Habitat management guidelines for the conservation of an emblematic species of Alpine timberline ecosystems, the black grouse: from fine-grained habitat selection to large-scale habitat suitability modelling

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Natalina Signorell

von Sur und S-chanf (GR)

Leiter der Arbeit:
Prof. Dr. R. Arlettaz
Abteilung Conservation Biology
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To Nona and Martin

Tilla Halder

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GENERAL INTRODUCTION

Mountain ecosystems belong to the last remote and relatively untouched regions of Europe and are often regarded as the last wilderness refuge in a landscape highly cultivated and modified by modern humans. Although the first human settlements in the Alps in the Neolithic were not only built along the lakeshores and in the large valleys, but also above the timberline, the high elevation regions remained relatively undisturbed by humans. This changed abruptly after the Second World War when tourism began to leave its traces. Tourism facilities, especially ski-lift installations, quickly expanded. Additionally, human penetration also increased in vulnerable, formerly relatively untouched ecosystems outside ski resorts (Muller et al., 1998; Ingold, 2005; Arlettaz et al., 2007; Delgado et al., 2007). Parallel to this trend, a change in farming practices took place. Traditional farming practices, such as extensive cattle grazing and meadow mowing, have progressively been abandoned, whereas intensification of agriculture has become widespread also in Alpine ecosystems. Several studies have shown that this change in farming practices can lower habitat heterogeneity and biodiversity in general (Garcia-Ruiz et al., 1996; Körner, 2000; Storch, 2000; Tasser & Tappeiner, 2002; Seeber & Seeber, 2005; Britschgi, Spaar & Arlettaz, 2006; Maurer et al., 2006).

The different impacts that act upon Alpine ecosystems do not remain without consequences for Alpine habitats and wildlife. These are, however, not always easy to name, as they are often very complex and vary in space and time (Körner, 2000; Tasser & Tappeiner, 2002; Tasser et al., 2007). Thus, it has been shown that human disturbance by recreational activities can not only change physiological processes and the behaviour of wild animals but also lower their survival and reproductive success (Taylor & Knight, 2003; Baltic, 2005; Ingold, 2005; Arlettaz et al., 2007). On the other hand, land-use changes may negatively influence habitat quality (Storch, 2000; Watson & Moss, 2004). Habitat quality, in turn, influences survival, reproductive output, physiological processes and behaviour of wild animals.

Habitat quality determines reproductive output and survival, i.e., ultimately aptitude and fitness (Tye, 1992; Pärt, 2001; Vickery et al., 2001). Therefore, maintenance and restoration of high quality habitats in anthropogenic landscapes is a key issue in conservation biology (Primack, 1998). In birds, the availability of high quality habitats is particularly crucial during the breeding period because of the high food demand by the young for optimal development (Britschgi, Spaar & Arlettaz, 2006). This might be especially true for precocial birds, which depend on a very unpredictable food source: it varies with season, weather, temperature, and last but not least the specific microhabitat. A high-quality breeding habitat is particularly crucial in boreal and alpine ecosystems, where the time window for reproduction is extremely short and where there is no possibility for a second brood.

The alpine black grouse (*Tetrao tetrix*) inhabits one of the most diverse ecotones, the timberline, where different ecosystems overlap. The black grouse is thought to be an indicator of ecosystem health (Storch, 2000) and may therefore play the role of an umbrella species as established for the capercaillie (*Tetrao urogallus*), a closely related species inhabiting upper subalpine forests (Suter, Graf & Hess, 2002). The habitat of the black grouse overlaps with habitats used for grazing livestock, habitats which are also very attractive for winter snow sports activities. The potential negative impact of human recreational activities and agriculture may therefore directly influence black grouse habitat quality. The black grouse is listed in the red list of Switzerland as potentially endangered mainly because its marginal populations are declining (www.birds-online.ch/, access: 03.04.2008). Additionally, in most European countries, a drastic decline in most black grouse populations can be observed (Klaus et al., 1990; Storch, 2000). Therefore, the Swiss ornithological institute has classified the black grouse as one of the 50 priority species in Switzerland which require specific conservation action plans (www.vogelwarte.ch/, access: 03.04.2008).

Previous investigations at the Division of Conservation Biology of Bern University (research in which I was involved; **fourth chapter**) have shown that the abundance of displaying black grouse males is smaller in areas with ski infrastructure than in remote, more natural areas with a low or diffuse presence of snow-sports people. However, it remained unknown what actually triggers this difference in lek size. In addition to disturbance by humans, habitat characteristics were also recognized as potentially co-acting factors. Black grouse population dynamics is principally governed by reproductive output (Klaus et al., 1990), with chicks' optimal growth and survival affected by arthropod food abundance and availability, especially during their first weeks of life. During my PhD study, we thus investigated the relationships between black grouse occurrence, food abundance and habitat characteristics during the reproductive season (Klaus et al., 1990), given that alteration of the breeding habitat could be a key factor in the decline of Alpine black grouse populations. A major focus of my PhD research was on microhabitat selection by hens, either breeding or non-breeding females, as well as cocks. To investigate habitat preferences, we radio-tracked free-ranging birds, comparing used (visited) and non-used (non-visited) parts of their home ranges. Non-visited locations consisted of randomly generated points within individual home ranges. Habitat selection analyses were conducted to compare habitat features of visited points with non-visited (i.e. random) locations. This comparison was the basis for the microhabitat selection analysis of chapter one, the habitat selection analysis at the home range level of chapter two and, finally, the modelling of habitat suitability and ecological niches for chapter three.

In the **first chapter** we investigated fine-grained habitat selection of breeding and non-breeding black grouse females and males. The best predictor of occurrence of breeding and non-breeding females and males was habitat heterogeneity within all vegetation layers (horizontal and vertical patchiness). Whereas vegetation composition played a role for breeding and non-breeding females, males were not selective towards specific plant species or phytosociological associations. For breeding females an optimal habitat profile could be drawn, which provides directly applicable recommendations for habitat management. These characteristic habitat preferences of breeding females are most probably due to the fact that breeding hens have to lead their chicks to patches where food for chicks peaks. We then investigated the relationships between food abundance and habitat type in more detail (**second chapter**). For that purpose, arthropod biomass was sampled in various habitats within typical timberline ecosystems, while a habitat type selection analysis was carried out for the hens at the home range level. Contrary to our expectations, the favourite habitat (a heterogeneous mosaic of different habitats) was not the one providing the highest arthropod food supplies (open grassland); this suggests that chick-rearing hens trade-off maximum food availability for vegetation shelter, i.e. protection from predators.

Chapters one and two showed which habitat features are important for black grouse, especially for breeding hens. They considered the local scale only, however. For conservation practitioners, it is essential to recognize where the most suitable habitats are available locally so as to target conservation action. In my **third chapter**, we thus developed a spatially-explicit habitat suitability model based on the results from the first two chapters, accounting for ecological niche discrepancies between the genders and females of different breeding statuses. Actually, different categories may have different requirements, which have to be considered in conservation planning. This analysis provides a thorough appreciation of the differences in ecological requirements of cocks and hens and allows visualizing the distribution of the most suitable habitats in the south-western Swiss Alps.

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CHAPTER ONE

Habitat heterogeneity as a key feature for wildlife persistence within Alpine timberline ecosystems: optimal habitat profile for the black grouse

Submitted

Habitat heterogeneity as a key feature for wildlife persistence within Alpine timberline ecosystems: optimal habitat profile for the black grouse

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Running title: Habitat heterogeneity as a key feature for Alpine wildlife

Abstract

1. The tourist industry has dramatically increased over the past decades in the European Alps. Landscapes and ecosystems have been degraded by ski infrastructure, whereas disturbance by snow-sport people causes stress in wildlife. As snow sports concentrate around the timberline, wildlife inhabiting this ecosystem is put at risk. Abandonment of grazing of Alpine pastures by domestic ungulates is an additional threat: this could lead to shrub and forest encroachment, altering traditional landscape heterogeneity and affecting biodiversity.
2. We used the black grouse, a vulnerable, indicator bird species of timberline ecosystems, to assess optimal habitat configurations, with the goal to provide guidelines for optimal ecosystem management. Fine-grained habitat selection was investigated during the breeding period in SW Switzerland and N Italy. We focused on breeding females, comparing their micro-habitat requirements with those of non-breeding females and males, as reproductive output is the principal determinant of black grouse population dynamics and is likely to depend on habitat quality. Using hierarchical Mixed Logistic Regression analyses and Akaike Information Criteria for model selection, we compared habitat features at radio-locations with those at random locations within individual home ranges in order to determine habitat preferences and optimal breeding habitat profile.
3. Habitat heterogeneity (horizontal and vertical patchiness) within all vegetation layers was the best predictor of birds' occurrence for all three bird classes. Habitat composition played a role for breeding and non-breeding females, but not for males. Females preferred a diverse, complex mosaic consisting of isolated mature coniferous trees (10-30%), scattered small trees in regeneration (< 3 m height) associated with shrub cover (30-40%), and Alpine grassland (10-30%, *Nardus stricta* as dominant species). Finally, both non-breeding females and males (but not breeding females) showed an avoidance of roads, forest tracks and walking paths.

4. *Synthesis and application.* These optimal proportions of habitat types may serve as guidelines for the maintenance and restoration of wildlife-hospitable timberline ecosystems. This could be achieved through corrective forestry measures and/or adapted grazing policies. Finally, in sensitive black grouse breeding habitat, walkers should be requested to stay on trails and tracks. These measures are likely to benefit Alpine timberline wildlife and biodiversity as a whole.

354 words

Key words: Bird conservation, fine-grained habitat selection, habitat heterogeneity, habitat quality, Alps, Alpine ecosystems, timberline, *Tetrao tetrix*

Introduction

In contrast to most lowland ecosystems, detrimental anthropogenic impacts on Alpine ecosystems are relatively new, but they have dramatically increased over the past decades (Muller et al., 1998; Körner, 2000; Wüthrich, 2001; Byers, 2005). The constantly growing winter and summer tourist industry results in an expansion of human facilities, especially ski-lift installations, and an increasing human penetration into vulnerable, formerly relatively untouched ecosystems outside ski resorts (Muller et al., 1998; Ingold, 2005; Arlettaz et al., 2007; Delgado et al., 2007). Moreover, a progressive abandonment of traditional farming practices, such as extensive cattle grazing and meadow mowing, can pose a severe additional threat to Alpine landscapes and biodiversity (Garcia-Ruiz et al., 1996; Körner, 2000; Storch, 2000; Tasser & Tappeiner, 2002; Seeber & Seeber, 2005; Britschgi, Spaar & Arlettaz, 2006; Maurer et al., 2006).

The effects of land use changes in mountainous regions on native flora and fauna are complex, variable in space and time (Körner, 2000; Tasser & Tappeiner, 2002; Tasser et al., 2007), and thus remain poorly understood. Anthropogenic impacts on Alpine wildlife population dynamics may operate through changes in habitat quality (Storch, 2000; Watson & Moss, 2004) and/or direct human disturbance (Taylor & Knight, 2003; Baltic, 2005; Ingold, 2005; Arlettaz et al., 2007). The maintenance or restoration of high quality habitats in semi-natural and anthropogenic landscapes is a key issue in conservation biology (Primack, 1998) as habitat quality determines reproductive output and survival, i.e. ultimately aptitude and fitness (Tye, 1992; Pärt, 2001; Vickery et al., 2001). The availability of high quality habitats is particularly crucial for breeding, because of the high food demand by the young for optimal development. Although habitat quality is determined by various factors, with different organisms having divergent resource requirements, i.e. partitioning ecological niches (Schoener, 1986), some basic habitat characteristics may still be shared in common by sympatric species. These may include habitat heterogeneity, as animal species richness mostly correlates positively with habitat structural diversity (Blondel, 1986), as well as low levels of disturbance by predators and humans (Olsson, Brown & Smith, 2002; Martin & Joron, 2003; Colwell et al., 2007).

In farmland ecosystems, spatial and temporal habitat heterogeneity, which may operate at different scales, has been shown to be pivotal for biodiversity (Benton, Vickery & Wilson, 2003). The same may be true for upper Alpine ecosystems, which have for long been managed by grazing, but information remains scarce. Compared to natural habitats, ski-runs and their vicinity harbour lower plant productivity and species richness, lower abundance and cover of woody plants, as well as reduced arthropod abundance and bird species diversity (Wipf et al., 2005; Rolando et al., 2007). This might explain why local populations of animals are locally less abundant in these habitats (Menoni & Magnani, 1998; Watson & Moss, 2004).

Alpine regions have become very attractive for outdoor recreational activities, snow sports in particular (Wüthrich, 2001). Their natural fragility due to highly specific plant and animal adaptations to extreme soil and climatic conditions render them especially vulnerable to human disturbance. As regards wildlife, effects include augmented stress (Arlettaz et al., 2007) and behavioural adjustments such as compensatory feeding, with associated extra energetic costs that all are likely to impact on fitness (Baltic, 2005). Disturbance may even lead to avoidance of otherwise suitable habitats and retreat into suboptimal zones (Taylor & Knight, 2003).

Among Alpine ecosystems, timberline habitats – which are situated at the interface between subalpine coniferous forests and adjacent dwarf shrub formations and Alpine pastures – are a naturally diverse ecotone, harbouring a high diversity of plants and animals (Camarero & Gutiérrez, 2002). Many of these species are highly specialized and occur principally in that habitat type (Schmid et al., 1998; Sippola, Siitonen & Punttila, 2002). Additionally, timberline ecosystems have increasingly become a refuge habitat for threatened bird species of intensive farmland such as the tree pipit (*Anthus trivialis*, Meury, 1998) or the linnet *(Carduelis* *cannabina*, Frey, 1998). At the same time, timberline ecosystems are also a favourite habitat for the development of snow sports such as skiing, snowboarding, mountaineering skiing and snow-shoeing.

The black grouse (*Tetrao tetrix*, Linné 1758) is one of the most emblematic representatives of the timberline fauna. Since grouse species are frequently viewed as indicators of ecosystem health (Storch, 2000), the black grouse is likely to play the role of an umbrella species for timberline ecosystems, as established for the capercaillie (*Tetrao urogallus*), a closely related species inhabiting upper subalpine forests (Suter, Graf & Hess, 2002). It is thus a good candidate for investigating the impact of land use changes upon Alpine wildlife as habitat alterations have been shown to subtly determine black grouse population dynamics (Zbinden, Salvioni & Stanga, 2003; Ludwig et al., 2008). In most West-European countries, black grouse populations are declining (Klaus et al., 1990; Storch, 2000). Habitat loss, degradation and/or fragmentation (Storch, 1991; Kurki et al., 2000; Sun et al., 2003), climatic variations (Lindström, 1996; Lindström et al., 1997; Zbinden & Salvioni, 2004) and disturbance caused by human activities (Bevanger, 1995; Arlettaz et al., 2007) are regarded as the main factors. The European Alps are also concerned by this decline, with several marginal populations far from the core distribution areas having shrunk dramatically over the past decades (Storch, 2000).

In the black grouse, reproductive output is the principal determinant of population dynamics (Klaus et al., 1990). As it is likely to depend principally on weather variation (Zbinden & Salvioni, 2004) and the quality of the reproductive habitat (Ludwig et al., 2008), we investigated fine-grained habitat selection of breeding females vs. non-breeding females and males, assuming that the preferences shown by breeding females would be highly indicative for setting priorities as to habitat management policies.

Methods

STUDY AREA

This study was conducted at seven different sites in southwestern Switzerland (canton of Valais, 46°12'N/7°20'E) and at two sites in northern Italy close to the Swiss border (Piemonte, Verbania Province, 46°06'N/8°18'E) within a habitat belt between 1400-2300 m altitude (Klaus et al., 1990). At six of the Swiss study sites larch *Larix decidua*, spruce *Picea abies* and, to a smaller extent, arolla pine *Pinus cembra* are the characteristic tree species of upper subalpine forests and the adjacent habitats. At the three sites on the southern slope of the Alps (Simplon area in southeastern Valais and Piemonte), the dominating tree species is larch. Dwarf shrubs (*Rhododendron ferrugineum*, *Vaccinium* sp., *Juniperus communis* ssp. *nana*, *Calluna vulgaris*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, etc.) and grasses (*Nardus stricta*, *Calamagrostis villosa*, etc.) form a characteristic understorey in all areas. The study regions are characterized by a subcontinental to continental climate with warm and dry summers, and cold, relatively wet winters (Reisigl & Keller, 1999).

RADIO-LOCATIONS AND RANDOM POINTS

Birds were first captured from snow burrows between January and March in 2003-2006. We used a 2 x 2.5 m mistnet stretched between two up to 6 m long telescopic fishing rods which was placed on the snow surface above visually pre-located, occupied igloos, this prior to actively flushing birds by the observer (Marti, 1985). Second, birds were mist-netted at leks during April-June in the same years. They were tagged with neck-laced radio-transmitters (Holohil Systems Ltd. Carp, Canada, RI-2D; 12 g, 29 x 19 x 15 mm for females; 15 g, 34 x 19 x 15 mm for males) with the permission of the Swiss Federal Office for the Environment, the Wildlife and Game service of Valais and the Italian and Piemontese environmental agencies. In July and August, i.e. during the breeding period, females were radio-located every day and males every second day for a period of 30 days in a row, resulting in 30 and 15 presence radio-locations for females and males, respectively. Males were only radio-tracked every second day due to our limited working capacity. Because the home range size increases asymptotically with the number of locations, we calculated the minimum number of locations necessary for estimating home range size from preliminary radiotracking data. For that we applied bootstrap simulations in the program ArcView GIS 3.3. (Environmental Systems Research Institute, California) in which the home range sizes were calculated as a function of an increasing number of randomly selected locations from the actual visited locations. Intensive radio-surveys of reproductive females started on the day chicks hatched. Bird radio-locations were obtained by triangulation and homing-in onto the animal (White and Garrot 1990). As soon as a location was obtained, a stick was planted at a mean distance of ca 20 m away from the bird, while recording the direction and distance from the stick to the bird. We proceeded so in order to avoid disturbing or flushing the bird. Additionally, a sketch of the surroundings was drawn to ensure that the exact bird location could be retrieved even after some weeks. At the end of the breeding season, exact coordinates of bird locations were collected with the help of a global positioning system (GPS; Garmin eTrex® Navigator, Garmin Corporation, Olathe, KS). These locations are henceforth referred to as visited points.

Our investigation of habitat selection results from a comparison of habitat features between visited points (radio-locations) and randomly defined, «non-visited» points generated within home ranges but outside the main activity areas. We assumed that non-visited points represent unsuitable or less suitable habitat. In a first step, we delineated individual home ranges as the Minimum Convex Polygon (MCP) encompassing all radio-locations of a given bird (White & Garrott, 1990, extension «animal movement» in ArcView GIS 3.3, Environmental Systems Research Institute, California). A buffer of 15 m breadth was added around the MCP (extended MCP). As visited points are often clumped in space we estimated the 70% Kernel isolines using again the extension «animal movement» in ArcView GIS 3.3 (Environmental Systems

Research Institute, California). Around each radio-location within the MCP a buffer of 30 m radius was drawn. The coordinates of the non-visited points were then randomly generated so as to lie inside the extended MCP but outside the 70% isolines and outside the 30 m radius buffer belts. A total of 30 and 15 non-visited points, i.e. equivalent to actual number of radio-locations, were defined for females and males, respectively.

HABITAT DESCRIPTORS MAPPING AND VARIABLES

At the end of the radiotracking season, habitat descriptors were mapped at each point (visited and non-visited locations) within a circle of 15 m radius. In order to eliminate between-observer bias, all mapping was performed by the first author of this article. Habitat descriptors were grouped in six different categories (habitat structure, habitat cover, plant community, topography, tourism footprint and food abundance) that we describe in detail below (Table 1). For some descriptors, the quadratic term was used to derive additional variables. If so, it was implicitly taken in addition to the linear term in order to model possible curvilinear habitat preferences along gradients.

Descriptors of habitat structure

Horizontal and vertical heterogeneities were described through a simple visual ordinal estimate of structure patchiness (three levels: low, middle and high). Horizontal patchiness described how much a habitat feature (distinguishing between «tall trees», «small trees», «shrub» as well as «grass», «bare ground» and «rock») changed along a virtual, 30 m long, horizontal transect through the point (low: 0-1 structural change; middle: 2-4 structural changes; high: >4 structural changes). Vertical patchiness described how many different height «levels» of a habitat feature were found along a similar transect (low: 0-1 structural height; middle: 2-4 different heights; high: >4 heights).

Moreover, average habitat feature height (ordinal variable, levels 0-3, from low to high), number of stumps and grazing activity (nominal variable, presence/absence) were also considered as structural descriptors since they shape habitat appearance. Descriptors of «habitat structure» were measured within four vegetation layers, i.e. mature trees (trunk ∅ > 20 cm, > 3 m height), small trees (trunk ∅ < 20 cm, height < 3 m), shrub (< 1 m), and herbaceous layer (Table 1).

Horizontal and vertical patchiness entered the analyses as linear functions since we hypothesized that the higher the patchiness the more likely the occurrence of black grouse. The same held for stumps: since they are an indicator for richly structured habitats and high biodiversity (Humphrey et al., 2002; Bütler & Schlaepfer, 2004) we assumed that they should correlate positively and linearly with black grouse habitat preferences. For average habitat feature height, however, we expected a quadratic relation with birds' occurrence: too small height would increase predation risk whereas too tall vegetation could impede the mobility of the birds and the accessibility of ground-dwelling arthropods for young chicks.

Descriptors of habitat cover

The percent cover of each habitat descriptor (Table 1) was estimated visually according to Braun-Blanquet (1951) within each vegetation layer, e.g. cover of a given plant species, of grasses (Graminaceae), of megaphorbs, and of bare ground and rocks. We included the linear and quadratic functions for all descriptors except for megaphorb and rock cover since they do not represent typical black grouse habitats and are likely to be avoided (Klaus et al., 1990).

Descriptors of plant communities

Percent cover of a given plant community was again visually estimated according to Braun-Blanquet (1951). Plant communities were classified according to Delarze et al. (1999) and included plant communities as well as other ground cover information such as bare ground, rocks, scree, etc. (Table 1). The classification by Delarze et al. (1999) was applied to each vegetation layer (see under Descriptors of habitat structure). The total percentage cover of the associations without the forest canopy cover summed up to 100%.

The linear and square forms of all plant community descriptors except rocks and scree were considered in the analysis in order to model possible curvilinear habitat preferences. The latter two descriptors were treated as linear variables only as we hypothesized that these variables are avoided by the birds given that they do not represent typical black grouse habitat (Klaus et al., 1990).

Descriptors of topography

Altitude (m above sea level), convexity, slope, southing (cosine of aspect) and easting (sinus of aspect) were used to describe the topography at given visited and non-visited locations. Since these descriptors influence the microclimatic conditions and shape the vegetation in a given habitat, they may play a role in fine-grained habitat selection. Black grouse prefer a specific altitude belt around the timberline, tending to avoid treeless zones and close forests (Klaus et al., 1990). Therefore, the quadratic function of altitude entered the analyses. Slope and exposition were treated as linear.

Descriptors of tourism footprint

We derived two habitat descriptors for tourism footprint, which were based on the presence/absence or Euclidean distance to the nearest infrastructure (road, forest track or walking trail) as these may affect black grouse habitat quality: vegetation may have changed in composition and/or cover due to new land use (Rolando et al., 2007) and/or human recreational activities can cause physiological stress in black grouse (Arlettaz et al., 2007).

We preferred distance to infrastructures rather than an estimate of their density because we could not objectively define the size of the window necessary for density calculations. Since we hypothesized that habitats near human facilities should be avoided, and habitat quality rises with the distance to human facilities, the linear function of the distance descriptor entered the analyses.

Descriptor of food abundance

As an estimate of arthropod food abundance, we used the number of anthills. Ants seem to be a crucial food source for the precocial chicks during their first weeks of life (Ponce, 1992b) and ant abundance may influence habitat selection pattern, especially in breeding females. Number of anthills entered the analyses as a linear function because we assume that the higher the arthropod abundance the more likely is chick-rearing hens' occurrence.

MODELLING AND MODEL SELECTION

General approach to model selection

We used logistic Mixed Effects Regressions to model black grouse habitat selection. To identify which variables best explain birds' presence and to avoid drawbacks inherent to stepwise regression (Whittingham et al., 2006), we applied an information theoretical approach for model selection: a priori defined sets of candidate models were ranked according to the principle of parsimony regarding best fit (Burnham & Anderson, 1998). We used unbiased Akaike Information Criterion differences and weights to hierarchize the candidate models (AICc, AICcw, respectively, Johnson & Omland, 2004). Model averaging gives a weighted coefficient estimate for each variable present in a set of candidate models and is traditionally used to get more robust estimates (Burnham & Anderson, 1998). However, since our models contained linear as well as quadratic variables, model averaging of parameter estimates was not possible. Thus, for each candidate set of models, only the model with the lowest AIC_c was retained. The selection probability of a given habitat category (described in Table 1, see also Table 2) was calculated as the sum of the AIC_c weights of those models where that category was included (Burnham & Anderson, 1998). Mixed Effects Models enabled the simultaneous analysis of all radiotracked individual birds pooled together, with individual being treated as a random effect and the habitat descriptors as fixed effects (Johnson et al., 2005).

Before running the analyses, we excluded, first, the descriptors that occurred only marginally or at very low densities (e.g. *Empetrum nigrum*, descriptor # 39 in Table 1). Second, we removed variables showing a high level of co-linearity (Spearman rank correlation coefficient, $r_s \geq |0.7|$). Of a correlated pair of variables, only that variable with biologically more meaningful information was retained, based on several studies (Zettel, 1974; Pauli, 1978, 1980; Marti, 1982; Zbinden, 1984; Ponce & Magnani, 1988; Klaus et al., 1990; Ponce, 1992a; Ponce, 1992b).

Variables expressing structural heterogeneity (category «habitat structure») and variables within the categories «habitat cover» and «plant communities» were logically grouped into sub-categories according to their belonging to a specific vegetation layer (see Descriptors of habitat structure and Table 1).

The detailed modelling sequence is described hereafter. All statistical analyses were performed using the R 2.4.1 software (lme4 library, R Development Core Team 2006).

Model selection within sub-categories

In a first step, we looked at single and combined contributions of the various habitat descriptors within the sub-categories of the three main categories «habitat structure», «habitat cover» and «plant community» (up to six variables per sub-category, see regrouping in Table 1), and retained the best model for subsequent analyses (Fig. 1).

Model selection within categories

In a second step, a global set of models was constructed within main categories (categories appear in bold in Table 1, third column), which included: a) the set of variables retained from each best single sub-category model, or b) the variables within the less complex categories «topography», «tourism footprint» and «food abundance» which now enter the modelling procedure (Fig. 1).

The set of variables within the categories «habitat structure», «habitat cover» and «plant communities» retained from each best single sub-category model was tested alone as well as was every possible combination of the sets of retained variables obtained from all sub-categories. The model with the lowest AIC_c value was retained for further modelling.

The variables within the categories «topography», «tourism footprint» and «food abundance» were tested alone 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 «habitat cover» and «plant community» into «habitat composition»

In a third step, we regrouped the categories «habitat cover» and «plant community» as they both express the cover characterization (plant species cover, rock cover, plant community, etc.) of the mapping locations. This newly constituted group was called «habitat composition» (Fig. 1). The computation of the best model was the same as for the modelling procedures mentioned above: each set of variables of the best model within «habitat cover» and «plant community» as well as the combination of the best models thereof were tested, and the model with the lowest AIC_c retained for the last step of the modelling procedure.

Best overall model

At step four, the set of explanatory variables of the single best model obtained for each category separately was used to build a new set of global candidate models in order to select the best overall model (Fig. 1). As the AIC_c enable ranking the models, but do not yield estimates of model performance, the latter was estimated with the KappaMax statistics (Kappa) as we have the same number of visited and non-visited points, i.e. a prevalence of 0.5 (Allouche, Tsoar & Kadmon, 2006). Bootstrap samples of equal size to the original data set were generated (Manly, 1997). The samples were chosen randomly and they replaced the original data set. For each bootstrap sample, we calculated the Kappa values and the Kappa standard deviation was determined from the whole sample. This method simulates the use of independent test data to evaluate the predictive performance of the original model (Vaughan & Ormerod, 2005). The model performance is considered poor when Kappa is lower than 0.4; good when Kappa is greater than 0.4 and smaller than 0.75, and excellent when Kappa is above 0.75 (Fielding & Bell, 1997).

Results

Altogether we radio-tracked and mapped the fine-grained habitat characteristics of 30 black grouse at nine study sites during the breeding season. There was, however, a bias in our sample towards males (n = 15) and non-breeding or unsuccessful reproductive females (n = 11) compared to females which successfully reared chicks (n = 4). Although 80% of the radio-tracked hens began incubation each year (2003-2006), only 28.6% of the incubating females could successfully raise their chicks. Failures were due either to nest failure (62.5%) or mortality of young chicks (37.5%). These values are similar to those from previous studies (30-60% and 34%, respectively, see the review by Klaus et al., 1990). A negative effect of radio-collars on survival and reproduction (Caizergues & Ellison, 1998) could not be assessed here.

The range of home range sizes was 9.8 – 18.5 ha (mean ± SD: 13.5 ± 3.6 ha, N = 4) for breeding females, 9.8 – 48.8 ha (18.1 ± 13.0 ha, N = 11) for non-breeding females and 4.0 – 80.0 ha (18.0 ± 19.2 ha, N = 15) for males.

«Habitat structure» was the most important habitat characteristic, showing a model selection probability of 100% for breeding and non-breeding females as well as males (Table 2). «Topography» had a selection probability over 50% for each bird class. «Habitat composition» was only important for breeding and non-breeding females (selection probabilities of 85% and 100%, respectively), whereas for males, the selection probability of this category was very low (12%). The selection probability of «tourism footprint» corresponded to 30% for breeding females, 93% for non-breeding females and 55% for males. Food abundance (i.e. number of anthills) showed selection probabilities lower than 30%.

For breeding females, variables expressing «habitat structure», «habitat composition» and «topography» were included in the best overall model ($AIC_cw_i = 0.4472$, Table 2), whereas «tourism footprint» and «food abundance» were not included. The overall quality of the best model was very good (Kappa = 0.88 ± 0.08). In contrast, the second best model had a probability of only 13% of being the best model ($AIC_cw_i = 0.1311$); it included, in addition to the above-mentioned categories, variables expressing «tourism footprint». The third best model included «food abundance» instead of «tourism footprint», and showed a similar weight as the second classified model ($AIC_cw_i = 0.1241$). The next models all had a probability lower than 10% to be selected as the best model.

For non-breeding females, a model with variables expressing «habitat structure», «habitat composition», «topography» and «tourism footprint» had the highest probability to be selected as the best model ($AIC_cw_i = 0.4433$, Table 2). The overall quality of the best model was excellent (Kappa = 0.83 ± 0.03). «Topography» was not included in the second and third best models ($AIC_cw_i = 0.\ 2899$ and $AIC_cw_i = 0.1040$, respectively), whereas «food abundance» was retained in the fourth best model only. From the fourth model downwards, the probability of being chosen as the best model was lower than 10%.

A model with variables expressing «habitat structure», «topography» and «tourism footprint» best explained the presence of male black grouse ($AIC_cw_i = 0.3017$). The quality of the best model was good (Kappa = 0.66 ± 0.05). However, the second best model had a similar probability to be selected as the best model ($AIC_cw_i = 0.2446$). It only included variables expressing «habitat structure» and «topography». The third best model included – besides «habitat structure» and «topography»– «tourism footprint» and «food abundance» ($AIC_cw_i = 0.1115$). All subsequent models had probabilities to be the best model all lower than 10%.

In the best models obtained for breeding, non-breeding females and males, retained variables describing horizontal and vertical patchiness of mature and small coniferous trees, shrubland and grassland all showed a positive association with the presence of birds (Tables 3–5). Only bare ground horizontal patchiness had a negative effect. Vertical patchiness was important within each vegetation layer, which was true for breeding females as well as for non-breeding females or males.

Variables describing «habitat composition» were only retained in models for habitat selection of breeding and non-breeding hens, whereas this category was not included in the best model for males (Table 2). Breeding females preferred a diversified habitat patchwork with a few scattered mature coniferous trees (larch and spruce) interspersed among a mosaic consisting of shrubland (mainly bilberry and Alpine rose; forest *Vaccinio-Piceion*, descriptor # 45 in Table 1) and Alpine grassland (descriptor # 66, with *Nardus stricta* as dominant species) (Table 3, Fig. 2a and Fig. 2c). Additionally, breeding hens showed a tendency to select rejuvenation of conifers within the above mentioned habitats (small tree *Vaccinio-Piceion*, descriptor # 50), which is obvious when the results are extrapolated onto the whole data set (Fig. 2b). Although many habitat descriptors appeared in the best model of non-breeding females, non-breeding hens did not show a pronounced preference, i.e. an optimum, for any of these habitat descriptors (Table 4, Fig. 2a-c). Both breeding and non-breeding females avoided rocky habitats.

In the category «topography», for breeding females, descriptors expressing altitude and slope and «convexity/concavity» were retained in the best model. Hens were less present at higher altitudes and preferred equal or concave topographies. Non-breeding females, in contrast, preferred convex topographies and were less present where the topography was straight. For males, only slope was retained; it showed a positive correlation with the presence of cocks, pointing to a preference for steeper mountainsides in that class.

For tourism footprint, there was an avoidance of tourism infrastructure by non-breeding hens and males, whilst breeding females appear to be indifferent towards them.

Food abundance (number of anthills) did not appear in the best or second best models describing habitat selection, neither for breeding, nor for non-breeding hens or cocks.

Discussion

The present study demonstrates that breeding and non-breeding black grouse females as well as males similarly show a high preference for patchy, heterogeneous microhabitats. Males showed no preference for a specific habitat composition, whereas habitat composition was important for females. Both breeding and non-breeding hens preferred a habitat mosaic consisting of an understorey of mixed shrubland interspersed with alpine grassland within a matrix dominated by isolated both mature and young (rejuvenation) coniferous trees. Our measures for structural heterogeneity were vertical and horizontal microhabitat patchiness, which merged together into global habitat heterogeneity. Habitat heterogeneity has been shown to be a key element for sustaining high biodiversity in ecosystems in general (Krüger & Lindström, 2001; Wilson, Fuller & Mather, 2002; Benton, Vickery & Wilson, 2003; Hamer et al., 2003; Tews et al., 2004; Koh, Lee & Lin, 2006) as well as in timberline Alpine ecosystems in particular (Molau, 2003; Dufour et al., 2006). We establish here in a quantitative way that habitat heterogeneity in timberline ecotones is essential for the occurrence of an emblematic element of the Alpine fauna. This provides support to the view that the black grouse plays the role of an umbrella species within timberline ecosystems as does the capercaillie (*Tetrao urogallus*) in nearby subalpine forests (Suter, Graf & Hess, 2002). Promoting optimal conditions for its survival are thus very likely to be beneficial to global Alpine biodiversity (Dufour et al., 2006).

Males do not show such a pronounced preference for some habitat composition as females do. This points to a possible sex-specific habitat selection, as demonstrated in ungulates (Conradt, Clutton-Brock & Thomson, 1999), carnivores (Rode, Farley & Robbins, 2006), elephants (Smit, Grant & Whyte, 2007), whales, seals, monkeys, fish and birds (Ruckstuhl & Neuhaus, 2000). One main reason leading to sex differential habitat selection is pronounced sex dimorphism (Ruckstuhl & Neuhaus, 2000). In the black grouse, females are smaller (960 g) than males (1311 g, Marti & Pauli, 1985), and have a completely different plumage coloration, cocks being black and white and hens cryptic brown. This marked dimorphism may be associated with different sex-specific anti-predator behaviour (cryptic plumage) and/or eco-physiological adaptations (body size) (Walsberg, 1982, 1985; Wolf & Walsberg, 2000). The latter may be crucial in mountainous ecosystems subjected to pronounced microclimatic variation (Körner, 1999).

The comparison of habitat compositions of breeding and non-breeding females suggests that these two classes differ in habitat selection pattern. Breeding females seem to have a narrower niche compared to non-breeding females. First, they prefer tall isolated, patchily distributed mature trees (10-20% within a radius of 15 m around a mapping point; Fig. 2). Second, they select zones with a relatively large cover of grassland (10-30%). And third, they are more restricted than non-breeding females to a given cover of rejuvenation of conifers associated with shrubland (mainly *Rhododendron ferrugineum* and *Vaccinium myrtillis*), with an optimum around 30-40%, although these results only emerged when an extrapolation onto the data set of breeding and non-breeding females was performed. The fact that cover of rejuvenation of conifers associated with shrubland was below 22% (Fig. 3b) in breeding hens could be due to our small sample size. Non-breeding females, in contrast, did not show a distinct habitat preference for any variable describing «habitat composition», suggesting more tolerance towards it. This difference in habitat use may be due to the need of breeding females to provide chicks with secluded shelters (regeneration trees and dense shrubland) and elevated biomasses of arthropods, the latter abounding in open and semi-open habitats (Signorell et al., submitted). Non-breeding females, in contrast, feed exclusively on plant material, i.e. do not require insect-rich zones; in the absence of chicks, they would also have less specific requirements regarding secluded shelters.

Our results suggest that non-breeding females and males both avoided roads, forest tracks and walking paths. Roads may impair habitat quality directly by modifying the landscape and the vegetation, and indirectly through a decrease of attractiveness due to increased human disturbance. This would add to the degradation of Alpine ecosystems by winter sport activities through the construction of ski infrastructure and the management of ski-runs (Ingold, 2005; Johnson et al., 2005) as well as steadily growing winter disturbance (Arlettaz et al., 2007). However, the fact that we found no sign of avoidance of walking trails and forest tracks in breeding females may be artefactual. It might be that our females classified as non-breeding hens did not initiate any brood or lost it because of human disturbance, or pressure exerted by predators profiting of human activities (Storch & Leidenberger, 2003; Wittwer et al., in prep.). After brood failure, they could simply have left their favourite breeding habitat towards zones less exposed to anthropogenic or predator pressure, which would be mirrored in an apparent pattern of avoidance of «tourism footprint». It might also be that the pressure for finding optimal habitat conditions for nesting as well as chick-rearing constrains the females to opt for risky habitats close to human activities.

Contrary to our expectation, exposition (easting and southing) had no effect on occurrence probability. This may be due to a too fine scale resolution (lack of sufficient contrast) in our habitat selection analysis, with most of our bird home ranges already on the most suitable aspects.

We could not find evidence of an association between habitat selection by breeding hens and occurrence of anthills. Ants are considered a key food source for chicks for they rely exclusively upon invertebrate food during the first 2-3 weeks of life, i.e. when growth rate peaks (Picozzi & Hepburn, 1984; Ponce & Magnani, 1988; Klaus et al., 1990; Ponce, 1992b). Yet, anthills are often hidden under dense shrub vegetation at the timberline, and some may have been missed in our visual mapping. More refined techniques to quantify actual arthropod availability – and not just ants – are required to better estimate the relationships between habitat selection and food supply (Patthey et al., submitted).

RECOMMENDATIONS FOR HABITAT MANAGEMENT

Alpine timberline ecosystems are currently increasingly threatened due to land-use changes and the growing negative impact of tourist activities upon flora and fauna (Ingold, 2005; Arlettaz et al., 2007, this study, see Fig. 3). Firstly, the construction and maintenance of ski-runs, chairlifts and cablecars for snow sports and summer recreational activities are associated with damages to the fragile native vegetation (Muller et al., 1998; Delgado et al., 2007). Shrubs, small trees and boulders are systematically removed to keep ski-runs smooth and free of obstacles, which leads to a homogeneous habitat dominated by grasses, i.e. reduced plant diversity (Dufour et al., 2006; Rolando et al., 2007; Tasser et al., 2007). Habitat homogenization also leads to a lower arthropod species richness and abundance on ski-runs, which in turn affects food abundance for insectivorous birds (Rolando et al., 2007). Secondly, the abandonment of traditional farming practices is another growing threat for Alpine timberline habitats (Storch, 2000; Maurer et al., 2006), as it also causes a loss of habitat heterogeneity. For instance, extensive cattle grazing actually maintains habitat heterogeneity, with abandonment of grazing resulting in encroachment by dwarf shrubs and forest, i.e. in the dominance of a few plant species and the emergence of monotonous habitats.

As habitat heterogeneity plays a central role for breeding and non-breeding female as well as male black grouse, it must be kept or restored both within and outside ski-resort areas. First, retaining patches of spontaneously growing shrubland and allowing natural seed rain from surrounding habitats (Urbanska & Fattorini, 2000) so as to recreate some habitat mosaic could prevent artificial homogenization of vegetation around ski-runs towards short grass. Additionally, transplants could be envisioned in habitats degraded by heavy machinery. Second, to counteract vegetation encroachment, i.e. progressive closure of vegetation often towards one single dominant plant species (Muller et al., 1998), traditional extensive farming practices like cattle grazing, or moderate goat grazing (Storch, 2000) should be maintained and encouraged all over the timberline. Some initial forestry interventions may be locally necessary where spontaneous reforestation is advanced in order to ensure good starting conditions where management through grazing of domestic animals is envisioned (Muller et al., 1998; Tasser et al., 2007).

Based on the outcome of this study we can provide simple guidelines for achieving an optimal breeding habitat patchwork for Alpine black grouse. We suggest the following approximate proportions of habitat types: 1) 30-40% of the area should consist of regeneration stands with scattered small (< 3 m) coniferous trees (spruce, larch and arolla pine) at a density of ca 20-30 trees/ha, 2) 10-30% of isolated mature conifers (again spruce, larch and arolla pine) at a density of ca 10-15 trees/ha, 3) these young and mature tree stands should be associated with an understorey of mixed Ericaceae shrubland (mainly *Rhododendron ferrugineum* and *Vaccinium myrtillis*) covering 30-40% of the area, and 4) 10-30% of alpine grassland (mainly

Nardion strictae and Festucion variae). Such a rich habitat mosaic should be regularly available within Alpine timberline ecosystems. Although our single-scale mapping does not allow estimating an optimum for spatial habitat pattern repetition along the narrow, ca 300 m wide altitudinal belt of timberline habitat, we suggest to repeat the proposed habitat pattern every 100 – 250 m horizontally along the timberline. The former distance is about three times our fine-grained habitat mapping scale, whereas the latter distance corresponds roughly to half the length of an average black grouse hen's home range stretching along the timberline (15 ha divided by 300 m of belt width). We would thus obtain between two and five mosaic repetitions per average hen's home range, with the resulting areas representing very convenient habitat management units.

In addition to vegetation management, access restrictions and path regulations should be implemented in optimal black grouse breeding habitat during the reproductive period, with the goal to keep walkers on trails and tracks for limiting human disturbance.

The habitat model developed here may be used in the future as a basis to map habitat suitability across the Alps using GIS technologies (satellite imagery) so as to delineate the best areas where corrective management measures would provide the greatest return on investment in terms of black grouse conservation, for instance by implementing habitat interventions firstly where forest encroachment is more advanced. If appropriately applied, these measures are likely to benefit other elements of biodiversity within Alpine timberline ecosystems.

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Table 1. Explanatory variables (n = 96, with individual variable reference code in the left most column) mapped in the field, regrouped in main categories (in bold) and subcategories (roman figures), with format (continuous, ordinal, categorical), function (quadratic or linear; for both continuous and ordinal variables), and levels (categorical variables: see nomenclature in the respective column; ordinal variables: 0–3, or 0–4). Variables belonging to the same sub-category are marked with vertical bars. A variable followed by brackets indicates that this variable has been eliminated to the profit of the variable whose reference code is given in parenthesis. See text for more details.

Descriptor #	Sub-category	Category Descriptor	Format	Function	Levels
		Habitat structure			
1	I.	Mature tree horizontal patchiness	ordinal	linear	0-3
2		Mature tree vertical patchiness (1)	ordinal	linear	0-3
3		Mature tree height (1)	ordinal	quadratic	0-3
4	II.	Small tree horizontal patchiness	ordinal	linear	0-3
5		Small tree vertical patchiness (4)	ordinal	linear	0-3
6		Small tree height	ordinal	quadratic	0-3
7	III.	Shrub horizontal patchiness	ordinal	linear	0-3
8		Shrub vertical patchiness	ordinal	linear	0-3
9		Shrub height	ordinal	quadratic	0-4
10	IV.	Herbaceous layer horizontal patchiness	ordinal	linear	0-3
11		Herbaceous layer vertical patchiness	ordinal	linear	0-3
12		Grass height	ordinal	quadratic	0-4
13	V.	Bare ground horizontal patchiness	ordinal	linear	0-3
14		Rock block size (44)	ordinal	linear	0-3
15		Rock horizontal patchiness (44)	ordinal	linear	0-3
16		Rock vertical patchiness (44)	ordinal	linear	0-3
17		Stumps	continuous	linear	
18		Grazing	nominal		Presence/absence
		Habitat cover			
19	I.	Total mature tree cover	continuous	quadratic	
20		Mature *Larix decidua* cover	continuous	quadratic	
21		Mature *Picea abies* cover	continuous	quadratic	
22		Mature *Pinus cembra* cover	continuous	quadratic	
23		Mature *Sorbus aucuparia* cover[a]	continuous	quadratic	
24	II.	Total small tree cover	continuous	quadratic	
25		Regeneration *Larix decidua* cover	continuous	quadratic	
26		Regeneration *Picea abies* cover	continuous	quadratic	
27		Regeneration *Pinus cembra* cover	continuous	quadratic	
28		Regeneration *Alnus viridis* cover	continuous	quadratic	
29		Regeneration *Salix* sp./*Betula* sp. cover[a]	continuous	quadratic	
30		Regeneration *Sorbus aucuparia* cover[a]	continuous	quadratic	
31	III.	Total shrub cover	continuous	quadratic	
32		*Vaccinium myrtillus* cover	continuous	quadratic	
33		*V. gaultherioides* cover	continuous	quadratic	

34		*V. vitis-idaea* cover[a]	continuous	quadratic
35		*Rhododendron ferrugineum* cover	continuous	quadratic
36		*Calluna vulgaris* cover (38)	continuous	quadratic
37		*Arctostaphylos uva-ursi* cover[a]	continuous	quadratic
38		*Juniperus communis ssp. nana* cover	continuous	quadratic
39		*Empetrum nigrum* cover[a]	continuous	quadratic
40	IV.	Total herbaceous cover (41)	continuous	quadratic
41		Graminaceae cover	continuous	quadratic
42		Megaphorb cover	continuous	linear
43	V.	Bare ground cover	continuous	quadratic
44		Rock cover	continuous	linear
		Plant community		
45	I.	Forest Vaccinio-Piceion	continuous	quadratic
46		Forest Junipero-Laricetum	continuous	quadratic
47		Forest Larici-Pinetum cembrae[a]	continuous	quadratic
48		Forest Abieti-Piceion[a]	continuous	quadratic
49		Forest Erico-Pinion mugo[a]	continuous	quadratic
50	II.	Small tree Vaccinio-Piceion	continuous	quadratic
51		Small tree Larici-Pinetum cembrae	continuous	quadratic
52		Small tree Junipero -Laricetum	continuous	quadratic
53		Small tree Alnenion viridis	continuous	quadratic
54		Small tree Salicenion waldsteinianae[a]	continuous	quadratic
55		Small tree Abieti-Piceion[a]	continuous	quadratic
56		Small tree Erico-Pinion mugo[a]	continuous	quadratic
57	III.	Very small tree Vaccinio-Piceion[a]	continuous	quadratic
58		Very small tree Larici-Pinetum cembrae[a]	continuous	quadratic
59		Very small tree Junipero -Laricetum[a]	continuous	quadratic
60		Very small tree Salicenion waldsteinianae[a]	continuous	quadratic
61		Very small tree Alnenion viridis[a]	continuous	quadratic
62		Very small tree Abieti-Piceion[a]	continuous	quadratic
63		Very small tree *Erico-Pinion mugo*[a]	continuous	quadratic
64	IV.	Nardion strictae	continuous	quadratic
65		Festucion variae	continuous	quadratic
66		Alpine grassland (variables # 67+68)	continuous	quadratic
67		Caricion ferruginea[a]	continuous	quadratic
68		Caricion curvulae[a]	continuous	quadratic
69		Calamagrostion arundinaceae	continuous	quadratic
70		Poion alpinae[a]	continuous	quadratic
71		Alchemillo-Poion supinae[a]	continuous	quadratic
72		Elyinion myosuroides[a]	continuous	quadratic
73	V.	Juniperion nanae	continuous	quadratic
74		Rhododendro-Vaccinion	continuous	quadratic
75		Loiseleurio-Vaccinion	continuous	quadratic
76		Epilobion angustifolii[a]	continuous	quadratic
77		Adenostylion allariae[a]	continuous	quadratic
78		Atropion belladonnae[a]	continuous	quadratic
79		Ericion carnarea[a]	continuous	quadratic
80		Rumicion alpini[a]	continuous	quadratic
81	VI.	Bare ground	continuous	quadratic
82		Rocks	continuous	linear
83		Snow bottoms[a]	continuous	linear
84		Scree[a]	continuous	linear

	Topography			
85	Altitude	continuous	quadratic	
86	Concavity/convexity	nominal		equal/concave/convex
87	Exposure	continuous	linear	
88	Slope	continuous	linear	
	Tourism footprint			
89	Infrastructure	nominal		presence/absence
90	Euclidean distance to the nearest road, track or path	continuous	linear	
	Food abundance			
91	Anthill number	continuous	linear	

[a] Variable excluded because it occurred only marginally or at very low densities within our study plots (<10%; see text for more details)

Table 2. Overview results of the model selection procedure for 4 breeding females, 11 non-breeding females and 15 black grouse males during the reproductive season. Only the best candidate models are presented (cumulative AIC_c weights = 0.95) among all possible combinations of the five categories. An x indicates a variable entering a given model. Also indicated are: number of model parameters (k), differences in small sample unbiased Akaike's Information Criterion scores (AIC_c Δ_i) and weights ($AIC_c w_i$) and Kappa statistic (± SD) for the best model. The model used is logistic mixed regression with, as dependent variable: visited/non visited location; fixed effects: habitat variables; and random effect: individual bird.

Habitat structure	*Habitat composition*	*Topography*	*Tourism footprint*	*Food abundance*	*k*	$AIC_c\Delta_i$	AIC_cw_i	*kappa*
Breeding females								
x	x	x			27	0.00	0.4472	0.88±0.08
x	x	x	x		29	2.45	0.1311	
x	x	x		x	28	2.56	0.1241	
x		x			16	3.21	0.0900	
x	x		x		26	3.56	0.0754	
x	x	x	x	x	30	4.97	0.0373	
x		x		x	17	5.12	0.0345	
x	x		x	x	27	5.60	0.0272	
1.000*	0.845*	0.882*	0.298*	0.232*				
Non-breeding females								
x	x	x	x		51	0.00	0.4433	0.83±0.03
x	x		x		50	0.85	0.2899	
x	x		x	x	51	2.90	0.1040	
x	x	x	x	x	52	3.16	0.0914	
x	x				49	5.61	0.0269	
1.000*	1.000*	0.570*	0.929*	0.224*				
Males								
x		x	x		19	0.00	0.3017	0.66±0.05
x		x			18	0.42	0.2446	
x		x	x	x	20	1.99	0.1115	
x		x		x	19	2.50	0.0864	
x			x		18	3.12	0.0634	
x					17	4.15	0.0379	
x			x	x	19	5.00	0.0248	
x	x				42	5.01	0.0247	
x	x	x			43	5.15	0.0229	

x	x		x		43	5.45	0.0197
x	x	x	x		44	5.61	0.0183
1.000*	0.116*	0.799*	0.552*	0.267*			

* selection probability (see text for explanation)

Table 3. Coefficients and standard errors of the habitat variables included in the best logistic mixed effects regression model predicting the occurrence of breeding black grouse females. Variables listed in Table 1 but not appearing here have not been retained in the final model. Quadratic terms are indicated as power 2. For enhancing clarity the estimates and standard errors of some quadratic terms were divided by 100 as indicated.

Breeding females	***Estimate***	***SE***
Intercept	598.1881	181.2921
Habitat structure		
Mature tree horizontal patchiness	0.9621	0.3430
Shrub horizontal patchiness	1.3314	0.5458
Shrub vertical patchiness	1.2676	0.5302
Herbaceous layer horizontalpatchiness	0.8037	0.6148
Herbaceous layer vertical patchiness	1.5760	0.4486
Grass height	6.4830	3.5368
Grass height^2	-0.9847	0.5795
Bare ground horizontal patchiness*	-0.2960	0.4876
Stumps	0.4791	0.3347
Grazing*	-0.2174	0.7099
Habitat composition		
Forest Vaccinio-Piceion	0.0949	0.0990
Forest Vaccinio-Piceion^2/100	-0.3368	0.2135
Small tree Vaccinio-Piceion	-0.3970	0.2534
Small tree Vaccinio-Piceion^2/100	1.7216	1.4534
Small tree Junipero-Laricetum*	0.0268	0.0966
Small tree Junipero-Laricetum^2/100*	0.0908	0.2703
Alpine grassland	0.0292	0.0626
Alpine grassland^2/100	-0.1036	0.0988
Calamagrostion arundinaceae	-0.1239	0.0613
Calamagrostion arundinaceae ^{2}/100	0.0931	0.0734
Rocks	-0.2444	0.1001
Topography		
Altitude	-0.5894	0.1767
Altitude^2/100	0.0140	0.0043
Concavity/convexity	2.5341	3.0146
Slope	0.6096	1.2617

* Estimate ± SE covers 0, indicating that the corresponding variable is irrelevant

Table 4. Coefficients and standard errors of the habitat variables included in the best logistic mixed effects regression model predicting the occurrence of non-breeding black grouse females. Variables listed in Table 1 but not appearing here have not been retained in the final model. Quadratic terms are indicated as power 2. For enhancing clarity the estimates and standard errors of some quadratic terms were divided by 100 as indicated.

Non-breeding females	***Estimate***	***SE***
Intercept	3.0662	4.1341
Habitat structure		
Mature tree horizontal patchiness	0.7916	0.3747
Small tree horizontal patchiness	1.8465	0.2899
Small tree height	-1.8614	0.9947
Small tree height^2	0.5046	0.2641
Shrub horizontal patchiness*	0.0809	0.2869
Shrub vertical patchiness	1.9946	0.3784
Shrub height	-1.0122	0.9560
Shrub height^2	-0.0015	0.2115
Herbaceous layer horizontal patchiness	1.2923	0.3278
Herbaceous layer vertical patchiness	2.1205	0.3088
Grass height	-4.0965	1.4362
Grass height^2	0.8033	0.2632
Habitat composition		
Total mature tree cover*	0.0518	0.0539
Total mature tree cover^2/100*	-0.0023	0.0678
Regeneration *Alnus viridis* cover	-0.1234	0.0671
Regeneration *Alnus viridis* ^{2}/100	0.2504	0.1030
V. myrtillus cover	-0.2377	0.0732
V. myrtillus cover^2/100	0.5368	0.2121
V. gaultherioides cover*	-0.0294	0.0699
V. gaultherioides cover^2/100*	0.1549	0.1730
Graminacea cover	0.0541	0.0612
Graminacea cover^2/100	-0.0986	0.0683
Megaphorb cover	0.2092	0.1733
Forest Vaccinio-Piceion	-0.0421	0.0440
Forest Vaccinio-Piceion^2/100	-0.0093	0.0709
Forest Junipero-Laricetum	-0.0320	0.0496
Forest Junipero-Laricetum^2/100	-0.1138	0.0937
Small tree Vaccinio-Piceion*	0.0229	0.0951
Small tree Vaccinio-Piceion^2/100*	-0.2651	0.3515
Small tree Junipero-Laricetum	-0.0963	0.0709
Small tree Junipero-Laricetum^2/100	0.0503	0.2088
Alpine grassland	-0.1161	0.0569
Alpine grassland^2/100	0.0429	0.0457
Nardion strictae	-0.0684	0.0377
Nardion strictae^2*/100*	0.0397	0.0614
Calamagrostion arundinaceae	-0.0660	0.0504
Calamagrostion arundinaceae^2/100	-0.0396	0.0395
Juniperion nanae	-0.1448	0.0460
Juniperion nanae^2/100	0.0446	0.0339
Rhododendro-Vaccinion	-0.0837	0.0471
Rhododendro-Vaccinion^2/100	0.0270	0.0360
Loiseleurio-Vaccinion	-0.1607	0.0600
Loiseleurio-Vaccinion^2/100	0.1496	0.0609

Bare ground	0.0208	0.0813
Bare ground^2/100	-0.3776	0.2122
Rocks	-0.1398	0.0447
Topography		
Convexity/concavity	0.9100	0.7627
Slope	-0.1310	0.5714
Tourism footprint		
Infrastructure	-2.1662	0.8024

[*] Estimate ± SE covers 0, indicating that the corresponding variable is irrelevant

Table 5. Coefficients and standard errors of the habitat variables included in the best logistic mixed effects regression model predicting the occurrence of black grouse males. Variables listed in Table 1 but not appearing here have not been retained in the final model. Quadratic terms are indicated as power 2.

Males	*Estimate*	*SE*
Intercept	-12.2852	2.3542
Habitat structure		
Mature tree horizontal patchiness	0.6672	0.1597
Small tree horizontal patchiness	0.5297	0.1701
Small tree height	1.9654	0.7084
Small tree height^2	-0.4819	0.1778
Shrub horizontal patchiness	0.2550	0.2304
Shrub vertical patchiness	0.8125	0.2277
Shrub height	-1.2030	0.6184
Shrub height^2	0.2479	0.1365
Herbaceous layer horizontal patchiness	0.5548	0.2115
Herbaceous layer vertical patchiness	0.5014	0.2184
Grass height	2.4746	1.5250
Grass height^2	-0.2909	0.2621
Bare ground horizontal patchiness	-0.4545	0.1754
Stumps	0.2101	0.0779
Topography		
Slope	0.0377	0.0166
Tourism footprint		
Infrastructure	-1.0488	0.6506

Figure captions

Fig. 1. Model selection theoretical approach design with arrows indicating the modelling steps. The main categories habitat structure, habitat cover and plant community consist of five to six sub-categories each. Categories of descriptors are indicated in bold. Variables are detailed in Table 1.

Fig. 2. Occurrence probability of breeding and non-breeding females with respect to percentage cover of most important habitat composition descriptors for breeding females (Table 3): a) scattered mature coniferous trees (larch *Larix decidua* and spruce *Picea abies* as the dominant species) with shrubland understorey (bilberry *Vaccinium myrtillis* and Alpine rose *Rhododendron ferrugineum* as dominant species), b) conifers rejuvenation (larch and spruce as the dominant species) with shrubland understorey (bilberry and Alpine rose as dominant species) and c) alpine grassland (*Nardus stricta* as the most common and dominant species). The other variables retained in the model were fixed at their mean values for producing these predictive graphs. Depicted distributions are limited to the range of values observed at actual mapping locations. Full dots: breeding females; crosses: non-breeding females; circles: extrapolation for breeding females based on the data of both breeding and non-breeding hens pooled together.

Fig. 3. Timberline ecosystems in the Alps: a) pristine habitats (Val d'Arolla, Valais, SW Switzerland; photograph by R. Arlettaz); b) area devoted to snow sports (Courchevel 1850, Savoie, France, photograph by G. Wittwer).

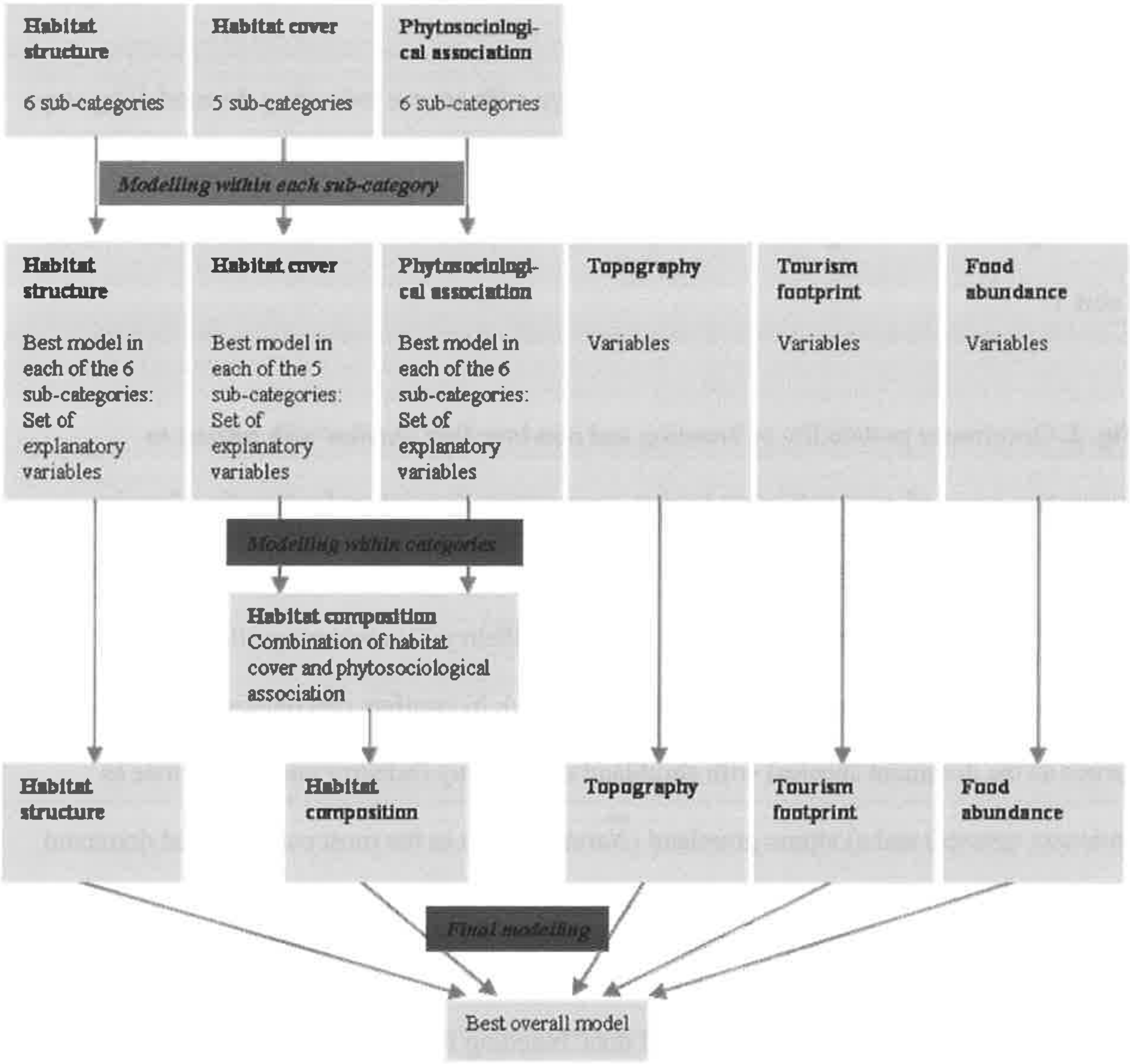
Habitat structure
6 sub-categories
Habitat cover
5 sub-categories
Phytosociological association
6 sub-categories
Modelling within each sub-category
Habitat structure
Best model in each of the 6 sub-categories: Set of explanatory variables
Habitat cover
Best model in each of the 5 sub-categories: Set of explanatory variables
Phytosociological association
Best model in each of the 6 sub-categories: Set of explanatory variables
Topography
Variables
Tourism footprint
Variables
Food abundance
Variables
Modelling within categories
Habitat composition
Combination of habitat cover and phytosociological association
Habitat structure
Habitat composition
Topography
Tourism footprint
Food abundance
Final modelling
Best overall model

Fig. 1

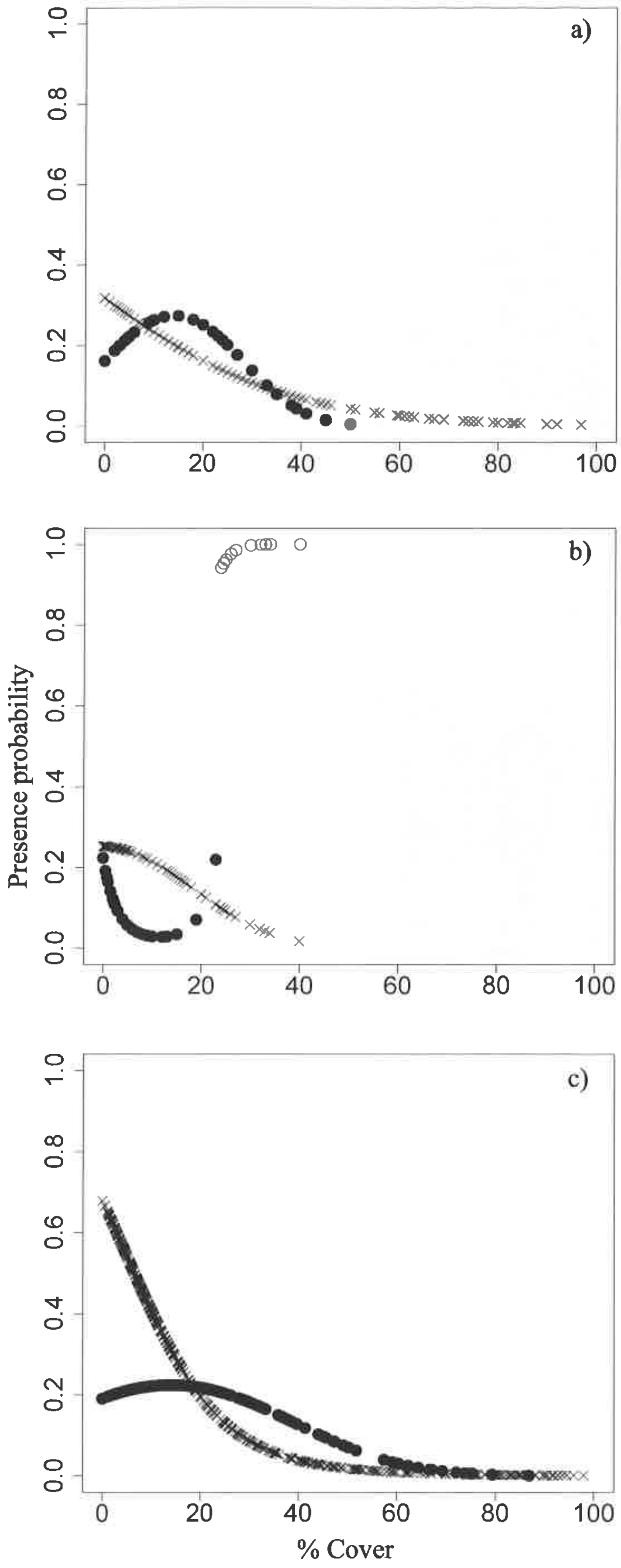
a)
b)
c)
Presence probability
% Cover
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100

Fig. 2

Fig. 3

CHAPTER TWO

Foraging habitat selection by black grouse (*Tetrao tetrix*) hens during reproduction: implications for the management of Alpine timberline ecosystems

Submitted

Foraging habitat selection by black grouse (*Tetrao tetrix*) hens during reproduction: implications for the management of Alpine timberline ecosystems

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Word count: 7485

Summary

1. Population dynamics of species with rapid generation turnover depends primarily on reproductive output and offspring survival. In birds, chick's optimal growth requires a protein-rich, easily digestible food such as arthropods, a food source that fluctuates seasonally and from year to year and varies in relation to habitat type and quality. Many birds thus select preferentially arthropod-rich habitats for breeding. However, arthropod-rich habitats may be traded-off against food-poorer habitats, e.g. when predation risk is high.
2. The black grouse (*Tetrao tetrix*) is a ground-nesting precocial bird species that has decreased dramatically in the last decades in several regions of Europe. Its decline has been associated with a drop of breeding success due to degradation of foraging conditions for chicks that are very sensitive to both habitat quality and weather fluctuations. In the Alps, black grouse inhabit heterogeneous timberline ecosystems that are characterized by a high seasonal and habitat specific variation in food availability. However, little is known about the relationship between arthropod abundance and habitat type as well as about habitat selection of breeding hens in relation to arthropod abundance.
3. We performed a habitat selection analysis for determining females' habitat preferences, and sampled arthropod abundance in different habitats, predicting higher food supplies in the favourite habitats. A comparison of the two datasets led to an interpretation of the pattern of habitat selection in the light of strategic trade-offs between trophic and behavioural constraints during reproduction.
4. Arthropod abundance differed significantly between habitats: open grassland and grassy shrubland yielded the highest biomass. Hens, however, avoided extensive open habitats, showing a marked preference for a mosaic of grassy shrubland with scattered trees. This suggests that food abundance *per se* is not the sole criterion for habitat selection by hens;

it is probably traded-off against shelter, i.e. predation risk, which is higher in open Alpine grassland.

5. *Synthesis and application.* The management of timberline ecosystems, aimed for instance at improving pastureland in the face of shrub and forest encroachment, should account for black grouse trophic and breeding habitat requirements: the restoration of extended areas of totally open pastureland ought to be avoided. Instead, a complex, heterogeneous habitat mosaic consisting of grassland and shrubland interspersed with scattered coniferous trees should be systematically promoted.

Word count: 370

Key words: Alpine timberline ecosystems, food abundance, arthropod phenology, trophic ecology, *Tetrao tetrix*

Introduction

The successful rearing of offspring is regarded as one of the most sensitive phases in the life history of animals with short generation lengths. It therefore plays a key role in lifetime reproductive success, a major determinant of fitness (Stearns, 1992). A crucial factor for the successful development of the offspring is a sufficient food source. As mammals depend on mother's milk, the food source for their offspring is more stable and predictable than for bird chicks that often depend on arthropods, a highly variable food source in space and time (Bolger et al., 2000). Arthropods provide a protein-rich and easily digestible food (Ponce, 1992b; Starling-Westerberg, 2001; Gregersen & Olstad, 2002). They are, however, highly dependent on a specific habitat and/or habitat quality (Duelli, Obrist & Schmatz, 1999; Nummelin & Zilihona, 2004), and their abundance shows high seasonal variation (Juen & Traugott, 2004; Leksono et al., 2005; Doblas-Miranda, Sánchez-Piñero & González-Megías, 2007). Moreover, since arthropods' behaviour is weather-dependent (e.g., Dennis & Sparks, 2006), availability of arthropod food for chicks largely depends on the prevailing weather conditions.

A second factor that determines reproductive success is predation that may dramatically reduce survival of the young (Hannon & Martin, 2006). Given that animals often expose themselves when in search for food, food abundance may be traded off against predation risk in habitat selection decisions. This is especially the case of precocial, ground-nesting birds whose chicks are flightless during their first weeks of life and depend on their mother for thermoregulation: these young follow their mother in quest of food, which renders them more conspicuous to aerial and terrestrial predators.

Predation level seems to have increased in human-disturbed ecosystems (Wüthrich, 2001; Storch & Leidenberger, 2003; Marzluff & Neatherlin, 2006). Human presence in tourist areas indirectly attracts predators due to numerous food remains close to infrastructure (Storch & Leidenberger, 2003; Wittwer et al., in prep.), with a higher abundance of opportunistic and generalist predators leading to increased nest and chick predation (Storch & Leidenberger, 2003; Watson & Moss, 2004). In boreo-alpine environments where the time window for reproduction is extremely short, the conjugated effects of high seasonality in arthropod availability and pronounced predation risk might represent real challenges to ground-nesting, precocial bird species such as grouse and waders.

We studied the Alpine black grouse (*Tetrao tetrix*), an emblematic ground-nesting and precocial bird species that inhabits timberline ecosystems. It is regarded as a good ecosystem indicator (Storch, 2000b). Black grouse populations have been continuously declining over the past decades, not only at low elevations in western and central Europe but also at the edge of their distribution in the Alps (Klaus et al., 1990; Hess, 2000). Principal threats for the Alpine populations have been claimed to be habitat alteration and fragmentation, and human disturbance (Storch, 2000a; Arlettaz et al., 2007).

Breeding success has been identified as an important component of population dynamics in many grouse species (e.g. Moss, Oswald & Baines, 2001). On the one hand, it highly depends on the prevailing weather conditions during reproduction (Zbinden & Salvioni, 2004). On the other hand, it is apparently linked to the quality of the breeding habitat which has been assessed, based mostly on expert knowledge, for black grouse (Pauli, 1974, , 1978; Marti, 1985a; Marti & Pauli, 1985; Ponce, 1992b; Starling-Westerberg, 2001; Zbinden & Salvioni, 2003), red grouse (Park et al., 2001) and capercaillie (Gregersen & Olstad, 2002). Good arthropod supplies are generally crucial for optimal grouse chicks' development and survival during their first weeks of life (Hannon & Martin 2006). For the black grouse, this time window is also regarded as the most sensitive phase of life history as it determines reproductive success and ultimately population dynamics (Rajala, 1974; Ellison, 1979; Klaus et al., 1990; Zbinden & Salvioni, 2004; Ludwig et al., 2008). For Alpine black grouse, there exists so far no quantitative study of arthropod biomass and phenology in different characteristic timberline habitats although this information would be essential for understanding the relationships between reproductive performance and habitat selection patterns in brood-rearing hens. Black grouse hens are expected to select arthropod-rich habitats and to time reproduction onto peaks of food abundance, which are usually occurring in the middle of the vegetation season (Atlegrim, 1991).

In continuation of a fine-grained habitat selection analysis (Signorell et al., submitted), this study aims at assessing arthropod abundance and phenology in different characteristic black grouse habitats, with emphasis on the breeding habitat and prey most likely to enter chicks' diet such as ants, beetles, grasshoppers, spiders and caterpillars (Ponce & Magnani, 1988; Klaus et al., 1990; Ponce, 1992b). We tested whether the habitat preference shown by females, especially brood-rearing hens, actually mirrors the pattern of habitat-specific arthropod abundances. For that purpose we first performed a habitat selection analysis with data collected from radiotracked birds, and, second, sampled arthropods in different habitats. The ultimate aim of the study was to apprehend the subtle habitat requirements of reproductive black grouse hens so as to optimize timberline ecosystem conservation management in the Alps. Indeed, pastureland has been decreasing dramatically in several parts of the Alps due to shrub and forest encroachment following abandonment of traditional land use by farmers, but there are currently new incentives to restore grassland for improving grazing conditions for livestock. It is essential that any habitat management policy accounts for the persistence of sensitive wildlife. The present work intends to contribute to define good management practices.

Material and Methods

STUDY AREAS AND HABITAT CHARACTERISATION

The study of arthropod abundance and phenology was conducted in the Alps of south-western Switzerland, in the cantons of Valais and Vaud, from June to August 2005. Three different sites were chosen, one site in the Central Alps (Aletsch, 46°22'N, 8°01'E), one in the Prealps (Les Diablerets, 46°19'N, 7°05'E) and one in the Southern Alps (Simplon, 46°15'N, 8°02'E).

The investigation of habitat selection by black grouse females was conducted in the summers 2004-2007 at 6 different sites in the canton of Valais (south-western Switzerland, 46°12'N/7°20'E), and at two sites in Piemonte, Verbania Province, close to the Swiss border (northern Italy, 46°06'N/8°18'E). Although a simultaneous study of arthropod abundance at actual hens' locations would have yielded more accurate data, we avoided disturbing the brood-rearing hens while radiotracking them. The arthropod study was thus carried out separately from the habitat selection analysis.

On the southern slope of the Alps (Simplon area in south-eastern Valais and Northern Italy), the dominating tree species of upper subalpine forests and the adjacent timberline is larch (*Larix decidua*), whereas in the other study areas spruce (*Picea abies*) and arolla pine (*Pinus cembra*) are also present. Dwarf shrubs (*Rhododendron ferrugineum*, *Vaccinium* sp., *Juniperus communis* ssp. *nana*, *Calluna vulgaris*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, etc.) and grasses (*Nardus stricta*, *Calamagrostis villosa*, etc.) represent a characteristic understorey in all areas. The study areas are characterized by a subcontinental to continental climate with warm and dry summers, and cold, relatively wet winters (Reisigl & Keller, 1999).

We defined 19 different habitat types according to their vertical and horizontal habitat structure, accounting additionally for a gradient of humidity impacting on the vegetation (Table 1). All habitat types are typically found in the home ranges of male and chick-leading female black grouse (henceforth referred to as breeding females) as well as of hens which had no clutch or lost their clutch or brood (henceforth referred to as non-breeding females) during the breeding season in the Alps (Signorell et al., submitted). These 19 habitat types were regrouped in 8 habitat categories with respect to habitat structure. Since the horizontal understorey structure plays a bigger role than the age of the trees (Signorell et al., submitted), we grouped together young and old forests that had the same understorey pattern (Table 1).

DELINEATION OF HOME RANGES AND GENERATION OF RANDOM POINTS

Birds were first captured from snow burrows between January and March in 2003-2006, when snow conditions were appropriate. We used a 2 x 2.5 m mist-net stretched between two up to 6 m long telescopic fishing rods. The net was placed on the snow surface above visually localized, potentially occupied igloos (Marti, 1985b). Second, birds were also mist-netted at leks from May to June with 1 m high and 6 m long groundnets. Caught birds were tagged with neck-laced radio transmitters (Holohil Systems Ltd. Carp, Canada, RI-2D; 12 g, 29 x 19 x 15 mm) with the permission of the Swiss Federal Office for the Environment, the Wildlife and Game Service of Valais and the Italian and Piemontese Environmental Agencies.

In July and August, i.e. during the brood-rearing period, females were radio-located every day for a period of 30 days in a row, resulting in 30 presence data points. Intensive radio-surveys of reproductive females started on the day chicks hatched. The locations were obtained by triangulation and homing-in onto the animal (White & Garrott, 1990) without disturbing and flushing the bird. The locations were marked with a pole and, at the end of the breeding season, exact coordinates of bird locations were obtained with a global positioning system (GPS; Garmin eTrex® Navigator, Garmin Corporation, Olathe, KS). These radio-locations are henceforth referred to as «visited points».

Individual home ranges corresponded to the minimum convex polygon that encompasses all radio-locations of a given bird (White & Garrott, 1990). We used ArcView GIS 3.3 for drawing the polygons («animal movement» extension, Environmental Systems Research Institute, California). Two buffer zones of 150 m altitude each were defined below and above the home range, i.e. perpendicular to the main slope, and 100 random points («non-visited points») were generated within them. The lateral boundaries of the buffer zones were thus a mere geometric prolongation of the lateral border of the home range, projected towards lower and upper altitudes, respectively. These buffers aimed at providing enough contrast for running the habitat selection analysis, which compares used with non-used habitats (see below). The lower buffer zone was likely to include more forested habitats, whilst the upper buffer was likely to enclose more open habitats than the average black grouse habitat. Buffers were restricted to lower and upper altitudes around the home range because lateral extension would potentially have overlapped with home ranges occupied by other hens, and might thus reflect a pattern of intraspecific competitive exclusion.

After the radiotracking season, we assigned one of the 19 habitat types to every visited and random point. Characterization of the habitats was done within a circle of 15 m radius around each point (Table 1).

ARTHROPOD ABUNDANCE AND DIVERSITY

A combination of pitfall trapping (epigeal fauna) and sweep-net sampling (epiphytic fauna) was used to estimate arthropod abundance (Standen, 2000) within 14 of the 19 different habitat types (Table 1). We did not include rocks and scree, bare ground, dense coniferous forest, river and other water bodies, adenostyles, willow herb and very dense raspberry as they are known to be avoided by the birds (Klaus et al., 1990; Signorell et al., submitted). Three pitfalls per habitat type were installed 5 m apart in a row and all 14 habitat types could be sampled at each study site, totalling 126 sampling plots. The pitfalls consisted of 8 cm deep PVC tubes (diameter of 7 cm), which were buried in the ground. An open plastic cup was placed in each tube. It contained ethylene-glycol both as a means to attract and kill the arthropods and as preservative. A quadratic piece of transparent PVC sheet installed 2-3 cm above the ground covered the pitfall, protecting it from rain. The pitfall traps were emptied every ten days between 20th June and 22nd August (n = 6 sampling events). This time window was chosen to be sure to sample arthropods during the most critical period ranging from hatching till chicks are four weeks old (Klaus et al., 1990, Fig. 3 down). In addition, at each trap clearance, a sweep-net sample was collected along two 10 m long transects aligned 1 m away from the pitfalls row. This epiphytic sample consisted of 10 strokes for each transect line according to the standardized sweep-net method proposed earlier (Oppermann, 1999; Di Giulio, Edwards & Meister, 2001; Britschgi, Spaar & Arlettaz, 2006). Our sampling design thus resulted in four samples, i.e. three pitfall trap samples and one sweep-net sample per habitat type and sampling event. The collected arthropods were conserved in small plastic bags in 70% Ethanol.

In the laboratory, the sampled arthropods were dried for 72 h at 60° C (cf. Southwood, 1978). Once dried, the cleaned arthropods were identified to order or suborder and categorized into 14 main groups according to Ponce (1988): Opiliones, Aranea, Diplopoda, Saltatoria, Dermoptera, Diptera, Hymenoptera without Formicidae, Formicidae, Coleoptera, Lepidoptera imagines, Lepidoptera larvae (caterpillars), Isopoda, Heteroptera and Homoptera. We then counted the number of individuals per group and measured their biomass to the nearest 0.001 g with a precision balance (Mettler Toledo PB303-L Delta Range, Greifensee, Switzerland). We calculated the mean arthropod dry biomass from 3 pitfalls per habitat type and sampling period.

Since breeding black grouse females show a high preference for diverse and richly structured habitats (Signorell et al., submitted), not only arthropod biomass but also species diversity could be a factor of habitat selection. We therefore additionally calculated a Shannon index of diversity (Shannon & Weaver, 1949), which was averaged for each habitat type and sampling period, using our 14 arthropod groups. We used only pitfall-trap samples, however, because sweep-netting represents an instantaneous sample which may be greatly affected by the prevailing weather conditions (see August II in Fig. 4b, when there was heavy rainfall).

WEATHER DATA

Since mobility of arthropods and therefore their availability for chicks is weather dependent, we calculated the average daily ambient temperature and cumulated precipitation for each sampling period for the weather station in Evolène-Villaz, Valais (46°7'N, 7°30'E; Federal office of Meteorology and Climatology, MeteoSwiss), which is located in the core of our study area.

STATISTICAL ANALYSIS

Habitat selection of hens

In order to analyse the habitat selection pattern at the home range level (Johnson, 1980) for each breeding and non-breeding female we compared the frequency distribution of used habitats (visited points within the home range) with the distribution of non-used habitats (random points from the buffer zones outside the home range). Because some habitat types had too low occurrences we had to regroup habitat types into upper habitat categories before performing the analysis (Table 1). We applied a randomized contingency table procedure (see Manly, 1997 for more details) to estimate the probability of any positive or negative deviation between observed and expected habitat category frequencies (10'000 iterations, program Actus2, G. F. Estabrook, University of Michigan, Ann Arbor, MI 48109-1048, USA, Estabrook & Estabrook, 1989; Arlettaz, 1999).

Arthropod data

We applied linear mixed-effects models with maximum likelihood estimation to test if biomass, number and diversity of arthropods estimated from pitfalls or sweep-net samples differed between habitat categories and varied among ten-day periods (Crawley, 2007). We used the same habitat categories as for the habitat selection analysis (Table 1) although habitat type was also a factor in the modelling. To account for our repeated (same plot measured several times) and nested (different plots and habitat types within the same study site) design, each «habitat type» was nested within «study site» and treated as the repeated factor. The nested term was treated as random effect. To get an estimate of the influence of the fixed effects «habitat category» and «ten-day period», we used ANOVA tests to compare the full model (containing both «habitat category» and «ten-day period» terms) with the simplified models, with only either «habitat category» or «ten-day period» term as suggested by Crawley (2007). Post-hoc contrast tests were used to compare the arthropod abundance between habitat categories. The analyses were performed with the software R 2.4.1 («nlme» library, R Development Core Team 2006). Variables were tested for homogeneity of variance and normality of residuals. All variables except Shannon index of diversity had to be log transformed ($\log_{10}(x+1)$). All values reported are means and standard deviations; p-values are two-tailed with rejection levels set at 5%.

Results

Altogether we captured 22 black grouse females. Only 15 of them were still alive at the beginning of the laying period. Eighty percent (n = 12) of the surviving females (n = 15) began incubation and 28.6% (n = 4) could successfully raise their chicks. We thus were able to radio-track four successful breeding females. Failures were due mostly to nest predation (n = 5) and a high mortality of young chicks during bad weather (N = 3, see also Klaus et al., 1990; Ludwig et al., 2008). In the subsequent habitat selection analysis, we shall also consider four non-breeding females which had their home ranges close to the four breeding hens.

Habitat category frequency distribution for breeding females differed significantly between visited points within their home range and non-visited random points outside the home range (χ^2, randomised contingency table procedures, all four p-values < 0.05, Fig. 1a). This difference was mostly due to a statistically significant preference for grassy shrubland with scattered coniferous trees (habitat # V, n = 3 hens out of 4), and an avoidance of grassland (habitat # II; n = 3 hens) and grassy shrubland (habitat # III; n = 2 hens).

Three out of the four non-breeding females showed significant differences in the frequency distribution of habitat category between visited and random points (χ^2, p-values < 0.05, Fig. 1b). The same main avoidance pattern as for breeding females emerged, although only one hen showed a significant preference for the same favourite habitat as breeding females: grassy shrubland with scattered trees (habitat # V).

A total number of 33’276 arthropods (298.7 g dry biomass) were collected with pitfall traps (epigeal fauna) and sweep nets (epiphytic fauna) during the six sampling events. The sample was dominated by Saltatoria (29.5% of biomass, 8.7% of number), Coleoptera (23.1% and 9.5%, respectively) and Formicidae (18.4% and 53.2%, respectively).

Epigeal and epiphytic arthropod dry biomass varied significantly between habitat categories (linear mixed-effects models, model comparison performed with ANOVAs; see methods for more details; p-values of < 0.0001 and 0.002 for epigeal and epiphytic prey, respectively) and throughout the season ($p < 0.0001$) (Table 2; Fig. 2a, e; Fig. 5). Given that arthropod number and biomass for pitfall trapping as well as sweep-netting were highly correlated (Spearman’s rank correlations; $r_s = 0.698$, $p < 0.001$ and $r_s = 0.744$, $p < 0.001$, n = 252 [i.e. 14 habitat types x 3 sites x 6 sampling events], for epigeal and epiphytic samples, respectively) we eventually restricted further analyses to biomass. There was a sharp fall in arthropod biomass between the last ten days of June and the first ten days of July 2005, apparently due to a cold spell (Fig. 3 top). Of the different habitat categories, grassland yielded, on average, the highest total biomass for both the epigeal and epiphytic entomofauna, followed by grassy shrubland (Appendix A; see also Fig. 2a, e and Fig. 5). Grassy shrubland with scattered trees and closed shrubland with scattered trees as well as closed shrubland showed, on average, lower biomasses (Appendix A). The biomass of Coleoptera differed significantly between habitat categories irrespective of the catching method (linear mixed models, p-values of 0.015 and < 0.0001 for pitfalls and sweep-netting, respectively; Table 2, Fig. 2b, f). A significant inter-habitat variation could be assessed for Saltatoria caught with sweep-netting and pitfall trapping (both p-values < 0.0001; Table 2, Fig 2c, g). Formicidae showed no significant inter-habitat variation (p-values of 0.212 and 0. 915 for the two sampling techniques, respectively; Table 2, Fig. 2d, h). All three categories showed again a significant seasonal effect as regards sweep-netting and pitfall trapping (Table 2). The biomass of Lepidoptera larvae, Opiliones and Aranaea showed a significant seasonal variation for both sweep-netting and pitfall trapping (Table 2). A significant inter-habitat variation could be assessed only for Opiliones and Aranaea caught with sweep-netting (p = 0.048; Table 2).

Saltatoria were the group of arthropods contributing most to the biomass collected with pitfalls and sweep-nets. They were especially abundant in grassland, showing a sharp biomass increase from late June until late July (Fig. 2c, g). In contrast, Coleoptera and Formicidae biomasses were larger in the early season and decreased progressively thereafter (Fig. 2b, d, f, h). Grassland yielded, on average, the highest dry biomass for both epigeal and epiphytic entomofauna at every sampling event (Appendix A).

Both epigeal and epiphytic biomass progressively decreased along a gradient from open towards closed habitats (habitats # II to VII; Appendix A, Fig. 5). We compared biomasses occurring in hens' favourite habitat (habitat # V, grassy shrubland with scattered trees) with biomasses of all other habitat categories: statistically significant differences were with habitat # II (grassland, a habitat avoided by hens) for sweep-netting (post-hoc contrast test, p = 0.003, Fig. 5) and with habitats # II and # III (grassland and grassy shrubland, both habitats avoided by chick-rearing hens) for pitfall trapping (p = 0.021 and p = 0.029, respectively, Fig. 5) which yielded higher total dry biomasses. Habitat # VII (dense forest) showed significantly lower biomasses as regards pitfall trapping (p = 0.036; Fig. 5).

The Shannon index of diversity of arthropods collected with pitfall traps showed a significant difference between habitat categories (linear mixed models, $p = 0.031$), with again a significant seasonal effect (p-value < 0.0001, Table 2 and Fig. 4), whilst there was no significant difference between habitat # V and any other habitat (all p-values > 0.05, Fig. 5).

Discussion

Our results establish that arthropod biomass, both epigeal and epiphytic, differs markedly between habitat categories, with all arthropod groups except beetles, being more abundant in grassland, followed by grassy shrubland with scattered trees, the latter being hens' favourite habitat. This suggests that breeding black grouse hens do not select the arthropod-richest habitats, but seemingly trade-off food abundance against vegetation cover in their pattern of habitat selection during reproduction.

Although most arthropods peaked in late June, which is about the middle of the vegetation period (and also when we started sampling), arthropod phenology was not the same for the three dominant taxa: whilst beetle and ant abundances were steadily decreasing from June to August, the biomass of grasshoppers, in contrast, increased continuously due to the successive instars to reach adult size. The second peak of abundance in late July was thus due mostly to the increase of grasshoppers, which may be an important food source for chicks in the Alps (Klaus et al., 1990; Ponce, 1992a). At that time of the year chicks are about 2-3 weeks old (Fig. 3 bottom, mean hatching date = July 12th), i.e. reach the very age when demand for protein-food is high (Klaus et al., 1990). This suggests that natural selection has prompted a close coincidence between the timing of reproduction and the availability of a rich food supply (Fig. 3 bottom). A similar temporal correspondence could be established for British black grouse and capercaillie (Baines, Wilson & Beeley, 1996). Availability and/or accessibility of arthropod food for black grouse chicks also depends on ambient temperature, with invertebrates being less active in adverse weather conditions. This occurred in our case in early July, with a sharp fall in arthropod biomass when persistent low temperatures and even casual snow falls occurred.

Asymmetric climate change, however, may jeopardize this delicate balance between the timing of breeding and the post-hatching survival as demonstrated in Finnish black grouse (Ludwig et al., 2006). In the Alps, May (egg-laying period) temperatures also appear to have increased much more than those in early summer (June-July, hatching time) since the 1970s (N. Zbinden, pers. comm.). If Alpine Black grouse hens similarly respond to spring climate warming by anticipating egg-laying (Ludwig et al., 2006), then chicks which are especially sensitive to adverse weather conditions during their first days of life (Zbinden & Salvioni, 2004) will experience a higher risk of exposure to cold than usual, i.e. higher mortality rates (Ludwig et al., 2006). Chick survival may be further affected if hatching takes place too early relative to peaks in arthropod food supply (this study).

Faecal investigations have so far demonstrated the importance of grasshoppers, beetles and ants in chicks' diet (Ponce & Magnani, 1988; Klaus et al., 1990; Ponce, 1992b). These three taxonomic groups also clearly dominated our sample. It might be, however, that other profitable arthropods also enter the diet of black grouse chicks but remain undetected through faeces inspection because of fewer chitinous parts meaning therefore fewer retrievable, recognizable fragments in the droppings (Ponce, 1992a; but see Fischbacher, 1996; Park et al., 2001). It has been suggested, for instance, that the non-sclerified caterpillars (which occurred only marginally in our sample) are an essential food source for black grouse chicks (Ponce & Magnani, 1988). The inefficacy of pitfall trapping and sweep-netting for catching caterpillars may have biased our sample (Duelli, Obrist & Schmatz, 1999). We believe, however, that these potential methodological artefacts would only slightly bias our results but not affect the general pattern we observed. Note that in boreal forests, capercaillie chicks are more bound to habitats with a rich supply of caterpillars (Wegge et al., 2005) than black grouse chicks (P. Wegge, pers. comm.). It is not known, however, whether the same pattern of dietary niche differentiation occurs in the Alps.

Although grassland, in particular Alpine pastures, yielded the highest overall biomass, both for the epigeal and epiphytic invertebrates, the abundance of the various arthropod groups differed markedly between habitats. In forested habitats, ants predominated, whereas beetles and especially grasshoppers played a considerable role in other habitats, which confirms previous findings (Picozzi & Hepburn, 1984; Ponce & Magnani, 1988; Klaus et al., 1990). Our breeding hens primarily selected grassy shrubland with scattered trees, i.e. old and young open forests with a heterogeneous grassy and shrubby understorey. They avoided very open habitats such as grassland and open shrubland, as well as closed habitats such as dense shrubland and forests. Non-breeding females showed the same habitat preference/avoidance pattern, although they appeared to be slightly less selective. These findings, in particular for breeding hens, corroborate our previous analysis of fine-grained habitat selection, which demonstrated the relevance of habitat structural and compositional heterogeneity for reproduction (Signorell et al., submitted). Additionally, this habitat may offer a more diverse palette of plants to growing chicks which gradually integrate more vegetative items into their diet (Klaus et al., 1990; Ponce, 1992b).

Our comparison of arthropod abundance in different habitat categories with the pattern of habitat selection indicates that breeding hens did not select the arthropod richest habitats, but directed their preference firstly towards richly-structured habitat matrices offering apparently slightly less favourable foraging conditions for invertebrate-eating young chicks. This pattern suggests that chick-rearing black grouse hens trade-off arthropod abundance against habitats offering lots of shelter opportunities (e.g. among shrub and below low coniferous tree branches) so as to reduce predation risks, which are presumably high in open grassland and shrubland. We showed that arthropod availability varies with respect to habitat, season and/or weather. It is thus likely to represent a serious limiting factor of breeding habitat suitability.-

Our study also demonstrates that green alder, which is spreading rapidly in many parts of the Alps following land abandonment by traditional grazing practices, encroaching and threatening the habitat of the black grouse and even overall timberline ecosystem biodiversity (Anthelme et al., 2001), represents an invertebrate-poor, thus unfavourable habitat for reproduction.

Finally, our results do not support the hypothesis that arthropod diversity (here measured through Shannon index of diversity based on our 14 main groups) may direct habitat selection decisions by hens. More refined studies based on an enhanced taxonomic resolution are needed to assess whether black grouse may play the role of an umbrella species for biodiversity within timberline ecosystems.

IMPLICATIONS FOR CONSERVATION

Timberline habitats offering high arthropod abundance and numerous shelter possibilities should be maintained or restored to provide suitable breeding conditions for black grouse. On one hand, shrub and forest encroachment could be mitigated by targeted forestry interventions. On the other hand, incentives to farmers for reinstating pastureland within the narrow belt of timberline ecosystems should be promoted; areas of totally open grassland should be absolutely avoided, however. The best compromise is certainly the maintenance and/or revitalization of a heterogeneous landscape matrix consisting of a mosaic of open Ericaceae shrubland interspersed with patches of grass, both associated with scattered young and mature coniferous trees at low density. Signorell et al. (submitted) provide the necessary guidance for achieving the best habitat configuration.

The question then arises how this mosaic matrix can be maintained in the long term. Traditional livestock grazing management by cattle and goats could be an option. They may be combined with forestry interventions when necessary. The potential of vegetation regulation by browsing deer whose populations are rapidly expanding in the Alps should also be evaluated: red deer may contribute to maintain the desired habitat composition and semi-open structure. Assuming that the black grouse may function as an umbrella species within timberline ecosystems (see Suter, Graf & Hess, 2002 for capercaillie), which should now be assessed, the promotion of its habitat would be likely to benefit an entire biocenose.

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Table 1. Habitat categories (I-VIII) and habitat types (1-19) used for habitat selection analysis and arthropod sampling, with indication of main structural and compositional features.

Habitat category	Habitat type		Vertical structure	Horizontal structure	Characteristics	Humidity
I Bare ground, rock, scree	1	Rocks/scree			> 75% cover	
	2	Bare ground			> 75% cover	
II Grassland	3*	Open young forest with grass cover	young trees	grass cover	> 75% grass	
	4*	Open old forest with grass cover	old mature trees	grass cover	> 75% grass	
	5*	Alpine pasture	pasture			
III Grassy shrubland	6*	Pasture with *Rhododendron*/*Vaccinium*	pasture & shrub		> 75% *Ericaceae*	wet
	7*	Pasture with *Rhododendron*/*Vaccinium*/*Juniperus*	pasture & shrub			medium
	8*	Pasture with *Juniperus*	pasture & shrub		> 75% *Juniperus*	dry
IV Closed shrubland	9*	Mixed *Rhododendron-Vaccinium* shrub	shrub		> 75% *Ericaceae*	wet
	10*	Mixed *Rhododendron-Vaccinium-Juniperus* shrub	shrub		*Ericaceae* & *Juniperus*	medium
	11*	*Juniperus* shrub	shrub		> 75% *Juniperus*	dry
V Grassy shrubland with scattered trees	12*	Open young forest with grass/*Ericaceae* cover	young trees	grass & *Ericaceae*		
	13*	Open old forest with grass/*Ericaceae* cover	old mature trees	grass & *Ericaceae*		
VI Closed shrubland with scattered trees	14*	Open young forest with *Ericaceae* cover	young trees	*Ericaceae*	> 75% *Ericaceae*	
	15*	Open old forest with *Ericaceae* cover	old mature trees	*Ericaceae*	> 75% *Ericaceae*	
VII Dense forest	16*	Dense *Alnus viridis* forest	dense bush			
	17	Dense forest	dense forest		> 75% tall trees	
VIII Others	18	River/water			> 75% water area	
	19	Adenostyle, willowherb, raspberry, etc.			> 75% cover	

* Habitat types in which arthropod supply was sampled.

Table 2. Linear mixed model on the effects of «habitat category» (see Table 1) and «ten-day period» on the biomass, number and Shannon index of diversity of arthropods sampled by pitfall-trapping (a-g) and sweep-netting (h-m). Model comparison was obtained through *a posteriori* ANOVAs between the full and sub-models (see text for more details). Df = degrees of freedom, AIC = Aikaike information criterion, logLik = log Likelihood, LRatio = Likelihood ratio, P-value = rejection probability: * < 0.05, ** < 0.01, *** < 0.001. The second model compares the full model with a model without «habitat category», thus estimating the effect of the latter. The third model compares the full model with a model without «ten-day period», thus estimating the effect of the latter factor.

	Source of variation	Df	AIC	logLik	L Ratio	P-value	
	Pitfall trapping (epigeal fauna)						
a)	Total biomass (all categories)						
	Full model	14	455.98	-213.99			
	«Habitat category» effect	9	474.39	-228.20	28.42	<0.0001	***
	«Decade» effect	9	625.83	-303.91	179.85	<0.0001	***
b)	Biomass of beetles						
	Full model	14	314.66	-143.33			
	«Habitat category» effect	9	318.82	-150.41	14.16	0.0146	*
	«Decade» effect	9	331.66	-156.83	27.01	<0.0001	***
c)	Biomass of grasshoppers						
	Full model	14	640.75	-306.38			
	«Habitat category» effect	9	659.90	-320.95	29.15	<0.0001	***
	«Decade» effect	9	716.70	-349.35	85.95	<0.0001	***
d)	Biomass of ants						
	Full model	14	187.96	-79.98			
	«Habitat category» effect	9	185.08	-83.54	7.12	0.2119	
	«Decade» effect	9	223.60	-102.80	45.64	<0.0001	***
e)	Biomass of Lepidoptera larvae						
	Full model	14	431.82	-201.91			
	«Habitat category» effect	9	430.46	-206.23	8.64	0.1244	
	«Decade» effect	9	453.16	-217.58	31.34	<0.0001	***
f)	Biomass of daddy-long-legs and spiders						
	Full model	14	390.34	-181.17			
	«Habitat category» effect	9	384.59	-183.30	4.25	0.5142	
	«Decade» effect	9	399.21	-190.61	18.87	0.0020	**
g)	Shannon index of diversity						
	Full model	14	-988.22	508.11			
	«Habitat category» effect	9	-985.95	501.98	12.27	0.0313	*
	«Decade» effect	9	-917.74	467.87	80.48	<0.0001	***
	Sweep-netting (epiphytic fauna)						
h)	Total biomass (all categories)						
	Full model	14	89.51	-30.75			
	«Habitat category» effect	9	98.72	-40.36	19.21	0.0018	**
	«Decade» effect	9	198.79	-90.39	119.28	<0.0001	***
i)	Biomass of beetles						
	Full model	14	303.67	-137.83			
	«Habitat category» effect	9	315.20	-148.60	21.53	<0.0001	***
	«Decade» effect	9	398.37	-190.18	104.70	<0.0001	***
j)	Biomass of grasshoppers						
	Full model	14	547.53	-259.76			
	«Habitat category» effect	9	560.34	-271.17	22.82	<0.0001	***
	«Decade» effect	9	566.87	-274.44	29.34	<0.0001	***
k)	Biomass of ants						
	Full model	14	175.09	-73.55			
	«Habitat category» effect	9	166.57	-74.29	1.48	0.9152	
	«Decade» effect	9	356.12	-169.06	191.03	<0.0001	***
l)	Biomass of Lepidoptera larvae						
	Full model	14	361.74	-166.87			
	«Habitat category» effect	9	361.91	-171.96	10.172	0.0705	
	«Decade» effect	9	390.07	-186.04	38.33	<0.0001	***
m)	Biomass of daddy-long-legs and spiders						
	Full model	14	190.54	-81.27			
	«Habitat category» effect	9	191.69	-86.85	11.15	0.0484	*
	«Decade» effect	9	389.69	-185.84	209.15	<0.0001	***

Figure captions

Fig. 1. Percentage frequency (%) of visited locations (filled column) and randomly generated points in buffer zones outside the home range (open column) in 4 breeding (a) and 4 non-breeding females (b) with respect to habitat category (Table 1). Randomization tests were carried out on overall absolute frequencies. Habitat categories with zero occurrence were not included in the analyses. Significant differences ($p < 0.05$) are depicted on column tops, with indication of the direction of selection (+: preferred habitat; –: avoided habitat). The number of symbols indicates the number of individuals out of four showing the selection pattern.

Fig. 2. Phenology of the mean arthropod dry biomass collected at three study sites for different habitat categories (see Table 1) from pitfall trapping (a-d) and sweep-netting (e-h). Shown are the total biomass (a, e) and the biomass of the three groups contributing most to total biomass (beetles; b and f, grasshoppers: c and g; ants: d and b).

Fig. 3. Top frame: seasonal variation in mean daily ambient temperature (averaged ± SD across the ten-day periods) and cumulated precipitation per arthropod sampling period at the station Evolène-Villaz, Valais. Bottom: breeding phenology of 9 radio-tracked hens (2004-2006) whose chicks hatched, including females whose chicks died after a few days (n = 5). Shown are the first four weeks of chick growth (bar) and the day the chicks were two weeks old (dot), i.e. when protein demand peaked.

Fig. 4. Seasonal trends in the mean Shannon index of diversity for arthropods collected with pitfall trapping (a) and sweep-netting (b) at our three study sites with respect to habitat category (Table 1 and Fig. 2).

Fig. 5. Mean dry arthropod abundance (black symbols) and Shannon index of diversity (grey symbols), averaged (± SD) across the 6 sampling events (Appendix A), with relation to habitat category for epigeal fauna (pitfall sampling, dots) and epiphytic fauna (sweep-netting, rhombus). Habitat selection pattern (+: preference; –: avoidance) for four breeding females and four non-breeding females is indicated on figure top; the number of symbols indicates the number of individuals out of four showing that selection pattern. Differences in arthropod abundance and diversity index were tested between habitat # V (favourite hens' habitat) and all other habitat categories; depicted by the horizontal bars are the significant differences ($p < 0.05$, from posthoc contrast tests) which occurred only between the most avoided habitat (# II) and the favourite habitat (# V). Symbols in the bar centre refer again to the response variables described above.

I	Bare ground, rocks, scree
II	Grassland
III	Grassy shrubland
IV	Closed shrubland
V	Grassy shrubland with scattered trees
VI	Closed shrubland with scattered trees
VII	Dense forest

▨ Visited points within the home range

☐ Randomly generated points outside the home range

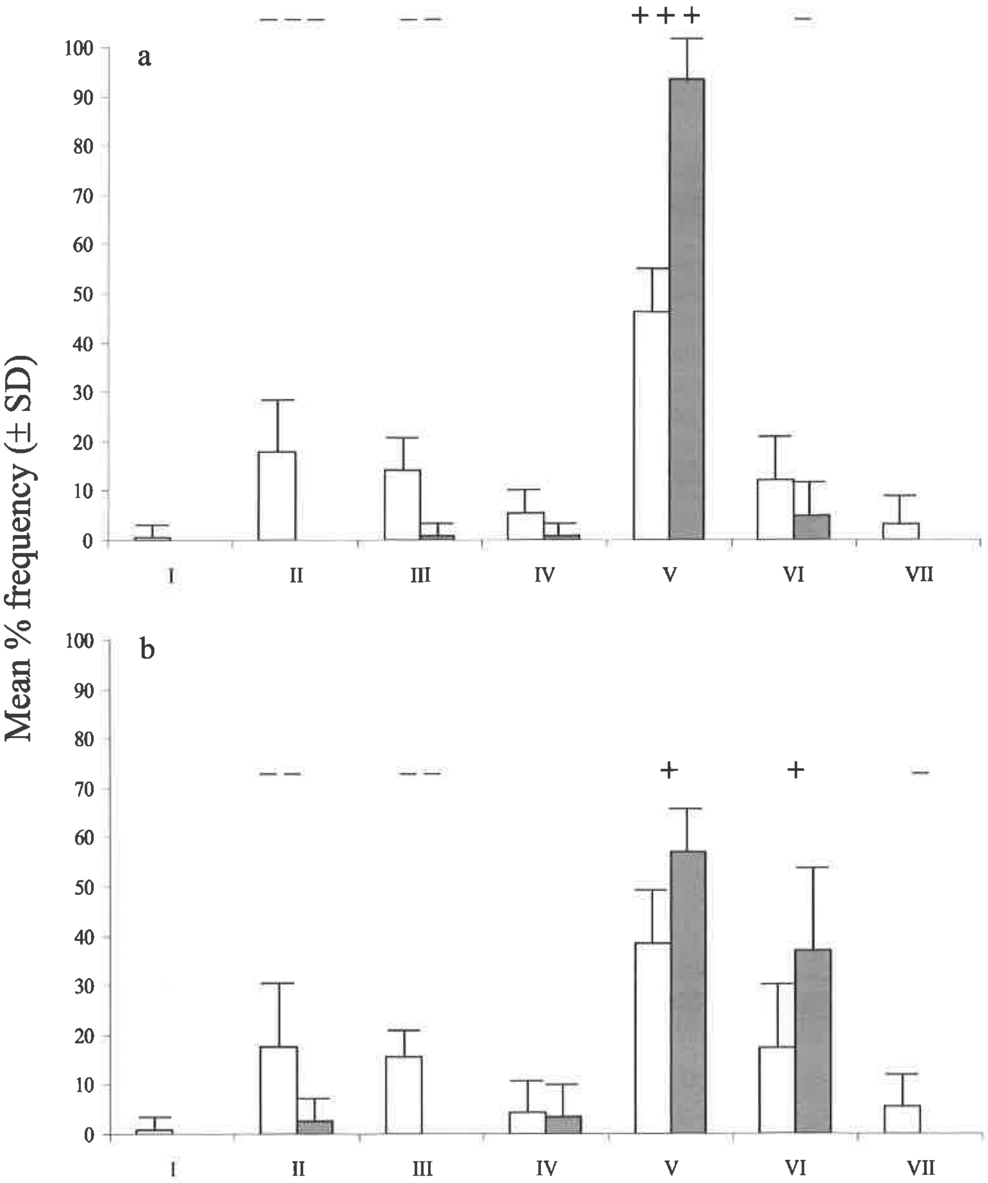

Fig. 1.

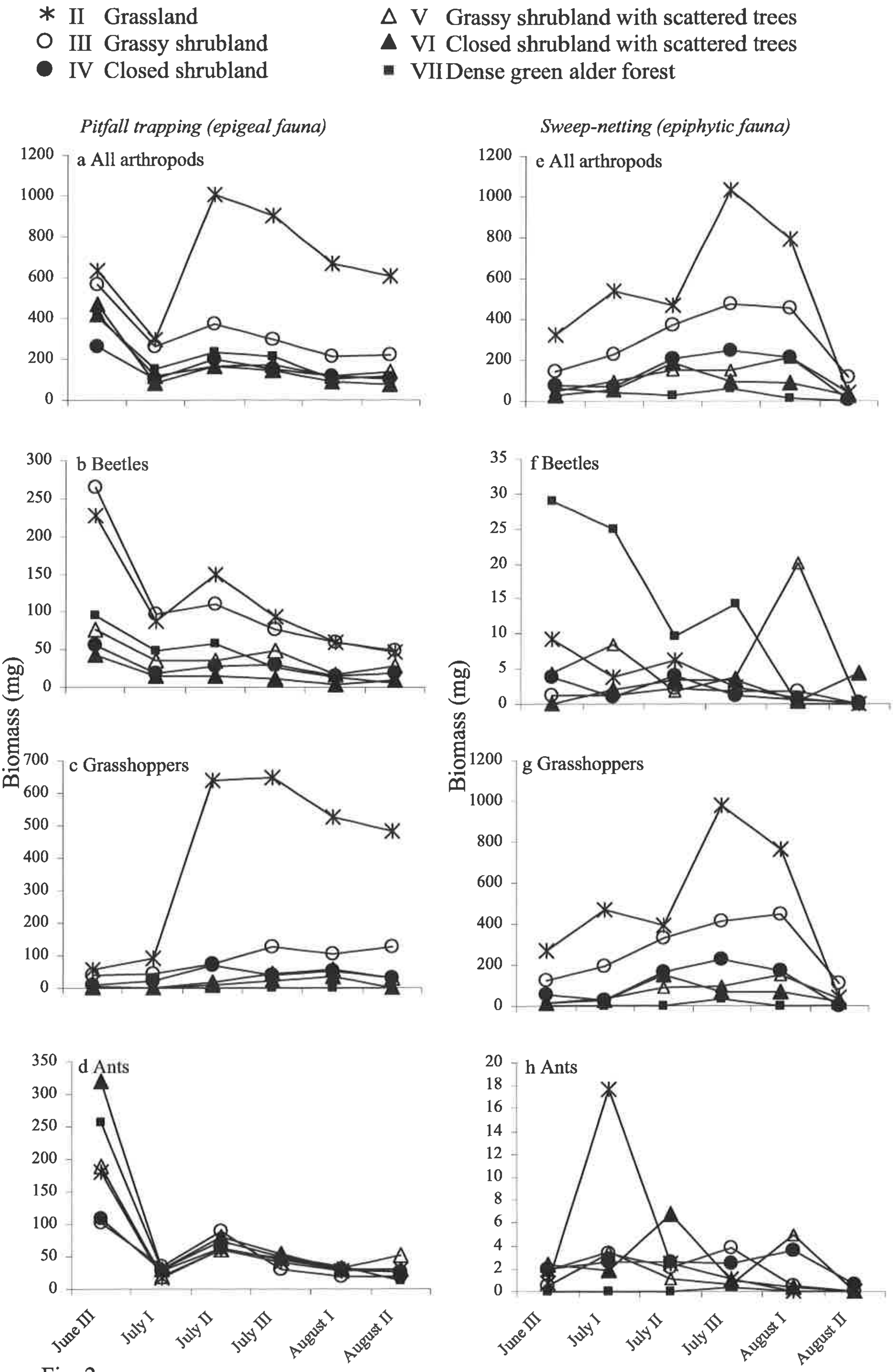
* II Grassland
○ III Grassy shrubland
● IV Closed shrubland
△ V Grassy shrubland with scattered trees
▲ VI Closed shrubland with scattered trees
■ VII Dense green alder forest
Pitfall trapping (epigeal fauna)
Sweep-netting (epiphytic fauna)
a All arthropods
b Beetles
c Grasshoppers
d Ants
e All arthropods
f Beetles
g Grasshoppers
h Ants
Biomass (mg)
June III
July I
July II
July III
August I
August II
0
200
400
600
800
1000
1200
50
100
150
250
300
350
500
700
5
10
15
20
25
30
35
2
4
6
8
12
14
16
18

Fig. 2.

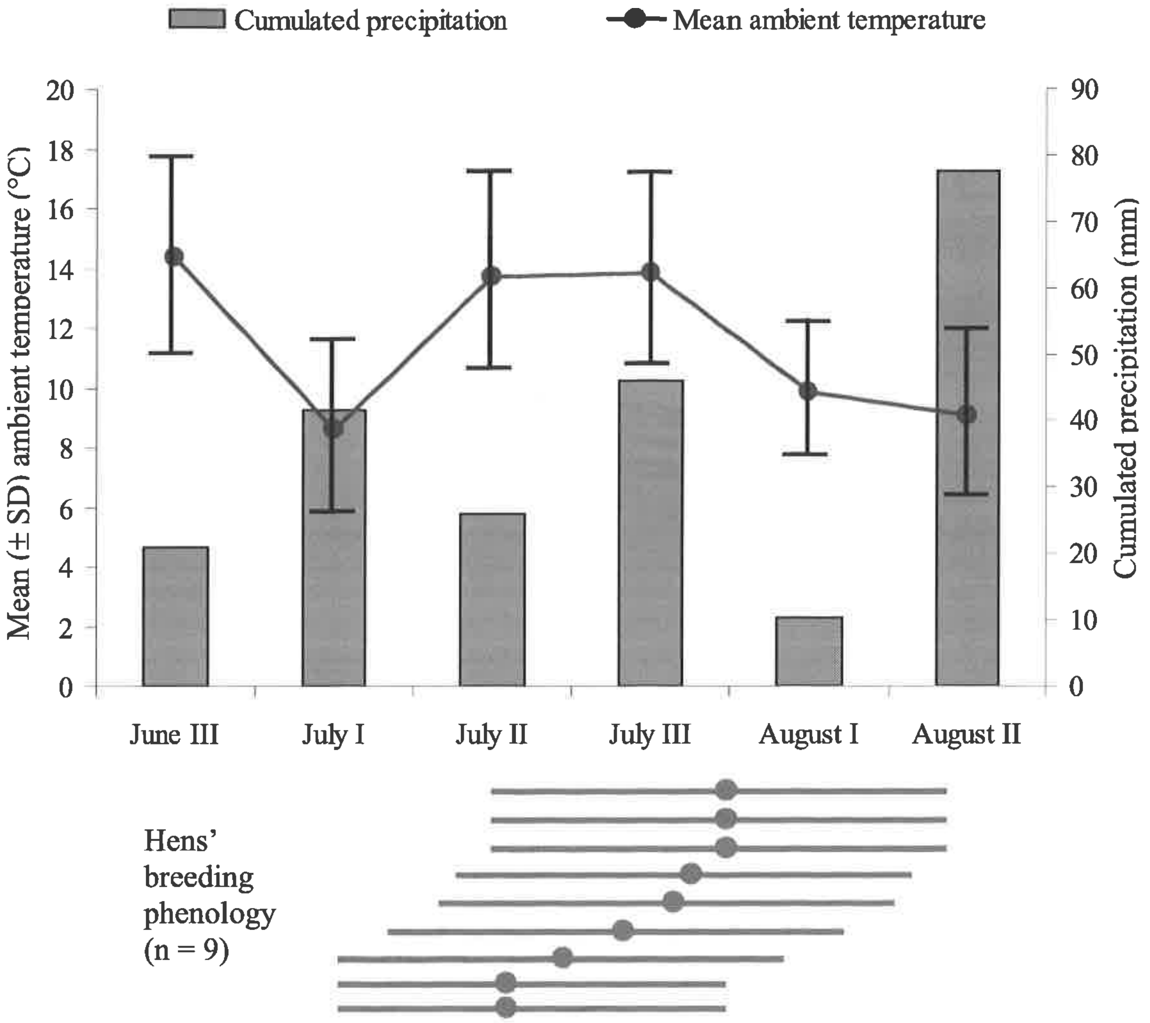
Cumulated precipitation
Mean ambient temperature
Mean (± SD) ambient temperature (°C)
0
2
4
6
8
10
12
14
16
18
20
Cumulated precipitation (mm)
0
10
20
30
40
50
60
70
80
90
June III
July I
July II
July III
August I
August II
Hens' breeding phenology (n = 9)

Fig. 3.

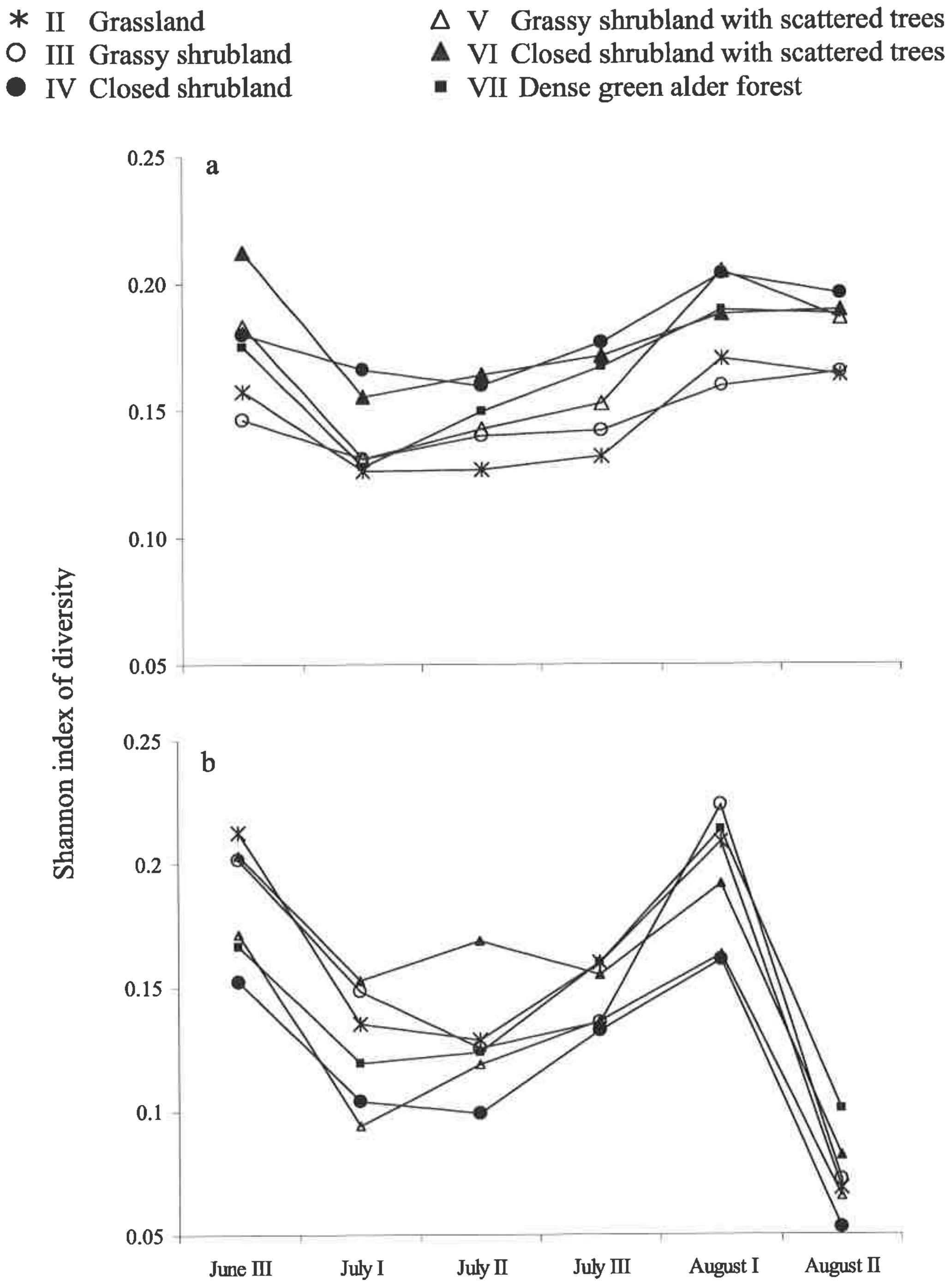
* II Grassland
○ III Grassy shrubland
● IV Closed shrubland
△ V Grassy shrubland with scattered trees
▲ VI Closed shrubland with scattered trees
■ VII Dense green alder forest
Shannon index of diversity
a
0.25
0.20
0.15
0.10
0.05
b
0.25
0.2
0.15
0.1
0.05
June III
July I
July II
July III
August I
August II

Fig. 4.

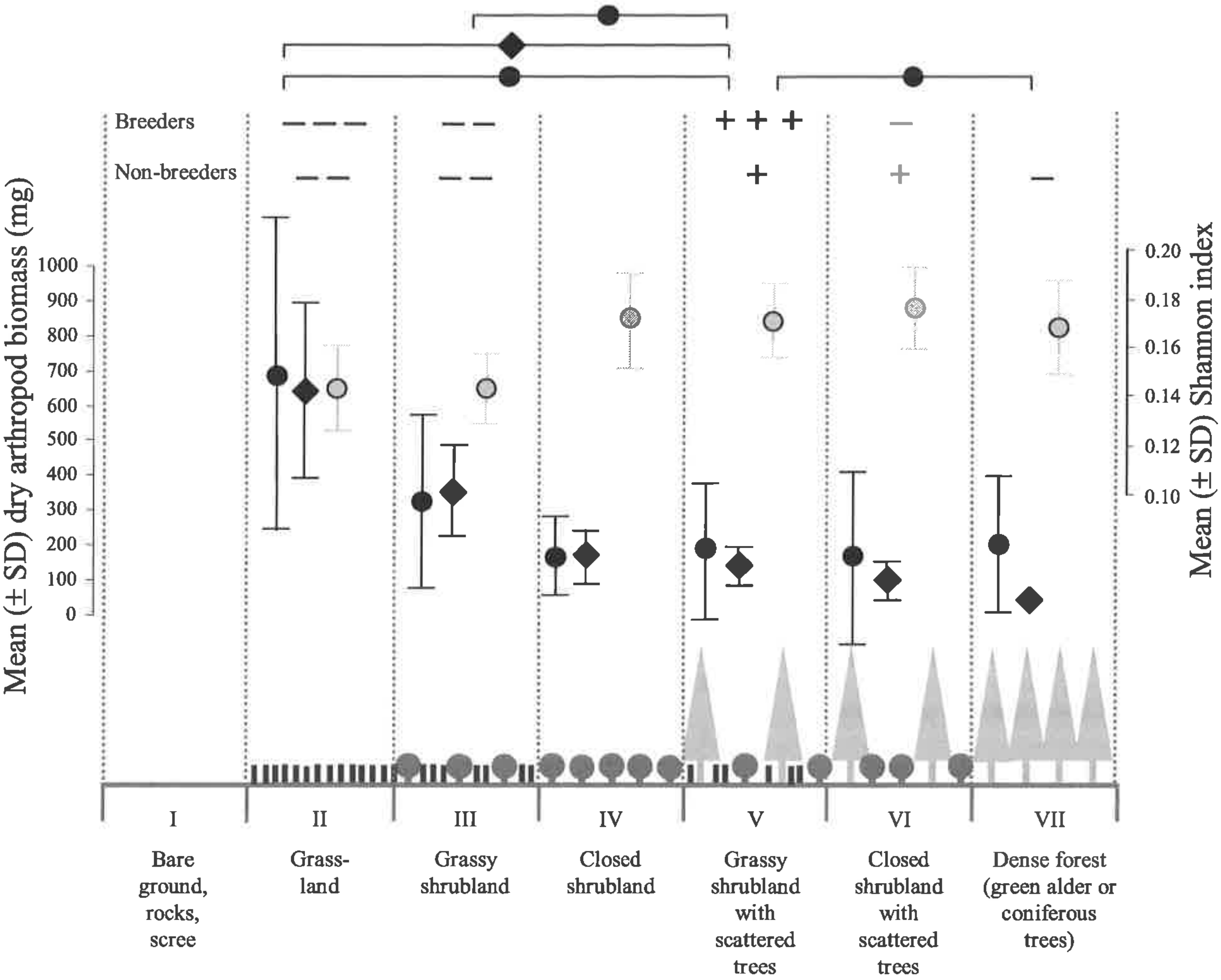
Breeders
— — —
— —
+ + +
—
Non-breeders
— —
— —
+
+
—
Mean (± SD) dry arthropod biomass (mg)
1000
900
800
700
600
500
400
300
200
100
0
0.20
0.18
0.16
0.14
0.12
0.10
Mean (± SD) Shannon index
I
Bare ground, rocks, scree
II
Grass-land
III
Grassy shrubland
IV
Closed shrubland
V
Grassy shrubland with scattered trees
VI
Closed shrubland with scattered trees
VII
Dense forest (green alder or coniferous trees)

Fig. 5.

Appendix A. Mean total dry epigeal and epiphytic arthropod biomass (averaged ± SD across the three study sites) sampled by pitfall trapping and sweep-netting from the last ten days of June to the second ten-day period of August) in six habitat categories (Table 1). Roman numbers indicate ten-day periods or habitat category (Table 1).

	Total dry arthropod biomass (mg)							
Sampling method Habitat category	June III	July I	July II	July III	August I	August II	Mean	SD
Pitfall trapping (epigeal fauna)								
II Grassland	636.1	297.2	1006.9	906.8	668.7	605.9	686.9	249.8
III Grassy shrubland	568.7	262.1	373.4	294.7	216.0	218.6	322.2	134.0
IV Closed shrubland	259.4	104.1	201.4	149.5	119.9	101.0	155.9	63.0
V Grassy shrubland with scattered trees	419.6	113.8	166.8	173.7	113.9	140.6	188.1	116.2
VI Closed shrubland with scattered trees	467.3	84.3	166.0	145.7	90.0	75.5	171.5	149.4
VII Dense green alder forest	404.4	149.2	235.6	214.9	101.2	118.6	204.0	111.5
Mean	459.3	168.5	358.3	314.2	218.3	210.0		
SD	132.5	89.3	326.9	295.5	225.2	200.0		
Sweep-netting (epiphytic fauna)								
II Grassland	323.6	534.7	469.1	1035.2	792.4	633.8	631.5	252.8
III Grassy shrubland	142.4	228.4	371.7	477.7	458.6	395.4	345.7	132.9
IV Closed shrubland	74.3	66.1	204.2	248.4	210.7	138.0	157.0	76.1
V Grassy shrubland with scattered trees	48.0	96.8	149.3	150.7	217.2	141.3	133.9	57.0
VI Closed shrubland with scattered trees	25.7	57.8	188.2	100.0	92.2	102.4	94.4	54.7
VII Dense green alder forest	64.3	44.3	26.7	58.7	16.0	24.2	39.0	19.8
Mean	113.1	171.4	234.9	345.1	297.8	239.2		
SD	110.4	190.2	159.6	369.6	285.1	230.2		
	Shannon index of diversity							
Pitfall trapping (epigeal fauna)								
II Grassland	0.158	0.124	0.125	0.131	0.170	0.164	0.145	0.021
III Grassy shrubland	0.146	0.130	0.138	0.137	0.159	0.158	0.145	0.012
IV Closed shrubland	0.180	0.156	0.157	0.169	0.204	0.195	0.177	0.020
V Grassy shrubland with scattered trees	0.182	0.129	0.142	0.150	0.205	0.186	0.166	0.029
VI Closed shrubland with scattered trees	0.212	0.152	0.163	0.171	0.188	0.189	0.179	0.022
VII Dense green alder forest	0.175	0.128	0.149	0.167	0.189	0.188	0.166	0.024
Mean	0.175	0.136	0.146	0.154	0.186	0.180		
SD	0.021	0.012	0.013	0.016	0.017	0.014		

CHAPTER THREE

Ecological niche modelling of male and female black grouse (*Tetrao tetrix*) and its implementations for conservation

Manuscript

Ecological niche modelling of male and female black grouse (*Tetrao tetrix*) and its implementations for conservation

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Summary

1. The quality of a habitat is a key determinant of aptitude and fitness in wildlife. Many different methods are available to assess habitat quality and different models are used to quantify it. Among them, habitat suitability modelling has become more and more established in habitat management and conservation issues. Habitat requirements, however, may not be identical for males and females or for reproductive and non reproductive individuals of one species, resulting in different ecological niches.
2. Differing ecological niches have consequences for conservation. The knowledge of spatial overlap between niches of individuals of different sexes or breeding status is crucial, especially in dimorphic animal species, where only one sex cares for the young. We focused on the endangered black grouse that lives at the timberline. In this species males show no parental care during chick rearing. Using GIS technologies and comparing visited, i.e. radio-tracked, locations with randomly generated points within individual home ranges using logistic mixed effects regressions we first mapped breeding and non-breeding female and male black grouse occurrence in southwestern Switzerland. Ecological Niche Factor Analysis was used to examine differences in niche parameters for breeding and non-breeding female and male black grouse.
3. Within an altitudinal belt of 1450 to 1750 m a. s. l. non-breeding females and males selected locations situated at the timberline and in adjacent open forests, whereas breeding females preferred locations at the treeline. Breeding females were highly selective and showed little tolerance towards deviations from their optimal habitat. In contrast, males and non-breeding females showed lower habitat restrictions and higher tolerance towards environmental variables.
4. *Synthesis and applications.* Habitat suitability maps provide a powerful tool to visualize high quality habitats and are therefore important in habitat conservation. As breeding

females' niches are much narrower than males', we recommend setting conservation and habitat management priorities on females' breeding habitat requirements.

Word count: 306

Key words: Habitat suitability, Ecological Niche Factor Analysis (ENFA), niche differentiation, timberline, Alps, *Tetrao tetrix*

Introduction

Habitat quality is thought to play a crucial role in population dynamics as it determines reproductive output and survival, i.e. ultimately aptitude and fitness (Tye, 1992; Pärt, 2001; Vickery et al., 2001). Moreover, the loss and degradation of habitats are the largest threats to wildlife populations (Johnson, 2005). The maintenance or restoration of high quality habitats especially in anthropogenic landscapes is therefore a key issue in conservation biology (Primack, 1998). Habitat quality is determined by various factors (Johnson, 2007), with different organisms having divergent resource requirements, i.e. differing ecological niches (Schoener, 1986). In different species, however, some basic habitat characteristics may be shared in common, like low predation risk, high food abundance and availability, richly structured habitats (Blondel, 1986; Blondel et al., 1990), as well as low levels of disturbance by humans. On the other hand, similar species may show divergent ecological niches (Sattler et al., 2007) as well as males and females and/or breeding and non-breeding females of one species (eg. Houston & Shine, 1993; Pasinelli, 2000; Pearson, Shine & How, 2002). Especially in highly dimorphic species and in species, where only one sex shows parental care habitat requirements may differ substantially between sexes (eg. Shine, Shine & Shine, 2003). This may be of great importance in conservation biology when defining habitat management measures.

Habitat quality can and should be assessed in many different ways and many models are used to quantify and analyse habitat quality (Johnson, 2005, 2007). Thus, habitat selection models predict that, relative to low-quality habitats, high quality habitats should be occupied for longer periods within a season and more consistently over years. The investigation of animals through time and the analysis of habitat descriptors in their selected habitats are thought to give an estimate of habitat quality (Sergio & Newton, 2003; Johnson et al., 2005). Since wildlife management often means habitat management, the habitat requirements of many species have to be known and very detailed knowledge of the habitat profiles is available (Comiskey et al., 2002; Ricankova et al., 2006; Smart et al., 2006; Souter et al., 2007). Habitat suitability mapping can be used to visualize potential regions, where habitat management would be meaningful and necessary. Habitat suitability mapping has become more and more established in habitat and wildlife management and is a powerful tool in conservation biology (Muntifering et al., 2006; Ray & Burgman, 2006).

Recently, it has been recognised that a basic concept in habitat suitability mapping is the niche breadth of a species, i.e. the tolerance of a species against different environmental variables (Hirzel et al., 2002; Sattler et al., 2007). Defining for example the conservation status of different species not only asks for knowledge of exact habitat requirements of species but also of the sensitivity of species towards variables (Sattler et al., 2007). However, this may be valid not only for different species but also for different sexes and/or breeding status of one single species. This is especially true in species where only one sex cares for the young and/or in highly dimorphic species, like waders and grouse. A potential difference in habitat requirements and niche breadth has consequences for conservation and knowledge about spatial niche overlap as well as tolerance is crucial to identify potential high habitat quality regions. To set conservation priorities right and define habitat management implementations in these species, knowledge about habitat requirements as well as niche breadth between sexes and/or individuals of a different breeding status may be crucial.

We studied the black grouse (*Tetrao tetrix*, Linné 1758), one of the most emblematic representatives of the timberline fauna. Since grouse species are frequently viewed as indicators of ecosystem health (Storch, 2000a), the black grouse may play the role of an umbrella species for timberline ecosystems, as established for the capercaillie (*Tetrao urogallus*), a closely related species that inhabits upper subalpine forests (Suter, Graf & Hess, 2002). Black grouse chicks are nidifugous and only females care for their young, leading them to habitat patches, where arthropod abundance is sufficient for growth and development

(Klaus et al., 1990). Black grouse females are smaller than males and they are brownish camouflaged whereas males have an almost entirely black plumage. The black grouse thus seems likely to be an appropriate species model for investigating differences in ecological niches within a species. In another study (Signorell et al., submitted-a), we could demonstrate that breeding females are more sensitive towards specific microhabitat variables, pointing at a narrower ecological niche than males and probably non-breeding females. Habitat characteristics have been shown to subtly determine black grouse population dynamics (Zbinden, Salvioni & Stanga, 2003; Ludwig et al., 2008). In most European countries, black grouse populations are declining (Klaus et al., 1990; Storch, 2000a). Habitat loss, degradation and/or fragmentation (Storch, 1991; Kurki et al., 2000; Sun et al., 2003), climatic variations (Zbinden, 1987; Lindström, 1996; Lindström et al., 1997) and disturbance caused by human activities (Bevanger, 1995; Arlettaz et al., 2007) are regarded as the main factors. The European Alps are also concerned by this decline, with several marginal populations far from the core distribution areas having shrunk dramatically over the past decades (Storch, 2000a). As core Alpine black grouse populations are more or less stable, protection and/or restoration of high quality habitats may be crucial for the long-term persistence of this species.

We first aimed at mapping occurrence probability of breeding and non breeding female and male black grouse using GIS technologies (satellite imagery) so as to delineate potential high quality habitats. Second, we modelled ecological niches (ENFA, Biomapper, Hirzel et al., 2002) to estimate spatial overlap between breeding and non-breeding females and males.

Material and methods

STUDY AREA

This study was conducted at seven different sites in south-western Switzerland (canton of Valais, 46°12'N/7°20'E) and at two sites in northern Italy close to the Swiss border (Piemonte, Verbania Province, 46°06'N/8°18'E) within a habitat belt between 1450-2300 m altitude (Klaus et al., 1990). At six of the Swiss study sites larch *Larix decidua*, spruce *Picea abies* and, to a smaller extent, arolla pine *Pinus cembra* are the characteristic tree species of upper subalpine forests and the adjacent habitats. At the three sites on the southern slope of the Alps (Simplon area in southeastern Valais and Piemonte), the dominating tree species is larch. Dwarf shrubs (*Rhododendron ferrugineum*, *Vaccinium* sp., *Juniperus communis* ssp. *nana*, *Calluna vulgaris*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*, etc.) and grasses (*Nardus stricta*, *Calamagrostis villosa*, etc.) form a characteristic understorey in all areas. The study regions are characterized by a subcontinental to continental climate with warm and dry summers, and cold, relatively wet winters (Reisigl & Keller, 1999).

DATA COLLECTION

Our occurrence probability mapping resulted from a comparison of GIS habitat descriptors, i.e., descriptor maps, of visited points (radio-locations) and randomly generated, non-visited points within individual home ranges but outside the main activity areas. We assumed that non-visited points represent unsuitable or less suitable habitat (but see also Hirzel et al., 2002). To achieve this, we first determined bird locations and based on these randomly generated non-visited points.

Bird locations

Birds were first captured from snow burrows (Marti, 1985) between January and March and mist-netted at leks during April-June in 2003-2006 (for details see Signorell et al., submitted-a; Signorell et al., submitted-b). Caught birds were tagged with neck-laced radio-transmitters (Holohil Systems Ltd. Carp, Canada, RI-2D; 12 g, 29 x 19 x 15 mm for females; 15 g, 34 x 19 x 15 mm for males) with the permission of the Swiss Federal Office for the Environment and the Wildlife and Game service of Valais. In July and August, i.e. during the breeding period, females were radio-located every day and males every second day for a period of 30 days in a row, resulting in 30 and 15 presence radio-locations for females and males, respectively. Males were only radio-tracked every second day due to our working capacity. As males have larger territories than females and move longer distances per day (Klaus et al., 1990), fewer locations were needed to get an accurate estimation of their home range size (for details see Signorell et al., submitted-a; for details see Signorell et al., submitted-b). Intensive radio-surveys of reproductive females started on the day chicks hatched. Bird radio-locations were obtained by triangulation and homing-in onto the animal (White and Garrot 1990), without disturbing or flushing the birds. At the end of the breeding season, exact coordinates of bird locations were collected with the help of a global positioning system (GPS; Garmin eTrex® Navigator, Garmin Corporation, Olathe, KS). These locations are henceforth referred to as «visited points».

Non-visited points

We delineated individual home ranges as the minimum convex polygon (MCP) encompassing all radio-locations of a given bird (White & Garrott, 1990). A buffer of 15 m breadth was added around the MCP. As visited points are often clumped in space we estimated the 70% Kernel density distribution. Around each radio-location within the MCP a buffer of 30 m was drawn. The coordinates of the non-visited points were then randomly generated so as to lie inside the MCP but outside the 70% density distribution and outside the buffer belts. An equivalent number of non-visited points were defined, i.e. 15 non-visited points for males and 30 for females.

GIS HABITAT DESCRIPTORS

We used an ecological approach estimating for each variable known to be important for breeding and non-breeding female and male black grouse (Signorell et al., submitted-a) descriptors available in GIS. We constructed several GIS habitat descriptor maps (Table 1) reflecting known habitat choices of black grouse during the breeding season (habitat structure, habitat composition, topography and tourism footprint, Signorell et al., submitted-a; Signorell et al., submitted-b). Since topography shapes the relief and strongly influences microclimate and hence phytosociological associations (Körner, 1999), different topographic descriptors were included besides spectral data and habitat descriptors (Dirnböck et al., 2003). We used the linear function for all habitat descriptors.

Topography

Topographic descriptors were derived from the digital elevation model (DEM, Swisstopo). Besides the more traditional descriptors of topography, namely «altitude», «slope», «easting» (sinus of exposition), «northing» (cosine of exposition) and «curvature» (shape of the surface along the direction orthogonal to aspect), we calculated «solar radiation», «flow» (flow direction of water out of each pixel), «runoff» (accumulation of rainfall units), «hill shade» (shadow a hill casts over the location with a certain azimuth and angle), and «upslope» (distance to ridges) and relief roughness («RoughnessA-F», Dirnböck et al., 2003, Table 1).

Habitat structure

In addition to the above mentioned descriptors of topography, our descriptors for habitat structure mainly included information extracted from satellite images (acquired during April, Mai, and August 1995, pixel resolution: 25 m). We used the images containing the reflectance bands visible green (500-600 nm wavelength), visible red (600-700 nm) and near infrared (750-1000 nm) (Dirnböck et al., 2003) and we derived texture measures and band transformations (Dirnböck et al., 2003). We calculated the standard deviation of each spectral band within a moving window of different radii as well as the normalized difference vegetation index (NDVI, e.g. Duncan et al., 1993).

Habitat composition

Topography shapes the relief and the prevailing microclimatic conditions and therefore influences habitat composition. Different habitat compositions show characteristic, different spectral patterns. Topographical as well as spectral data can therefore be used as descriptors of habitat composition (Table 1). In addition to these descriptors, we calculated the density of isolated trees as well as the density of forest and forest edges within circles of 25, 50, 75, 100 and 125 m radius.

Tourism footprint

The Euclidean distance as well as the density of pedestrian roads, forest tracks, roads and ski lifts or cableways within circles of 25, 50, 75, 100 and 125 m radius were our descriptors of tourism footprint.

OCCURRENCE MODELS

To predict the occurrence of breeding and non-breeding female and male black grouse, we used logistic mixed effects regressions with a logit function. Our response variable was whether a point was visited or not (1/0). Mixed Effects Models enabled the simultaneous analysis of all radiotracked individual birds pooled together, i.e. locations nested within individual, with individuals being treated as random effects and the different descriptors as fixed effects (Johnson et al., 2005).

Before running the analyses, we excluded the habitat descriptors that occurred only marginally or at very low densities (< 10% occupancy). Second, we removed descriptors showing a high level of co-linearity (Spearman rank correlation coefficient, $r_s \geq |0.7|$). Out of a correlated pair of descriptors, we chose descriptors pointing towards smaller scaled features (e.g., within a 50 m radius instead of 100 m), as small scale heterogeneity was important for habitat selection (Signorell et al., submitted-a).

In a first step, a full model including all descriptors was run. Second, we successively excluded by hand the least significant descriptor until we got a model with significant descriptors only. To get an estimate of model performance, the final model was estimated with the KappaMax statistics. KappaMax, however, is sensitive on the prevalence, but as we had the same number of visited and non-visited points, i.e. a prevalence of 0.5, KappaMax can be applied (Allouche, Tsoar & Kadmon, 2006). Bootstrap samples of equal size to the original data set were generated (Manly, 1997). For each bootstrap sample, we calculated the KappaMax values and among all samples, the KappaMax mean and standard deviation were determined. This method simulates the use of independent test data to evaluate the predictive performance of the original model (Vaughan & Ormerod, 2005). The model performance is considered poor when KappaMax is lower than 0.4; good when KappaMax is between 0.4 and 0.75, and excellent when KappaMax exceeds 0.75 (Fielding & Bell, 1997). We additionally calculated the threshold value for the occurrence probabilities: it describes the value where the visit probability changes from non-visited to visited.

OCCURRENCE PROBABILITY MAPS

We extrapolated the logistic model into space in order to construct occurrence maps. We limit extrapolation to the range of elevations of 1450 – 2300 m a. s. l. which corresponds to the range where black grouse can be observed (own data, and Klaus et al., 1990). The probability (π) of a point to be visited is equal to (Quinn & Keough, 2002):

$$\pi(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_i x_i)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_i x_i)}$$

where β_0 is the intercept, β_i the coefficients of the descriptors and x_i the descriptor maps.

We used ArcView GIS 3.3 (Environmental Systems Research Institute, California) for calculation of MCPs and 70% Kernel density distribution, ArcGIS 9.1, its Spatial Analyst extension (Environmental Systems Research Institute, California), IDRISI32 (Clark Labs) and Biomapper (Hirzel et al., 2002) for GIS analyses. Statistical analyses were performed with the R statistical package (package nlme, Version 2.4.1).

ECOLOGICAL NICHE FACTOR ANALYSIS (ENFA) FOR MALES, BREEDING AND NON-BREEDING FEMALES

Hirzel and colleagues (2002) described in detail the principles and procedure of ENFA. Briefly, ENFA summarizes the overall information in two indices: «marginality» and «specialisation». «Marginality» maximizes the multivariate distance of the eco-geographical variables between the cells occupied by males, breeding or non-breeding females and the cells within the whole reference area. We used the total area of individual home ranges as reference area. «Specialisations» are the second and subsequent factors of an ENFA and they account for the decreasing residual variance after removal of upper-ranked explanatory factors (Sattler et al., 2007). They denote to which extent the distribution of the eco-geographical variables of males, breeding and non-breeding females is narrow with respect to the overall distribution of the variables in the whole reference area. The tolerance of males, breeding and non-breeding females towards eco-environmental factors can be measured as the inverse of «specialisation». «Marginality» and «specialisation» are uncorrelated factors and the major information is contained within the first factors (Hirzel et al., 2002). A global «marginality» factor close to 1 means that the species lives in a very particular habitat relative to the reference set. A randomly chosen set of cells is expected to have a tolerance of 1, i.e. any value below 1 indicates some form of specialisation (Sattler et al., 2007).

Similar to the occurrence models, we removed descriptors showing a high level of co-linearity (Spearman rank correlation coefficient, $r_s \geq |0.7|$) and used in principle the same GIS-derived variables as for the calculation of the occurrence maps. The distributions of the eco-geographical variables were normalized, when necessary, by the Box-Cox algorithm (Sokal & Rohlf, 1994) or they were log transformed ($\log_{10}$).

Evaluation

We evaluated the ENFA accuracy by means of 10-fold cross validation (Fielding & Bell, 1997). The presence data set was divided randomly into 10 partitions of equal sizes. Each partition was used in turn to evaluate the predictions computed by a model calibrated on the other nine partitions. 10 values for each evaluation measure were thus calculated, summarized by their mean and standard deviation. We used the Boyce index *B4* (Boyce et al., 2002) which provides a continuous assessment of model predictive power (Hirzel et al., 2006). Following the method used by Sattler and colleagues (2007) we defined four classes of habitat suitability and counted how many presence points of the evaluation partition fell into each. This provided a predicted-to-expected frequency (PE, Boyce's area-adjusted frequency) of presence for each of them if they're combined with the total area covered by each class in the home ranges. The Boyce index *B4* was finally computed by the Spearman's rank between the

PE and the class rank, varying from -1 to 1, with 0 indicating a random model (Boyce et al., 2002; Hirzel et al., 2006).

Results

We radio-tracked a total of 30 black grouse at nine study sites during the breeding season. There was, however, a bias in our sample towards males (n = 15) and non-breeding or unsuccessful reproductive females (n = 11) compared to females which reared chicks (n = 4). Although 80% of the radio-tracked hens began incubation each year (2003-2006), only 28.6% of the incubating females could successfully raise their chicks. Failures were due either to nest failure (62.5%) or mortality of young chicks (37.5%). These values are similar to those from previous studies (30-60% and 34%, respectively, see the review by Klaus et al., 1990). A negative effect of radio-collars on survival and reproduction (Caizergues & Ellison, 1998) could not be assessed here.

OCCURRENCE PROBABILITY MAPS

After elimination of the correlated descriptors according to our criteria described in the previous section, we ended up with 35 uncorrelated descriptors (Appendix A). This was mainly because we included different radii for one single descriptor and the chosen descriptors for one group (e.g., roughness) often were only marginally different from each other (Table 1).

In the final model for breeding females, descriptors of topography, habitat structure, habitat composition and tourism footprint were included (Table 2). The KappaMax value was good (0.56±0.04), the threshold value was set on 0.6. The final model of non-breeding females contained the same descriptors as for breeding females (Table 3). Its Kappa value was slightly less good (0.48±0.05) with a threshold value of 0.6. The final model for males performed much worse, with a Kappa-value of 0.37±0.06 and a threshold value of 0.5. It only contained descriptors of topography, habitat structure and habitat composition (Table 4). Breeding females selected habitats with a higher relief roughness («Roughness A» and «Roughness F_{min}») but avoided habitats where the diversity of hill shading is large («Roughness C», Table 2). Breeding females chose locations, where the dominance of spectral band value 3 («Spectral texture C», visible red) as well as the mean NDVI («Mean NDVI 08.1998») were low. They avoided locations with abundant large trees within a radius of 50 m («Isolated trees 50 m») as well as pedestrian roads («Pedestrian roads»).

The results are ambiguous with respect to relief roughness for non-breeding females (Table 4): some descriptors describing relief roughness are avoided («Roughness A», «Roughness C with azimuth 180 and angle 40», «Roughness F_{max}» and «Roughness F_{min}»), whereas others are selected for («Flow», «Roughness B», «Roughness C with azimuth 270 and angle 10»). Non-breeding females chose locations where the vegetation reflected visible red less (600-700 nm wavelengths; «Spectral band value 3»). Diversity of spectral texture («Spectral texture B») was avoided. Spectral dominance («Spectral texture C») of spectral band value 3 (visible green) within a 3x3 pixel window is avoided, but selected for band value 2 within a 7x7 pixel window. Non-breeding females chose locations, where the mean NDVI («Mean NDVI 08.1998») was high. Forest tracks and roads were avoided.

For males, too, the results concerning relief roughness are ambiguous (Table 4): some descriptors describing relief roughness are avoided («Roughness A», «Roughness B» and «Roughness F_{max}»), whereas others were selected for («Roughness C with an azimuth of 180 and an angle of 40» and «Roughness F_{min}»). Males preferred locations where the vegetation reflected visible green less (500-600 nm wavelengths, «Spectral band value 2»). Spectral diversity was avoided («Spectral texture B»), whereas locations with higher mean NDVI («Mean NDVI 08.1998») were selected for.

The resulting habitat suitability maps within an altitudinal belt of 1450 to 2300 m a. s. l. for breeding and non-breeding females as well as for males are shown in Figures 1 to 3. Especially non-breeding females and males show a lower probability to be present in habitats at the upper edge of the altitudinal distribution of black grouse (2000 to 2300 m. a. s. l., Fig. 1 to 3). Forested habitats seem to be preferred by all three bird groups. However, the high preference of breeding females for habitats at the lower edge of the altitudinal distribution of the black grouse is probably an artefact due to the extrapolation in elevations where breeding females usually are not present (own data, see discussion).

ECOLOGICAL NICHE FACTOR ANALYSIS (ENFA) FOR MALES, BREEDING AND NON-BREEDING FEMALES

A high global marginality value of 1.38 for black grouse breeding females indicates that hens with chicks searched for very particular habitats compared to their availability in the home ranges of all individuals. This is also supported by a low tolerance of 0.23 which points at a high specialisation and relatively low tolerance towards deviations of their optimal habitat profile.

A comparatively much lower marginality of 0.65, combined with a higher tolerance index of 0.77 indicates that black grouse males' habitat choices during the breeding period are much less specific and that they show higher tolerance towards deviations of their optimal habitat.

The same holds for non-breeding females: they show a similar marginality like males (0.58) and a slightly lower tolerance (0.67) towards deviations from their optimal habitat.

The Boyce index *B4* used for cross-evaluating the habitat suitability models was highest for non-breeding females (mean ± SD, 0.92 ± 0.10) followed by breeding females (0.87 ± 0.15) and males (0.76 ± 0.53). The Boyce indices for hens were near their theoretical maximum of 1, attesting very good predictive power. The mean Boyce index of males was also quite high, but the large standard deviation points to low model robustness.

Discussion

In this study we present occurrence maps for black grouse females and males during the breeding period. We assumed that the occurrence probability of birds reflects habitat suitability: the higher the occurrence probability the more suitable a habitat. Habitat suitability and occurrence probability maps can thus be used as synonyms, although we are aware of the limitations in using habitat selection as an index for habitat quality and suitability (Johnson, 2007).

Habitat suitability modelling showed that breeding females selected locations where relief diversity and spectral texture is higher (low dominance of one spectral band value within a window of 5x5 pixels) compared to non-visited locations. This points towards a selection of richly structured habitats, which confirmed our previous results (Signorell et al., submitted-a). We found that breeding females preferred open locations with a low density of isolated trees. This may underline their need for habitats at the tree line, where big and small trees are patchily distributed.

In addition, we calculated ecological niches for males, breeding and non-breeding females. We showed that breeding hens are much more selective towards specific habitat variables in their home range than males and non-breeding females. Additionally, their tolerance towards deviations from their optimal habitat profile is much smaller than for males and non-breeding females. This is expected as breeding females of precocial birds have to lead their chicks to good and predator safe feeding grounds. Like in many other bird species, chick's diet differs from that of adults, consisting mainly of protein rich arthropod food

(Klaus et al., 1990). Therefore, habitat requirements during the breeding period should differ between breeding hens on the one hand and non-breeding females and males on the other hand. Differences in ecological niches has been demonstrated for highly related and cryptic species (Sattler et al., 2007) as well as for different sexes in different species (Pearson, Shine & How, 2002; Breed et al., 2006; Cook et al., 2007). Habitat suitability modelling offers the opportunity to define regions of high conservation priority, conflict zones or areas, where habitat management would be necessary (e.g. Glenz et al., 2001; Comiskey et al., 2002; Gibson et al., 2004). However, different ecological niches for males and females may complicate conservation priority settings: in highly dimorphic species where only one sex shows forms of parental care, knowledge of the ecological niches of the two sexes is often crucial and it must be of great concern in conservation biology. It namely entails decisions where to put conservation priorities and knowledge of the spatial overlap of males and females may be crucial in this decision taking process.

Single species habitat conservation always bears the problem that only this specific species is protected, not a whole ecosystem, unless the species plays the role of an umbrella species (Andelman & Fagan, 2000). Many grouse species are indicators of ecosystem health (Storch, 2000b) and may therefore act as umbrella species in their specific habitats, as it has been shown for the capercaillie (*Tetrao urogallus*, Suter, Graf & Hess, 2002). Additionally, although core Alpine black grouse populations are more or less stable over time, marginal populations of the Alps as well as most European black grouse populations have declined during the last decades (Klaus et al., 1990; Hess, 2000). Alpine countries therefore have a high responsibility for the conservation of their black grouse populations. Protecting high quality habitats for Alpine black grouse could therefore be one possibility of ensuring stable populations in the future. In the black grouse, population dynamics are thought to be tightly linked with reproductive output (Klaus et al., 1990). As black grouse females are the sex that cares for the young and shows narrower ecological niches than males, putting conservation priorities on high quality breeding habitats would ensure the long term continued existence of black grouse populations in the Alps. We therefore propose that habitat management should in priority focus on the requirements of breeding females.

Inherent to models are, however, limitations to the immediate applicability for habitat management and some considerations have to be kept in mind while interpreting habitat suitability maps (Fielding & Bell, 1997; Seoane et al., 2005; Ray & Burgman, 2006). As our modelling is based on only few individuals and only on a few regions of south-western Switzerland, extrapolation in locations where little or no data exists may be problematic. Additionally, as the data points of one individual are not independent of each other, spatial autocorrelation cannot be effectively excluded. In Alpine timberline ecosystems, where microclimatic conditions can change within meters (Körner, 1999), the resulting complexity and diversity of landscapes may pose a challenge in effective modelling habitat suitability maps. As the relationships between species and habitat features are scale-dependent (Lee et al., 2002; Boyce et al., 2003; Graf et al., 2005) habitat descriptors defined at one scale may not be successful in predicting species occurrence at another scale. For modelling occurrence maps, descriptors thought to be important at a very small scale, i.e. microhabitat may therefore not be suitable in predicting species occurrence at the landscape scale.

RECOMMENDATIONS FOR HABITAT MANAGEMENT

Based on this study, we can propose where in the region of southwestern Switzerland habitat conservation and eventually management should ideally be applied to prevent further shrinkage of high quality breeding habitats. This adds to the results of our previous studies on habitat selection (Signorell et al., submitted-a; Signorell et al., submitted-b) that suggested, which habitat management implementations would be adequate. Because the reasons may be manifold why apparently suitable habitats are actually not inhabited by a certain species conservation of still existing high quality regions should have priority. In conservation biology, prevention of loss of good habitats for a species is of key concern (Primack, 1998). This is often also economically an interesting solution. In these habitats, adequate habitat management would be meaningful to ensure optimal breeding habitat conditions also in the future. Furthermore, based on our ecological niche modelling, we propose setting conservation priorities on habitat requirements of breeding hens, because they are less tolerant towards deviations from their optimal habitat.

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Table 1. Topographic, spectral and spectral-textural descriptors as well as descriptors for habitat and tourism footprint with their derivation and underlying ecological features (Dirnböck et al., 2003).

	Descriptors of:						
Descriptor	Habitat structure	Habitat composition	Topography	Tourism footprint	Derivation	Underlying ecological feature	N
Altitude		x	x		Elevation (m a. s. l.)	Temperature, course of the timberline	1
Slope		x	x		Slope	Accumulation of scree and snow, avalanches, rockfall, insolation	1
Easting		x	x		East-exposed fraction of aspect	Wind-, rainshadow	1
Southing		x	x		South-exposed fraction of aspect	Insolation	1
Curvature$_{max}$	x	x	x		Shape of the surface along the direction of aspect	Influences moisture, accumulation of scree and snow, insolation	1
Curvature$_{min}$	x	x	x		Shape of the surface along the direction orthogonal to aspect	Influences acceleration and deceleration of flow and therefore erosion and moisture	1
Solar radiation		x	x		Calibrates radiances	Insolation, moisture, dryness	7
Flow	x	x	x		Flow direction	Moisture, flow	1
Runoff	x	x	x		Accumulation of rainfall units	Moisture, flow	1
Hill shade		x	x		Hillshade, azimuth/angle: 90/10, 180/10,270/10, 270/30	Insulation, moisture, dryness	5
Upslope			x		Distance to ridges	Wind-, rainshadow, scree and snow accumulation, moisture	1
Roughness A	x	x	x		Standard deviation of Easting in a radius of 1-5 pixels (25-125 m) around the location	Relief roughness. The more diverse the exposures in in a location, the rougher the relief	5
Roughness B	x	x	x		Standard deviation of Southing in a radius of 1-5 pixels (25-125 m) around the location	Relief roughness. The more diverse the exposures in a location, the rougher the relief	5
Roughness C	x	x	x		Standard deviation of Hill shade in a radius of 1-5 pixels (25-125 m) around the location	Relief roughness. The more diverse the exposures in a location, the rougher the relief	2 5
Roughness D$_{max}$	x	x	x		Mean of Curvature$_{max}$ in a radius of 1-5 pixels (25-50 m) around the location	Relief roughness. The more diverse the curvatures in a location, the rougher the relief	5
Roughness D$_{min}$	x	x	x		Mean of Curvature$_{min}$ in a radius of 1-5 pixels (25-50 m) around the location	Relief roughness. The more diverse the curvatures in a location, the rougher the relief	5
Roughness E$_{max}$	x	x	x		Standard deviation of Curvature$_{max}$ in a radius of 1-5 pixels (25-50 m) around the location	Relief roughness. The more diverse the curvatures in a location, the rougher the relief	5
Roughness E$_{min}$	x	x	x		Standard deviation of Curvature$_{min}$ in a radius of 1-5 pixels (25-50 m) around the location	Relief roughness. The more diverse the curvatures in a location, the rougher the relief	5

Roughness F_{max}	x	x	x		Roughness D_{max}/Roughness E_{max} in a radius of 1-5 pixels (25-125 m) around the location	Relief roughness	5
Roughness F_{min}	x	x	x		Roughness D_{min}/Roughness E_{min} in a radius of 1-5 pixels (25-125 m) around the location	Relief roughness	5
Spectral band value	x	x			2 = near infrared (750-1000 nm); 3 = visible red (600-700 nm); 4 = visible green (500-600 nm)	Spectral reflection, absorption and transmission of vegetation cover	9
Spectral texture A	x	x			Standard deviation of spectral band values 2-4 in a 3x3, 5x5 and 7x7 pixel window	Spatial heterogeneity of the vegetation cover	2 7
Spectral texture B	x	x			Diversity of spectral band values 2-4 in a 3x3, 5x5 and 7x7 pixel window	Spatial heterogeneity of the vegetation cover	2 7
Spectral texture C	x	x			Dominance index of spectral band values 2-4 in a 3x3, 5x5 and 7x7 pixel window	Spatial heterogeneity of the vegetation cover	2 7
Spectral texture D	x	x			Fragmentation index of spectral band values 2-4 in a 3x3, 5x5 and 7x7 pixel window	Spatial heterogeneity of the vegetation cover	2 7
Spectral texture E	x	x			Number of different classes of spectral band values 2-4 in a 3x3, 5x5 and 7x7 pixel window	Spatial heterogeneity of the vegetation cover	2 7
NDVI	x	x			Normalized difference vegetation index (04., 05. and 08. 1998)	Leaf area index, chlorophyll content, above-ground phytomass, vegetation cover	3
mean NDVI	x	x			Mean of the normalized difference vegetation index in a radius of 1-5 pixels (25-125 m) around the location (04., 05. and 08. 1998)	Leaf area index, chlorophyll content, above-ground phytomass, vegetation cover	1 5
Isolated trees		x			Density of isolated trees in a radius of 1-5 pixels (25-125 m) around the location	Openness of forest, estimation of course of timberline	5
Forest edge		x			Density of forest edge in a radius of 1-5 pixels (25-125 m) around the location	Openness of forest, estimation of course of timberline	5
Forest		x			Density of forest in a radius of 1-5 pixels (25-125 m) around the location	Openness of forest, estimation of course of timberline	5
Pedestrian roads, distance and density				x	Euclidean distance to the nearest walking path, density of pedestrian roads in a radius of 1-5 pixels (25-125 m) around the location	Index of human disturbance/tourism footprint	6
Forest tracks / roads, distance and density				x	Euclidean distance to the nearest forest track or road, density of forest tracks and roads in a radius of 1-5 pixels (25-125 m) around the location	Index of human disturbance/tourism footprint	6
Ski lifts / cableways, distance and density				x	Euclidean distance to the nearest ski lift or cableway, density of ski lifts and cableways in a radius of 1-5 pixels (25-125 m) around the location	Index of human disturbance/tourism footprint	6

Table 2. Coefficients, standard errors and p-values of the GIS-descriptors included in the best logistic mixed effects regression model predicting the occurrence of breeding black grouse females. Descriptors listed in Table 2 but not appearing here have not been retained in the final model. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, Kappa = 0.56 ± 0.04 (mean ± SD).

	estimate	SE	p	
Intercept	35.054	6.394	0.000	***
Altitude	-0.008	0.002	0.001	***
Roughness A 50m	9.726	2.516	0.000	***
Roughness F_{min} 50m	1.277	0.484	0.008	**
Roughness C (180/40) 50 m	-30.515	8.287	0.000	***
Spectral texture C (bd3, 5x5)	-11.675	5.060	0.021	*
Mean NDVI 08.1998 50m	-32.809	6.176	0.000	***
Isolated trees 50 m	-0.491	0.155	0.002	**
Pedestrian roads (Euclidean distance)	0.009	0.003	0.001	***

Table 3. Coefficients, standard errors and p-values of the descriptors included in the best logistic mixed effects regression model predicting the occurrence of non-breeding black grouse females. Descriptors listed in Table 2 but not appearing here have not been retained in the final model. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, Kappa = 0.48 ± 0.05 (mean ± SD).

	estimate	SE	p	
Intercept	5.289	2.934	0.071	.
Altitude	-0.003	0.001	0.015	*
Flow	0.005	0.001	0.000	***
Roughness A 50m	-4.409	1.336	0.001	***
Roughness B 50m	3.774	1.416	0.008	**
Roughness C (180/40) 50 m	-16.740	3.233	0.000	***
Roughness C (270/10) 50 m	5.819	2.136	0.006	**
Roughness F_{max} 100m	-1.601	0.475	0.001	***
Roughness F_{min} 100m	-1.294	0.361	0.000	***
Spectral band value 3 (05.1998)	-0.016	0.003	0.000	***
Spectral texture B (bd4, 3x3)	-0.894	0.421	0.034	*
Spectral texture C (bd3, 5x5)	-5.486	1.595	0.001	***
Spectral texture C (bd2, 7x7)	3.244	1.163	0.005	**
Mean NDVI 08.1998 50m	5.935	1.304	0.000	***
Forest tracks, roads (Euclidean distance)	0.001	0.000	0.000	***

Table 4. Coefficients, standard errors and p-values of the descriptors included in the best logistic mixed effects regression model predicting the occurrence of black grouse males. Descriptors listed in Table 2 but not appearing here have not been retained in the final model. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, Kappa = 0.37 ± 0.06 (mean ± SD).

	estimate	SE	p	
Intercept	2.159	1.089	0.047	*
Roughness A 50m	-5.898	1.502	0.000	***
Roughness B 50m	-4.433	1.534	0.004	**
Roughness C (180/40) 50 m	14.866	4.158	0.000	***
Roughness F_{max} 100m	-1.734	0.611	0.005	**
Roughness F_{min} 100m	0.881	0.405	0.029	*
Spectral band value 2 (28.05.1998)	-0.075	0.034	0.027	*
Spectral texture B (bd4, 3x3)	-1.263	0.421	0.003	**
Mean NDVI 08.1998 50m	6.387	1.647	0.000	***

Figure captions

Fig. 1. Occurrence probability of breeding female black grouse in southwestern Switzerland within an altitudinal belt of a) 1450-2300 m a. s. l. and b) 1750-2300 m a. s. l.

Fig. 2. Occurrence probability of non-breeding female black grouse in southwestern Switzerland within an altitudinal belt of 1450-2300 m a. s. l.

Fig. 3. Occurrence probability of male black grouse in southwestern Switzerland within an altitudinal belt of 1450-2300 m a. s. l.

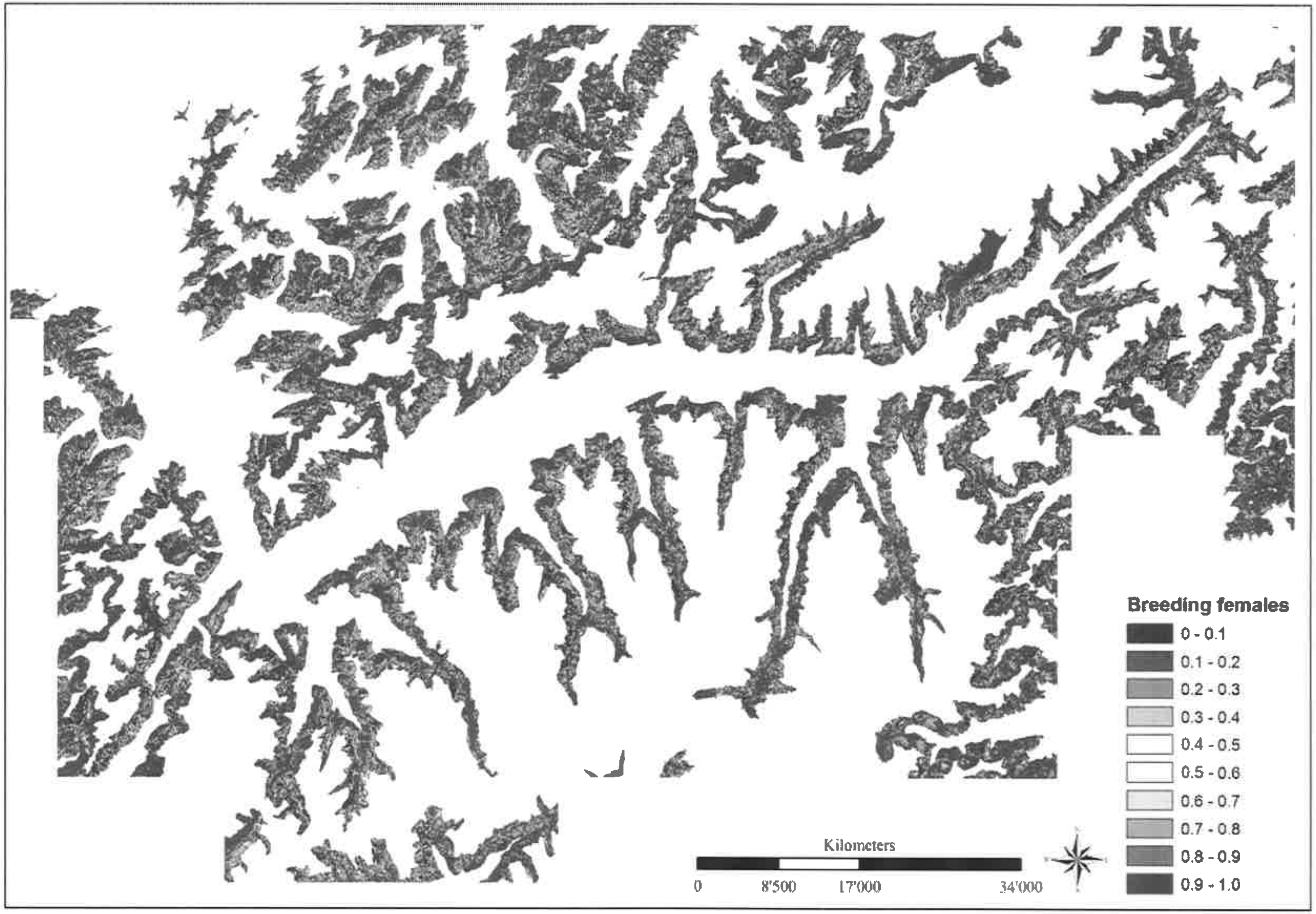
Breeding females
0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0
Kilometers
0
8'500
17'000
34'000

Fig. 1a.

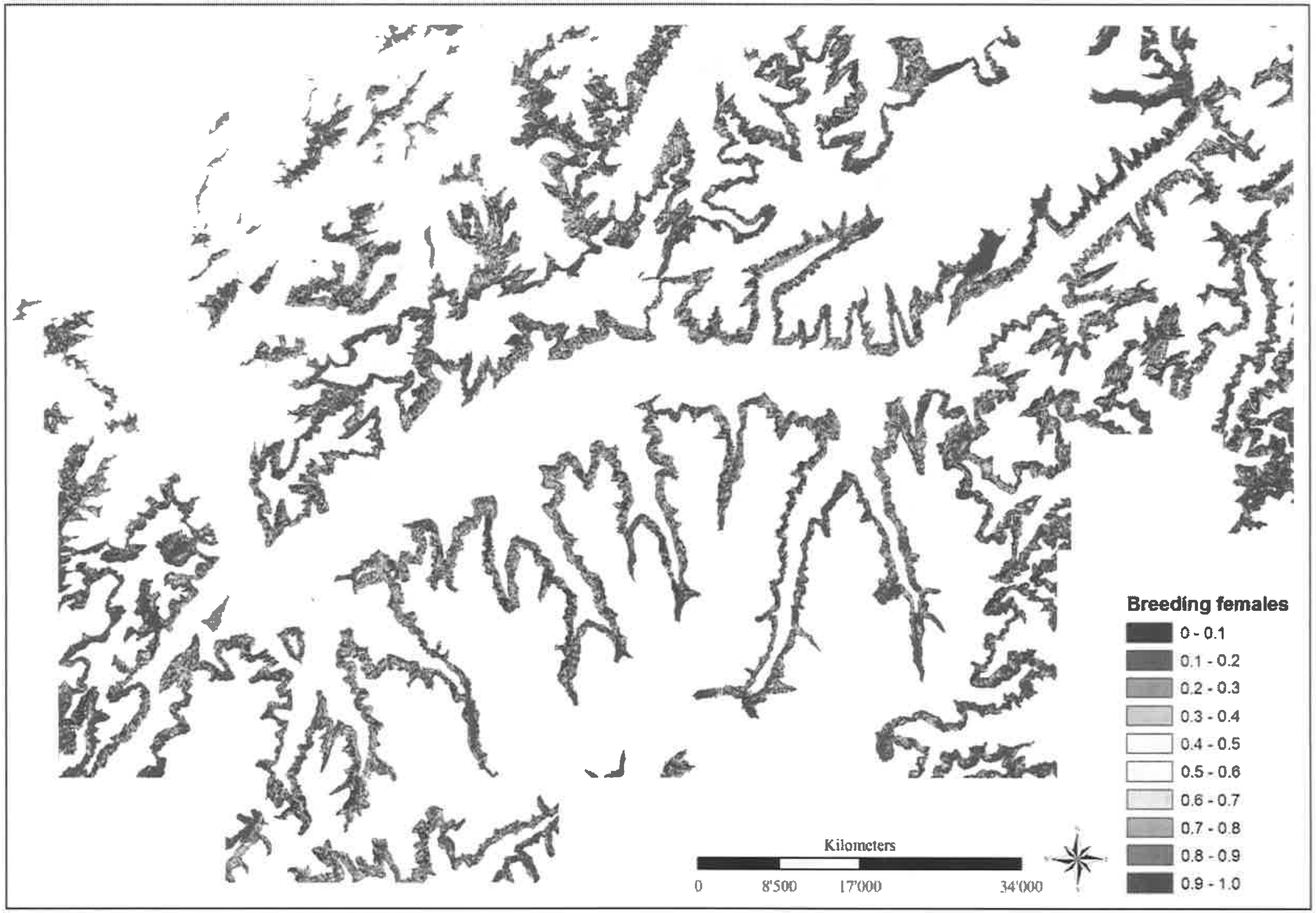
Breeding females
0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0
Kilometers
0
8'500
17'000
34'000

Fig. 1b.

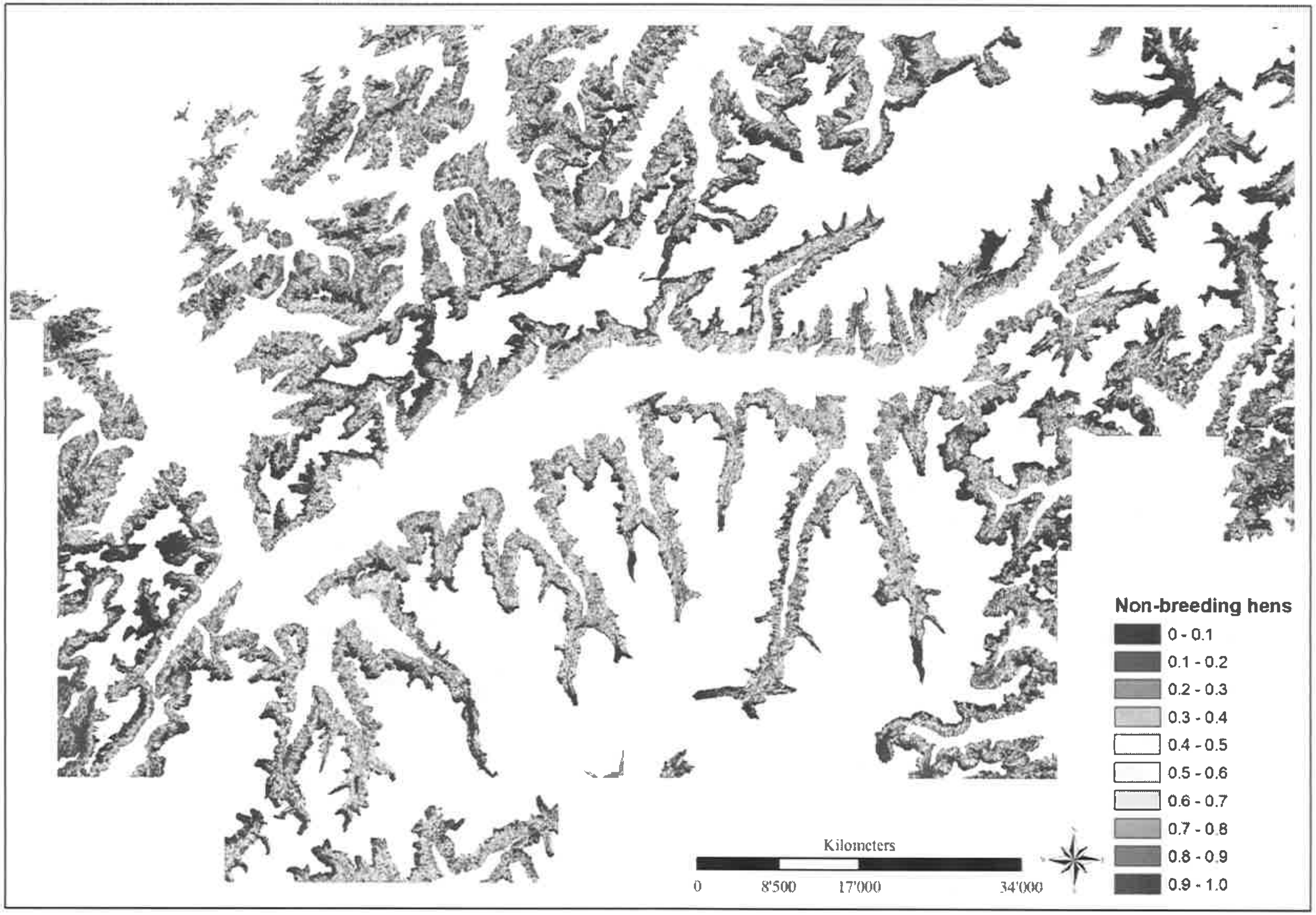
Non-breeding hens
0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0
Kilometers
0
8'500
17'000
34'000

Fig. 2.

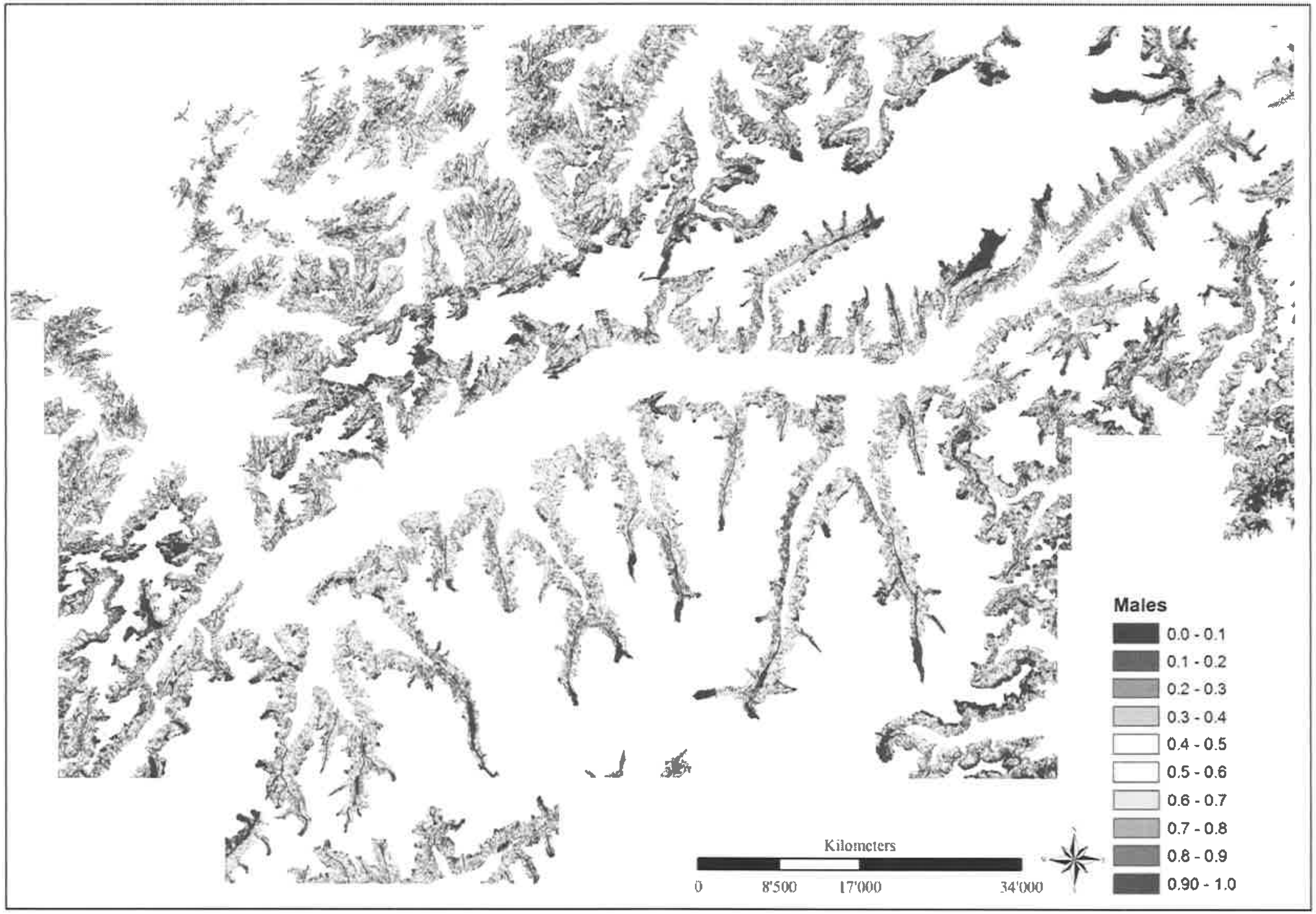
Males
0.0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.90 - 1.0
Kilometers
0
8'500
17'000
34'000

Fig. 3.

Appendix A. Descriptors retained for further modelling, after elimination of correlated descriptors and descriptors which occurred only marginally or at low densities. For further details see text.

Descriptors
Altitude
Slope
Easting
Southing
Curvature$_{max}$
Curvature$_{min}$
Flow
Upslope
Roughness A 50 m
Roughness B 50 m
Roughness C (180/40) 50 m
Roughness C (270/10) 50 m
Roughness F$_{max}$ 50 m
Roughness F$_{max}$ 100 m
Roughness F$_{min}$ 50 m
Roughness F$_{min}$ 100 m
Spectral band value 2 (08.1998)
Spectral band value 3 (05.1998)
Spectral band value 4 (04.1998)
Spectral texture A (bd3, 50m)
Spectral texture B (bd3, 3x3)
Spectral texture B (bd4, 3x3)
Spectral texture C (bd2, 3x3)
Spectral texture C (bd2, 7x7)
Spectral texture C (bd3, 3x3)
Spectral texture C (bd3, 5x5)
Spectral texture C (bd4, 3x3)
Spectral texture C (bd4, 5x5)
Spectral texture C (bd4, 7x7)
Mean NDVI 08. 1998 50 m
Isolated trees 50 m
Forest 50 m
Pedestrian roads (Euclidean distance)
Pedestrian roads 50 m
Forest tracks, roads (Euclidean distance)

CHAPTER FOUR

Impact of snow sports infrastructures and activities on the abundance of Alpine wildlife

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Impact of snow sports infrastructures and activities on the abundance of Alpine wildlife

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5920 words

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Summary

1. Tourism and leisure activities have increased continuously all over the world during the past decades, exerting a growing pressure upon naturally fragile ecosystems such as mountainous habitats. Disturbance by snow sports (free-riding skiing, mountaineering skiing, snowboarding and snowshoeing) and related infrastructures elicit stress upon wildlife, which may have serious negative demographic consequences. We tested the effect of human winter disturbance by snow-sports infrastructures and activities on wildlife abundance in the European Alps. The black grouse was chosen as a model as it is a declining, emblematic species of vulnerable timberline habitat, the latter being also the favourite habitat for snow sports activities.
2. We used Poisson regressions, firstly, to determine the relationships between black grouse abundance (number of displaying cocks along census transects) vs. presence of snow-sports infrastructures, hunting pressure and habitat characteristics (vegetation typology) at 15 natural sites (null or very low level of anthropogenic disturbance) and 15 ski-resorts in the south-western Swiss Alps; secondly, to construct spatially-explicit predictive abundance models, either pre-interactive models (natural conditions, i.e. in the theoretical absence of human infrastructures and snow sports activity) vs. post-interactive models (presently prevailing conditions).
3. Snow sports infrastructures (i.e. presence of ski resorts) and habitat typology were the principal determinants of black grouse abundance whereas hunting pressure had no discernable effect. Ski resort had a strong negative effect on the number of displaying cocks, which led to a halving of local density in ski resort sites, this after controlling for the confounding effect of habitat type.
4. *Synthesis and applications.* Conservation action plans for black grouse should aim at reducing the multiple negative effects generated by snow sports infrastructures and activities. Vegetation patchiness i.e. a mosaic of shrubs and grasses must be maintained

along ski-pistes. Wintering preserves where human penetration is banned or strictly limited should be promoted, even within ski resorts. Spatially explicit human-wildlife conflict maps can be constructed from the present model for delineating the most likely efficient protection areas.

Key words: Ski resorts, habitat quality, human disturbance, snow-sports, hunting, ski lifts, Alpine ecosystems, *Tetrao tetrix*

Introduction

Tourism and other public recreational activities have been continuously increasing over the past decades, even in the most remote areas of the world (Wüthrich, 2001). They potentially constitute a new threat to endangered and vulnerable animal species. The impact of these trendy activities on wildlife are often complex and variable in space and time, with their actual effects still remaining poorly understood (Taylor & Knight, 2003;Blumstein et al., 2005; Ficetola et al., 2007; Sutherland, 2007). Human disturbance such as repeated flushing events may induce stress (Arlettaz et al., 2007) and extra energetic costs (Baltic, 2005; Williams, Lusseau & Hammond, 2006), often constraining animals to occupy suboptimal habitats (Marti, 1986; Taylor & Knight, 2003), which may affect the reproductive (Watson & Moss, 2004) and survival functions, and overall fitness (Ellenberg et al., 2006; Mullner, Linsenmair & Wikelski, 2004). This may ultimately lead to a reduction of local population density (Mallord et al., 2007; Rolando et al., 2007).

Mountainous and alpine ecosystems are especially at risk due to their natural fragility (Ingold, 2005) and a steady increase of recreational activities such as free-riding snow sports (Arlettaz et al., 2007; Watson & Moss, 2004). Animals inhabiting alpine habitats have a finely-tuned winter energetic balance for coping with the harsh conditions which have deeply modulated their physiology (Marchand, 1996). In addition, the creation of ski facilities has profoundly modified the landscape through total destruction, degradation and/or fragmentation of the original natural habitats (Rixen et al., 2004; Rixen, Stoeckli & Ammann, 2003; Wipf et al., 2005). The progressive abandonment of traditional farming practices, such as cattle grazing, may further reduce the overall richness and attractiveness of these habitats for wildlife due to diminished heterogeneity and mosaicity of the natural features (Bignal & McCracken, 1996; Blanco, Tella & Torre, 1998; Laiolo et al., 2004). Moreover, it has been established that nearby human settlement, such as ski huts, the density of generalist predators may be artificially increased by the deposition of food remains and other garbage (Storch &

Leidenberger, 2003). Finally, hunting, which bears great cultural and economic value in the Alps (Ingold, 2005), could additively impact on wildlife populations which are already weakened by other factors and reduce their abundance (Baines & Lindén, 1991; Gauthier et al., 2001).

The black grouse (*Tetrao tetrix*) is an emblematic, threatened game bird of the Alps, which is likely to play the role of an umbrella species for Alpine ecosystems (Storch, 2000). The species lives the year round within the narrow timberline belt (1800-2300 m elevation) where most ski infrastructures and snow-sport activities in the Alps concentrate. Black grouse populations are declining in several parts of their geographic distribution (Storch, 2000). In the Alps, severe declines have been reported locally in the recent past, especially in marginal areas far from core distribution range (Hess, 2000; Zbinden, Salvioni & Stanga, 2003). The International Union for the Conservation of Nature has suggested that this decline is linked to the spreading of winter sports although scientific evidence is lacking (Storch, 2000).

The aim of the present study was to quantify and rank the various threats ultimately affecting black grouse population dynamics in the north-western European Alps, namely to assess the relative impact of ski resort settlement and snow sports activities, as well as hunting pressure, on black grouse abundance, while controlling for the effect of habitat type (plant community).

Material and methods

STUDY AREA

The study was conducted in the Alps of the cantons of Valais and Vaud (southwestern Switzerland, 46°10' N, 7°20' E) within an elevation belt between 1400-2300 m altitude (Klaus et al., 1990), on each side of the Rhône valley which extends from the Lake of Geneva to the Rhône glacier. The climate is characterized by warm and dry summers and cold, relatively wet winters.

BLACK GROUSE ABUNDANCE

Black grouse abundance was estimated from the spring density of lekking males between mid April and the end of May 2005. Males display just above or at the timberline level. Fifteen ski resorts (≥ 1 skilift, chair lift or cable car each) and 15 natural sites (outside ski resorts, no ski infrastructure) were chosen across the area. The criterion for selecting these 30 sites was the possibility that one observer was able to see with telescope (20-40x magnification) cocks displaying along a 1.5 km transect at the timberline from a vantage point situated on the opposite side of the valley at the same elevation as the transect; this was to avoid that the censusing activity interferes with birds' behaviour. That transect length corresponds to the mean distance recorded between black grouse leks in the Alps (Klaus et al., 1990) and so we limited the risk to miss a lek. Each transect was censused three times throughout the season, at the beginning, middle and at the end of the courtship period, respectively (Klaus et al., 1990). The visit sequence to the sites was randomized pairwisely, ensuring an equal temporal distribution to ski resorts and natural sites for each period within the season. Surveys started at dawn and consisted of three periods of 15 minutes observation, with two gaps of 15 minutes in-between. The maximum number of simultaneously observed cocks along the 1.5 km transect in one of the nine 15 minutes' observation sessions was our estimate of black grouse local abundance.

PREDICTORS OF ABUNDANCE

Habitat typology

We mapped 13 different habitat types along the 1.5 km long transects (Table 2), which encompassed all habitats present in the altitudinal habitat belt where black Grouse occur.

Mapping was performed during the summer from a walk along the transect at the average altitudinal distribution of displaying cocks. Along this «elevation isocline», we collected GPS coordinates at each habitat type boundary. This enabled us to estimate the local proportions for each of the 13 habitat types. In order to reduce both the number of variables and variable interdependency, we performed a principal component analysis (PCA) on these percentage values. The main factor(s) encompassing most of the system variance (principal components: PC-1 to PC-n) was/were used for subsequent analyses (HABITAT predictors). The actual number of retained principal components was determined with the broken-stick method (Jackson, 1993).

Snow-sport infrastructures and activities

We used the density of skilifts (including all types of snow-sport cable infrastructures such as skilifts, cable cars and chair lifts) as a proxy of landscape alteration by installations *and* winter human disturbance (the two factors are confounded in the present study). As we ignored up to which distance from ski-installations skiers may move (off-piste activities, see Arlettaz et al. 2007), potentially representing a source of disturbance, we constructed GIS raster maps with, first, skilift density within circular moving windows of radii from 250 to 1500 m, with an increment of 250 m in between; and, second, distance to skilifts. Raster maps had a cell size of 625 m^2. As with habitat variables, we performed a PCA on these GIS skilift maps. For the analyses, we retained the first principal component (PC-1) that explained 80% of the overall variance. PC-1 correlates negatively with mean distance to skilifts, and positively with densities of skilifts within different radii. It is thus an measure or index of «ski-infrastructures and snow-sport activities» (SKILIFTS, Table 2). Mean values of this PC-1 map were extracted for each census transect.

Hunting pressure

In some Alpine cantons of Switzerland, black grouse cocks can still be hunted during late autumn outside federal and cantonal game reserves. We calculated the density of shot birds for each community (the smallest administrative unit across the country) and year. To estimate density, the reference area within a community was restricted both to the altitudinal belt traditionally occupied by black grouse (1400-2300 m) and to the area subjected to hunting, after excluding hunting reserves. The mean shooting bags of the comprehensive time series 2000-2004 (long term cumulative effect) as well as for the sole year 2004 (short term effect) were considered separately. On the basis of the geo-referenced maps, we calculated a density of shot birds within circular moving windows of similar radii as for SKILIFTS. Principal component analyses were run with the five resulting variables (250-1500 m radii, 250 m increment). The first component for, respectively, the years 2000-2004 (96% of variance), and 2004 separately (95% of variance), were retained. They were used as indices of «hunting pressure» (HUNTING) as they correlated positively with hunting bag densities. Mean values of the resulting PC-1 maps were extracted for each census transect.

MODELLING BLACK GROUSE ABUNDANCE WITH RESPECT TO SKI INFRASTRUCTURES, HABITAT TYPOLOGY AND HUNTING PRESSURE

We used log-linear Poisson regressions to model black grouse abundance as a function of habitat typology, ski infrastructures and snow-sport activities, and hunting pressure. We followed an information-theoretic approach (Burnham & Anderson, 1998; Johnson & Omland, 2004; Rushton, Ormerod & Kerby, 2004). We defined seven candidate models (Table 1) resulting from the combinations of the three main groups of predictors: HABITAT, SKILIFTS and HUNTING. The competing models were ranked according to the «small sample unbiased» Akaike Information Criterion (AIC_c) differences and weights. We used a two-stage process. Firstly, we selected the best set of predictors within each group of predictors. Among all possible combinations of these predictors (e.g., PC-1 to PC-n of the

HABITAT group), we retained the predictors that were included in the variable combinations that had an AIC_c difference not greater than 2 compared to the best submodel (i.e. the best model within the group of predictors; Burnham & Anderson, 1998). Secondly, we integrated these sets of predictors, where appropriate, in the seven candidate models. Our approach allowed firstly to decrease the number of predictors and to select the most likely explanatory predictors during the first step of the process, and secondly to avoid testing all possible combinations of predictors which would have dramatically inflated the number of candidate models at the second stage. We estimated the relative importance of each group of predictors by summing the AIC_c weights for each group across all models that contained that group of predictors. According to Burham & Anderson (1998), this sum corresponds to a "selection probability". Finally, we used a model-averaging approach to estimate coefficients and 95% confidence intervals (CI) for each predictor in a final, general model (Burnham & Anderson, 1998). The predictive performance of the final model was evaluated with the Spearman rank correlation test coupled to a randomization procedure. We generate 1000 bootstrap samples of equal size to the original data set by sampling them randomly with replacement. For each bootstrap sample, we recalculated the model coefficients. We used them and the original data set to predict the black grouse abundance and to estimate the correlation between the predicted and the observed abundance. We computed the mean of Spearman statistics and its standard deviance. This method simulate the use of independent test data to evaluate the predictive performance of the original model (Vaughan & Ormerod, 2005). Moreover, we considered the correlation to be significant if the spearman tests where more than 950 times significant (with a *p-value* <0.05) among the 1000 bootstraps (Manly, 1997).

CONSTRUCTING LARGE-SCALE ABUNDANCE MAPS

The habitat typology segment of the black grouse abundance model was based on precise field-mapped data. Such detailed habitat typology maps did not exist across the entire study area contrary to the self-constructed GIS HUNTING and SKILIFTS maps. It was thus not possible to directly and spatially extrapolate the restricted data about the relationships between local bird abundance and habitat type to a larger reference area. In order to construct predictive abundance maps for black grouse, we had thus to find GIS surrogates of the HABITAT principal components; we proceeded as follows. Firstly, we extracted monthly indices of vegetation growth (NDVI, see Pettorelli et al., 2005) from three LANDSAT-5 satellite images taken in April, Mai and August 1998, respectively. In subsequent analyses, we retained the first principal component obtained through a PCA conducted on these three NDVI. Secondly, for each of the three same monthly satellite images, we run a separate PCA using the six reflectance bands in the visible (blue, green, red), near-infrared, shortwave, and thermal infrared portions of the electromagnetic spectrum, again using PC-1 for each seasonal image in the following analyses. Another PCA was finally carried out on these three retained principal components in order to integrate the information drawn throughout the season. Thirdly, we used a vectorial habitat database (Swisstopo, 2005) to calculate the density of isolated trees, bushes, open forests and closed forests, in circular moving windows. The same radii as for the other predictors were used (see above) and, likewise, the first factor(s) of a PCA applied onto these density maps were kept for further analyses. Then, we performed stepwise (forward and backward) linear regressions to model surrogates of the HABITAT PC. The independent variables were the GIS habitat predictors created previously and their quadratic term. Here, we used stepwise modelling instead of model averaging since we firstly wanted to obtain a simple and robust model and, secondly, were not interested in the composition of that model (Whittingham et al., 2006).

A «post-interactive» abundance map with present-day environmental characteristics was generated by applying the black grouse abundance model using the HABITAT surrogates, as well as the SKILIFTS and HUNTING maps. Similarly, a final «pre-interactive» abundance map (i.e. in the theoretical case of absence of ski infrastructures and related snow-sport activities) was created by using the abundance model; this time, however, the overall SKILIFTS predictor was hold constant at its average value obtained from the natural sites.

We used the geographical information system ArcGIS 9.1, its Spatial Analyst extension (Environmental Systems Research Institute, California), the IDRISI32 (Clark Labs) and Biomapper softwares (Hirzel, Hausser & Perrin, 2002) for GIS analyses. Statistical analyses were performed with the R statistical package (Version 2.4.0, R Development Core Team, 2006). We checked for variance homogeneity and normality of regression residuals.

Results

MODEL SELECTION

Between 1-20 black grouse cocks (average ± SD: 5.6 ± 4.2) were observed along the thirty 1.5 km long census transects.

During the first stage of the model selection process, two hunting pressure predictors (HUNTING 2004 PC-1 and HUNTING 2000-2004 PC-1) and two HABITAT predictors (HABITAT PC-2 and PC-5) provided substantial support to the black grouse abundance pattern within their respective predictor group. They were thus retained for the second stage of modelling and integrated in the seven subsequent candidate models.

Among the set of candidate models, the SKILIFTS and HABITAT variables were the most likely ecological correlates of black grouse abundance (selection probabilities of 0.999 and 0.996 respectively, Table 1). In comparison, HUNTING predictors had a very low probability to be linked with black grouse abundance (selection probability of 0.124). The obviously best model is constituted of a combination of SKILIFTS and HABITAT predictors (AIC_c weight = 0.90; Table 1), with a good predictive power as shown by the significant correlation between observed and predicted abundance ($r_s = 0.54 \pm 0.08$, $p < 0.05$). Models with other combinations of predictors had much lower probabilities to be the best model.

BLACK GROUSE ABUNDANCE MODEL

In the averaged model, HABITAT PC-5 had the strongest effect among habitat predictors. The influence of this factor on black grouse abundance was negative. Since the factor HABITAT PC 5 is negatively correlated with the variable «mixed *Rhododendron-Vaccinium* shrubs» (Table 2), the latter habitat type had the greatest positive effect on black grouse abundance. In contrast, the variable «rocks and scree» is positively correlated with the factor HABITAT PC-5, establishing a negative association between «rocks and scree» and black grouse abundance. The second «habitat typology» factor (HABITAT PC-2) had a negative influence on black grouse abundance. That factor was negatively correlated with the habitat type «open old forest with grass/*Ericaceae* groundcover», which means a positive effect of that habitat type on black grouse abundance. The factor «ski-resort index» (SKILIFTS PC-1) had a negative effect on black grouse abundance, meaning that a higher density of ski-lifts and a lower distance to skilift decrease the abundance of black grouse (Table 2). According to their PC loadings, higher skilifts densities within radii of 500 to 1000 m have a stronger negative effect than a higher skilift density close to the transect (250 m) (Table 2). The two HUNTING predictors were not correlated with black grouse abundance; their coefficients overlapped with zero (0.0041, 95% CI: -0.0058 – 0.0139; -0.0045, CI: -0.0142 – 0.0053, for the two HUNTING predictors, respectively) and the HUNTING predictors had a very low model selection probability (Table 2).

We thus predicted black Grouse abundance in function of the SKILIFTS predictor by holding constant the HABITAT predictors at their mean value, and without considering any effect of HUNTING. The mean predicted black Grouse abundance in natural sites (i.e. areas without skilifts) is 6.6 cocks per linear transect and 4.2 in ski resorts (areas with ≥ one skilift) (Fig. 1).

BLACK GROUSE ABUNDANCE MAP

It was possible to find adequate GIS surrogates of the HABITAT predictors selected in the averaged final model (see electronic Appendix). The linear regressions between the field-based HABITAT predictors and their GIS surrogates showed good predictive power (HABITAT PC-2 = 1.00 ± 0.18 * HABITAT PC-2 GIS surrogate, $p < 0.0001$, $R^2 = 0.49$; HABITAT PC-5 = 1.00 ± -0.09 * HABITAT PC-5 GIS surrogate, $p < 0.0001$, $R^2 = 0.80$). The actual and pre-interactive abundance maps highlighted a spatially negative effect of ski resorts presence on black grouse abundance on large areas (Fig. 2).

Discussion

This study provides the first quantitative evidence that ski infrastructures and related snow sports activities negatively impact on Alpine wildlife abundance on a large scale: Black grouse density was ca. 50% higher in natural than in anthropized sites after accounting for the effect of habitat type (given that scattered and open forests are the most favourable habitat type). Ski infrastructures thus not only provoke a reduction in abundance of birds and spiders through the modification and destruction of native vegetation within a 100-200 m belt along ski-pistes (Rolando et al., 2007; Wipf et al., 2005), they also affect an emblematic and threatened wildlife species on a much broader scale, predominantly within 500–1000 m, and up to 1500 m from skilifts.

A negative effect of ski infrastructures and snow sports activities on black grouse abundance is probably due to a combination of different factors: 1) habitat destruction or alteration (Ingold, 2005); 2) higher predation rate caused either by habitat fragmentation which increases foraging opportunities of predators (Storch, Woitke & Krieger, 2005), or by food remains deposition which may enhance density of predators (Storch & Leidenberger, 2003); 3) increase of direct disturbance by humans that induce higher stress levels (Arlettaz et al., 2007) and extra-energetic costs (Baltic, 2005); 4) additional mortality due to collisions with cables (Miquet, 1986). At this stage, we still do not know which factor(s) contribute most to lowering black grouse density, which calls for new refined investigations. In order to better identify key human disturbance factor(s), actual winter disturbance intensity should be quantified by measuring actual number of ski or snowshoe traces away from ski-pistes (Arlettaz et al., 2007) rather than by applying a crude skilift index as in the present study. The present study confirms former views that open, either young or old forest stands with a wide *Ericaceae*-grass cover represent black grouse's favourite habitat (Swenson & Angelstam, 1993; Storch, 2000; Pearce-Higgins et al., 2007). A common feature across black grouse range is the availability of richly-structured open habitats with a mixture of shrubs and grasses. In contrast, unproductive habitats such as rocks and screes, as well as open habitats such as alpine pastures, which expose birds to predators, had a negative effect upon black grouse abundance in Southwestern Switzerland.

We did find any link between hunting pressure and black grouse abundance. It is therefore likely that hunting is principally a compensatory mortality trigger in our study area (Zbinden, Salvioni & Stanga, 2003) where harvesting is in general low (between 104 and 187 cocks shot down yearly in 2000-2004 on an area of about 5'000 km^2). Hunting most probably causes only local population reductions, especially where harvesting is intensive over the years such as in highly accessible areas with a good road network. The currently relatively low harvesting level in the Swiss Alps contrasts with the situation in the UK where hunting mortality has been established to be additive (Baines & Lindén, 1991). Although the hunting regime had no discernable effect on black grouse abundance, at least compared to other more decisive factors dictating abundance such as habitat type and presence of ski infrastructures, it would be interesting to see, however, if hunting may affect local survival and population dynamics. The development of capture-recapture models with marked birds could provide decisive hints and lead to the development of spatially-explicit hunting plans adapted to local geographic context.

CONSERVATION IMPLICATIONS

The Alpine vegetation is generally severely damaged by skiing and the preparation of ski-runs (Rixen et al., 2004; Wipf et al., 2005): shrubs, small trees and grass cover are generally reduced in height and density in order to smooth the ski-pistes. Moreover, the roads network is generally made denser to facilitate the access and maintenance of the installations (Ingold, 2005). Thus, optimal habitat of black grouse, which we have shown to be an essential determinant of its abundance, is threatened where it overlaps with ski resorts. The conservation or restoration of a patchy shrub-grass vegetation cover should be promoted along ski-pistes and roads, at timberline elevation. Where the preservation of a vegetation patchwork is not possible or where damages have already been too severe, restoration methods such as safe-site islands, i.e. small undisturbed patch of native plants (Urbanska, 1997), grass seeding (Bayfield, 1996) and transplants of native grass (Fattorini, 2001) may be applied so as to accelerate the recolonization process of the native vegetation. In areas where closure of vegetation and bush encroachment occurred after abandonment of Alpine summer pastures (Laiolo et al., 2004), forestry measures should be envisioned such as tree thinning and removal of dense bush cover (Y. Magnani, *pers. comm.*) or extensive farming practices like goat, sheep or cattle grazing should be promoted (Storch, 2000).

The present study could not identify the proximate mechanisms which affect black grouse abundance and are likely embedded within our general estimates for ski infrastructures and snow-sport activities, which mostly impact on local bird density. Previous studies, however, have shown that black grouse have, firstly, to cope with a more pronounced stress challenge in the ski resorts and ski mountaineering areas than in natural, undisturbed sites (Arlettaz et al., 2007); secondly, that repeated flushing events induce an immediate stress response (Arlettaz et al., 2007); and, thirdly, that extra energetic costs are higher in disturbed birds (Baltic, 2005). The creation of specific wintering preserves within ski resorts may therefore improve the survival of black grouse, potentially leading to an increase of their local abundance. In this objective, our «pre-interactive» abundance map (abundance of black grouse in the theoretical absence of ski infrastructures and related snow-sport activities) offers the opportunity to locate the most suitable sites for creating such winter refuges, as far as vegetation conditions have not been too much degraded. In these refuges, human penetration should be banned or limited to a minimum. Such refuges could furthermore be used for educating snow sports people about wildlife conservation issues.

Based on our results, we predict that regions of the Alps where black grouse habitat is naturally suboptimal (massive shrub encroachment, absence of open forest stands, etc.) and which furthermore harbour extended ski resorts will experience severe decreases of their black grouse populations. This problem seems especially acute at the periphery of distribution, e.g. in the Swiss Prealps (Zbinden, Salvioni & Stanga, 2003). In more central locations, where populations are stable, further negative demographic trends are to be expected if snow sports activities continue to expand, which seems very likely (Ingold, 2005). Consequently the previous mitigation measures should be implemented at an early stage and are likely to benefit other elements of biodiversity within that ecosystem.

Our spatial abundance model may serve as a tool for creating or modifying routes for skilift-infrastructures which are as little detrimental to wildlife as possible. Presently, there is an ongoing rationalisation of ski facilities, with secondary skilifts being dismantled, whilst the capacity of principal facilities is increased in capacity. Alternative skilift routes may be evaluated by virtually modifying the landscape and comparing directly their effect on black grouse abundance. The comparison of such scenario maps, or of the «pre-interactive» map with a map of snow-sports activities will enable to recognize, in a spatially-explicit manner, zones of high potential human-wildlife conflicts so as to optimize the sustainable management of ski resorts.

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Table 1. Summary of the model selection procedure for predicting Alpine black grouse abundance. The candidate models (see the combinations of X) include the following descriptors: habitat type (HABITAT), ski-infrastructures and snow-sport activities (SKILIFTS) and hunting pressure (HUNTING). Models have been ranked according to their Akaike's Information Criterion (AIC_c) weights. K indicates the number of parameters used in the model.

Model description					
SKILIFTS	HABITAT	HUNTING	k	Delta AIC_c	AIC_c weights
X	X		4	0.00	0.872
X	X	X	6	3.91	0.123
X			2	11.05	0.003
	X		3	14.36	0.001
X		X	4	14.85	0.001
	X	X	5	16.05	0.000
		X	3	27.03	0.000
0.999[1]	0.996[1]	0.124[1]			

[1] Selection probability (see material and methods for more details)

Table 2. The SKILIFTS and the two HABITAT variables derived from a principal component (PCA) analysis, included in the averaged Poisson regression model of black grouse abundance. Loadings are the correlation coefficients of each original variable onto the principal components (PC). SKILIFTS PC-1 is composed of five densities of skilifts (calculated in circles of 250 to 1500 m radii) and the distance to skilifts.

SKILIFTS PC-1 (80%)		**HABITAT PC-2 (9.8%)**		**HABITAT PC-5 (7.0%)**	
Variable	Loading	Variable	Loading		Loading
Density r250	-0.81	*Juniperus* shrubs	0.37	Rocks and scree	0.36
Density r500	-0.94	Open old forest with Ericacea	0.28	*Juniperus* and pasture	0.35
Density r750	-0.97	*Alnus* forest	0.27	*Rhododenron /Vaccinium* and pasture	0.34
Density r1000	-0.96	Open young forest with Ericacea	0.23	Open young forest with grass	0.23
Density r1500	-0.90	Open young forest with grass	0.16	Typical alpine pasture	0.16
Distance	0.51	Rocks and scree	0.14	Open old forest with grass/Ericaceae	0.14
		Rhododenron /Vaccinium and pasture	0.11	Open young forest with Ericacea	0.08
		Typical alpine pasture	0.10	Open old forest with grass	0.05
		Juniperus and pasture	0.03	*Juniperus* shrubs	0.03
		Mixed *Rhododendron-Vaccinium* shrubs	-0.05	Open young forest with grass/Ericaceae	-0.03
		Open old forest with grass	-0.37	Open old forest with Ericacea	-0.05
		Open young forest with grass/Ericaceae	-0.39	*Alnus* forest	-0.42
		Open old forest with grass/Ericaceae	-0.55	Mixed *Rhododendron-Vaccinium* shrubs	-0.59
Poisson regression					
coefficient	0.051		-0.125		-0.222
SE	0.014		0.054		0.065

Figure captions

Figure 1. Predicted Alpine black grouse abundance relative to ski-infrastructures and snow-sport activities. Abundance was allowed to vary with the «ski-infrastructures and snow-sport activities» (SKILIFTS PC-1) while HABITAT covariates were held at their mean values.

Figure 2: Illustration of the effect of ski infrastructures (black lines) and snowsports activities on spatial density of black grouse (n = number of cocks per horizontal transect of 1.5 km) in the ski resort of Verbier, Valais. A) Satellite view; blue: snow cover, dark green: closed forests; dark red: shrubland; light green: pasture; violet: built areas. B) Actual abundance map (post-interactive). C) Pre-interactive abundance map (theoretical distribution in the absence of ski infrastuctures). The negative effect of infrastructures is clearly recognizable. The model used is presented in Table 2.

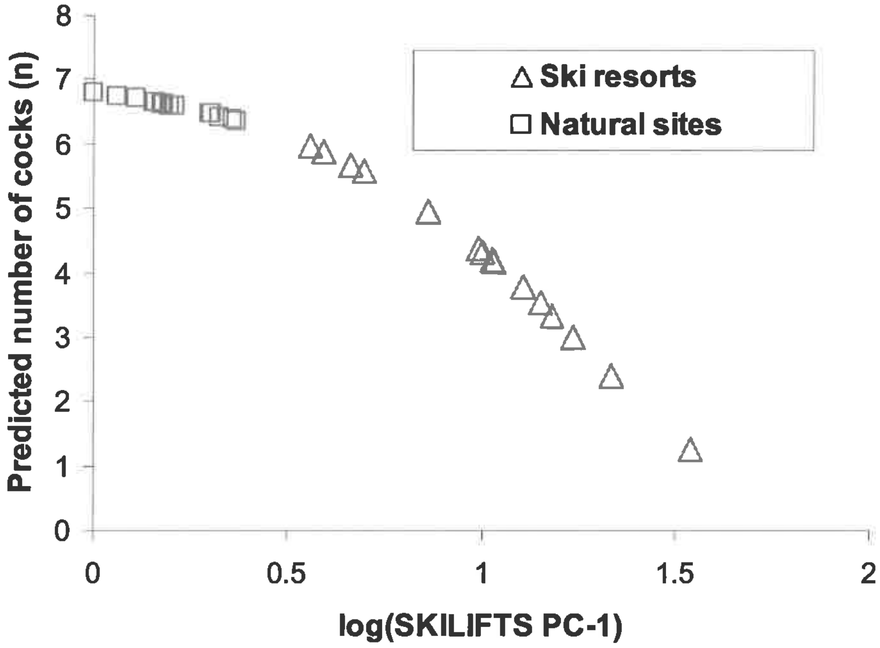
8
7
6
5
4
3
2
1
0
Predicted number of cocks (n)
0
0.5
1
1.5
2
log(SKILIFTS PC-1)
△ Ski resorts
□ Natural sites

Fig. 1

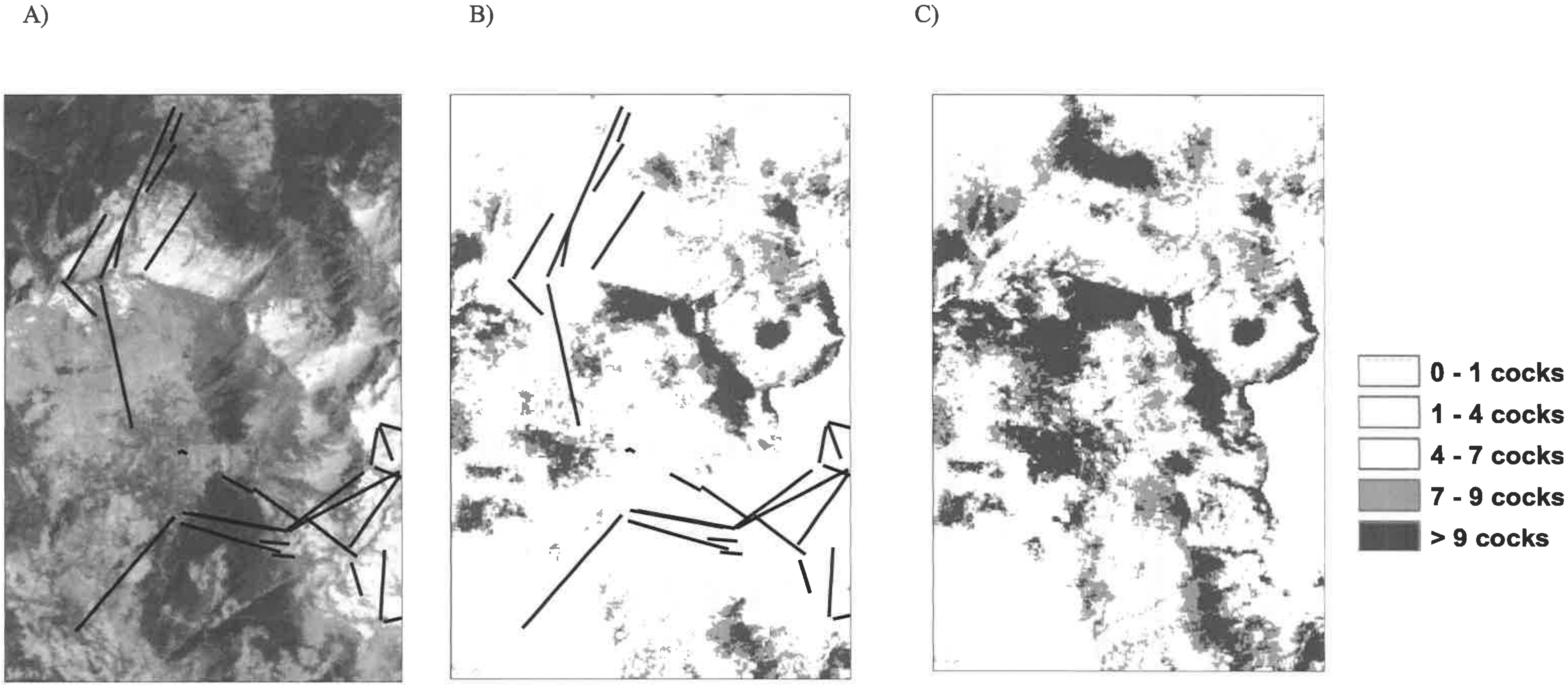

Fig. 2

Electronic appendix: Composition of the GIS HABITAT surrogates

Results of the stepwise linear regression (both direction) between field-based HABITAT PC-2 and PC-5 with the list of candidate GIS habitat variables (see Material and methods: „Constructing large-scale abundance maps"). Each GIS variable is itself a principal component and the variance it explains within that PCA is shown. GIS variables not retained by the stepwise process are also presented (NR).

			HABITAT PC-2		**HABITAT PC-5**	
GIS Variables		***Variance***	***Estimate***	***p value***	***Estimate***	***p value***
Intercept			1.64	0.0115	-1.05	0.0185
NDVI	PC-1	78%	1.75	0.0031	NR	
	PC-2	20%	-1.75	0.0343	NR	
Reflectance bands	PC-1	39%	-1.44	0.0011	0.19	0.0333
	PC-2	33%	NR		-0.35	0.0039
	PC-3	14%	NR		-0.87	0.0237
isolated trees	PC-1	87%	NR		-0.21	0.0085
	PC-1$^{\wedge 2}$		NR		NR	
	PC-2	10%	1.50	0.0235	-2.53	0.0007
	PC-2$^{\wedge 2}$		NR		-2.77	0.0009
open forests	PC-1	73%	NR		-0.03	0.1135
	PC-1$^{\wedge 2}$		NR		NR	
	PC-2	16%	NR		NR	
	PC-2$^{\wedge 2}$		NR		NR	
closed forests	PC-1	83%	NR		-0.22	0.0291
	PC-1$^{\wedge 2}$		NR		NR	
	PC-2	12%	NR		NR	
	PC-2$^{\wedge 2}$		NR		4.71	0.0032
bushes	PC-1	73%	NR		NR	
	PC-1$^{\wedge 2}$		NR		NR	
	PC-2	13%	0.48	0.0529	NR	
	PC-2$^{\wedge 2}$		NR		NR	
Adjusted R-squared:			0.40		0.72	
p-value:			0.003		<0.001	
F-statistic:			4.88		9.33	
Degree of freedom:			5 and 24		9 and 20	

GENERAL CONCLUSION

This works highlights first the importance of a richly structured and diverse habitat, where different vegetation elements merge together and create a high structural heterogeneity. Both breeding and non-breeding black grouse hens as well as males preferred microhabitats in their home ranges which showed a high vertical and horizontal patchiness, this in all vegetation layers. Whereas males were not very sensitive towards vegetation composition, females, in particular breeding females, showed clear preferences towards specific plant communities. Although non-breeding females preferred certain habitat features in their home ranges, a clear habitat profile could be drawn for breeding females. Breeding hens selected open forests at the timberline with a mosaic of old and young trees and a richly structured understorey consisting of grasses and different shrub species. An optimal habitat profile consists of a diverse, complex mosaic comprising isolated mature coniferous trees (10-30% of area), scattered small trees in regeneration (< 3 m height) associated with shrub cover (30-40%), and Alpine grassland (10-30%, *Nardus stricta* as dominant species).

The clear preference of breeding females for a specific habitat results from their need to lead the chicks to arthropod rich and predator safe habitats. Actually, breeding hens probably trade-off arthropod abundance for predator avoidance; they avoided the arthropod richest habitats (open Alpine grassland) which offer low or no cover against avian and mammalian predators.

The specific habitat requirements of breeding females and their close relationship towards microhabitats which offer enough arthropod abundance and/or availability for their chicks as well as predator-safe feeding grounds may render them especially vulnerable to even slight habitat changes. As brood losses are very frequent due to the high sensitivity of chicks towards adverse weather, a decrease of breeding habitat quality would highly impact on population dynamics of this species. The maintenance and restoration of high quality breeding habitats seems therefore an important issue for the conservation of Alpine black grouse populations. By modelling ecological niches, we could additionally show that breeding females are especially sensitive towards specific habitat variables and show low tolerance towards deviations from their optimal habitat profiles. Our habitat suitability model identifies rather large regions where optimal breeding habitat conditions still occur.

Finally, we could show in a complementary study (chapter four), that not only the «natural» heterogeneity of the habitat matters but that snow-sports infrastructure itself affects habitat suitability.

CONSERVATION RELEVANCE

The habitat requirements of black grouse populations in Europe have been investigated mostly in the northern and north-western areas of the continent (e.g., Klaus et al., 1990; Swenson & Angelstam, 1993; Baines, 1995b; Pearce-Higgins et al., 2007; Storch, 2007), which has led to effective local habitat management (e.g., Baines, 1995a). Several studies have documented a direct link between habitat alteration and negative demographic trends (e.g., Baines & Hudson, 1995; Baines, 1996; Baines & Summers, 1997; Storch, 2000; Warren & Baines, 2002; Storch & Leidenberger, 2003). Yet, habitat requirements for the Alps had not been the focus of detailed investigations so far, which has led to habitat management recommendations based mostly on expert-knowledge. My research provides decisive insights into fined-grained habitat requirements, i.e. the necessary scientific evidence which, hopefully, will influence habitat management policies. I would recommend focusing on the restoration of optimal habitat for breeding females because black grouse demography depends largely on reproductive output and chick survival. If such measures can be implemented on a large scale, one can expect positive demographic developments. Finally, I recommend combining local management of the breeding habitat with corrective measures as regards winter disturbance (undisturbed winter refuges, chapter 4). Optimally, these two series of measures should overlap spatially to obtain an enhanced positive effect on populations.

Despite of the expansion of human facilities and snow-sports infrastructure as well as changes in human land use practices in the Alps, Alpine ecosystems have still a high biodiversity potential, especially in remote regions. In contrast to most European black grouse populations, Alpine black grouse core populations seem to be rather stable on these days. Protecting and preserving these populations is the responsibility of all Alpine countries. I hope that this work may contribute to better management policies and the preservation of this emblematic species of the Alps.

ADDITIONAL RESEARCH AND OUTLOOK

Based on the present habitat suitability map, dynamic breeding habitat change could be modelled (through e.g. aerial pictures and satellite imagery) so as to evaluate where habitat changes have been more rapid during the last decades in black grouse breeding habitats. This could be used to delineate regions where habitat restoration would be most effectively implemented. In addition, spatially explicit human-wildlife conflict maps could be constructed for the winter situation so as to delineate the most beneficial areas to create winter refuges. An overlay of the summer (this thesis) and winter models would even enable us to locate areas where summer and winter interventions could be implemented in conjunction.

Studies published in peer-reviewed journals are often not accessible to practitioners such as foresters, farmers and game-keepers, as well as to people involved in the tourism industry. To some extent, this may explain why management decisions remain mostly based on expert knowledge. To ensure an efficient knowledge transfer relying on evidence-based approaches, scientists have the task to convey decisive information for promoting efficient management in a way which is readily accessible to practitioners (e.g. oral presentations, brochures and leaflets). There are certainly lots of foresters and farmers who would be keen to manage upper subalpine forests in a way that improves conditions for black grouse and other species benefiting from habitat heterogeneity. In Alpine regions where human presence is high, e.g. close to tourist resorts, there are also lots of locals concerned by nature and wildlife preservation who would be ready to take measures to mitigate disturbance by sport and recreational activities. Some areas have already implemented winter refuges to protect wildlife (e.g. Grisons in the Eastern Swiss Alps), although those were not specifically designed for black grouse preservation. Additionally, the Swiss Alpine Club (SAC) is currently launching a campaign for reducing disturbance of wildlife by snow-sport activities such as ski-touring and snow-shoeing in natural and semi-natural Swiss mountain ecosystems. The future will tell us whether such measures can preserve the sensitive wildlife of our mountains.

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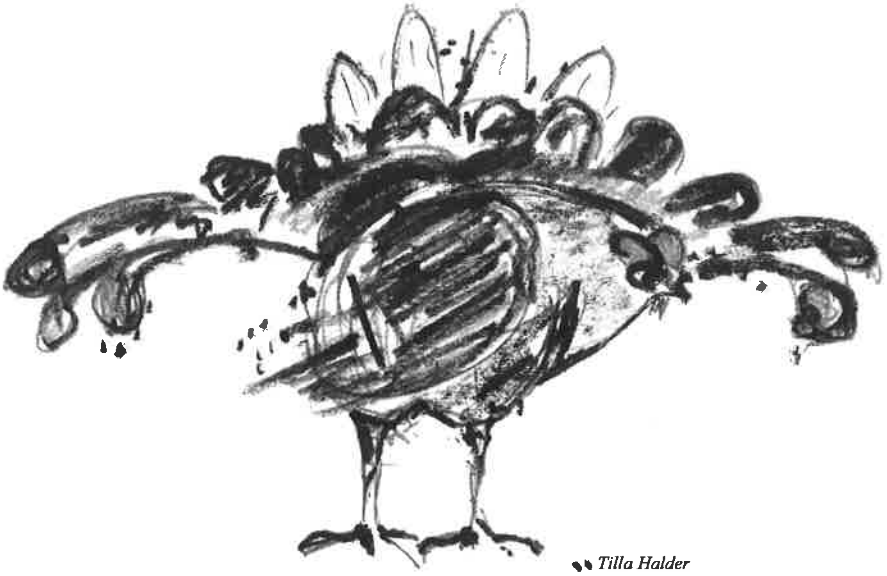

Tilla Halder

CURRICULUM VITAE

PERSONAL DATA

Name	Natalina Signorell
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EDUCATION

1981-1987	Primary school in St. Moritz
1987-1994	Secondary school at the Lyceum Alpinum in Zuoz
June 1994	Diploma, Swiss maturity, Typus B

STUDIES

1994-1995	Study of medicine at the University of Lausanne
1995-1997	Basic course biology I (botany and zoology) at the University of Basel
1997-2001	Main course biology I at the University of Basel
Mai 2000-Mai 2001	Diploma work at the Swiss Ornithological Station Sempach (PD Dr. L. Jenni und Prof. Dr. B. Bruderer) on the growth and development of young barn swallows depending on different factors
Mai 2001	Diploma at the University of Basel

FURTHER TRAININGS

Oct. 1998-June 2000	Course in field ornithology in Chur (Dr. Ch. Meier-Zwicky)
Oct. 2001-Juni 2002	Trip-leader course in ornithology in Zürich (Zürcher Vogelschutz)
Oct. 2001-Okt. 2005	Training at the "Höheres Lehramt" of the University of Zürich
Jan. 2004-May 2008	PhD at the University of Bern, Conservation Biology, (Dr. Prof. Raphaël Arlettaz) on "Habitat management guidelines for the conservation of an emblematic species of Alpine timberline ecosystems, the black grouse: from fine-grained habitat selection to large-scale habitat suitability modelling"

Periods of practical trainings

Summer 1998	Three-month period of practical training at the Swiss National Park
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Jan. 2003-März 2003	Scientific employee at the “Amt für Jagd und Fischerei” of the Canton of Grison
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