a central role for both females and males, must be promoted wherever possible. Such a varied mosaic is threatened in the European Alps due to shrub and forest encroachment after

**Table 2** Coefficients, with 95% confidence intervals, of the habitat variables included in the averaged Logistic Mixed Effects model predicting the occurrence of black grouse males and breeding females, during the chick-rearing season, in the Swiss and Italian Alps

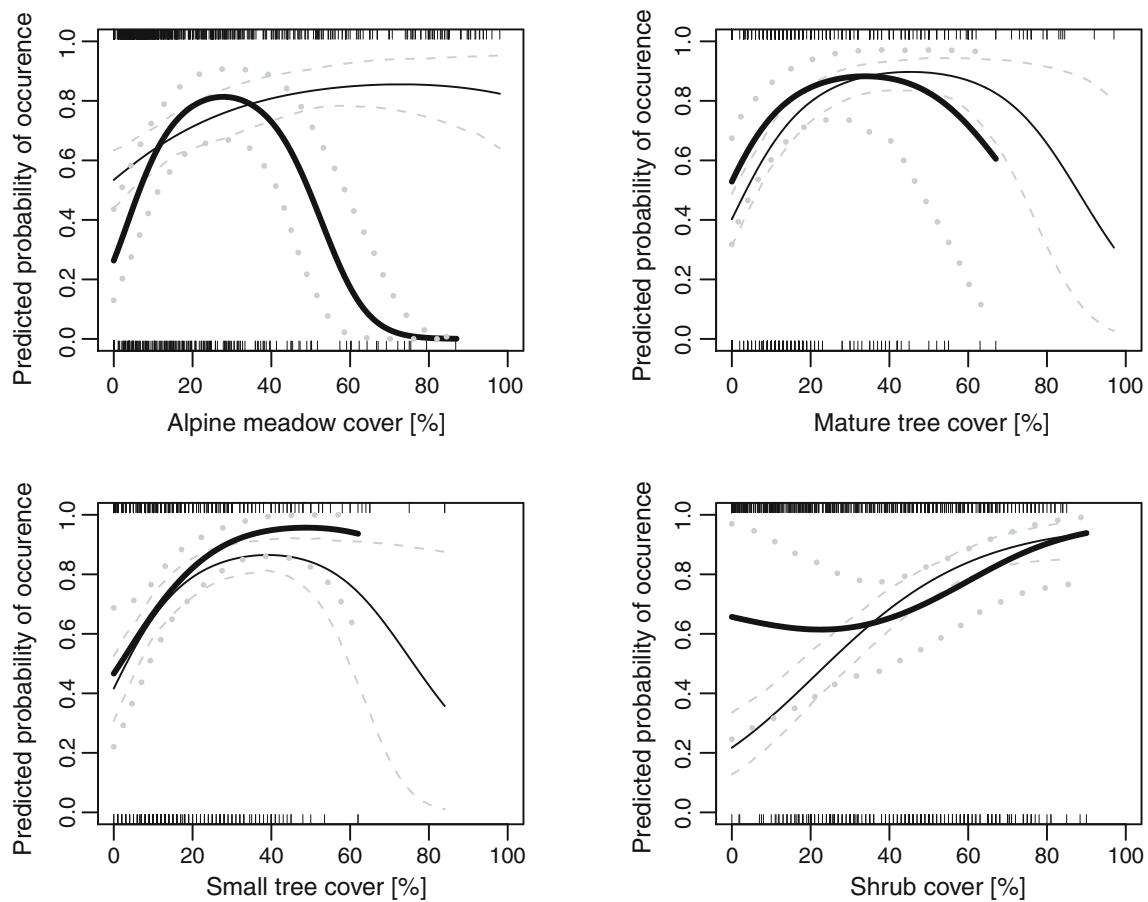
Habitat variables	Successful breeding females			Unsuccessful breeding females			Males		
	Estimate	CI (2.5%)	CI (97.5%)	Estimate	CI (2.5%)	CI (97.5%)	Estimate	CI (2.5%)	CI (97.5%)
Intercept	-18.07	-28.4	-7.7408 <sup>a</sup>	0.910049	-7.017	8.8368	-12.4175	-17.12	-7.7108 <sup>a</sup>
<b>Vegetation structure</b>									
Mature tree horizontal patchiness	0.9272	0.2594	1.59497 <sup>a</sup>	0.757128	0.0508	1.46348 <sup>a</sup>	0.66665	-0.218	1.55173
Small tree horizontal patchiness				-1.556841	1.0516	2.06207 <sup>a</sup>	0.53217	-0.091	1.15579
Small tree height				-1.35547	-3.201	0.48987	1.96519	1.1578	2.77262 <sup>a</sup>
Small tree height <sup>2</sup>				0.404253	-0.081	0.88975	-0.48072	-1.229	0.2672
Shrub horizontal patchiness	1.462	0.4357	2.48826 <sup>a</sup>	-0.11065	-0.629	0.40775	-0.24699	-0.158	0.65152
Shrub vertical patchiness	0.8058	-0.123	1.73504	1.70303	1.03	2.37604 <sup>a</sup>	0.80777	0.2176	1.39793 <sup>a</sup>
Shrub height				-1.28791	-2.998	0.42183	-1.16612	-4.342	2.01008
Shrub height <sup>2</sup>				0.044991	-0.337	0.42737	0.24599	-0.431	0.92333
Herbaceous layer horizontal patchiness	0.8193	-0.326	1.96472	1.227811	0.6142	1.84139 <sup>a</sup>	0.55009	0.2315	0.86866 <sup>a</sup>
Herbaceous layer vertical patchiness	1.536	0.6613	2.41075 <sup>a</sup>	2.024734	1.4683	2.58121 <sup>a</sup>	-0.5165	-1	2.03334
Grass height	7.318	0.7638	13.8722 <sup>a</sup>	-3.23812	-5.917	-0.5593 <sup>a</sup>	2.46628	-2.223	7.15516
Grass height <sup>2</sup>	-1.21	-2.305	-0.1151 <sup>a</sup>	0.636521	0.1488	1.12423 <sup>a</sup>	-0.28772	-0.821	0.24515
Bare ground horizontal patchiness	-0.3825	-1.339	0.57418				-0.45352	-0.923	0.01579
Stumps	0.5086	-0.11	1.12698				0.20335	-1.122	1.5286
<b>Vegetation composition</b>									
Total mature tree cover				0.034204	-0.064	0.13266			
Total mature tree cover <sup>2</sup> /100				-9.22E-05	-0.001	0.00114			
Regeneration <i>Alnus viridis</i> cover				-0.12627	0.241	-0.0113 <sup>a</sup>			
Regeneration <i>Alnus viridis</i> <sup>2</sup> /100				0.252609	0.0771	0.42812 <sup>a</sup>			
<i>V. myrtillus</i> cover				-0.20913	-0.342	-0.0766 <sup>a</sup>			
<i>V. myrtillus</i> cover <sup>2</sup> /100				0.506545	0.12	0.89309 <sup>a</sup>			
<i>V. gaultherioides</i> cover				0.006426	-0.116	0.12893			
<i>V. gaultherioides</i> cover <sup>2</sup> /100				0.050266	-0.238	0.33846			
Graminacea cover				0.082559	-0.024	0.18933			
Graminacea cover <sup>2</sup> /100				-0.11178	-0.233	0.00983			
Megaphorb cover				0.212075	-0.101	0.5255			
Forest Vaccinio-Piceion	0.05085	-0.138	0.23948	-0.02192	-0.101	0.05724			
Forest Vaccinio-Piceion <sup>2</sup> /100	-0.166	-0.591	0.25932	-0.00375	-0.131	0.12375			
Forest Junipero-Laricetum				0.018332	-0.07	0.10621			
Forest Junipero-Laricetum <sup>2</sup> /100				-0.15591	-0.331	0.01879			
Small tree Vaccinio-Piceion	-0.9867	-1.604	-0.3695 <sup>a</sup>	0.007035	-0.156	0.17055			



Small tree <i>Vaccinio-Piceion</i> <sup>2</sup> /100	4.903	0.5773	9.22872 <sup>a</sup>	-0.18836	-0.773	0.39676
Small tree <i>Junipero-Laricetum</i>	0.1417	-0.043	0.32659	-0.04128	-0.168	0.0858
Small tree <i>Junipero-Laricetum</i> <sup>2</sup> /100	-0.183	-0.687	0.32072	-0.04378	-0.432	0.3443
Alpine grassland	0.0094	-0.103	0.12181	-0.11544	-0.224	-0.0066 <sup>a</sup>
Alpine grassland <sup>2</sup> /100	-0.07	-0.241	0.10052	0.051124	-0.034	0.1359
<i>Nardion strictae</i>				-0.05973	-0.127	0.00771
<i>Nardion strictae</i> <sup>2</sup> /100				0.033609	-0.075	0.14225
<i>Calamagrostion arundinaceae</i>	-0.09828	-0.207	0.01072	-0.05104	-0.146	0.04387
<i>Calamagrostion arundinaceae</i> <sup>2</sup> /100	0.064	-0.075	0.20316	-0.04078	-0.112	0.03026
<i>Juniperion nanae</i>				-0.12685	-0.213	-0.0407 <sup>a</sup>
<i>Juniperion nanae</i> <sup>2</sup> /100				0.059	0.0037	0.11434 <sup>a</sup>
<i>Rhododendro-Vaccinion</i>				-0.05979	-0.15	0.03072
<i>Rhododendro-Vaccinion</i> <sup>2</sup> /100				0.021438	-0.045	0.08819
<i>Loiseleurio-Vaccinion</i>				-0.1598	-0.273	-0.0469 <sup>a</sup>
<i>Loiseleurio-Vaccinion</i> <sup>2</sup> /100				0.152172	0.0418	0.2625 <sup>a</sup>
Bare ground				0.0034	-0.144	0.15124
Bare ground <sup>2</sup> /100				-0.29152	-0.666	0.08327
Rocks	-0.1874	-0.363	0.0119 <sup>a</sup>	-0.1156	-0.203	0.0282 <sup>a</sup>
Topography						
Convexity/concavity				0.27979	-0.713	-1.27235
Convexity/concavity				-0.05097	-0.546	0.44363
Slope						
<b>Human infrastructure and tourism</b>						
Infrastructure	-0.9754	-4.323	2.37228	-1.76199	-3.212	-0.3117 <sup>a</sup>
Distance to roads	-0.01299	-0.02	-0.0055 <sup>a</sup>			

Quadratic terms are indicated as  $x^2$ . To improve clarity, the estimates and standard errors of some quadratic terms were divided by 100

<sup>a</sup>Confidence intervals do not overlap 0, indicating the importance of the corresponding habitat variable



**Fig. 2** Predicted probability of occurrence of successful (*bold lines*) and unsuccessful (*thin lines*) breeding black grouse females, during the chick-rearing season, in the Swiss and Italian Alps, with respect to various vegetation covers (alpine meadow, mature trees and small trees, shrub; 95% CI). Occurrence probability was allowed to vary

with the species vegetation cover under consideration, while other vegetation covers were held constant at their mean values. Observed cover values are shown as *small bars* for successful (along *lower horizontal axis*) and unsuccessful (*upper horizontal axis*) breeding females

abandonment of traditional land-use by farmers (e.g. forest pasturing) and, more locally, too intensive grazing. The destruction of the field layer is also pronounced in tourist (especially ski) resorts. In the latter areas, retaining patches of shrubland and allowing natural seed rain from surrounding areas (Urbanska and Fattorini 2000) could be a first measure in preventing artificial homogenization of vegetation along ski slopes; re-vegetation could also be envisaged in areas damaged by heavy machinery. In timberline meadows, vegetation encroachment should be counteracted by traditional extensive farming practices, such as cattle grazing or moderate goat grazing (Storch 2007), but intensive pasturing resulting in monotonous open grassland should be discouraged. In localised areas where spontaneous reforestation is very advanced, some initial forestry work may even be necessary in order to establish favourable conditions for reinstating grazing (Muller et al. 1998; Tasser et al. 2007).

It was not possible to dissociate the effects of human infrastructure from the effects of human disturbance on the occurrence of breeding females. We nevertheless recommend, as a safety measure, the restriction of human access to sensitive chick-rearing areas, as well as the implementation of visitor-steering measures, such as the canalisation of tourist movement along designated paths, during the chick-rearing season.

The habitat model developed here may be used in the future as a basis for mapping habitat suitability across the Alps using GIS and satellite images. This may enable delineation of the areas where corrective management measures would provide the greatest return on investment, for instance where forest or shrub encroachment is more advanced. If appropriately applied, the above management recommendations are likely to benefit also other elements of biodiversity within Alpine timberline ecosystems.

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