Suitable habitat for ptarmigan (*Lagopus muta helvetica*) in the Swiss Alps and its response to rapid climate change in the 21st century – a multiscale approach

Diploma thesis

presented by Rasmus Revermann

Potsdam, December 2006

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Supervisors:

Dr. Boris Schröder,

Potsdam University,

Institute of Geoecology

Dr. Niklaus Zbinden,

Schweizerische Vogelwarte

Sempach

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1. General introduction

1.1 Motivation

Major effort of ecological research during the past decade aims at an estimation of the response of species and ecosystems on potential global change. Since At the latest with the last IPCC synthesis report 2001 (IPCC, 2001) scientific community agrees with an ongoing human induced climate change. The report forecasts a rise of global mean temperature of 1.4 – 5.8°C for the coming century.

High mountains in many parts of the world are susceptible to the impacts of a rapid changing climate (Beniston, 2005). They exhibit a very complex climate system and climatic parameters, in particular temperature and precipitation rates shift rapidly over very short distances. Hence, the patterns of climate change in these regions are expected to differ from the rest of the globe: The climatic warming experienced since the early 1980ies in the Alps is approx. three fold as strong as the global climate signal (Diaz and Bradley, 1997). Therefore, the "tops of the world" are excellent study sites for the early detection of climate change and the investigation of the response of ecosystems and species to the changing environment.

It is generally agreed that species distribution is largely triggered by climatic factors, determined by the species physiological tolerance. Therefore, they are expected to track climate warming by migration towards the poles or to higher elevation (Archaux, 2004). Latitudinal migrations correlated to climate warming have already been detected for bird species (e.g. Thomas and Lennon, 1999) and altitudinal shifts have been observed in a few cases (e.g. Pounds et al., 1999). However, changes in the altitudinal range of birds in the French Alps have been correlated to site specific factors rather than to climate alterations (Archaux, 2004).

With this study, I would like to illustrate the possible response to rising temperatures of a high alpine bird species, the ptarmigan. This bird is perfectly adapted to the environmental conditions prevailing at high elevation and has narrow temperature preferences, making it an ideal study object to investigate potential uphill forcing of its habitat.

1.2 Objectives of the study

The aim of the study is to predict the impact of climate change on ptarmigan in the Swiss Alps. This study comprises two parts: First, the investigation of key factors determining ptarmigan habitat today applying statistical species distribution modelling. Since habitat selection is a multi scale process, analysis is conducted on three different scales. Second, predictions for spatial distribution for climate change scenarios are calculated. The scenarios base on the current state and are developed following an approach similar to bioclimatic envelopes.

The thesis is structured as follows: the first part introduces to the ecology and distribution of the species under study. Furthermore, the data acquisition, especially the data on territory scale, is described in detail. The second part contains the manuscript for a scientific publication. Third, the appendix offers closer insights into conducted analyses and gives additional information on the results.

2 Species under study: Ptarmigan (*Lagopus muta* Montin 1776)

The ptarmigan is with a body mass of 400-600 g one of the smallest grouse (Burkhardt and Schmid, 2001). Within the order of the Galliformes the grouse form a distinct and homogenous group. Therefore some authors (e.g. Potapov and Flint, 1989) consider them as a separate family, the Tetraoninae, whilst others regard them as a subfamily only. The ptarmigan is a typical bird of arctic and alpine regions and hence well adapted to cold climates. The most outstanding feature distinguishing grouse from other galliform birds are feathered feet (tarsi) and toes serving as “snowshoes”. During winter time ptarmigan rests in snow burrows.

Literature cites more than 20 subspecies of ptarmigan, which often evolved due to geographical separation after retreat of inland ice sheets in post glacial periods (Johnsgard, 1983; Potapov and Flint, 1989).

Fig. 1: Ptarmigan: left hand winter plumage, right hand summer plumage (Photos by C. Morerod (left) and R. Revermann (right)

2.1 Population size and distribution

Ptarmigan is widely distributed in the northern hemisphere. From a circumpolar distribution reaching up to 83°N and beyond in northern Greenland to the recently detected southernmost population at 38°N in the Pamir mountains in Tadjikistan ptarmigan inhabits alpine and arctic regions (Fig. 2 and 3, Storch, 2000). The populations in Scotland, the Pyrenees and the Alps are considered as glacial relict populations. In contrast to the population of the Alps, the smaller ptarmigan population of the Pyrenees are genetically impoverished and display great divergence to populations in Norway. Nonetheless a significant isolation-by-distance effect has been detected (Caizergues et al., 2003). Due to potential habitat loss and forcing upwards of ptarmigan caused by climate change, this effect may even increase.

Fig. 2: Worldwide distribution of ptarmigan (taken from (Cramp and Simmons, 1980)

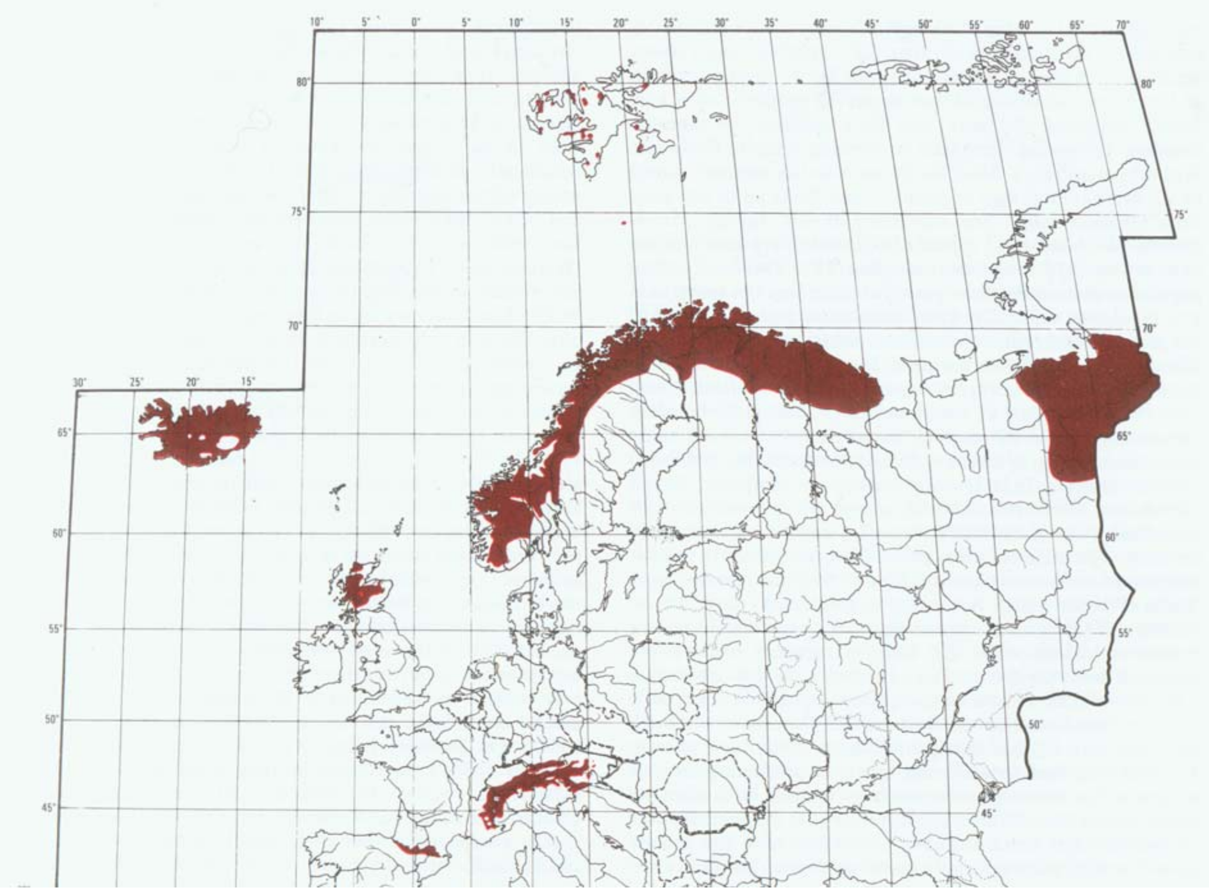


Fig. 3: Ptarmigan distribution throughout Europe (taken from (Cramp and Simmons, 1980)

In central Europe ptarmigan is a sedentary, monogamous breeding bird, though the bird exhibits seasonal up- and downhill migrations (Glutz von Blotzheim et al., 1973). Suitable habitat is patchily distributed and hence population densities are low. At the southern edge of the Alps they reach densities up to 0.35-1.60 pairs/km^2 only (Favaron et al., 2006). In contrast, at the foothills of the Alps in the north of Switzerland (Augustmaterhorn BE) Huber and Ingold (1991) recorded seven territorial cock per km^2 within one year. However, alpine ptarmigan populations exhibit cycling fluctuations of 5-8 year periods (Cattadori et al., 1999; Favaron et al., 2006).

Bossert et al. (1983) designate climatic factors as possible reasons for fluctuations of population size. Furthermore, Bossert (1980) clarifies that mild winters are responsible for declining populations but early snowfall, late snow melt or late frosts can weaken ptarmigan population, as well.

2.2 Habitat and food sources

Typical breeding habitats in central Europe are located between 1,900 and 2,600 m asl. At the southern slope of the Alps they tend to be higher than at the northern slope (Fig. 3, Schmid et al., 1998). Ptarmigan prefers highly structured slopes above timberline. A typical ptarmigan habitat features small scale alterations of wind exposed ridges, snow dells and slopes covered by boulders and debris. It offers look-outs and shelter at the same time.

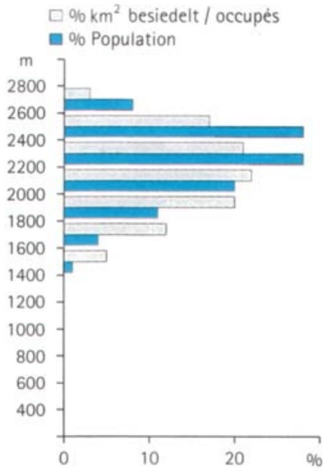


Fig. 4: Altitudinal distribution of ptarmigan in Switzerland (taken from (Schmid et al., 1998)

Ptarmigan is herbivorous, feeding on dwarf shrubs such as heather (*Calluna vulgaris)*, alprose (*Rhododenron* spp.), bilberry (*Vaccinium* spp.), dwarf willows (*Salix* spp.) and in later summer even alpine herbs (Bossert, 1980; Fasel and Zbinden, 1983; Marti and Bossert, 1985). Depending on the season, it feeds on buds, flowers, shoots, leaves or berries. The use of trees as food source (e.g. *Larix decidua* or *Pinus cembra*) has rarely been reported apart from strong winters (Glutz von Blotzheim, et al., 1973).

2.3 Threats and conservation status

In northern latitudes ptarmigan still occupies most of its original distributional range due to its wide distribution in areas with low human population density and inaccessible habitats. In contrast to these regions, the population in central Europe suffers from detrimental effects of human activities. The main threats emanate from alpine tourism, hunting, or habitat destruction (e.g. excessive grazing). Direct disturbance by human presence, loss of habitat due to expansion of ski-resorts and collisions with skiing facilities has been reported (reviewed by Storch, 2000). Future substantial loss of habitat has to be expected due to global warming. As indicated by Bossert et al. (1980; 1983) irregularities in climate related to snow cover and (late) frost, can result in population decrease. Moreover, an upward shifting of vegetation communities will lead to a drastic decrease of the alpine vegetation belt which represents the food source of ptarmigan (Theurillat and Guisan, 2001).

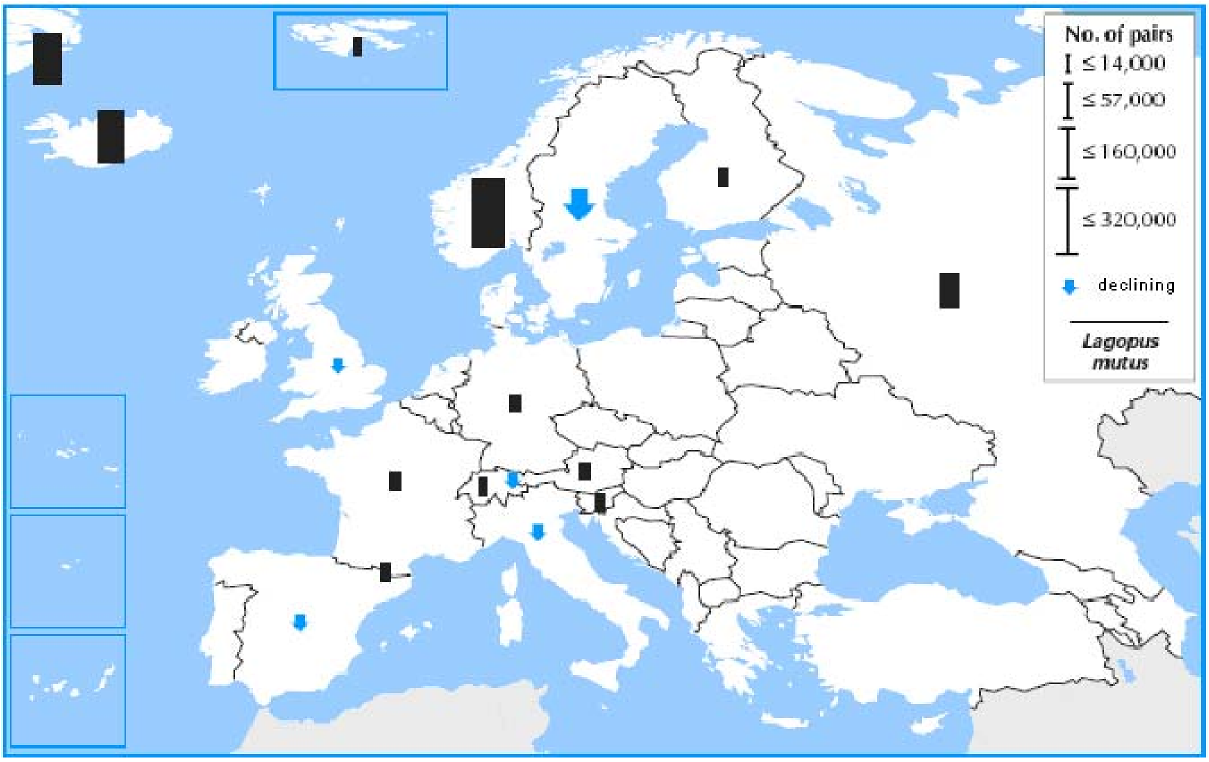


Fig. 5: Population size of ptarmigan and its development in European countries (taken from (Burfield and Bommel, 2004)

World wide ptarmigan population is not estimated to be threatened. IUCN (1996) lists the ptarmigan as at “lower risk” (least concern) and CITES (1998) does not denote it in the Appendices (Storch, 2000). The Swiss population of 12,000 – 15,000 individuals is regarded as not threatened (Schmid et al., 1998). Nevertheless, ptarmigan is registered in some national red data books, e.g. Germany. Ptarmigan is also listed in the Emerald Network (Council of Europe, 2006), the European wide counterpart of NATURA 2000, shaping a paneuropean network of reserves. This elucidates the continental wide importance of the ptarmigan population in the Swiss Alps.

3. Research area and data

3.1 Research area

The study was conducted in Switzerland, a central European country. Geologically the country can be classified into three regions: the Jura, a calcerous mountain range in the Northwest with altitudes of 400-1700 m asl. covering 10% of the surface of the country; the Midlands (30% of the surface), a lowland corridor of 50 – 100 km width stretching between the Jura and the other mountain range, the Alps. The latter are a comparatively young mountain range originated from an unfolding starting in the Tertiary. They are composed of a variety of different rocks and reach altitudes exceeding 4000 m asl. With 60% they cover the main part of Switzerland.

Since ptarmigan occurrence has only been reported for the Alps the study concentrates on this region. However, predictions of potential habitat are made for the whole country. For species data I used presence-absence data rather than abundance data as these are more suitable for species distribution modelling of rare or sparsely distributed species such as the ptarmigan (Cushman and McGarigal, 2004).

3.1.1 Study on macro-scale

The study on macro-scale bases on the Swiss breeding bird Atlas (Schmid et al., 1998). The data were sampled during a large field campaign carried out in the years 1993-1996. This atlas provides countrywide information on the incidence of all breeding birds on a grid with a cell size of 1 km. Together with geodata-bases delivering potential predictor variables, the atlas provides excellent conditions for species distribution modelling (for details on species data and environmental variables please refer to the appendix).

3.1.2 Study on territory scale

To study ptarmigan's habitat requirements on territory scale, I selected nine sites with known ptarmigan occurrence (Fig. 6). These sites reflect the characteristic types of ptarmigan habitats in Switzerland, ranging from the northern distributional range at the foothills of the Alps over the central Alps to the southern edge of the distribution in the canton Ticino.

At these sites, I mapped ptarmigan's incidence during breeding season from May to July 2005. Ptarmigan can most easily be observed in the early morning when cocks get active at about one hour before sunrise. Activity ends at about eight o'clock.

Fig. 6: Location of the study sites on territory scale and altitudinal range of Switzerland

The cocks can be easily located by their call whereas it is difficult to detect them at daytime due to their good camouflage. Furthermore, the findings of fresh faeces, egg shells or footprints in the snow served as indicator for the presence of ptarmigan (Fig. 7).

Fig. 7: evidence for the incidence of ptarmigan: footprints, egg shell, faeces and direct sighting

As additional information for ptarmigan's incidence, especially as support for the verification of absence areas, I used data collected in former surveys made by collaborators of the Swiss Ornithological Institute or in the context of the annual monitoring programme of frequent Swiss breeding birds (by Swiss Ornithological Institute Sempach, MhB). The archive of these surveys offers detailed maps showing where the bird has been observed in subsequent years. At some smaller sites (Jatzhorn, Schinberg, Piz Darlux, Glänlischopf and Hörnli) the delineation of occupied and not occupied areas was carried out solely on the basis of MhB data. As precondition for the election of the sites ptarmigan had to be observed at the same locations in subsequent years.

In the following, I give a rough description of the studied sites in respect to their environmental conditions and the suitability for ptarmigan:

Study site Aletsch

The study area resides at a ridge stretching from SW to NE along the lower part of the glacier "Großer Aletsch". The ptarmigan population at the Aletsch is probably the best studied in the alpine region; here, Bossert and Marti (cf Bossert, 1980; Marti and Bossert, 1985) conducted detailed studies about ptarmigan's ecology and behaviour and from that time on there are yearly records of ptarmigan population.

The area is characterized by dense ericaceous dwarf shrubs and *Salix helvetica* with scattered *Pinus cembra* trees growing at the lower altitude areas. With increasing altitude *Salix herbacea* and short Ericaceae dominate the flora.

The whole area is strongly influenced by tourist activities: several ski runs, ski lifts and teleferics traverse the south-east facing slopes and many highly frequented hiking trails cross the area. However, within this region the highest density of ptarmigan in Switzerland has been recorded (Schmid et al., 1998).

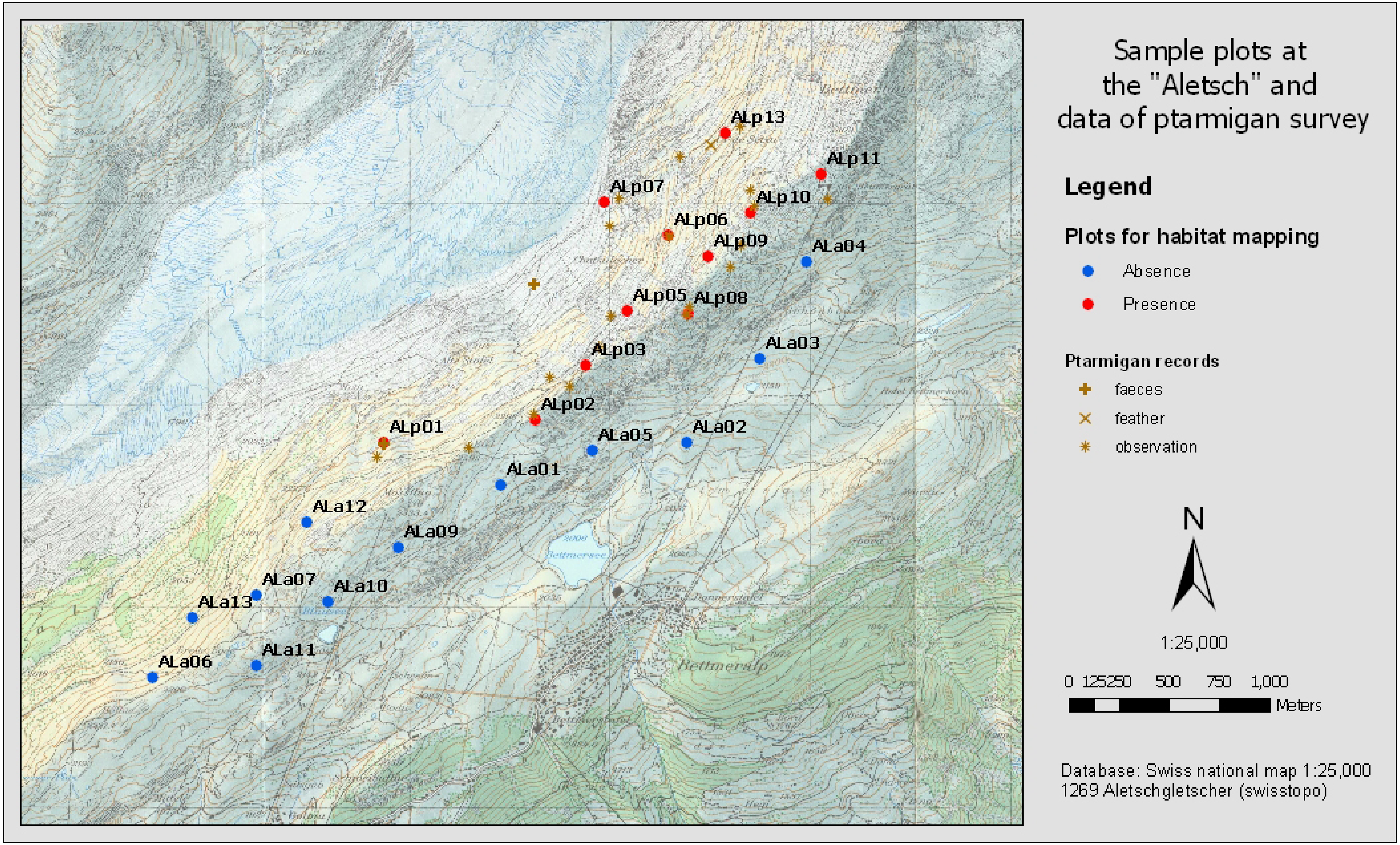


Fig. 8: Map of the study site "Aletsch". The map shows the sample plots and the results from the ptarmigan survey which served as basis for the delineation of presence and absence areas; data of former surveys that contributed to that process are not shown.

Basòdino

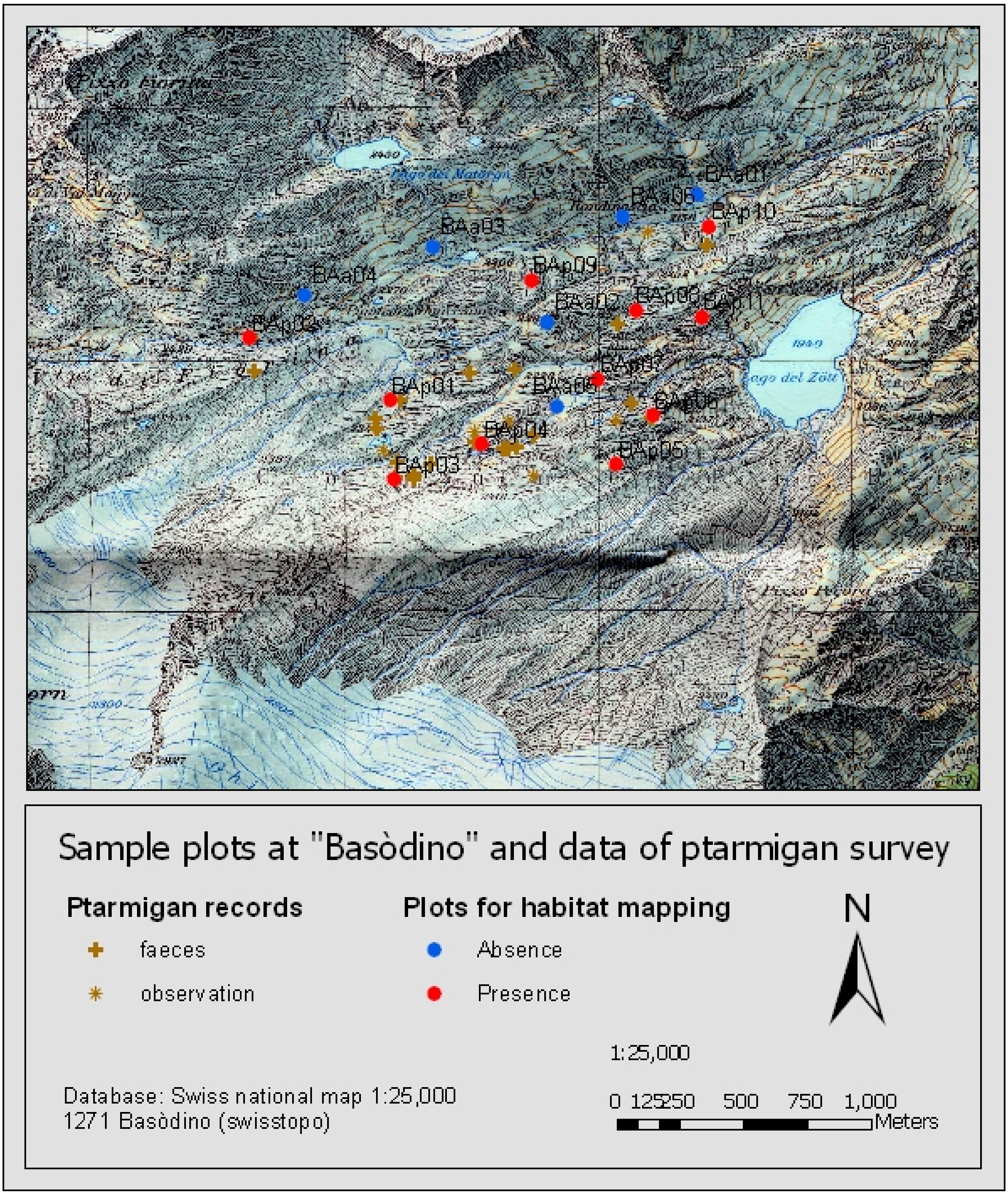


Fig. 9: Map of the study site "Basòdino"

The map shows the sample plots and the results from the ptarmigan survey which served as basis for the delineation of presence and absence area; data of former surveys that contributed to that process are not shown.

This study site is situated below the Basòdino glacier at an elevated plain shaped by glacier activities in the last centuries. The glacier itself is of small size and retreating 50 m year^{-1} (oral correspondence with locals). However, in comparison to the other sites in this study, snow cover lasts longer. Moreover, the ptarmigan habitats at Basódino distribute over an elevated plain below the glacier instead of a concentration of habitats to the surroundings of the ridge.

Pizzo Erra/Biasca

Pizzo Erra is the mountain peak of the SE-NW orientated ridge following the Tecino valley. The natural appearance of the Western side of the mountain top of Pizzo Erra is strongly altered by constructions for avalanche protections; the eastern part still has its natural physiognomy.

Ptarmigan habitats concentrate on the northeast facing slopes and the ridge. The absence area is characterized by brushes of *Alnus viridis* at the eastern slope. On the other side of the ridge, sheep pasture and the timberline composed of *Larix deciduda* and *Picea abies* delimit the suitable habitat.

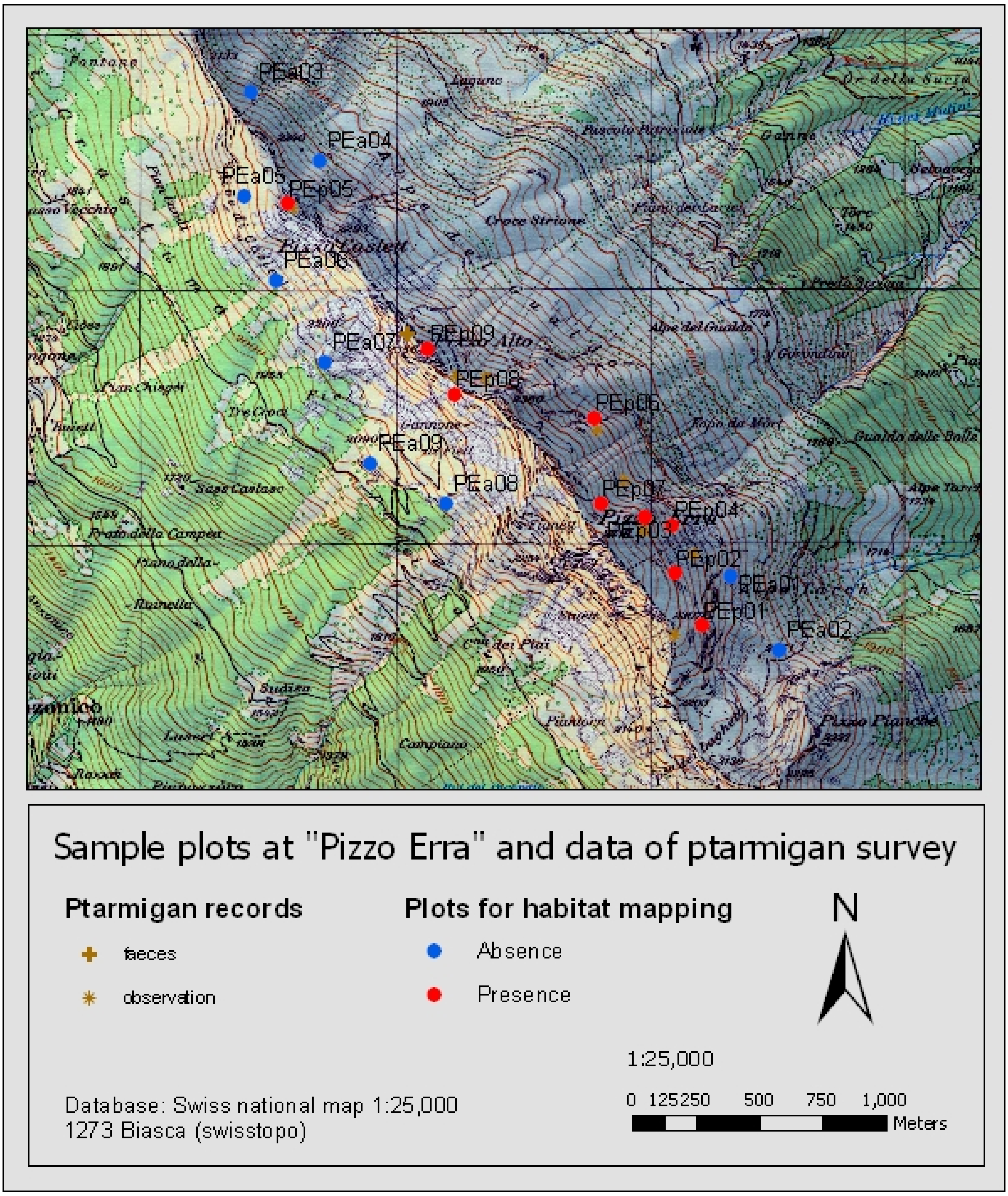


Fig. 10: Map of the study site "Pizzo Erra"

The map shows the sample plots and the results from the ptarmigan survey which served as basis for the delineation of presence and absence areas; data of former surveys that contributed to that process are not presented.

Gaggio/Belinzona

The Gaggio represents a low situated habitat at the southernmost edge of the ptarmigan distribution in Switzerland. Suitable habitat distributes closely along the ridge; especially the steep and rough north facing slopes are inhabited by ptarmigan. The south facing slope is intensively grazed by sheep during breeding season; ptarmigan frequents these parts during cold winters only (Fasel and Zbinden, 1983) (see the appendix for a map).

Jatzhorn/Davos

Even though Jatzhorn is imbedded in the vast skiing areas surrounding the city of Davos, the study site is not directly influenced by skiing activities and can only be reached on a hiking trail. Steep slopes with crystalline rocks and spare vegetation cover characterize the area occupied by ptarmigan. The lower situated parts of the slope, covered by shrub vegetation (especially *Rhododendron ferrugineum* and *Vaccinium myrtillus*), do not serve as ptarmigan habitat. (see the appendix for a map)

Piz Darlux/Albulapass

The mountains surrounding Piz Darlux are developed as a small skiing resort. Hence, Alp pastures dominate the landscape. However, off the beaten track ptarmigan occurs on a north-west facing slope partly covered by small boulders. (for the map see the appendix)

Hörnli/Arosa

This is another area strongly influenced by skiing and hiking tourism. Habitats concentrate on ridges where human activities are limited and ericaceous shrubs are frequent. The areas which are not occupied by ptarmigan are among others the ski runs, composed of extensive grassland with small patches of Ericaceae (see the appendix for a map).

Schinberg/Beckenried

Together with Glänlichopf/Buchs this site differs from the ones listed above: they feature calcareous bedrock, typical for the northern slopes of the Alps. Consequently, the food plant *Rhododendron ferrugineum* is substituted by *Rhododendron hirsutum*. The site is hardly influenced by skiing tourism but by grazing cattle (see the appendix for a map).

Glänlichopf/Buchs

This is the most northern site within this study and situated at the foothills of the Alps. With altitudes of around 200 m asl Glänlichopf is comparatively low and represents the northern edge of ptarmigan distribution in Switzerland. Due to the calcareous bedrock vegetation composition differs from most of the remaining sites. Yet, Alp pastures and dwarf shrubs characterize the landscape (see the appendix for a map).

4. Paper

Suitable habitat for ptarmigan (*Lagopus muta helvetica*) in the Swiss Alps and its response to rapid climate change in the 21st century – a multiscale approach

Submitted as:

Rasmus Revermann[1], Hans Schmid[2], Reto Spaar[2], Niklaus Zbinden[2], Christian Marti[2], Boris Schröder[1]. Suitable habitat for ptarmigan (*Lagopus muta helvetica*) in the Swiss Alps and its response to rapid climate change in the 21st century – a multiscale approach

[1]Institute of Geoecology, University of Potsdam, D-14415 Potsdam, Germany;
[2]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

4.1 Abstract

This paper presents a multiscale modelling approach to predict the current and future spatial distribution of ptarmigan (*Lagopus muta*), a high alpine grouse species.

Since there is no single appropriate scale for analysing ecological patterns, the study aims to quantify the scale-dependent determining factors of ptarmigan's breeding habitat. Hence, I perform species distribution modelling on various scales: i.e. on territory level and on countrywide macro-scales with resolutions of 1 km^2 and 100 km^2, respectively. Data on species incidence and potential predictor variables rely on the Swiss Breeding Bird Atlas and are derived from various geo-data bases for macro-scale. Territory scale data were obtained during a field campaign in breeding season.

The results show the scale dependency of the explanatory power of predictors: On the one hand at territory scale, variables depicting topography and structure of the habitat have great predictive power. On the other hand at macro-scale these variables play a minor role and predictors concerning vegetation types and bioclimate determine ptarmigan habitat instead. However, comparing the two macro-scales I found that with increasing grain size bioclimatic predictors gain importance. Furthermore, I developed scenarios for the response of ptarmigan population in Switzerland on climate change. The results show that a species, which is actually not threatened, may run into the severe risk of suffering from decreasing potential habitat. Climate change scenarios show an upward shift of suitable habitat driven by bioclimatic factors alone. In the most pessimistic scenario for the year 2070 this upward shift exceeds 300 m, accompanied by a decrease in area by approximately 50%.

Keywords: ptarmigan, *Lagopus muta helvetica*, species distribution modelling, generalized linear model, glm, Swiss Alps, climate change, multiscale

4.2 Introduction

Alpine regions are susceptible to the impacts of rapid climate change since environmental conditions change extremely within very short horizontal and vertical distances. The species representing the ecosystems of these high mountain regions are highly adapted to this environment and often limited by climatic factors. Therefore, the world's high ranging mountains are ideal study sites to analyse the consequences of a changing climate (Beniston, 2003).

The scientific community has agreed that there is no doubt about human induced climate change (IPCC, 2001) and species are already responding to this phenomenon (Hughes, 2000; Parmesan and Yohe, 2003). Generally speaking, there are two ways of response: adaptation or distributional shift (Huntley et al., 2006). Mobile species such as birds are amongst the first expected to react, and migration is one of their major adaptive responses: Thomas & Lennon (1999) detected a northward shift of British breeding birds by 18.9 km within a 20-year period; Huntley et al. (2006) predicted a shift of potential geographical distribution of birds up to 1,000 km within the 21st century.

Here I present a study about the ptarmigan (*Lagopus muta helvetica*), a species which might already be affected by small climate changes (cf Bossert, 1980; Bossert, Marti and Niederhauser, 1983). The ptarmigan is an arctic bird species which is also abundant in isolated glacial relict populations in a few European mountain ranges such as the Alps. In central Europe it occurs in regions above the timberline reaching up to the glaciers. The species is highly adapted to the harsh conditions prevailing at these elevated sites. In Switzerland, the breeding territories are distributed at altitudes ranging from 1,900 to 2,600 m asl (Schmid et al., 1998). As all grouse, the ptarmigan is herbivorous, only the chicks partly prey on insects. It prefers diversely structured slopes covered by dwarf shrubs and boulders offering good look-outs and hideaways (Glutz von Blotzheim, et al., 1973). High quality habitats are patchily distributed and home ranges therefore tend to be large (Favaron et al., 2006).

Today, there is a stable population of ca. 12,000 to 15,000 individuals in the Swiss Alps which is considered to be not threatened but may become so in the next decades because of decreasing suitable habitat (Schmid et al., 1998). With this work, I elucidate the actual habitat requirements of the ptarmigan and its possible response to rising temperatures due to climate change.

The objectives of my study are:

(i) Detecting the key factors determining the ptarmigan's distribution,
(ii) Predicting suitable habitat in Switzerland at current conditions,
(iii) Developing scenarios for the potential future distribution of ptarmigan, and
(iv) Supporting the ongoing discussion about the effects of global change by providing relevant distributional data about a species of public interest.

In order to find answers for these questions, I applied statistical species distribution modelling (SDM) using a glm-approach. In recent years, this kind of model has become common to successfully address conservation issues (Pearce and Ferrier, 2001), to estimate biodiversity (MacNally et al., 2003) and to predict distributional changes on the basis of environmental modifications (Guisan et al., 2006; Rudner et al., 2007).

As starting point for my research, I use the "Atlas on Swiss breeding birds" (Schmid et al., 1998). This atlas provides a good overview of the species distributional range and population size. SDMs aid to deepen insights by extrapolating the distributional patterns for the entire extent of the study area and not for the observation sites only. Beyond that, they provide a probabilistic output and hence highlight areas which are especially suitable. Moreover, SDMs go beyond pure distributional analyses offering insights into causal relationships of species occurrence and their environment – or at least provide testable hypotheses. Therefore, they represent a powerful tool for conservation issues especially in respect to the expected need of dynamic strategies on the grounds of rapid changes due to global change.

The importance of the observed spatial scale has been pointed out in several studies since habitat selection is a multi-scaled process (Brambilla et al., 2006; Oppel et al., 2004). The spatial scale on which response and explanatory variables are sampled strongly influences the discovered relationships (cf Cushman and McGarigal, 2004; Mackey and Lindenmayer, 2001). Therefore, single habitat variables may vary in their predictive power on different scales as shown, for instance by Thompson and McGarigal (2002) and Graf et al. (2005), for birds with large home ranges. To detect spatially dependent differences in the response of ptarmigan, I performed SDMs on various spatial scales corresponding to ecological levels: On territory scale and on two regional scales (with a resolution of 1 km^2 and 100 km^2) covering entire Switzerland.

Concerning the temporal scale, we have to assume an equilibrium situation of species distribution throughout years (Austin, 2002; Guisan and Zimmermann, 2000). Although ptarmigan is a resident bird, it exhibits up- and downhill migrations in summer and winter time respectively. The breeding season is the only time in the year when ptarmigan sticks to a territory. Therefore all data on incidence were collected during this time and hence all models and results given here refer to the breeding habitat. Despite the assumption of a static population at current conditions, SDMs are able to predict the impacts of a changing environment on potential habitat. In order to determine the response of ptarmigan to rapid climate change I apply an approach similar to bioclimatic envelope models (BEMs, Pearson and Dawson, 2003; Thuiller, 2003, 2004). Adopting the results of a recent study about regional climate change in Switzerland (Frei, 2004) I calculated scenarios for the years 2030, 2050 and 2070. These scenarios show the future distribution of potential ptarmigan habitat and illustrate its forcing uphill.

4.3 Methods

4.3.1 Research area and data

During a two month period of field work, I obtained data on territory scale in the breeding season 2005 on nine selected sites. These sites are distributed over the Swiss Alps covering the core distribution range of ptarmigan in the central Alps and reaching to the edge of the distributional range at the southern slope of the Alps.

At each spot I mapped areas which were occupied and non-occupied by ptarmigan. An occupied territory was identified by recognition of calling cocks in the early morning, sightings at daylight or by indirect evidence such as fresh findings of feathers, faeces or footprints. Accordingly, an area was declared as unoccupied if none of the signs mentioned were recorded within two days of observation. After mapping the bird’s incidence, I randomly selected sample plots sized 25 x 25 m^2 within occupied and non-occupied areas to survey environmental variables. To avoid pseudoreplication, I set a minimum distance of 300 m in between of each plot, which corresponds to the distance between centres of two territories of 12 ha according to Bossert (1995). For each plot I mapped explanatory variables representing the presumed autecological requirements of ptarmigan such as food availability, heath, topographic situation and habitat structure (see App. 1 for predictor variables on territory scale).

For the two macro-scale analyses, I used data from the Swiss breeding bird atlas (Schmid et al., 1998) collected in the years 1993-1996 and mapped with a grid size of 1 km^2. Additionally, I used data observed during the Monitoring programme of frequent Swiss Breeding Birds carried out annually by the Swiss Ornithological Institute as well as individual observations gathered by the same institution. Since there are no ptarmigan records reported from the Jura and the lowland, I did not incorporate absence data from these regions for modelling. In this way, I focused the analysis on recent potential habitat and achieved a more balanced prevalence, which is advantageous for modelling (McPherson et al., 2004).

The surveys for the breeding bird atlas were carried out up to altitudes of 2,500 m asl., thus there are no absence data available above that altitude. In order to improve the model's validity with respect to altitude, I generated pseudo-absence data by random-based selection (cf Engler et al., 2004). In order to decrease the probability that a presence plot was picked erroneously, I set a minimal altitude of 3,000 m asl. for selection since successful breeding has only been reported below this altitude (Schmid et al., 1998). In total I chose 63 pseudo-absence plots representing 5% of the total absences.

I selected potential predictors based on literature (e.g. Glutz von Blotzheim, Bauer and Bezzel, 1973) and expert knowledge. Information on these predictors were gathered from various geodatabases with the same resolution as the response variable (1 km^2): Bioclimatic data from BIOCLIM (Swiss Federal Research Institute WSL), land use and vegetation data from GEOSTAT (Swiss Federal Statistical Office) and data on vegetation geography from the "Atlas on Vegetation Types" (Hegg et al., 1993). Furthermore, I added data describing the topographic situation and its variability by carrying out a digital terrain analysis (Wilson and Gallant, 2000). For modelling at the resolution of 100 km^2 I used the same database. All variables were aggregated using ESRI ArcGis™ 9.0 (Spatial Analyst Toolbox).

4.3.2 Statistical analysis

I applied a generalized linear model approach (glm) using a logistic regression model as this model type suits a binary response (presence or absence of ptarmigan) very well (Hosmer and Lemeshow, 2000). A glm furthermore allows the use of different scaled variables in the same theoretical frame (Yee and Mitchell, 1991).

I started by screening the potential explanatory variables in preliminary analyses of univariate models according to Hosmer & Lemeshow (2000). To consider hump-shaped response curves, I additionally included all squared terms. I selected only those predictors that yielded AUC-values exceeding 0.7 for the macro-scale and 0.6 for the territory scale. The AUC (area under the receiver operating characteristic (ROC) curve) is a threshold-independent measure of the discriminatory power of the model (Fielding and Bell, 1997; Zweig and Campbell, 1993). AUC-values range from 0.5 (same predictive power as the null-model) to 1 (denoting perfect discrimination Fielding and Bell, 1997).

To check for multicollinearity between these predictors, I used a two-sided Spearman rank-correlation-test (r_s) setting a threshold of $|r_s| > 0.7$ for two correlated variables (Fielding and Haworth, 1995).

As a decision criterion for omitting one of the two correlated variables, I applied hierarchical partitioning (Chevan and Sutherland, 1991; Heikkinen et al., 2005; Mac Nally, 2002). This method allows to estimate the amount of explained variance each predictor contributes alone (independent effect) and conjoint with others (joint effect). I also used hierarchical partitioning as a tool to determine the effect each variable contributes to the final models.

The remaining set of predictors was subjected to a stepwise backward variable selection in order to find the most parsimonious model with the best predictive power. I compared the final models evolving from selection with AIC (Akaike Information Criterion, (Akaike, 1974) and BIC (Bayes Information Criterion, (Schwarz, 1978). BIC is a more conservative selection criterion, while, in contrast, applying AIC delivers more complex models (Reineking and Schröder, 2006). After variable selection, all two-way interactions between the selected variables were added that significantly improved the model (checked by a χ^2-test) (Hosmer and Lemeshow, 2000).

4.3.3 Model checking: evaluation and validation

A common problem working with spatial data in statistical modelling approaches is spatial autocorrelation. This violates the model assumption of independency of the observations and may result in a misleading interpretation of ecological relationships (e.g. Lichstein et al., 2002). Therefore, I checked the final models for residual spatial autocorrelation by calculating Moran's *I* (Moran, 1950) and visualizing the effective distance by correlograms.

To assess the performance of the final models, I calculated AUC for discrimination and R^2_N for calibration and refinement (Harrell, 2001; Nagelkerke, 1991). Additionally, I computed Cohen's kappa (Cohen, 1960) and the slope of the calibration curve (Reineking and Schröder, 2006). According to Hosmer & Lemeshow (2000), an AUC-value exceeding 0.9 reflects an outstanding discrimination. Monserud & Leemans (1992) proposed a similar evaluation criterion for kappa, assigning models with $\kappa > 0.85$ the predicate excellent. Backhaus et al. (2000) refer to an R^2_N of 0.4 already as a good fit. To check for model optimism arising from model assessment on training data, I used bootstrapping as a method for internal validation (for applications in species distribution models see Reineking and Schröder, 2003; Verbyla and Litvaitis, 1989)).

4.3.4 Extrapolation in space and time

I provide predictions for the potential ptarmigan habitat in Switzerland on the basis of the macro-scale models. For each grid cell, I predict the probability of occurrence. To derive binary predictions I apply the cut-off probability (P_{crit}): $P_{crit} = P_{kappa}$, referring to the cut-off probability where kappa is maximized (Schröder, 2006).

To investigate the effect of climate change on ptarmigan habitat in Switzerland, I adopted the change of climatic predictors calculated in a probabilistic study carried out by Frei (2004). Frei derived predictions for Switzerland from Global Circulation Models (GCMs) and Regional Climate Models (RCMs). Table 1 shows the presumed temperature rise for the years 2030, 2050 and 2070. For each year three scenarios are calculated: a median scenario representing the best estimation of the temperature rise and a minimum and a maximum scenario representing the lower and the upper limit of a 95% confidence interval.

Table 1: Presumed temperature changes due to climate warming in [°C] forecasted by (Frei, 2004). Minimum and maximum represent the lower and upper level of a 95% confidence interval.

Scenario	Minimum	Median	Maximum
2030	0.6	1.45	2.6
2050	1.4	2.75	4.9
2070	1.9	3.9	7.1

All statistical computing was performed with the statistical package “R 2.2.0” (R Development Core Team, 2006) and the libraries “Hmisc” and “Design” for logistic regression models (Harrell, 2001), “hier.part” for hierarchical partitioning (Mac Nally and Walsh, 2004), “spdep” (Bivand, 2002) and “ncf” (Bjørnstad and Falck, 2001) for spatial autocorrelation analysis. For plotting ROC-plots I used the software “ROC plotting and AUC Calculation”(Schröder, 2006). To facilitate model interpretation through visualization of response surfaces, I used the software “lr-mesh” (Rudner, 2004).

4.4 Results

4.4.1 Territory scale

The final model for territory scale resulting from variable selection with AIC contains six predictors plus one quadratic term (Tab. 2). Out of the six predictors, three describe the vegetation composition and cover, two are related to topography, and one depicts the abiotic habitat structure. The predictor 'vegetation-free area' shows a hump-shaped response.

Table 2: Explanatory variables of the final model on territory scale. The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance. β = slope, S.E. = standard error (β), p = p-value, independent (I) and total (T) effect [%], derived by hierarchical partitioning. Evaluation criteria: AUC=0.968, R^2_N=0.802, Kappa=0.855. (n=83, prevalence=0.49)

Model for ptarmigan on territory scale (based on AIC selection)					
Predictors	β	S.E.	p	I-effect	T-effect
Intercept	-10.636	2.886	<0.001	-	-
vegetation-free area	23.339	9.107	0.010	22.1	27.6
Vegetation-free area (^2)	-21.332	10.844	0.049	-	-
Variability of topography	0.748	0.487	0.124	20.1	23.1
Vertical structure elements	0.674	0.408	0.099	14.3	19.1
Vaccinium uliginosum spp. incidence	4.353	1.482	0.003	19.6	12.8
Aspect (cosine transformed)	2.394	0.901	0.008	16.9	10.2
Juniperus communis spp. cover	-9.242	5.874	0.116	7.0	7.2

The comparative model resulting from using BIC consists of a subset of the AIC model containing only four predictors but neither describes habitat structure nor discriminates between preferred or avoided vegetation. Furthermore, it exhibits worse performance criteria and shows greater optimism (App. 18).

4.4.2 Macro-scale

Since the available sample size was manifold bigger on macro-scale, I applied BIC for variable selection. AIC yielded very complex models containing many two-way interactions impeding a reasonable ecological interpretation. Moreover, internal validation reveals greater overfitting of the AIC-based models.

Tab. 3: Explanatory variables of the final model on macro-scale (resolution 1 km^2)

The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance. β = slope, S.E. = standard error (β), p = p-value, independent (I) and total (T) effect [%], derived by hierarchical partitioning. Evaluation criteria: AUC=0.954, R^2_N=0.746, Kappa=0.0.761. (n=2099, prevalence=0.37)

Model for ptarmigan on macro-scale at 1 km^2 resolution (based on BIC selection)					
1-km^2 macro-scale model	β	S. E.	p	I effect [%]	T effect [%]
Intercept	-9.117	1.024	<0.001		
Mean July temperature [°C]	2.196	0.232	<0.001	17.3	20.1
Mean July temperature ^2	-0.101	0.012	<0.001	-	-
Low, loose vegetation [%]	-0.086	0.015	<0.001	20.4	19.5
Wood [%]	-0.057	0.006	<0.001	22.2	19.2
Agriculture [%]	0.02	0.007	0.006	16.3	15.6
Snow bed vegetation [%]	1.73	0.543	0.001	11	11.1
Snow bed vegetation ^2	-0.065	0.021	0.003	-	-
Profile curvature	-21.566	2.939	<0.001	8.6	8.4
Alp pasture [%]	0.047	0.014	<0.001	4.1	6.1
Alp pasture * July temp.	-0.008	0.001	<0.001	-	-
Snow bed veg. * July temp.	-0.009	0.004	0.02	-	-

At the resolution of 1 km^2, 12 predictors remain in the final model including three quadratic terms and one two-way interaction (Tab. 3). The majority of predictors describe vegetation and land use, whereas only one is a topographic parameter (profile curvature) indicating the preference for mountain tops and ridges. Fig. 11 displays the response curve regarding 'Alp pasture' and 'July temperature'. It reflects the unimodal response of 'July temperature' and the interaction between both predictors becomes apparent: At lower altitudes an increasing coverage with alp pasture reduces the probability of ptarmigan occurrence.

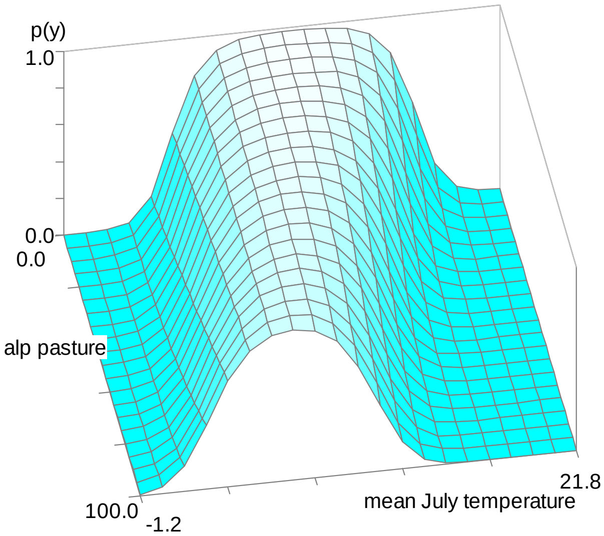


Fig. 11: Three dimensional response surface of the two predictors 'alp pasture' and 'mean July temperature' (including quadratic and interaction term). The remaining predictors had the following values (representing a habitat with intermediate suitability): low, loose vegetation: 5% cover, wood: 10% cover, agriculture: 0% cover, snow bed vegetation: 0.5 % cover and profile curvature: -0.04

At the resolution of 100 km^2 (Tab. 4) the predictor set of the final model partly differs from the one at finer grain size: Bioclimatic predictors gain increased importance. Thus 'annual precipitation rate' and 'July water budget' additionally entered the final model. Nevertheless, predictors related to land cover still are of main importance, especially the variables representing food availability, e.g. snow bed vegetation or low, loose vegetation. Topographic variables do not play any role at this coarse resolution.

Tab. 4: Explanatory variables composing the final model on macro-scale (resolution 100 km^2)
The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance. β=slope, S.E.=standard error, p= p-value, independent (I) and total (T) effect [%], derived by hierarchical partitioning. Evaluation criteria: AUC=0.967, R^2_N=0.960, Kappa=0.961. (n=465, prevalence=0.52)

Model for ptarmigan on macro-scale at 100 km² resolution (based on BIC selection)					
Predictor	*β*	S.E.	p	T [%]	I [%]
Intercept	21.986	6.988	0.002	-	-
Mean July temperature [°C]	-2.059	0.461	<0.001	27	32.4
Snow bed vegetation [%]	0.366	0.112	0.001	22.2	22.2
Low, loose vegetation [%]	0.796	0.206	<0.001	13.8	12
Low, loose vegetation ^2	-0.008	0.002	0.001	-	-
Open rock crevice vegetation [%]	0.334	0.144	0.021	9.9	7.1
Open rock crevice vegetation ^2	-0.004	0.002	0.019	-	-
Conifer forest [%]	-0.036	0.020	0.079	9.2	9
Dwarf shrub heath [%]	0.356	0.090	<0.001	8.9	8.3
Precipitation year [mm]	-0.014	0.004	<0.001	4.7	3.8
Water budget July [mm]	0.104	0.024	<0.001	4.3	5.1
Snow bed vegetation * water budget July	-0.003	0.001	0.007	-	-

4.4.3 Model evaluation and validation

All models show excellent performance regarding all criteria (Table 5). The internal model validation via bootstrap exhibits a slight optimism respective to R^2_N on territory scale; on macro-scale the effect can be neglected. The slope of the calibration curve reveals slight overconfidence on territory scale and of the model at the 100 km^2 resolution.

Table 5: Results of model evaluation and validation on territory and on macro-scale

Indices are given before (index original) and after internal validation via bootstrapping with 2000 replicates (index corrected). Model optimism is defined as the difference between the performance on training and test data, hence the corrected index=original index - optimism.

Scale	Criterion	Original index	Optimism	Corrected index
Territory	AUC	0.968	0.000	0.968
	R^2_N	0.802	0.067	0.735
	slope	1.000	0.222	0.788
Macro-scale 1 km^2	AUC	0.954	0.000	0.954
	R^2_N	0.746	0.007	0.739
	slope	1.000	0.026	0.974
Macro-scale 100 km^2	AUC	0.997	0.000	0.997
	R^2_N	0.96	0.017	0.943
	slope	1.000	0.189	0.811

4.4.4 Residual spatial autocorrelation

At the 1 km^2 scale, there is a significant degree of positive spatial autocorrelation in the raw data but only marginal autocorrelation in the final model. This can be reduced to a non significant level if an autologistic model is estimated by adding an autocovariate (Fig. 12). However, performance criteria (AUC, R^2_N) do not show any improvement compared to the non spatial model (see App 21). At the resolution of 100 km^2, I detected no severe spatial autocorrelation in the residuals.

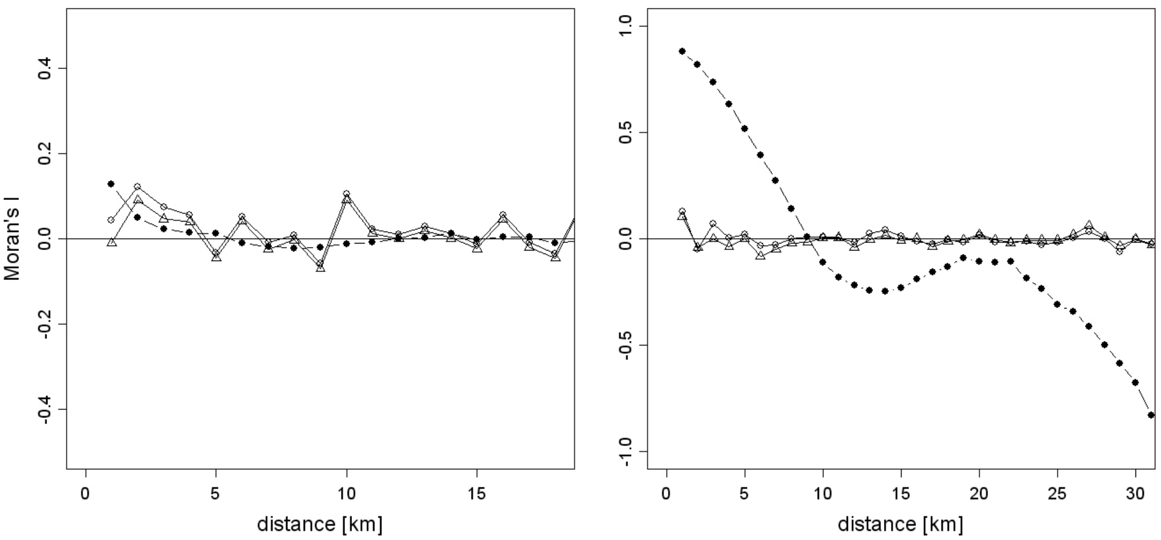


Fig. 12: Correlogram for residual spatial autocorrelation on macro-scale (A: at the resolution of 1 km², B: at the resolution of 100 km²) for raw data (filled points), the non-spatial model (circles) and the spatial autologistic model (triangles). Moran's I-values are given for different lag distances. Expected value in absence of autocorrelation (straight line) in (A) -0.0005 and in (B) –0.0022; note the different scales in Fig. A and B.

Global Moran's *I*: A: raw data: 0.13 ($p < 0.01$), non-spatial model: 0.01 ($p = 0.02$), residuals spatial model: 0.00 ($p = 0.23$); B: raw data: 0.31 ($p < 0.01$), residuals non-spatial model: 0.00 ($p = 0.13$), residuals spatial model: 0.01 ($p = 0.81$).

4.4.5 Climate change scenarios

The mean July temperature was the only climatic predictor remaining in the final model at the fine resolution (1 km²). At the coarser resolution (100 km²), 'annual precipitation rate' and 'water budget July' were additionally included in the final model but have comparatively little influence (see hierarchical partitioning, Tab. 4). Figure 13 and 14 show the prediction for the current state and future development of suitable habitat for ptarmigan in Switzerland; a summary in numbers is given in Tab. 6. The area [km²] with a probability of occurrence (P) exceeding $P_{crit} = P_{kappa}$ declines from 9,441 for the prediction at recent conditions by one fourth in the maximum scenario 2050. Presuming the maximum scenario for 2070, I expect a decrease by almost the half of suitable habitat.

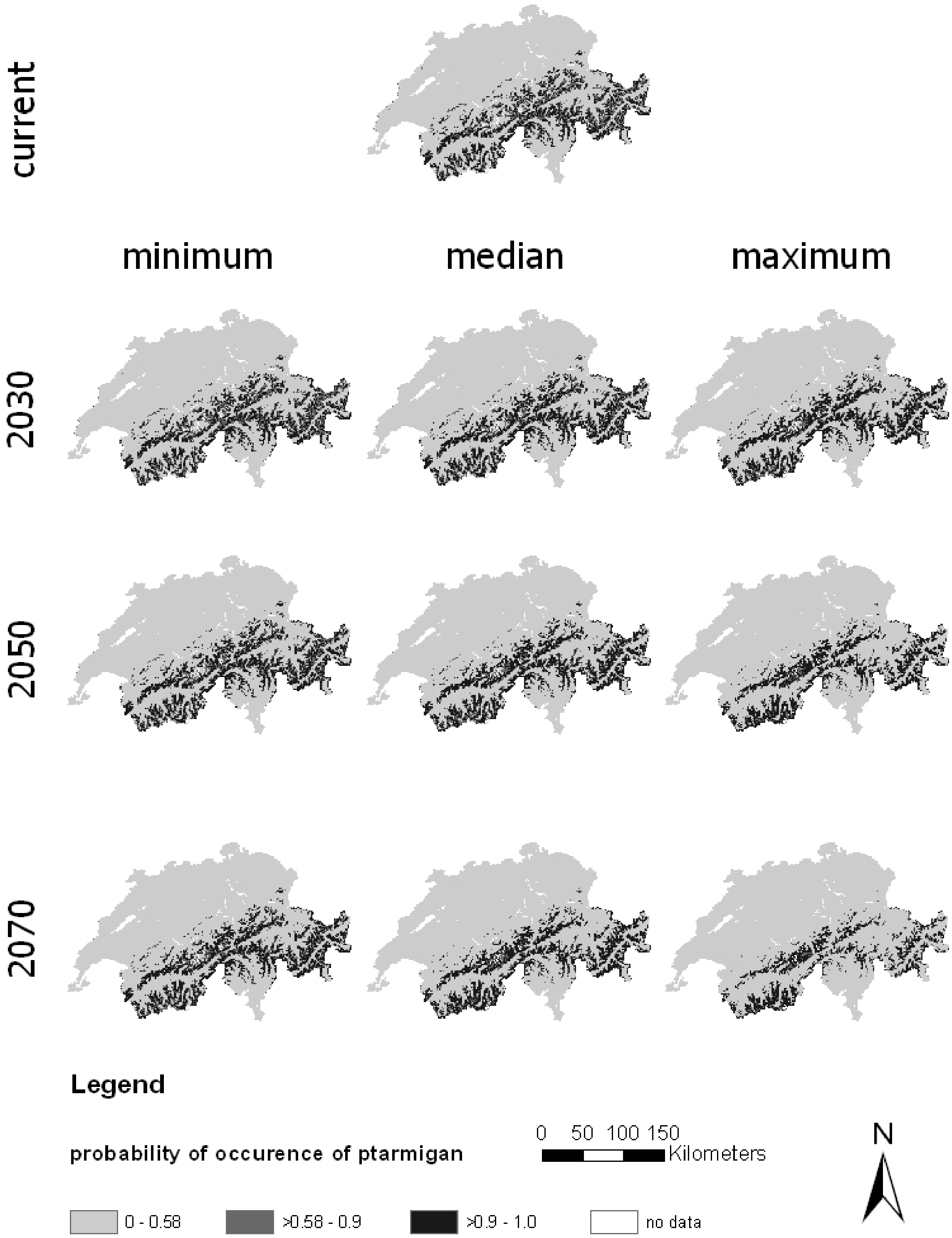


Fig. 13: Map of the potential ptarmigan habitat in Switzerland at current stage and at scenarios for climate change according to Table 1. Grid cells (grain size 1 km^2) with $P > P_{kappa} = 0.580$ are assumed as suitable; cells with values of $P>0.9$ are considered as extremely suitable.

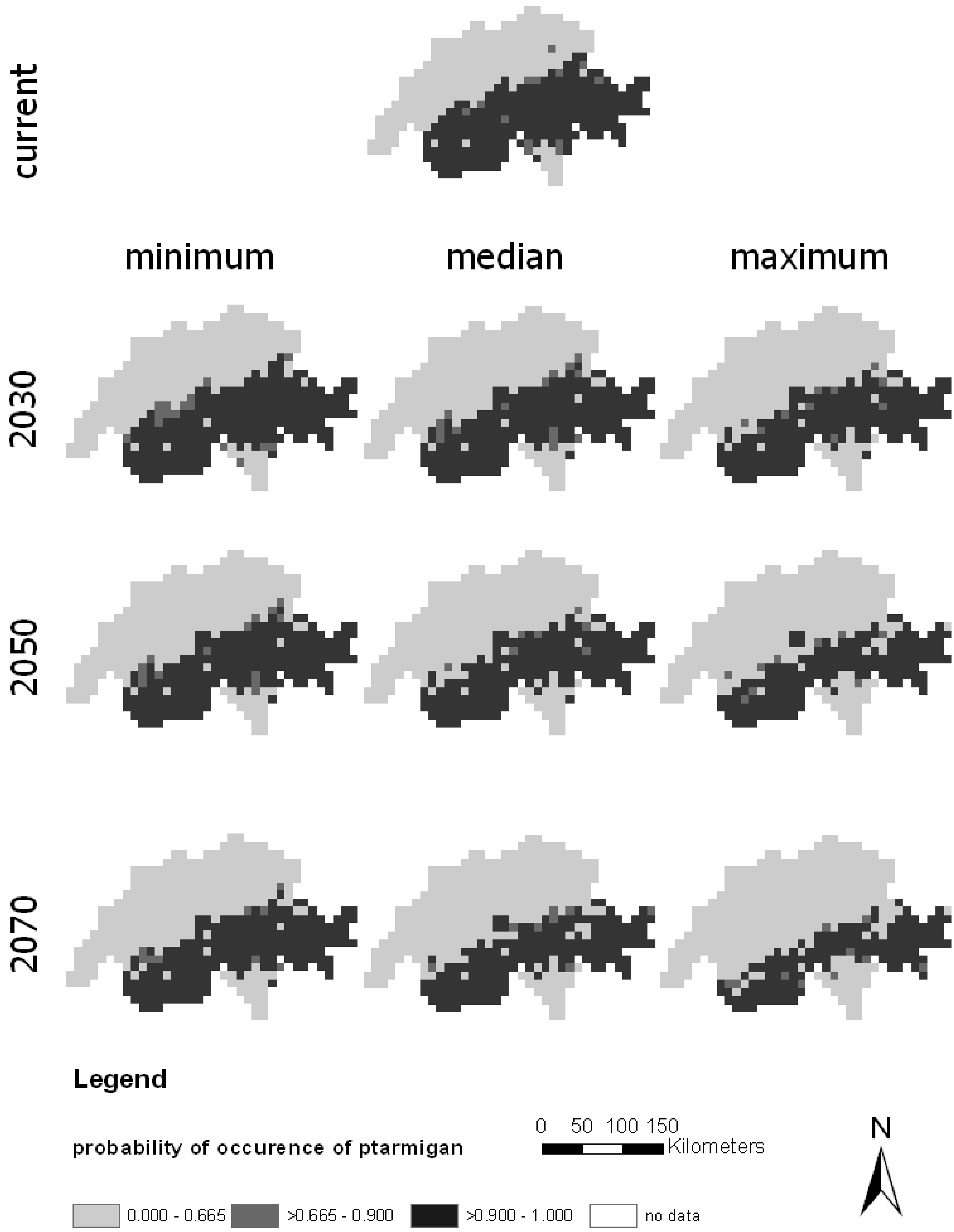


Fig. 14: Map of the potential ptarmigan habitat in Switzerland at current stage and at scenarios for climate change according to Table 1. Grid cells (grain size 100 km^2) with $P > P_{kappa} = 0.665$ are assumed as suitable; cells with values of $P > 0.9$ are considered as extremely suitable.

Tab. 6: The influence of rising mean July temperature on potential habitat of ptarmigan for minimal, median and maximal scenarios for the years 2030, 2050 and 2070. Habitat is estimated as suitable if $P_{(ptarmigan)} > P_{kappa}$.

scenario/		current		2030			2050			2070	
resolution			min	median	max	min	median	max	min	median	max
	Δ July temp. °C	0	0.61	1.45	2.6	1.4	2.75	4.9	1.9	3.9	7.1
1 km^2	Σ P(ptarmigan)	9806	9718	9469	8888	9489	8797	7251	9270	8014	5438
	Pot. habitat [km^2]	9441	9427	9219	8708	9229	8605	7105	9048	7875	5408
	Decrease [%]	-	0.1	2.4	7.8	2.2	8.9	24.7	4.2	16.6	42.7
	Med. of altitudinal distr. [m]	2102	+30	+70	+122	+68	+128	+225	+90	+177	+325
100 km^2	Σ P(ptarmigan)	242	231.9	216	196.5	216.9	194.5	168.2	207.7	180.2	142.3
	Pot. habitat [km^2]	23800	22700	20900	19200	20900	18900	16300	20100	17500	14000
	Decrease [%]	-	4.6	12.2	19.3	12.2	20.6	31.5	15.5	15.5	41.2
	Med. of altitudinal distr. [m]	1373.5	+28	+86	+140	+86	+160	+256	+105	+220	+307

The rise in mean July temperature does not only affect the extent of potential habitat but as well the altitudinal range of dispersal. I assume an upward shift of 325 m calculated for the 1 km^2 resolution and 307 m for the 100 km^2 resolution from current situation to the maximum scenario by the year 2070. This upward shift is more or less constant, with a median shift of 46.9 m/°C at the 1 km^2 and 55.0 m/°C at the 100 km^2 resolution respectively (Tab. 6).

4.5 Discussion

4.5.1 Suitable habitat

On territory scale, ptarmigan habitat can be described as sites with intermediate cover of vegetation. Densely vegetated plots, especially with high vegetation, as well as vegetation-free areas represent suboptimal habitats (Tab. 2). North-facing slopes are preferred reflecting the strong climatic limitation of ptarmigan: The species tolerates summer temperatures up to 16°C only. This also explains the preference of habitats with a large variation in relief since the birds can adapt to short-term weather fluctuations by taking advantage of differences in site-specific climate (variability of topography contributes 23% to total explained variance, Tab. 2). Furthermore, the vertical structure, which had an independent effect of 15% plays an important role. These abiotic structure elements serve as lookouts or hideaways.

Obviously, vegetation cover and vegetation types are elementary for herbivorous species like the ptarmigan. Surprisingly, a few of the most important food plants e.g. alprose (*Rhododendron spp.*) and blueberry (V*accinium myrtillus*) (Fasel and Zbinden, 1983; Glutz von Blotzheim, Bauer and Bezzel, 1973; Marti and Bossert, 1985) do not serve as suitable predictors whereas the presence of bog blueberry (*V. uliginosum*) remains an explanatory variable in the final model. This can be explained by the fact that *Rhododendron spp.* and *V. myrtillus* frequently have been observed on grazed alp pastures and on south-facing slopes, i.e. on comparatively warm locations and thus unsuitable habitat.

For *Juniperus communis spp.*, a negative coefficient was estimated. This plant has not been identified as a food source although it sometimes occurs in ptarmigan habitat (Fasel and Zbinden, 1983; Marti and Bossert, 1985). In general, *Juniperus* is bound to warmer locations such as exposed sites receiving higher insolation and thus serves as a predictor for unsuitable habitat.

The determinants on large-scale depict vegetation types and land use; altogether they account for 72% of the total effect in the final model at the finer and for 64% at the coarser resolution (Tab. 3 and 4). However, the most important predictor is 'mean July temperature'. The temperature reflects the altitudinal range in which ptarmigan finds suitable conditions. At higher latitudes, e.g. Scandinavia, these conditions spread over vast areas where ptarmigan is widely distributed. In the Alps, the necessary requirements concentrate to regions in altitudes between 1,900 and 2,600 m asl. (Schmid et al., 1998).

Besides temperature, there are other variables which implicitly reflect specific altitudinal ranges, e.g. certain vegetation types such as snow bed vegetation (positively correlated with ptarmigan occurrence) or forests (negative correlation).

The variables `low and loose vegetation´ and `snow bed vegetation´, at 100 km^2 resolution as well as ericaceous dwarf shrubs represent food availability for ptarmigan in the final model. These variables include important food plants, i.e. ericaceous dwarf shrubs and *Salix* species (cf. Fasel and Zbinden, 1983; Marti and Bossert, 1985). The species avoids vegetation exceeding dwarf shrubs in height which is shown in univariate analysis on territory scale (App. 1). The timberline therefore represents the absolute lower limit for ptarmigan distribution.

Concerning land use, the models show that cultivated land is unsurprisingly not suitable for ptarmigan. Alp pastures are the only form of human land use in the range where ptarmigan occurs. The univariate analysis on macro-scale shows a positive correlation with the probability of the occurrence of ptarmigan whereas findings on territory scale indicate a negative correlation (grazing and extended herbal layer both show negative coefficients, cf. App. 1). The interaction term 'Alp pastures' * `mean July temperature´ elucidates this contradiction: High altitude Alp pastures indicate suitable habitat, whereas low altitude Alp pastures have contrary consequences (Fig. 11). Nevertheless, I am convinced that Alp pastures themselves do not represent potential habitat for ptarmigan, rather their neighbourhood indicates suitable habitat patches within the atlas square.

4.5.2 Scale dependency

According to my previous assumptions, the results show that there are different habitat variables governing habitat suitability for ptarmigan on different spatial scales. That means that the predictive power of predictors varies with scale (Graf et al., 2005).

Despite the fact that I were not able to work with exactly the same pool of available predictor variables, I found evidence for great discrepancy between territory scale and the two macro-scales whereas the models at large scale are quite similar. Topographic predictors (besides altitude and closely correlated variables e.g. slope or curvature) describe processes effective only at small scales, e.g. shelter on the basis of topographic variability or landscape structure elements. But with increasing scale, their predictive ability diminishes until they loose their predictive power at the largest scale. Downscaling, therefore, would require consideration of information about topography and vertical structure of habitat patches.

It has often been stated that the major drivers of species distribution are climatic factors and that land cover plays a minor role (cf Thuiller et al., 2004). The reason is that land cover can widely be explained through climate. This is true for continental-wide scales and indeed the results clearly show that bioclimatic predictors gain predictive power on the coarser resolution. Herein, my results coincide with the findings of Luoto et al. (2006) asserting that bioclimatic predictors are large-scale determinants, amended by land cover variables at finer resolutions.

Grain size seems not to be of any bigger influence regarding the response to global change. Though the predicted potential habitat area diverges drastically between the scales: The model for the coarse resolution estimates an area of more than the double size of the one at the finer resolution (Tab. 6).

4.5.3 Predictive performance of the models

Recent reviews of procedures applied for validating species distribution models (Fielding, 2002; Guisan and Thuiller, 2005; Pearce and Ferrier, 2000) emphasize that model validation is indispensable and recommend multiple assessments of different measures of model performance. Furthermore, McPherson et. al. (2004) pointed out, that the use of threshold independent measures, e.g. AUC, should be preferred as they are not sensitive to prevalence (unlike e.g. Cohen's Kappa). The models proof excellent performance in all applied measures (AUC, R^2_N, Kappa) applying them on training and test data (Tab. 6).

A standard check for spatial autocorrelation (Moran's I) reveals little positive autocorrelation in the residuals (Fig. 2). Since the autologistic model shows equal model performance but exhibits slightly higher overfitting (see App. 3) I used the non-spatial model for further investigation.

4.5.4 Climate change

The pros and cons of bioclimatic envelope models (BEM) used for prediction of future species distributions are recently discussed (Davis et al., 1998; Hampe, 2004; Pearson and Dawson, 2003). Common arguments put forward against BEMs are the missing incorporation of biological interactions and dispersal limitations. However, I follow the argumentation outlined by Pearson (2004) stating that in spite of lacking dynamics, BEMs can contribute a lot to the understanding of species response to climate change. They represent the only tools available because the understanding of the underlying mechanistic processes is still quite insufficient. Moreover, the amount of required data would be enormous and hence process-based model approaches are not applicable. Nevertheless, we have to be aware of the shortcomings and possibilities of such envelope models while interpreting the results.

Our model does not solely rely on bioclimatic predictors but includes variables covering many aspects of the abiotic niche. For climate change modelling, I assume a status quo for these predictors and do not account for additional anthropogenic induced alterations in, for instance, land use. Furthermore, the calculation lacks any considerations of changes in vegetation composition which probably will occur. But the results of recent research dealing with the future dispersal and shifting of vegetation belts in alpine regions diverge (for a review see Theurillat and Guisan, 2001). According to this study (2001), profound changes may be expected from plus 3°C and beyond. Although a complete shift of vegetation belts is unlikely, the alpine belt - i.e. the core area of ptarmigan - would suffer the strongest effects. For a "plus 3.3°C scenario", Theurillat & Guisan (2001) forecast a reduction by 63% in area of the alpine layer. One has to add the fact that physiogeographic factors may differ seriously in upslope areas. This would especially harm vegetation communities which depend on areas without strong inclination such as snow bed vegetation (Theurillat and Guisan, 2001) - a main food resource of ptarmigan during breeding season.

Although some studies deal with responses of food plants used by ptarmigan to climate change, the results remain unclear. For example, V*accinium myrtillus* and *Rhododendron ferrugineum* could undergo severe injury on the grounds of late frosts after early snowmelt induced by warmer climate (Neuner et al., 1999; Ögren, 1996), but the opposite is shown in Tolvanen (1997), as well.

Conferring to the model, ptarmigan shows a strong negative correlation with forested areas. Consequently, an upward shift of the timberline would cause shrinkage of potential habitat. Observations from a mountain ridge close to the Aletsch glacier (Bossert, 1995/ my data from territory scale analysis) indicate that even small trees colonizing unforested area (in that case *Pinus cembra*) impede colonization by ptarmigan.

Altogether, there are many uncertainties about how environmental conditions in the alpine region will change. Nevertheless, we can assume a significant rise in temperature, globally (IPCC, 2001) and locally in Switzerland (Frei, 2004; Frei et al., 2006). My study indicates that climate, especially summer temperature, is a main driving factor for ptarmigan distribution in Switzerland. The scenarios show that already small changes of temperature during the breeding season will force the species upwards. I can conclude that there are reserves of suitable habitat in high mountain regions offering adequate conditions in terms of vegetation and topography. Nevertheless, habitat is shrinking, though the calculated upward shift, with a median of 46.9 m/°C, is much lower than one would expect presuming a purely temperature driven distribution, namely a shift of ca. 160 m/°C (Hughes, 2000). Anyhow, in case of a temperature rise exceeding 4°C (maximum scenario 2050, median and maximum scenario 2070), I predict a strong decline in suitable habitat.

Since I presume static conditions for habitat-determining factors besides climate I have to expect a more severe development. Moreover, I do not regard effects of transient dynamics or habitat isolation and loss of connectivity due to forcing the species to mountain tops far apart from each other. I therefore point out that the scenarios present a conservative approach representing the lower limit of decrease in potential habitat for ptarmigan I expect in future.

4.6 Conclusion

I present a model frame for predicting suitable habitat for ptarmigan in alpine regions on local territory scale and on regional macro-scale at two different resolutions. This approach outlines the scale-dependent habitat requirements of ptarmigan. My work can be a helpful tool for conservation purpose as conservationists have to adapt their strategies to a dynamic environment. Furthermore I show that the predicted changes in climate will have a severe effect on ptarmigan distribution: I forecast a distributional shift induced already by changes below the internationally agreed target of 2°C to which global warming should be restricted (IPCC, 2001). If temperature rise exceeds 4°C ptarmigan population will probably decrease drastically. These are effects provoked by climate change alone; there may be other effects, e.g. genetic isolation due to loss of habitat connectivity, changing biotic interactions, shifting vegetation composition and transient dynamics, contributing to or worsening this development. It will be a promising approach for further research to link these processes to species distribution models.

5. Zusammenfassung

Ziel der vorliegenden Arbeit ist die Bestimmung der Habitatpräferenzen des Alpenschneehuhns (*Lagopus muta helvetica*) in den Schweizer Alpen. Darüber hinaus sollen Vorhersagen für die räumliche Verbreitung des potenziellen Habitats sowie für dessen Veränderung aufgrund des Klimawandels getroffen werden.

Das Alpenschneehuhn ist eine hoch alpine Vogelart, die optimal an das Leben in kalten Klimaten angepasst ist. Mit 12 000 – 15 000 Individuen gilt das Schneehuhn in der Schweiz bislang als nicht gefährdet. Aufgrund des Klimawandels könnte das Schneehuhn jedoch durch starken Rückgang geeigneter Habitate massiv im Bestand gefährdet werden.

Um die entscheidenen Faktoren zu bestimmen, die die aktuelle Verbreitung des Alpenschneehuhns steuern, finden statistische Habitatmodelle Anwendung. Über die kausalen Zusammenhänge der Verbreitung hinaus sind Habitatmodelle in der Lage, die räumliche Verbreitung der Arten für nicht untersuchte Gebiete oder unter veränderten Umweltbedingungen vorherzusagen. Dazu werden Daten über biotische und abiotische Umweltfaktoren und Angaben bezüglich des Vorkommens und Nichtorkommens der Art benötigt.

Da die bei der Habitatselektion wirksamen Faktoren stark skalenabhängig sind, basiert diese Studie auf einem mehrskaligen Ansatz. Auf drei verschiedenen Skalen wird der Zusammenhang zwischen Schneehuhnvorkommen und umgebender Umwelt untersucht: auf der Ebene von Brutzeit-Revieren (10 - 12 ha) und auf zwei Atlasebenen, die die gesamte Schweiz abdecken (mit Auflösungen von 1 km^2 bzw. 100 km^2). Als Datengrundlage für die Revierskala dienen Daten, die während einer Habitatkartierungen in der Brutsaison 2005 gesammelt wurden. Auf der Atlas Ebene steht mit dem Schweizer Brutvogelatlas aus den Jahren 1993-

1996 und mit Information über mögliche Prädiktoren aus diversen Geodatenbanken (Vegetation, Landnutzung, topographische Situation und Bioklima) eine exzellente Datengrundlage zur Verfügung. Um Vorhersagen über die Auswirkungen des Klimawandels auf den Lebensraum des Alpenschneehuhns treffen zu können, werden Szenarien für die Jahre 2030, 2050 und 2070 erstellt, basierend auf Ergebnissen einer probabilistischen Klimaprojektion für die Schweiz.

Die Ergebnisse zeigen, dass auf Revierebene vor allem topographische Faktoren wichtig sind, während auf der Makro-Skala neben der Vegetation vor allem bioklimatische Faktoren (insbes. die mittlere Juli Temperatur) eine große Rolle bei der Habitatselektion spielen. Die Bedeutung bioklimatischer Faktoren nimmt mit abnehmender Auflösung zu.

Die Szenarien für den Klimawandel zeigen eine Abnahme des potenziell geeigneten Habitats mit steigender Juli Temperatur. Im pessimistischsten Szenario für das Jahr 2070 nimmt dies fast um die Hälfte ab. Dies liegt vor allem daran, dass sich das potenzielle Habitat des Alpenschneehuhns aufgrund des engen klimatischen Toleranzbereiches der Art in höhere Lagen verschiebt. In diesem Szenario liegt das potenzielle Verbreitungsgebiet um mehr als 300 m höher als heute. Im Median verschiebt es sich um 46,9 m (+/- 1,3 m) pro 1°C Erwärmung der mittleren Juli Temperatur. Es bleibt zu betonten, dass es sich bei diesen Szenarien um konservative Ansätze handelt, denn in die Betrachtung fliessen lediglich veränderte bioklimatische Faktoren ein. Andere Faktoren wie etwa veränderte Vegetationszusammensetzung oder sich wandelnde biotische Interaktionen sind nicht berücksichtigt und können den Effekt noch zusätzlich verstärken.

6. References

Akaike, H. 1974. A new look at statistical model identification. - *IEEE Trans. Autom. Control* 19: 716-22.

Archaux, F. 2004. Breeding upwards when climate is becoming warmer: no bird response in French Alps. - *Ibis* 146: 138-44.

Austin, M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. - *Ecol. Model.* 157: 101-18.

Backhaus, K., et al. (2000) *Multivariate Analysemethoden - Eine anwendungsorientierte Einführung*, 9., überarb. & erw. Aufl. edn. Springer, Berlin.

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. - *Clim. Change* 59: 5–31.

Beniston, M. 2005. Mountain climates and climatic change: an overview of processes focusing on the European Alps. - *Pure Appl. Geophys.* 162: 1587-606.

Bivand, R. 2002. Spatial econometrics functions in R: Classes and methods. - *J. Geograph. Syst.* 4: 405-21.

Bjørnstad, O.N. and Falck, W. 2001. Nonparametric spatial covariance functions: Estimation and testing. - *Environ. Ecol. Stat.* 8: 53-70.

Bossert, A. 1980. Winterökologie des Alpenschneehuhns (*Lagopus mutus* Montin) im Alteschgebiet, Schweizer Alpen. - *Ornith. Beob.* 77: 121-66.

Bossert, A. 1995. Bestandsentwicklung und Habitatnutzung des Alpenschneehuhns L*agopus mutus* im Aletschgebiet (Schweizer Alpen). - *Ornith. Beob.* 92: 307-14.

Bossert, A., et al. 1983. Zur Bestandsentwicklung des Alpenschneehuhns (*Lagopus mutus* Montin) im Aletschgebiet (Zentralalpen) von 1973-1983. - *Bulletin Murithienne* 101: 39-49.

Brambilla, M., et al. 2006. Factors affecting breeding habitat selection in a cliff-nesting peregrine *Falco peregrinus* population. - *J. Ornithol.* 147: 428-35.

Burfield, I. and Bommel, F.v. (2004) *Birds in Europe. Population estimates, trends and conservation status.* BirdLife International, Cambridge.

Burkhardt, M. and Schmid, H. (2001) *Vögel in der Schweiz* Schweizerische Vogelwarte, Sempach.

Caizergues, A., et al. 2003. Population genetic structure of rock ptarmigan Lagopus mutus in Northern and Western Europe. - *Mol. Ecol.* 12: 2267-74.

Cattadori, I.M., et al. 1999. Synchrony, scale and temporal dynamics of rock partridge (*Alectoris graeca saxatilis*) populations in the Dolomites. - *J. Anim. Ecol.* 68: 540-49.

Chevan, A. and Sutherland, M. 1991. Hierarchical partitioning. - *Am. Statist.* 45: 90-96.

Cohen, J. 1960. A coefficient of agreement for nominal scales. - *Educt. Psych. Measure.* 20: 37-46.

Council of Europe. (2006, last access: 17.11.2006, 11:26). Emerald Network. In. http://www.coe.int/t/e/cultural_co%2Doperation/environment/nature_and_biological_diversity/ecological_networks/the_emerald_network/02General_information.asp#TopOfPage.

Cramp, S. and Simmons, K.E. (1980) *Handbook of the Birds of Europe, the Middle East and North Africa - The birds of the Western Palearctic,* Oxford.

Cushman, S.A. and McGarigal, K. 2004. Patterns in the species-environment relationship depend on both scale and choice of response variables. - *Oikos* 105: 117-24.

Davis, A.J., et al. 1998. Making mistakes when predicting shifts in species range in response to global warming. - *Nature* 391: 783-86.

Diaz, H.F. and Bradley, R.S. 1997. Temperature variations during the last century at high elevation sites. - *Clim. Change* 36: 253-79.

Engler, R., et al. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. - *J. Appl. Ecol.* 41: 263-74.

Fasel, M. and Zbinden, N. 1983. Kausalanalyse zum Verlauf der südlichen Arealgrenze des Alpenschneehuhns *Lagopus mutus* im Tessin. - *Ornith. Beob.* 80: 231-46.

Favaron, M., et al. 2006. Spacing behaviour and habitat use of rock ptarmigan (*Lagopus mutus*) at low density in the Italian Alps. - *J. Ornithol.* 147: 618-28.

Fielding, A.H. (2002). What are the appropriate characteristics of an accuracy measure? In *Predicting Species Occurrences: Issues of Accuracy and Scale*, p 271–80. Island Press, Covelo, CA.

Fielding, A.H. and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence-absence models. - *Environ. Conserv.* 24: 38-49.

Fielding, A.H. and Haworth, P.F. 1995. Testing the generality of bird-habitat models. - *Conserv. Biol.* 9: 1466-81.

Frei, C. (2004). Die Klimazukunft der Schweiz - Eine probabilistische Projektion. In *Die Schweiz im Jahre 2050 (Entwurf).*

Frei, C., et al. 2006. Future change of precipitation extremes in Europe: an intercomparison of scenarios from regional climate models. - J. *Geophys. Res.* 111: D06105.

Glutz von Blotzheim, U.N., et al. (1973). Handbuch der Vögel Mitteleuropas. In, Vol. 5. Galliformes und Gruiformes, p 699. Akad. Verlagsgesellschaft, Frankfurt a. M.

Graf, R.F., et al. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. - *Landscape Ecol.* 20: 703-17.

Guisan, A., et al. 2006. Making better biogeographical predictions of species' distributions. - *J. Appl. Ecol.* 43: 386-92.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. - *Ecol. Letters* 8: 993-1009.

Guisan, A. and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. - *Ecol. Model.* 135: 147-86.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. - *Global Ecol. Biogeog.* 13: 469-71.

Harrell, F.E., Jr. (2001) *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis* Springer, New York.

Hegg, O., et al. (1993) *Atlas schutzwürdiger Vegetationstypen der Schweiz* Bundesamt für Umwelt, Wald und Landschaft, Bern.

Heikkinen, R.K., et al. 2005. New insights into butterfly-environment relationships using partitioning methods. - *Proceedings of the Royal Society B.* doi:10.1098/rspb.2005.3212.

Hosmer, D.W. and Lemeshow, S. (2000) *Applied logistic regression*, 2nd edn. Wiley, New York.

Huber, B. and Ingold, P. 1991. Bestand und Verteilung der Territroien des Alpenschneehuhns Lagopus mutus am Augustmaterhorn BE. - *Ornith. Beob.* 88: 1-7.

Hughes, L. 2000. Biological consequences of global warming: is the signal already. - *Trends Ecol. Evol.* 15: 56-61.

Huntley, B., et al. 2006. Potenital impacts of climatic change upon geographical distributions of birds. - *Ibis* 148: 8-28.

IPCC. 2001. Climate Change 2001: Synthesis Report. - *Cambridge University Press*.

Johnsgard, P.A. (1983) *The grouse of the world* University of Nebraska Press, Lincoln.

Lichstein, J., W., et al. 2002. Spatial autocorrelation and autoregressive models in ecology. - *Ecol. Monogr.* 72: 445-63.

Luoto, M., et al. 2006. The role of land cover in bicoclimatic models depends on spatial resolution. - *Global Ecol. Biogeogr.* 16: 34-42

Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. - *Biodiversity Conserv.* 11: 1397–401.

Mac Nally, R. and Walsh, C.J. 2004. Hierarchical partitioning public-domain software. - *Biodiversity Conserv.* 13: 659-60.

Mackey, B.G. and Lindenmayer, D.B. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. - *J. Biogeog.* 28: 1147-66.

MacNally, R., et al. 2003. Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America. - *Biol. Conserv.* 110: 21-31.

Marti, C. and Bossert, A. 1985. Beobachtungen zur Sommerkativität und Brutbiologie des Alpenschneehuhns *Lagopus mutus* im Alteschgebiet (Wallis). - *Ornith. Beob.* 82: 153-68.

McPherson, J., et al. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? - *J. Appl. Ecol.* 41: 811-23.

Monserud, R.A. and Leemans, R. 1992. Comparing global vegetation maps with Kappa statistic. - *Ecol. Model.* 62: 275-93.

Moran, P.A.P. 1950. Notes on continuous stochastic phenomena. - *Biometrika* 37: 17-23.

Nagelkerke, N.J.D. 1991. A note on general definition of the coefficient of determination. - *Biometrika* 78: 691-92.

Neuner, G., et al. 1999. Readiness to Frost Harden druing the Dehardening Period Measured In Situ in Leaves of *Rhododendron ferrugineum* L. at the Timberline. - *Flora* 194: 289-96.

Ögren, E. 1996. Premature dehardening in *Vaccinium myrtillus* during a mild winter: A cause for winter dieback? - *Funct. Ecol.* 10: 724-32.

Oppel, S., et al. 2004. Habitat selection by the Pale-headed brush-finch, *Atlapetes pallidiceps*, in southern Ecuador: implications for conservation. - *Biol. Conserv.* 118: 33-40.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. - *Nature* 421: 37-42.

Pearce, J. and Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. - *Ecol. Model.* 133: 225–45.

Pearce, J. and Ferrier, S. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. - *Biol. Conserv.* 98: 33-43.

Pearson, R.G. and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? - *Global Eco. Biogeogr.* 12: 361-72.

Pearson, R.G. and Dawson, T.P. 2004. Bioclimate envelope models: what they detect and what they hide - response to Hampe (2004). - *Global Ecol. Biogeogr.* 13: 471-73.

Potapov, R.L. and Flint, V.E. (1989) *Handbuch der Vögel der Sowjetunion*, Wittenberg Lutherstadt.

Pounds, J.A., et al. 1999. Biological response to climate change on a tropical mountain. - *Nature* 398: 611-15.

Reineking, B. and Schröder, B. (2003). Computer-intensive methods in the analysis of species-habitat relationships. In *Gene, Bits und Ökosysteme - Implikationen neuer Technologien für die ökologische Theorie* (eds B. Breckling, H. Reuter and A. Mitwollen), Vol. 9, pp. 165-82. Peter Lang, Frankfurt am Main.

Reineking, B. and Schröder, B. 2006. Constrain to perform: regularization of habitat models. - *Ecol. Model.* 193: 675-90.

Rudner, M. 2004. LR_Mesh. Response surfaces for logistic regression models. - URL: *http://www.uni-oldenburg.de/landeco/21343.html*.

Rudner, M., et al. 2007. Integrated grid based ecological and economic (INGRID) landscape model – a tool to support landscape management decisions. - *Environmental Modelling and Software* 22: 177-87.

Schmid, H., et al. (1998) *Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996.* Schweizerische Vogelwarte, Sempach.

Schröder, B. (2006). ROC & AUC-Calculation - evaluating the predictive performance of habitat models. URL: http://brandenburg.geoecology.unipotsdam.de/users/schroeder/download.html.

Schwarz, G. 1978. Estimating the dimension of a model. - *Ann. Stat.* 6: 461-64.

Storch, I. (2000) *Grouse Status Survey and Conservation Action Plan 2000–04* IUCN, Gland, Switzerland and Cambridge, UK and the world, Pheasant Association, Reading UK.

Theurillat, J.-P. and Guisan, A. 2001. Potential impact of climate change on vegetation in the european Alps: a review. - *Clim. Change* 50: 77-109.

Thomas, C.D. and Lennon, J.J. 1999. Birds extend their ranges northwards. - *Nature* 399: 213.

Thompson, C.M. and McGarigal, K. 2002. The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). - *Landscape Ecol.* 17: 569-86.

Thuiller, W. 2003. BIOMOD - optimizing predictions of species distributions and projecting potential future shifts under global change. - *Glob. Change Biol.* 9: 1353-62.

Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. - *Glob. Change Biol.* 10: 2020-27.

Thuiller, W., et al. 2004. Do we need land-cover data to model species distributions in Europe? - *J. Biogeog.* 31: 353-62.

Tolvannen, A. 1997. Recovery of the bilberry (*Vaccinium myrtillus* L.) from artificial spring and summer frost. - *Plant Ecol.* 130: 35-39.

Verbyla, D.L. and Litvaitis, J.A. 1989. Resampling methods for evaluation of classification accuracy of wildlife habitat models. - *Environ. Manage.* 13: 783-87.

Wilson, J.P. and Gallant, J.C. (2000) *Terrain analysis: principles and applications* Wiley, New York.

Yee, T.W. and Mitchell, N.D. 1991. Generalized additive models in plant ecology. - *J. Veg. Sci.* 2: 587-602.

Zweig, M.H. and Campbell, G. 1993. Receiver-Operating Characteristic (ROC) Plots: a fundamental evaluation tool in clinical medicine. - *Clin. chem.* 39: 561-77.

7. Appendix

App. 1: Set of predictor variables territory scale. Variables describing plant species were tested as cover (percentage) and as incidence (binary); I display the one with better performance only. For each variable, estimates of median and MAD are given for absence and presence plots separately. Results for univariate logistic regression analysis are shown giving the p-value, Area under ROC curve (AUC) and R^2 after Nagelkerke (R^2_N). Further the sign of the correlation with the response variable is displayed. (n= 83, prevalence = 0.49).

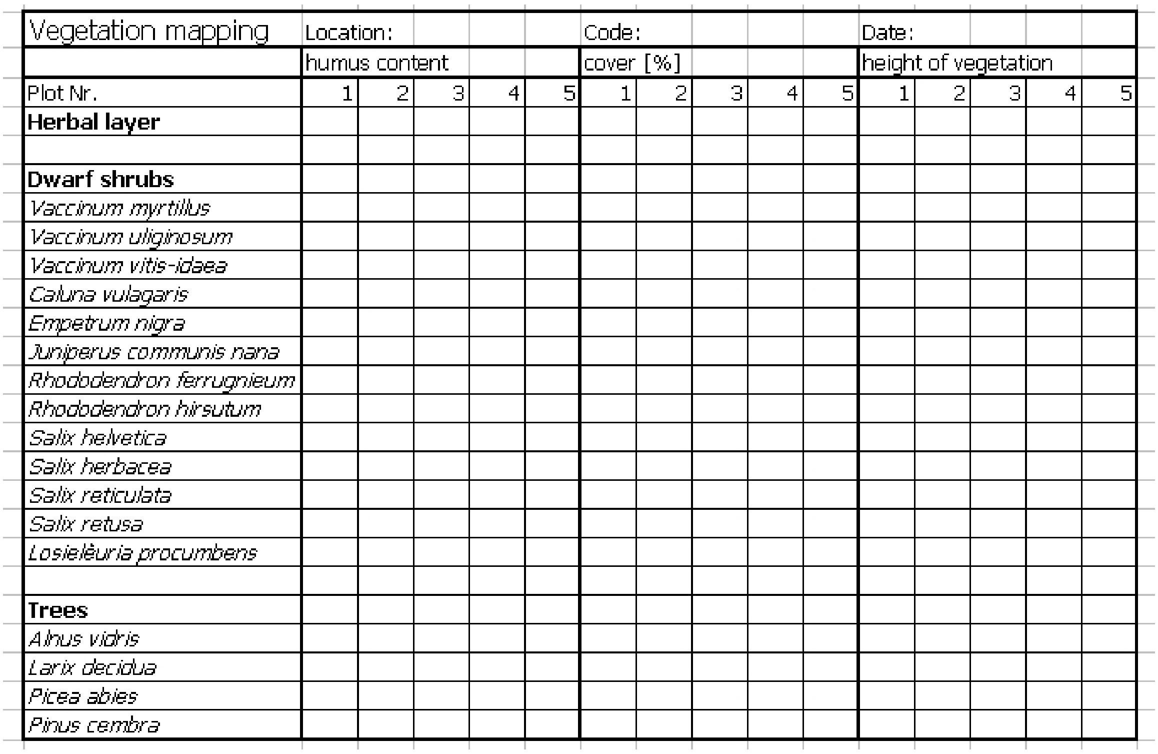
	Ptarmigan present (n=41)		Ptarmigan absent (n=42)		Univariate	analysis		
Predictor variable	Median	MAD	Median	MAD	P	AUC	R^2_N	Correlation
Topography								
aspect beers transformed	0.674	0.595	1.096	0.611	0.191	0.587	0.030	-
aspect cosines transformed	0.407	0.432	-0.165	0.718	0.005	0.680	0.130	+
aspect sinus transformed	-0.105	0.692	0.276	0.651	0.307	0.557	0.020	-
distance to peak [m]	330	190	555	270	0.305	0.623	0.020	-
distance to ridge [m]	240	230	345	215	0.862	0.582	0.000	-
altitude above sea level [m]	2275	63	2188	69	0.012	0.696	0.120	+
distance to settlements [m]	890	350	825	290	0.425	0.532	0.010	+
distance to skiing area [m]	1430	780	845	695	0.240	0.620	0.020	+
inclination [°]	33	8	32.5	4.5	0.196	0.582	0.030	+
topographic elements [No.]	4	1	3	1	0.001	0.749	0.280	+
plan curvature [cat]	2	1	2	1	0.150	0.583	0.040	-
profile curvature [cat]	1	0	2	1	0.011	0.660	0.110	-
Habitat structure/ disturbance								
hiding possibilities [cat]	2	1	1	0	<0.001	0.779	0.330	+
grazing by cattle [cat]	1	1	2	1	<0.001	0.721	0.220	-
grazing by wildlife [cat]	1	0	1	0	0.517	0.560	0.010	+
anthropogenic disturbance [cat]	1	1	1	1	0.039	0.635	0.070	-
Vegetation and resources								
number of trees >2 m height	0	0	0	0	0.075	0.603	0.100	-
tree cover {%]	0	0	0	0	0.039	0.612	0.170	-
dwarf shrub cover [binary]	1	-	1	-	0.027	0.595	0.120	+
herbal layer cover {%]	0.2	0.1	0.3	0.25	0.002	0.654	0.190	-

Ericaceae cover {%]	1	-	1	-	0.013	0.619	0.160	+
Vaccineae [binary]	1	-	1	-	0.014	0.618	0.110	+
Vaccinium myrtillus [%]	0	0	0.063	0.0625	0.088	0.618	0.050	-
Vaccinium uliginosum [binary]	1	0	1	0	0.003	0.654	0.170	+
Vaccinium vitis-idaea [binary]	0	0	0	0	0.859	0.509	0.000	-
Rhododendron spp. [binary]	1	0	1	0	0.052	0.593	0.060	+
Loiseleuria procumbens [binary]	0	0	0	0	0.005	0.648	0.130	+
Empetrum nigra [binary]	0	0	0	0	0.214	0.564	0.030	+
Juniperus communis spp. [%]	0	0	0.006	0.0063	0.028	0.628	0.100	-
Salix spp. [binary]	1	-	0	-	0.001	0.673	0.170	+
Salix herbacea [binary]	0	0	0	0	<0.001	0.684	0.230	+
vegetation free area [%]	0.3	0.2	0.1	0.1	<0.001	0.822	0.330	+
vegetation height, average [cm]	7	3	15	6	<0.001	0.776	0.320	-
vegetation height, maximum [cm]	25	8	35	19	0.050	0.694	0.130	-
Shannon diversity index	1.077	0.23	1.099	0.38	0.363	0.513	0.010	+
evenness Shannon index	0.603	0.106	0.668	0.128	0.504	0.572	0.010	-
Simpson diversity index	0.883	0.073	0.762	0.085	0.001	0.792	0.290	+
evenness Simpson index	1.021	0.085	0.916	0.079	0.004	0.766	0.200	+
Number of shrub species	6	1	5.5	2.5	0.057	0.607	0.060	+
humus content of soil [%]	3	1.1	2.8	0.9	0.786	0.425	0.000	-
mean deepness of soil [cm]	9.75	2.5	14.5	5	0.002	0.705	0.190	-

App. 2: Datasheet for ptarmigan survey and habitat mapping

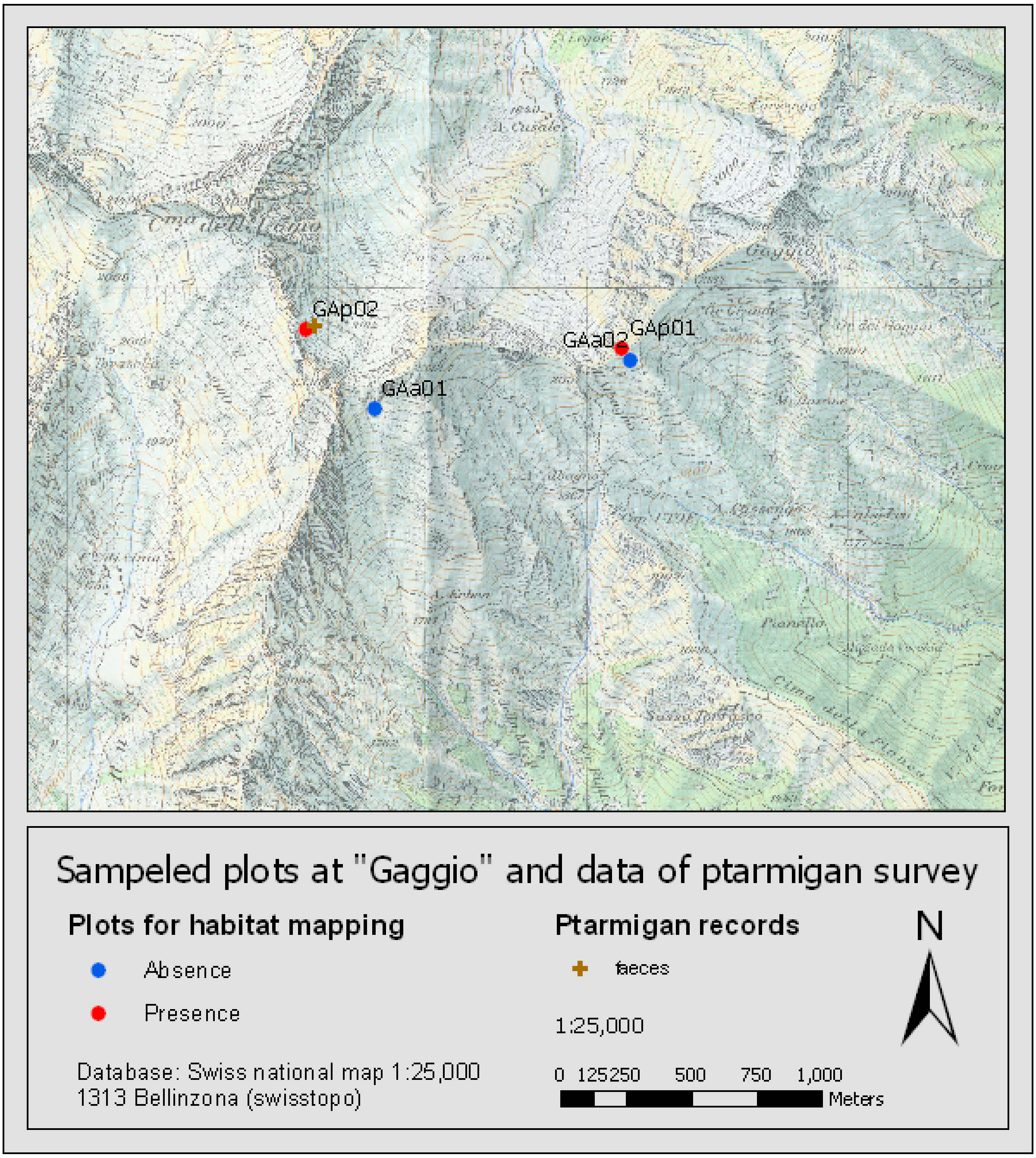
Data sheet ptarmigan survey and habitat mapping 2005				
Study area				
Code of location:		No.:		
Date:		Time of day:		
X coordinate:				
Y coordinate:				
Ptarmigan survey				
proof of ptarmigan´s occurrence	sighting	call	footprints	faeces
Weather	Cloudiness	Wind	Temperature	Visibility
Topography				
altitude asl. [m]		Aspect [°]		
Inclination of slope [°]		profile curvature		
Distance to ridge [m]		plan curvature		
Topographic features	Slope ( ) valley ( ) knoll ( ) sink ( ) ridge ( ) boulder field ( ) erosion path ( ) steep face ( ) terrain step ( ) caldera ( ) costa ( )			
Soil				
Humus content [%]		area covered by soil [%]		
Soil depth [m]				
Geology				
crystalline		non crystalline		
Vegetation				
No. of trees height > 2 m				
Cover [%]				
Moss & fern				
Herbal layer				
Dwarf shrubs				
Trees				
Vegetation free				
land use	no/nothing	low/seldom	medium	high/frequent
Distance to settlements/huts				
Dist. to ski runs/services				
Grazing by cattle				
Grazing by wild animals				
Ski run				
anthropogenic disturbance				
Intensity of land use				
Structure	no/nothing	low/seldom	medium	high/frequent
Vertical				
Horizontal				
Snow dell vegetation				
Look-outs				
Shelter				
Structure elements vert. > 2 m				
Foto				
Film No.		Picture No.		
Comments				

App. 3 : Datasheet for vegetation survey. All species of shrubs and trees were mapped within the plot sized 25 x25 m. Within this plot five subsamples were mapped with a size of 5 x 5 m in respect to humus content, vegetation height and cover.

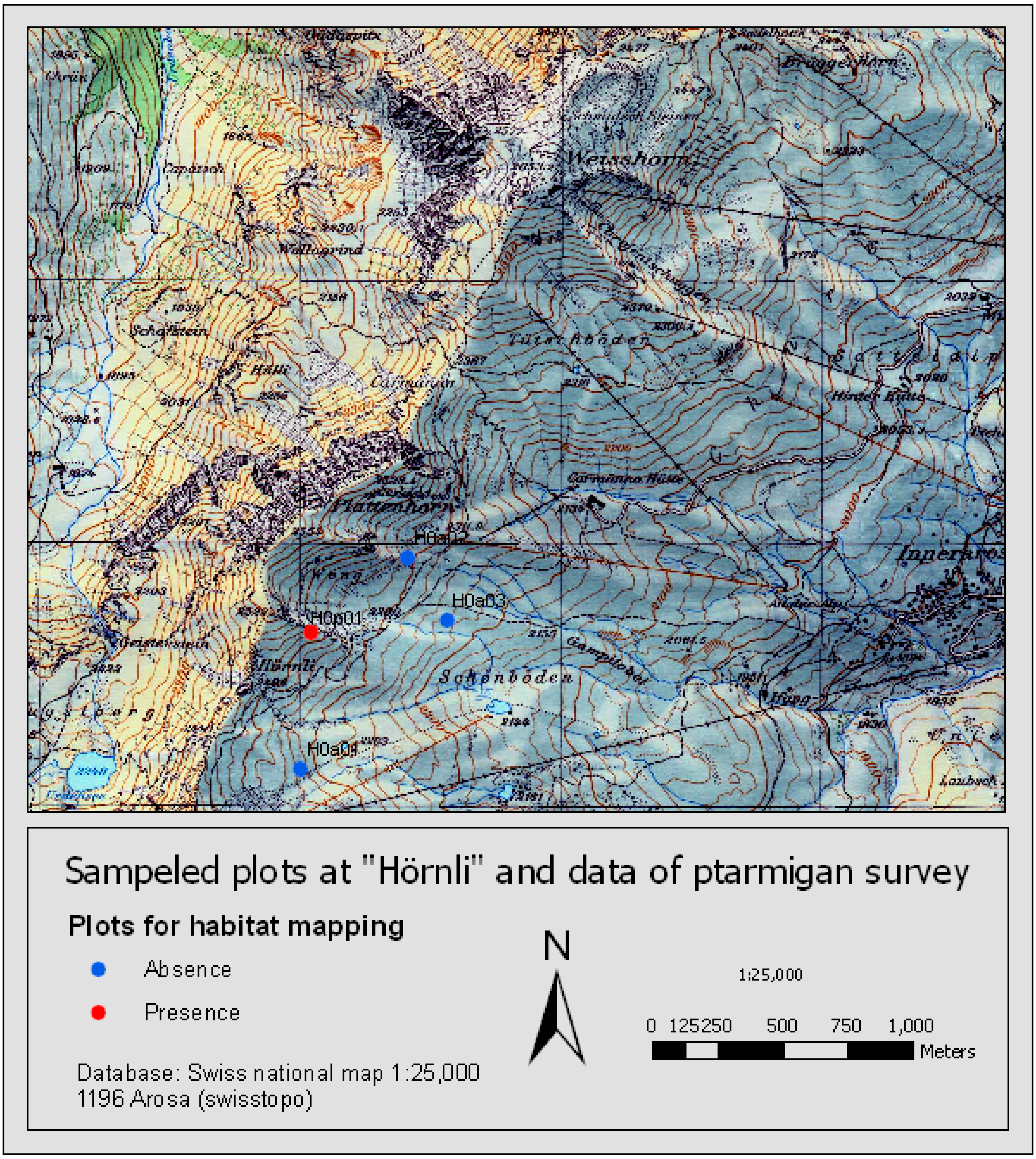


Vegetation mapping	Location:					Code:					Date:				
	humus content					cover [%]					height of vegetation				
Plot Nr.	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Herbal layer															
Dwarf shrubs															
Vaccinum myrtillus															
Vaccinum uliginosum															
Vaccinum vitis-idaea															
Caluna vulagaris															
Empetrum nigra															
Juniperus communis nana															
Rhododendron ferrugnieum															
Rhododendron hirsutum															
Salix helvetica															
Salix herbacea															
Salix reticulata															
Salix retusa															
Losielèuria procumbens															
Trees															
Alnus vidris															
Larix decidua															
Picea abies															
Pinus cembra															

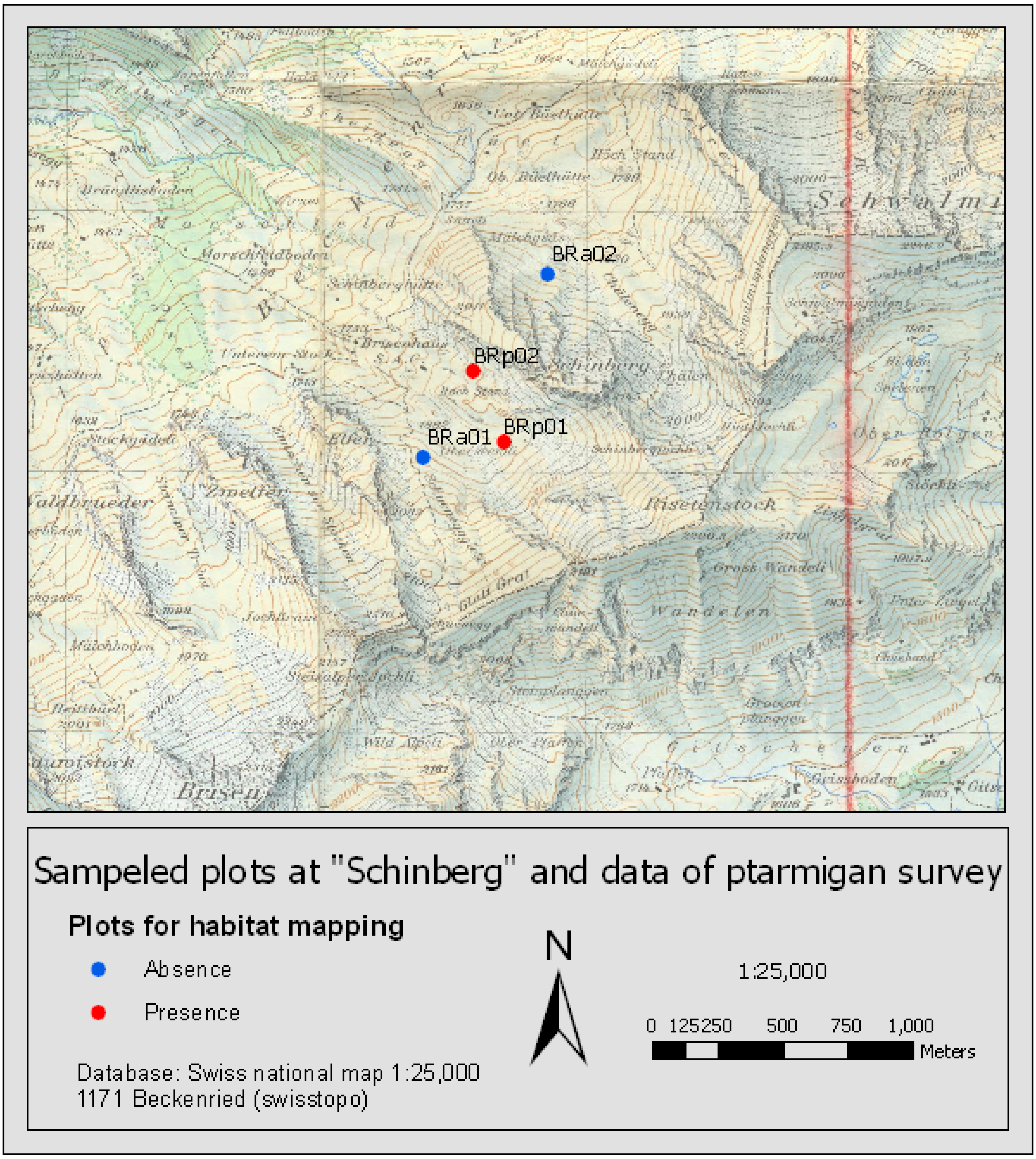
App. 4: Ptarmigan survey at Gaggio/Belinzona: location of sample plots and records of ptarmigan's incidence



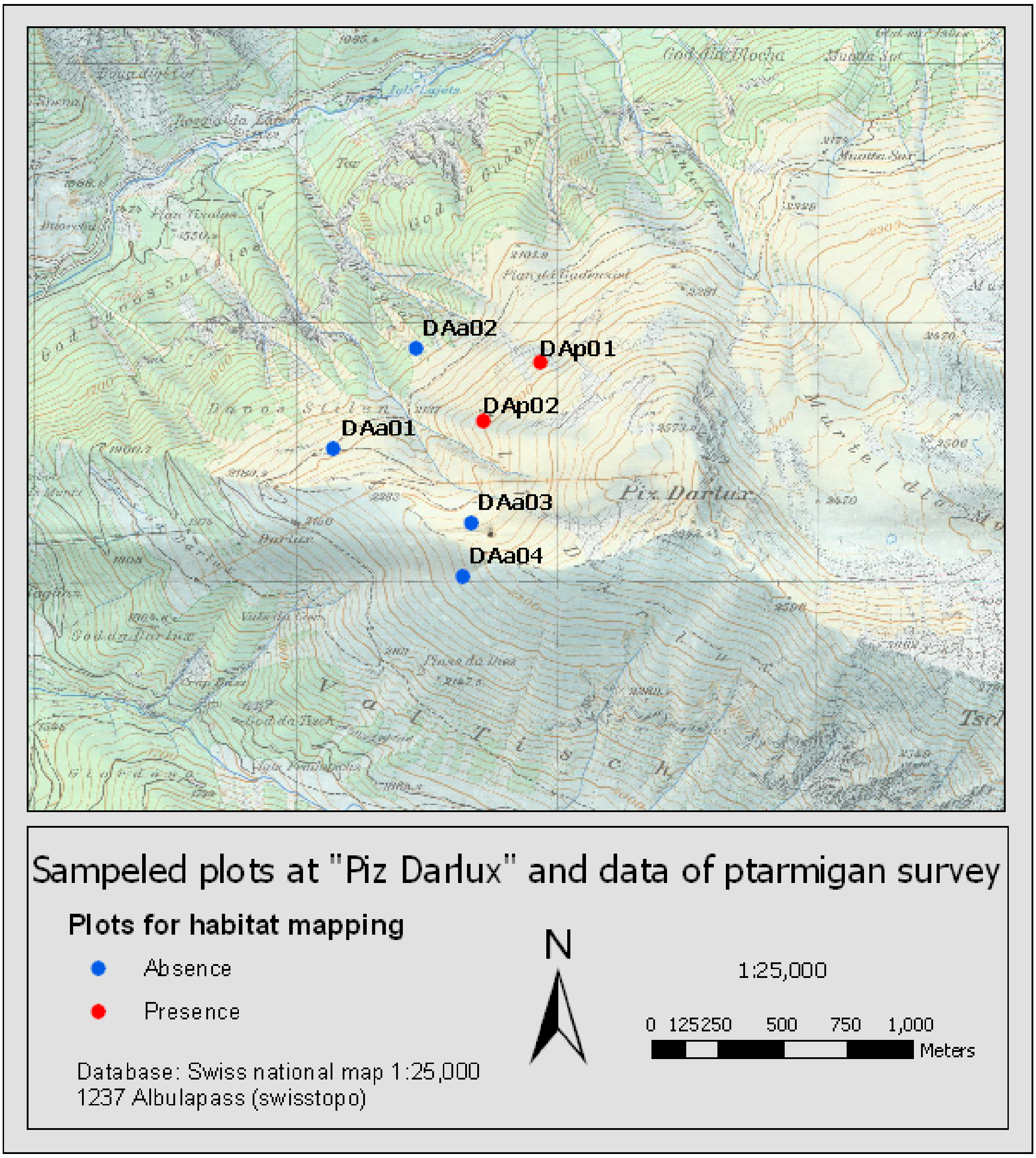
App. 5: Ptarmigan survey at Glänlishopf/Buchs: location of sample plots



App. 6: Ptarmigan survey at Schinberg/Beckenried: location of sample plots



App. 7: Ptarmigan survey at Piz Darlux/Albulapass: location of sample plots



App. 8: Photos of the sample plots

Aletsch (occupied habitat)

Piz Darlux/Albulapass (not occupied)

Basòdino (occupied habitat)

Basòdino (occupied habitat)

Gaggio/Belinzona (ridge occupied, lower part of the southern slope not)

Schinberg/Beckenried (not occupied)

Glänlischopf/Buchs (south facing grazed slope, not occupied)

Glänlischopf/Buchs (occupied habitat)

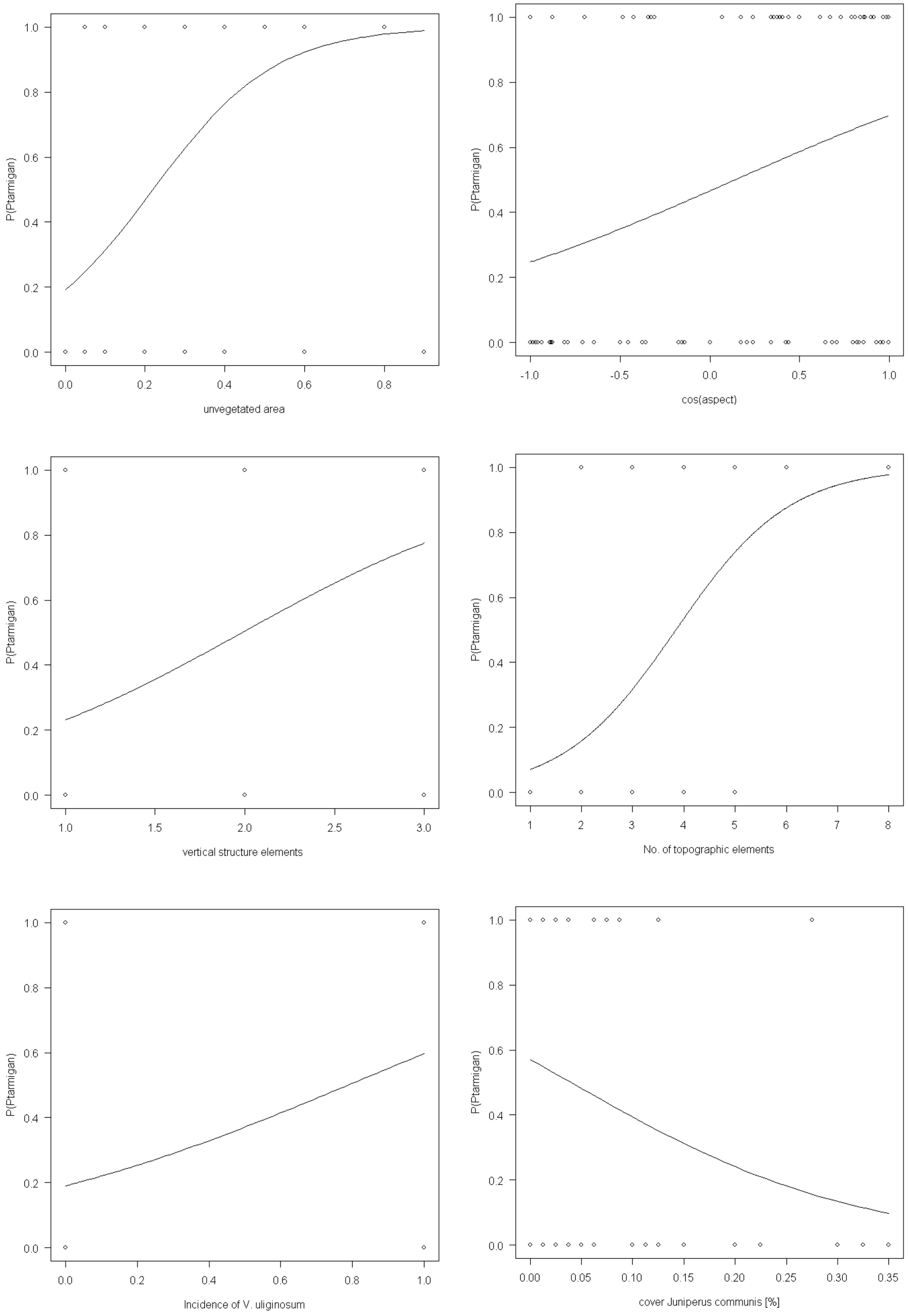
Hörnli/Arosa (occupied habitat)

Jatzhorn/Davos (occupied habitat)

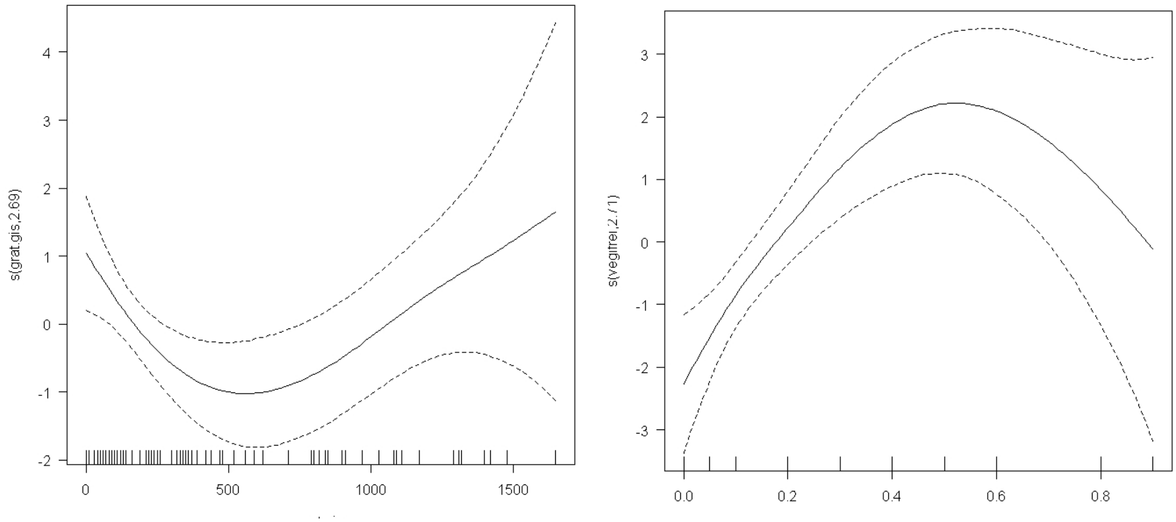
Pizzo Erra/Biasca (occupied habitat)

Pizzo Erra/Biasca (occupied habitat)

App. 9: Plots of univariate models for all variables composing the final model on territory scale (for remaining variables and the other scales see CD)



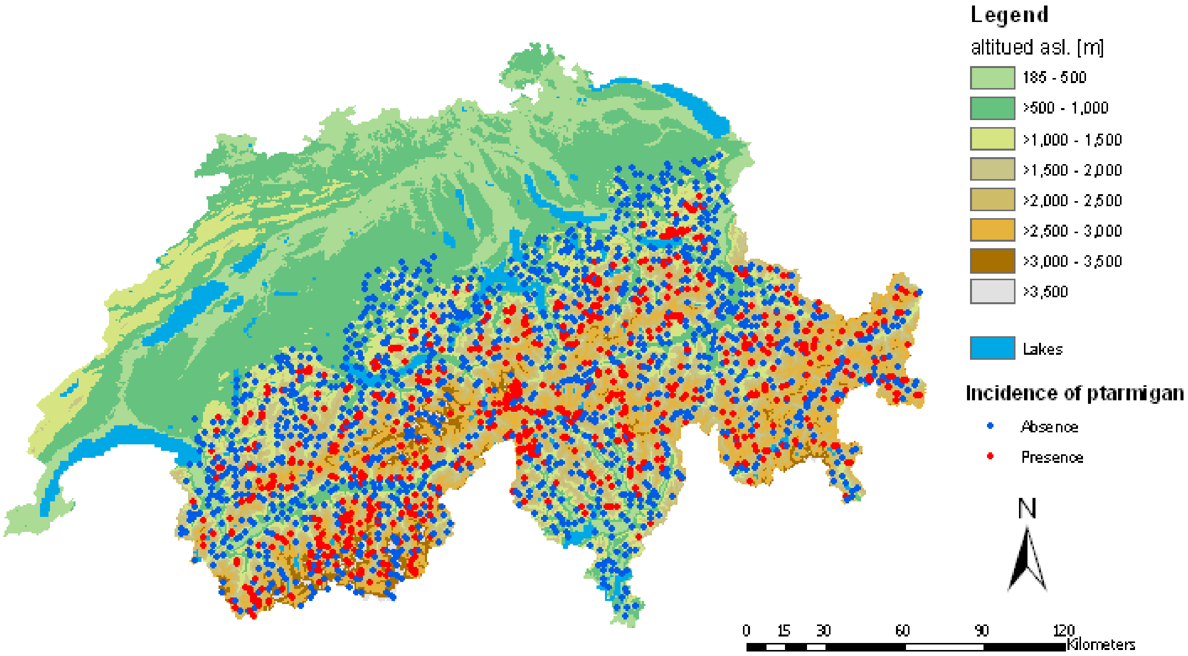
App. 10: Plots for univariate GAMs (general additive models) for those predictors showing a hump-shaped response (on territory scale)



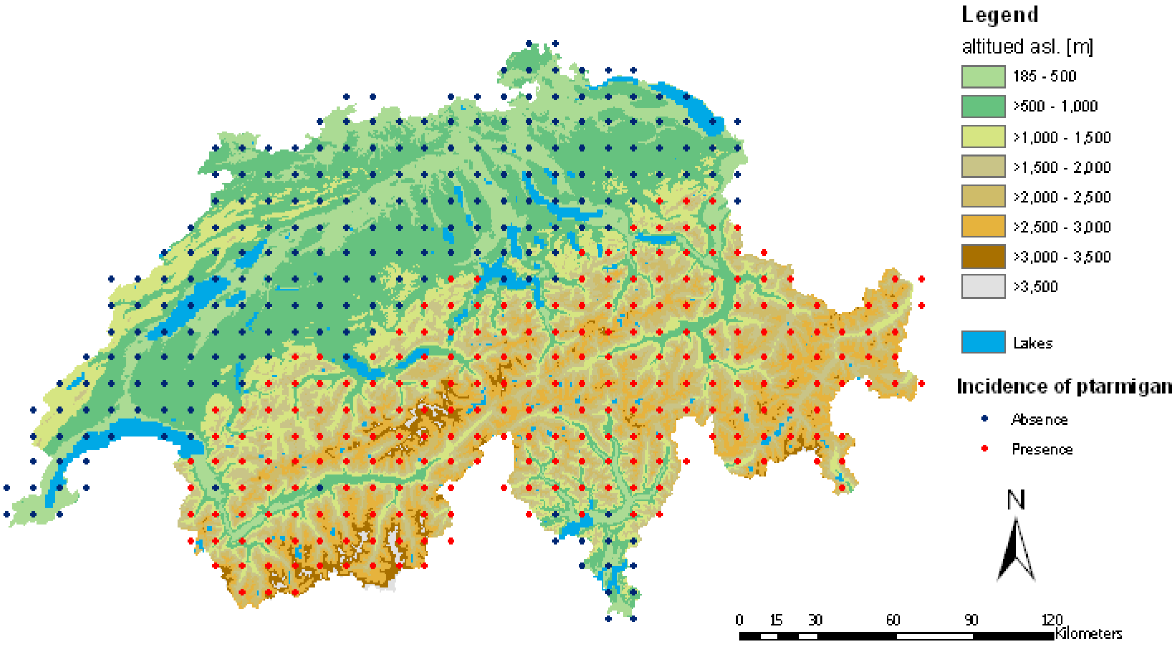
distance to closest ridge [m]

vegetation free area [%]

App. 11: Data on ptarmigan´s incidence on macro-scale at the resolution of 1 km². There are no records of ptarmigan from the Jura and the Midlands, hence only ptarmigan data from the Alps were used for species distribution modelling at this scale.



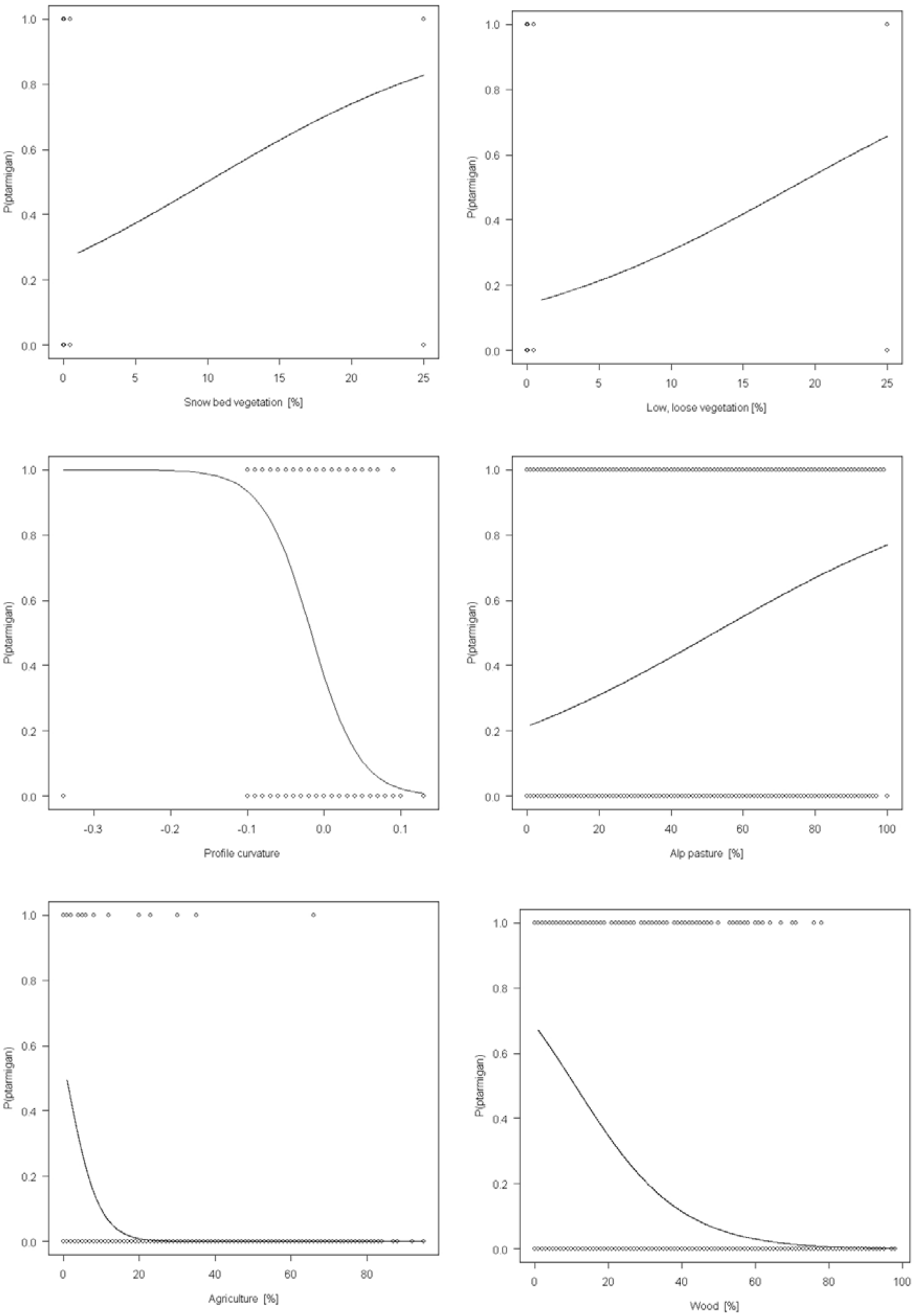
App. 12: Species data on macro-scale (100 km² resolution)



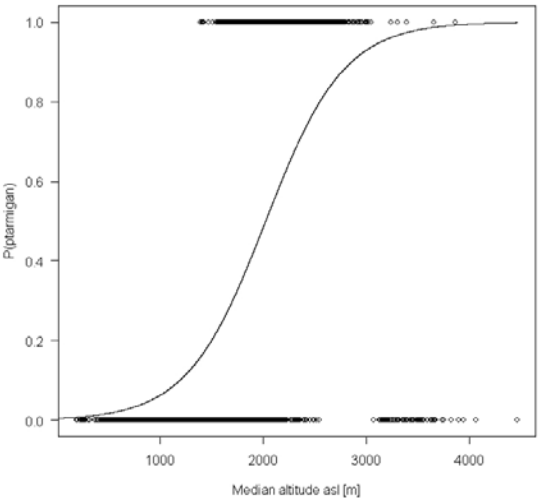
App. 13: Univariate analysis of predictors on macro-scale (1 km^2). Model performance (AUC and R^2_N) and the algebraic sign of the model coefficient (β) is displayed.

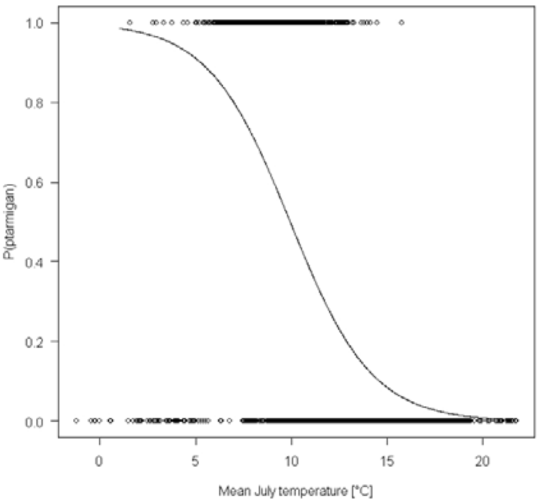
Predictor	Predictor abbreviation	AUC	R^2_N	algebraic sign of β
Days	DEGDAYS30	0.862	0.458	-
Insolation July	RADJUL	0.715	0.152	+
mean July temperature	TEMPJUL	0.875	0.426	-
mean year temperature	TEMPYEAR	0.874	0.423	-
Shrubs	N4.97	0.793	0.267	-
Wood	NBS1.97	0.845	0.41	-
Agriculture	NBS5.97	0.787	0.423	-
Alp pastures	NBS10.97	0.713	0.147	+
Derilict land	NBS14.97	0.829	0.346	+
Vegetation free	NBS15.97	0.863	0.225	+
Settlements	NBS16.97	0.819	0.389	-
Agriculture without	NBS2.8.97	0.786	0.417	-
Poor vegetation cover	KVS3	0.753	0.307	+
Low, loose vegetation	KVS4NEU	0.807	0.344	+
Dense, high sedge and grass meadows	KVS7	0.723	0.224	-
Deciduous forest	KVS15	0.757	0.312	-
Groves	KVS19	0.717	0.203	-
Open rock crevice vegetation	K20	0.738	0.23	+
Loose pioneer vegetation	K30	0.783	0.327	+
Snow bed vegetation	K55	0.777	0.256	+
high pastures	K80	0.814	0.443	-
Shady deciduous forest	K140	0.715	0.282	-
Closed, coniferous forest	K180	0.715	0.202	-
Alluvial forest	K190	0.738	0.228	-
Snow bed vegetation (silicate)	V25	0.725	0.214	+
Snow bed vegetation (calcareous)	V168	0.701	0.134	+
Subalpine dwarf heath	V169	0.733	0.178	+
Minimal altitude asl	MINH.HE	0.874	0.398	+
Median altitude asl	MEDIANH.HE	0.892	0.439	+
Maximal altitude	MAXH.HE	0.894	0.443	+
Flow accumulation	FLOWACCUMU	0.71	0.138	-
Contributing area	CONTRIBUTI	0.71	0.208	-
Curvature	CURVATURE	0.72	0.185	+
Profile curvature	CURV.PROF	0.735	0.197	-
Dwarf shrubs	RR.ZWERG2	0.733	0.17	+
Forest	RR.WALD	0.795	0.397	-

App 14: Plots of univariate models for selected variables on macro-scale (1 km² resolution)

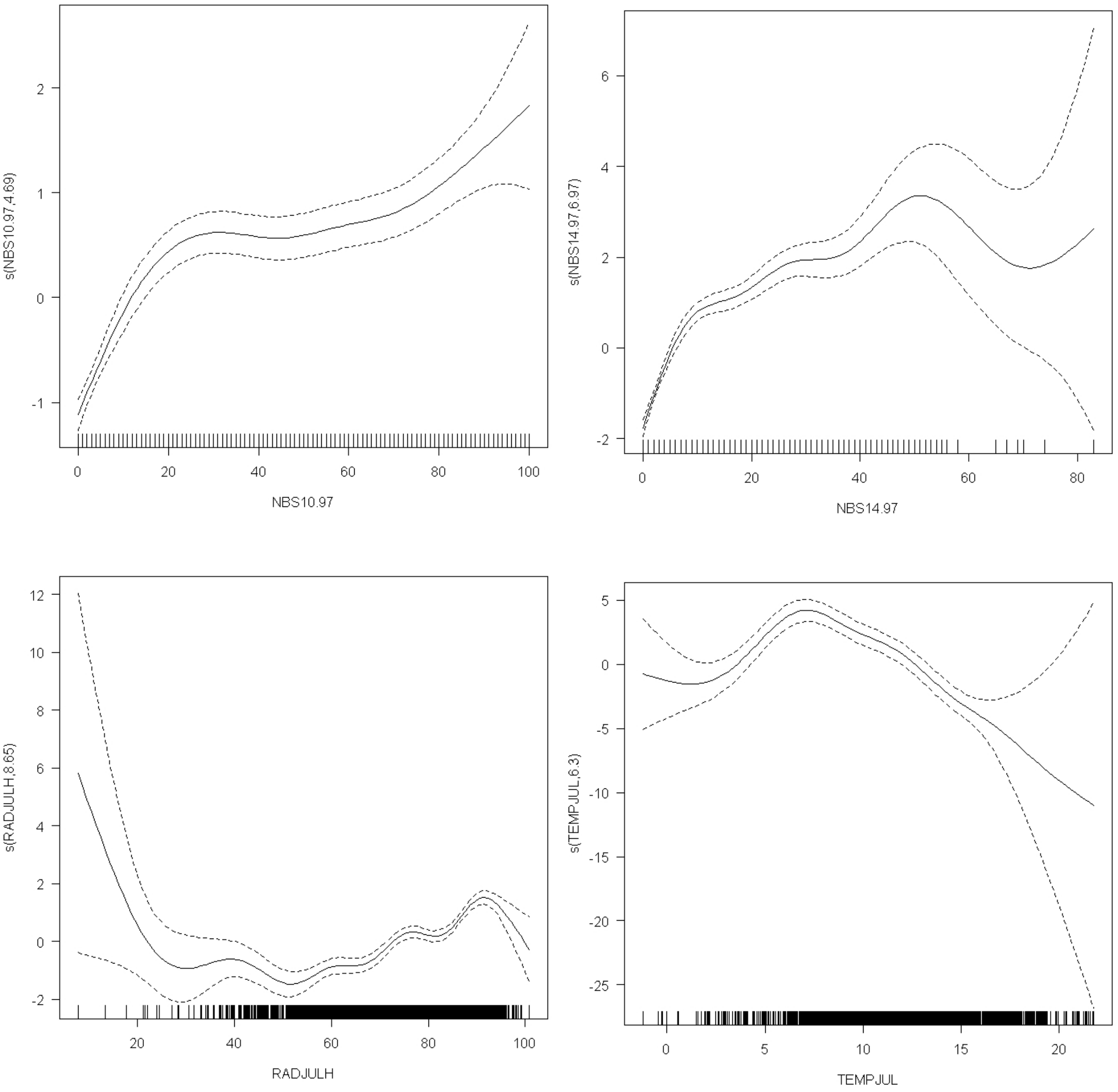


App. 14 continued



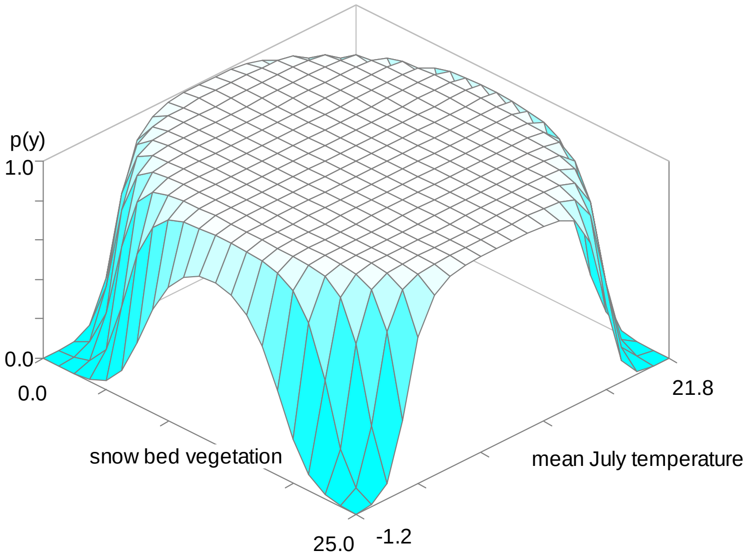


App. 15: univariate GAMs at macro scale (resolution 1 km²) for those predictors that enter the final model (glm) with its linear and its squared term.



App. 16: Three dimensional response surface, final model macro-scale at the resolution of 1 km^2 illustration the interaction term 'snow bed vegetation' * 'mean July temperature'

The response variable $P_{(ptarmigan)}$ and the predictors 'snow bed vegetation' and 'mean July temperature' are shown continuously. The remaining predictors are considered as a constant presuming the following values: low, loose vegetation 5% cover, wood 10% cover, agriculture 0% cover, Alp pasture 30 % cover and profile curvature=-0.04 representing a habitat with intermediate suitability.



App. 17: Univariate analysis of predictors on macro-scale (100 km^2). Model performance (AUC and R^2_N) and the algebraic sign of the model coefficient (β) is displayed.

Predictor	Predictor abbreviation	AUC	R2N	algebraic sign of beta
Days	DEGDAYS30	0.862	0.458	-
Insolation July	RADJUL	0.715	0.152	+
mean July temperature	TEMPJUL	0.875	0.426	-
mean year temperature	TEMPYEAR	0.874	0.423	-
Coppice	N4.97	0.793	0.267	-
Wood	NBS1.97	0.845	0.41	-
Agriculture	NBS5.97	0.787	0.423	-
Alp pastures	NBS10.97	0.713	0.147	+
Derilict land	NBS14.97	0.829	0.346	+
Vegetation free	NBS15.97	0.863	0.225	+
Settlements	NBS16.97	0.819	0.389	-
Agriculture without	NBS2.8.97	0.786	0.417	-
Poor vegetation cover	KVS3	0.753	0.307	+
Low, loose vegetation	KVS4NEU	0.807	0.344	+
Dense, high sedge and grass meadows	KVS7	0.723	0.224	-
Deciduous forest	KVS15	0.757	0.312	-
Groves	KVS19	0.717	0.203	-
Open rock crevice vegetation	K20	0.738	0.23	+
Loose pionier vegetation	K30	0.783	0.327	+
Snow bed vegetation	K55	0.777	0.256	+
high pastures	K80	0.814	0.443	-
Shady deciduous forest	K140	0.715	0.282	-
Closed, coniferous forest	K180	0.715	0.202	-
Alluvial forest	K190	0.738	0.228	-
Snow bed vegetation (silicate)	V25	0.725	0.214	+
Snow bed vegetation (calcerous)	V168	0.701	0.134	+
Subalpine dwarf heath	V169	0.733	0.178	+
Minimal altitude asl	MINH.HE	0.874	0.398	+
Median altitude asl	MEDIANH.HE	0.892	0.439	+
Maximal altitude	MAXH.HE	0.894	0.443	+
Flow accumulation	FLOWACCUMU	0.71	0.138	-
Contributing area	CONTRIBUTI	0.71	0.208	-
Curvature	CURVATURE	0.72	0.185	+
Profile curvature	CURV.PROF	0.735	0.197	-
Dwarf shrubs	RR.ZWERG2	0.733	0.17	+
Forest	RR.WALD	0.795	0.397	-

7.1 Alternate models

There are many possible “final models”. The variable set of the final model depends on various factors, e.g. the applied selection criterion (AIC or BIC), the thresholds applied in the preliminary univariate screening or the decision which predictor is omitted of a pair of correlated variables.

App. 18: alternate model territory scale, backward stepwise selection with BIC. The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance. β = slope, S.E. = standard error (β), p = p-value, independent (I-effect) and total effect (T-effect) [%], derived by hierarchical partitioning. Model performance (corrected index): AUC=0.957 (0.956), R^2_N=0.773 (0.699), Cohen’s Kappa=0.881, slope of calibration curve=0.763

Model for ptarmigan on teritory scale (based on BIC selection)					
Predictor	β	S.E.	p	I-effect	T-effect
Intercept	-10.548	2.599	<0.001	-	-
Vegetation-free area [%]	25.479	8.392	0.002	35.9	37.5
Vegetation-free area (^2)	-20.215	8.997	0.025	-	-
Variability of topography	0.775	0.407	0.057	25.4	31.3
Vaccinium uliginosum spp. incidence	4.082	1.361	0.003	18.6	17.4
Aspect (cosine transformed)	2.54	0.792	0.001	20.1	13.8

App. 19: Alternate final model on territory scale. The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance. β = slope, S.E. = standard error (β), p = p-value, independent (I-effect) and total effect (T-effect) [%], derived by hierarchical partitioning. AUC=0.957 (0.957), R^2_N=0.752 (0.738), Cohen's Kappa=0.773, slope of calibration curve=0.949.

Alternate model for ptarmigan on territory scale (AIC selection)					
Predictor	β	S.E.	p	I-effect	T-effect
Intercept	-6.993	2.470	0.005	-	-
Vegetation-free area [%]	0.320	0.107	0.003	30.9	35.9
Vegetation-free area (^2)	-0.003	0.002	0.034	-	-
Vertical structure elements [No.]	0.792	0.439	0.072	20.1	24.8
Vaccinium uliginosum spp. incidence	4.607	1.696	0.007	23.9	16.7
Aspect (cosine transformed)	1.978	0.880	0.025	15.5	13.2
Juniperus communis spp. cover [%]	-15.496	7.317	0.034	8.7	9.3
Distance to ridge [mm]	-8.475	4.532	0.062	0.9	0.0
Distance to ridge (^2)	5.787	3.566	0.105	-	-

App. 19 shows an alternate model for territory scale. This model reflects a fact often observed by field ornithologists: ptarmigan seems to prefer areas close to the ridge. This is valid particularly for populations at the edge of the distribution, i.e. at comparatively warm conditions (cf Fasel and Zbinden, 1983). However, in the alternate model the predictor distance to the ridge shows a hump-shaped response. This indicates that habitats close to the ridge and those further away, but not those at intermediate distances, represent suitable conditions (see plot of the univariate gam in App. 10). At the first glance there is no reasonable ecological explanation. At the majority of the sample sites habitats close to the ridge indeed are preferred. At Basòdino however, this predictor does not play any bigger role as suitable habitat distributes over an elevated plain.

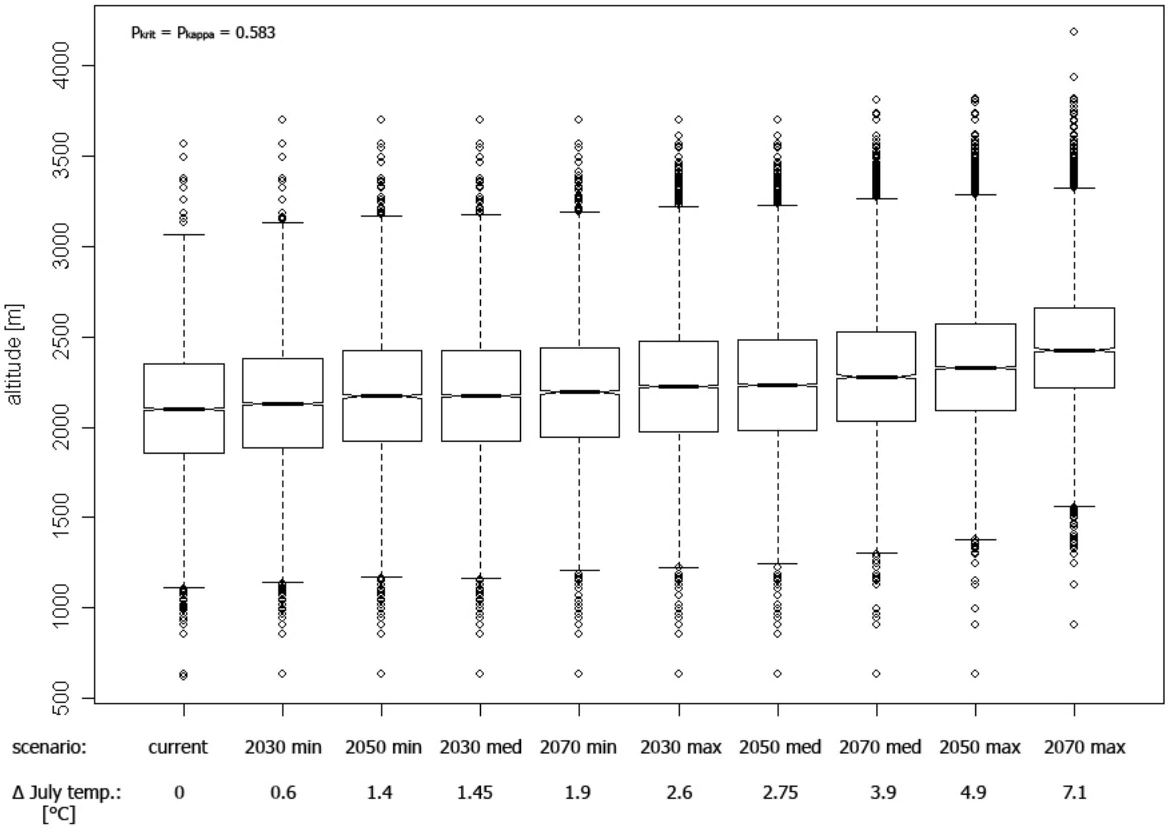
App. 20: Alternate model macro-scale (1 km² resolution, AIC-selection). The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance (calculated for linear effects only). β = slope, S.E. = standard error (β), p = p-value. Model performance (corrected index): AUC=0.957 (0.957), R^2_N=0.752 (0.738), Cohen's Kappa=0.773, slope of calibration curve=0.949.

Model for ptarmigan on macro-scale at 1 km² resolution (based on AIC selection)					
Predictor	β	S.E.	P	I effect [%]	T effect [%]
Intercept	-9.917	1.983	<0.001	-	-
Mean July temperature	2.253	0.295	<0.001	12.4	14.2
Mean July temperature (^2)	-0.106	0.014	<0.001	-	-
Agriculture	-0.073	0.017	<0.001	12.9	13.8
Wood	-0.053	0.008	<0.001	13.4	13.5
Derelict land	0.025	0.021	0.235	11.7	11.1
Derelict land (^2)	-0.001	0	0.077	-	-
Low, loose vegetation	-0.084	0.041	0.041	10.9	11
Snow bed vegetation	1.585	0.558	0.005	7.8	7.9
Snow bed vegetation (^2)	-0.058	0.022	0.008	-	-
Open rock crevice vegetation	0.016	0.007	0.022	7.5	7
Dense, high sedge and gras meadows	-0.015	0.007	0.039	7.1	6.8
profile curvatue	-23.1	3.096	<0.001	6.6	5.9
Insolation July	0.051	0.041	0.211	4.6	4.5
Insolation July (^2)	-0.001	0	0.053	-	-
Alp pastures	0.028	0.021	0.181	5.3	4.3
Alp pastures (^2)	0	0	0.115	-	-
Alp pastures * mean July temp.	-0.007	0.002	<0.001	-	-
Snow bed vegetation * mean July temp	-0.007	0.004	0.1	-	-
Snow bed vegetation * Alp pastures	-0.001	0	0.01	-	-
Low, loose vegetation * insolation July	0.001	0.001	0.01	-	-

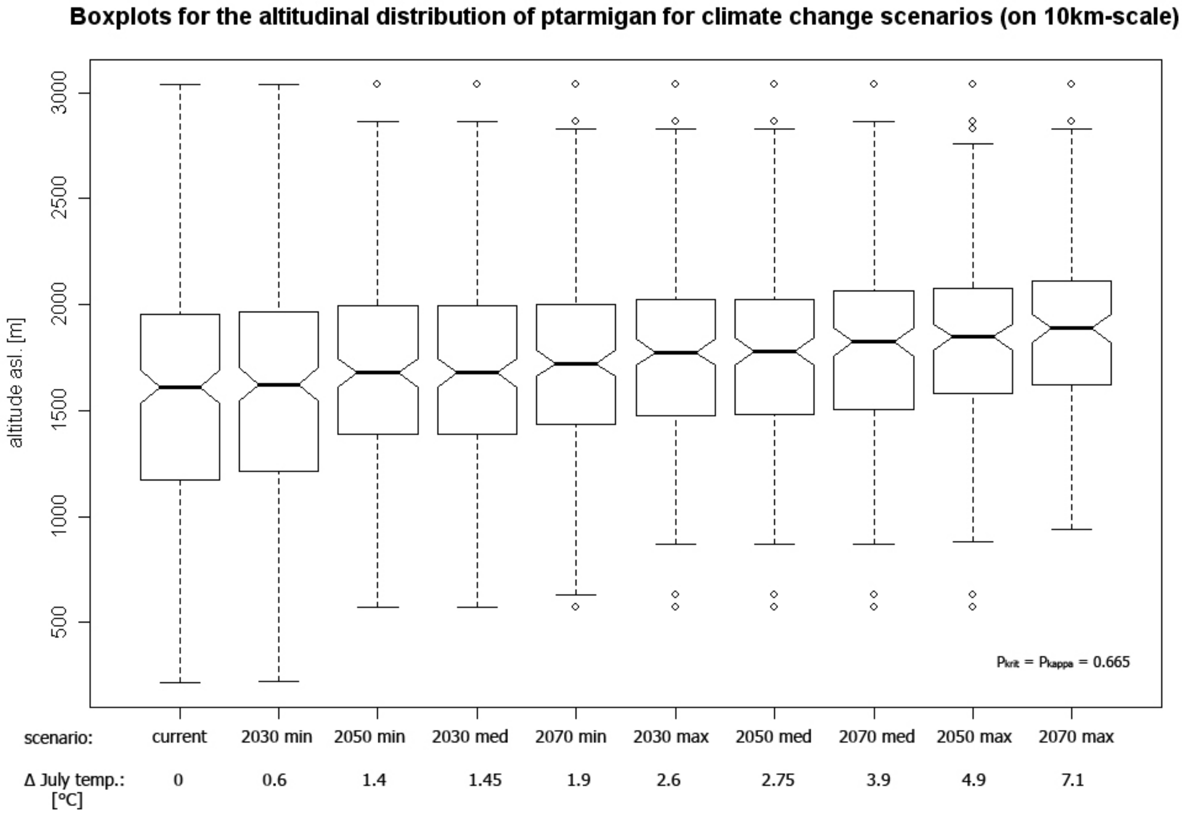
App. 21: Autologistic model on macro-scale (1 km^2, BIC selection). The variables are ordered in respect to their total (independent + joint) contributing effect to the explained variance. β = slope, S.E. = standard error (β), p = p-value, independent (I-effect) and total effect (T-effect) [%], derived by hierarchical partitioning. Model performance (corrected index): AUC=0.954 (0.954), R^2_N=0.748 (0.739), Cohen's Kappa=0.766, slope of calibration curve=0.966.

Autologistic model for ptarmigan on macro-scale at 1 km^2 resolution (based on BIC selection)					
Predictor	β	S. E.	p	I effect [%]	T effect [%]
Intercept	-9.105	1.037	<0.001	-	-
Mean July temperature	2.123	0.238	<0.001	14.7	17.7
Mean July temperature (^2)	-0.099	0.012	<0.001	-	-
Agriculture	-0.081	0.015	<0.001	18	17.2
Wood	-0.056	0.006	<0.001	19.8	16.9
Low, loose vegetation	0.023	0.008	0.003	14.2	13.7
Snow bed vegetation	1.275	0.547	0.02	9.1	9.8
Snow bed vegetation (^2)	-0.05	0.022	<0.001	-	-
Autocovariate	0.736	0.48	0.125	8.9	8.8
Profile curvature	-22.047	3.077	<0.001	9.4	7.4
Alp pastures	0.048	0.014	<0.001	3.7	5.4
Dwarf shrub heath	1.054	0.524	0.044	2.2	3.1
Dwarf shrub heath (^2)	-0.043	0.021	0.042	-	-
Alp pastures * mean July temp.	-0.008	0.002	<0.001	-	-

App. 22: The altitudinal distribution of ptarmigan for minimum, median and maximum scenarios for the years 2030, 2050 and 2070 ordered in respect to temperature rise at the resolution of 1 km^2 resolution. The boxplots show the altitudinal distribution of all raster cells with predicted presence of ptarmigan ($P_{(Ptarmigan)}>P_{crit}=P_{kappa}=0.583$). The median altitudinal shift betrays 46.9 m per 1°C temperature rise (MAD=1.1 m).



App. 23: Altitudinal distribution of ptarmigan for minimum, median and maximum scenarios for the years 2030, 2050 and 2070at 100 km^2 resolution. The boxplots show the median of the altitude of all raster cells with predicted presence of ptarmigan ($P_{(Ptarmigan)}>P_{crit}=P_{kappa}=0.665$). The median altitudinal shift betrays 55.0 m per 1°C temperature rise (MAD=3 m).



App. 24: for further on statistical analyses, R-Codes, species and environment data etc. please refer to the annexed CD.

8. Acknowledgements

An dieser Stelle möchte ich mich bei allen bedanken, die mich bei und während dieser Arbeit unterstützt haben. Insbesondere natürlich bei meinen beiden großartigen Betreuern Boris Schröder und Niklaus Zbinden. Boris Schröder möchte ich dafür danken, dass er stets ein offenes Ohr für meine Fragen und Anliegen hatte und sich immer (!) Zeit für seine Diplomanden genommen hat, auch wenn es noch so viele Paper zu schreiben gab. Niklaus Zbinden hat mich insbesondere vor und während der Feldarbeiten mit seinen langjährigen Schneehuhnerfahrungen unterstützt. Gleiches gilt für Christian Marti, der mich mit auf meine erste Schneehuhnexpedition zum Aletsch genommen hat. Ein großes „merci vielmal" geht an das gesamte Team der Schweizerischen Vogelwarte Sempach, die mich sehr nett empfangen und beherbergt haben!

Neben der wissenschaftlichen Unterstützung konnte ich immer auf den Rückhalt meiner Familie zählen. Meine Eltern Helma und Peter haben mich nicht nur ideel und finanziell jahrelang unterstützt, sondern waren auch beim zweiten Teil der Feldarbeiten logistisch eine große Hilfe. Dank gilt auch meinen beiden Brüdern Tobias und Ole.

Viel geholfen hat mir auch mein Potsdamer zu Hause, die rote Küche 51, mit all ihren MitbewohnerInnen und Gästen, die ich jetzt hier gar nicht alle aufzählen kann. Natürlich nicht zu vergessen, meine Freundin Phrenie, die immer für mich da war und oft Gesellschaft im Golmer Container geleistet hat.

Nicht zu letzt möchte ich mich bei allen denjenigen bedanken, die Korrektur gelesen haben, Jens, Phrenie, Björn, Damaris, Jörn und Tobias, die mit mir die Mittags- und Kaffepausen draußen in Golm verbracht haben und Jule, die mich währenden der Feldarbeiten zeitweise begeleitet hat.

Zu erwähnen sind auch noch der DAAD, der mir für den Aufenthalt in der Schweiz ein Stipendium gewährt hat, die Unterstützung der Heinrich Böll Stiftung mit ihrem Studienstipendium und der Verein Pro Natura der mich während der Feldarbeiten auf der Riederalp kostenlos im Aletsch Hüttli beherbergt und verköstigt hat!

Hiermit versichere ich abschliessend, die Arbeit selbständig verfasst zu haben und keine weiteren als die angegeben Hilfsmittel und Quellen verwendet zu haben.

Rasmus Revermann, 20.12.2006