Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems

Patrick Patthey[1], Sven Wirthner[1], Natalina Signorell[1] and Raphaël Arlettaz[1,2,3,*]

[1]*Zoological Institute, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland;*
[2]*Swiss Ornithological Institute, Valais Field Station, Nature Centre, 3970 Salgesch, Switzerland; and* [3]*The Ecology Centre, University of Queensland, St Lucia, QLD 4072, Australia*

Summary

1. Tourism and leisure activities have increased continuously all over the world during the past decades, exerting a growing pressure upon naturally fragile ecosystems, such as mountainous habitats. Recent studies have established that disturbance by outdoor winter sports (e.g. skiing, snowboarding and snowshoeing) is a source of stress for wildlife. This may in turn affect its abundance, but we still lack quantitative evidence.

2. We tested the effect of outdoor winter sports (ski lifts and related recreational activities) on the abundance of the alpine black grouse *Tetrao tetrix*, a vulnerable indicator species of the timberline ecosystem, the favoured habitat for outdoor winter sports in the European Alps.

3. Generalized linear models and a model selection approach were used to rank environmental factors influencing black grouse abundance and to make predictions about population status in the theoretical absence of ski resorts. We modelled the number of displaying cocks along census transects in spring, as a function of habitat characteristics (vegetation structure and typology), ski lift density and hunting pressure at 15 natural sites (none or a very low level of anthropogenic disturbance) and 15 ski resorts in the south-western Swiss Alps.

4. Ski lift density and habitat typology were the principal determinants of black grouse abundance, whereas hunting pressure had no discernable effect. Ski lifts and related winter sport activities had a strong negative effect on the number of displaying cocks, which may have led to a mean 36% reduction of local abundance in ski lift areas, as determined after controlling for the confounding effect of habitat type.

5. *Synthesis and applications*. Conservation action plans for black grouse should aim at reducing the multiple negative effects generated by outdoor winter sports (ski facilities and related winter sport activities). First, vegetation patchiness (i.e. a mosaic of grassy shrubland with scattered trees) should be maintained along ski runs. Secondly, wintering preserves where human access is banned or strictly limited should be promoted within ski resorts. Spatially explicit human–wildlife conflict maps can be constructed from the present model to allow delineation of those areas likely to become effective protection areas.

Key-words: AIC, alpine ecosystems, habitat quality, human disturbance, hunting, ski lifts, *Tetrao tetrix*, winter recreation

Introduction

Tourism and other public recreational activities have been continuously increasing over the past decades, even in the most remote areas of the world. They potentially constitute a new threat to endangered and vulnerable wildlife. The impact of these increasingly popular activities on wildlife is often complex and variable in space and time, with their actual effects still poorly understood (Taylor & Knight 2003; Blumstein *et al*. 2005; Sutherland 2007). Human disturbance, such as repeated flushing events of resting wildlife by people practicing outdoor winter sports, may evoke stress responses (Arlettaz *et al*. 2007). This is often associated with compensatory behavioural adaptations and incurs additional energetic costs (Baltic 2005; Williams, Lusseau & Hammond 2006). Repeated disturbance often constrains animals to occupy suboptimal habitats (Taylor & Knight 2003; Thiel *et al*. 2008), and may affect reproductive and survival functions

*Correspondence author. E-mail: raphael.arlettaz@nat.unibe.ch

as well as overall fitness (Mullner, Linsenmair & Wikelski 2004; Watson & Moss 2004). The combination of these detrimental effects will ultimately lead to a reduction of local population density, if not species richness (Mallord *et al.* 2007; Rolando *et al.* 2007; Walker, Naugle & Doherty 2007).

Through the steady increase of the winter tourism industry mountainous and alpine ecosystems are put at risk due to their natural fragility. The construction of ski lifts has profoundly modified the landscape through total destruction, degradation and/or fragmentation of the original natural habitats (Wipf *et al.* 2005). Animals inhabiting alpine habitats already have a finely-tuned physiology for coping with the harsh winter conditions (Marchand 1996). They now in addition have to cope with disturbance generated by winter sport activities (Arlettaz *et al.* 2007). It has also been established that close to mountain hostels and restaurants, the density of generalist predators may be artificially increased by the availability of food remains and other garbage (Storch & Leidenberger 2003). Independent of the increase of winter tourism, the progressive abandonment of traditional farming practices, such as cattle grazing, may further reduce the overall species richness and attractiveness of these habitats for wildlife due to diminished heterogeneity and patchiness of the landscape (Laiolo *et al.* 2004). Finally, hunting, which bears great cultural and economic significance in the Alps, could additively impact on the dynamics of wildlife populations that are already weakened by other factors (Baines & Lindén 1991).

The black grouse *Tetrao tetrix* is a key indicator species of timberline ecosystems, which is suffering a decline in parts of its geographic distribution (Storch 2007). In the Alps, severe declines have been reported locally in the recent past, especially in marginal areas far from the species' core distribution range (Zbinden, Salvioni & Stanga 2003). Alpine black grouse live almost all year-round within the narrow timberline belt [1800–2300 m above sea level (a.s.l.)], where most ski facilities and related winter recreation concentrate. The International Union for the Conservation of Nature (IUCN) has suggested that this decline is linked to the spread of winter sports, although scientific evidence is lacking (Storch 2007).

The aim of the present study was to quantify and rank the various threats affecting black grouse population dynamics in the north-western European Alps. Specifically, we assess the relative impact of ski lifts and related outdoor winter sport activities, as well as hunting pressure, on black grouse abundance, while controlling for the effect of habitat type.

Methods

STUDY AREA

The study was conducted in the Swiss Alps, within the cantons of Valais and Vaud (south-western Switzerland, 46°10′N, 7°20′E), between 1400–2300 m a.s.l. (Klaus *et al.* 1990). The study area is situated on both sides of the Rhône Valley, which extends from the Lake of Geneva to the Rhône glacier and covers an area of about

3000 km^2. The dominant tree species of the upper subalpine forests and the adjacent timberline is larch *Larix decidua*, with arolla pine *Pinus cembra* present in the centre of the study area. Spruce *Picea abies* dominates the more marginal areas in the Prealps. Dwarf shrubs (*Ericaceae*, *Rhododendron ferrugineum* L., *Juniperus communis* L.) and grasses (*Nardus stricta* L., *Calamagrostis villosa* L., etc.) represent the understorey. The climate is sub-continental to continental, with warm, dry summers, and cold, relatively wet winters (Reisigl & Keller 1999).

BLACK GROUSE ABUNDANCE

Black grouse abundance was estimated by counting lekking males displaying at or above the timberline, along transects, in spring 2005. Fifteen ski resort and 15 'natural' sites were chosen with the following key selection criterion: the presence of a lookout (accessible on foot) from which an observer could recognize (using a telescope) cocks displaying along a 1·5 km transect situated on the opposite side of the valley at the same elevation, without interfering with the birds' behaviour. The mean ($\pm$ SD) observation distance was 2·1 $\pm$ 1·1 km; this did not differ between natural sites and ski resorts (*t*-test, $t = 0.25$, $P = 0.80$). Disturbed sites were all located within ski resorts, with at least one ski facility (e.g. ski lift) crossing the transect and several other facilities in the surroundings. The natural sites were areas with minimal or limited disturbance by outdoor winter sports – including ski mountaineering – and absence of ski lifts within a radius of 3 km around the centre of the transect. Transects were distributed across the study area at least 1·5 km apart and averaging ($\pm$ SD) 4·6 $\pm$ 3·4 km. As adult male black grouse are sedentary (Klaus *et al.* 1990; P. Patthey *et al.* unpublished data), mean natal dispersal distance for juvenile males in the Alps (Caizergues & Ellison 2002) and mean recorded distance between leks along the timberline in the Alps (Klaus *et al.* 1990) is ~1·5 km; thus, the distribution of transects reduced the risk of counting the same cocks on two different transects and consequently, any risk of interdependency between transects. Censuses were performed three times during the season from mid-April until late May (Klaus *et al.* 1990). Detection probability was high as black grouse males with their black plumage were highly conspicuous against the snow background. The sampling protocol for site visits was randomized in a pairwise fashion, ensuring equal number and timing of visits to ski resort and natural sites during each of the census period. Surveys started at dawn and consisted of three 15-min periods of observation, separated by 15-min gaps. Local abundance of black grouse was estimated as the maximum number of displaying cocks observed simultaneously, in any of the nine 15-min censuses, in a habitat belt along each transect (100 m below and 200 m above the timberline).

PREDICTORS OF ABUNDANCE

Habitat typology

We mapped 13 different habitat types along the transects (including a 20-m buffer), which encompassed all main habitats present in the altitudinal belt where black grouse occur. Mapping was performed by the same observer in August 2005, by walking along each transect at the average elevation of displaying cocks. We recorded the boundaries of each habitat type with a Global Positioning System (GPS; Garmin eTrex Summit, Garmin Ltd, USA). Habitat types were characterized based on the vertical and horizontal vegetation structure, and accounting for a humidity

gradient (Supporting Information Table S1). This enabled us to estimate the local proportion of each of the habitat types. To reduce both the number of variables and their interdependency, we performed a principal component analysis (PCA), based on these proportions. The five main factor(s) encompassing most (63%) of the system variance (principal components PC-1 to PC-5; selected with the broken-stick method; Jackson 1993) were used in subsequent analyses (thereafter HABITAT predictors). Principal components were standardized.

Ski lifts and winter sport activities

We used ski lift density as a proxy for landscape-habitat alterations by outdoor winter sports and disturbance by sportspeople in winter. These two factors are thus confounded in the present study. As we could not assess how far skiers may move from ski lifts (off-piste, or free-riding recreation, see Arlettaz *et al.* 2007), potentially representing a source of disturbance, we constructed several GIS raster maps. First, we estimated ski lift density (length of all types of lift wire per surface [m 100 m^{-2}]) within circular buffers of 250, 500, 750, 1000 and 1500 m radii. Secondly, we built a sixth map of the minimum distance to the nearest ski lift cable. Raster maps had a cell size of 625 m^2. As with habitat variables, we performed a PCA on these GIS ski lift maps. For further analyses, we retained only the first principal component (PC-1), which explained 80% of the overall variance. PC-1 correlates negatively with mean distance to ski lifts, and positively with densities of ski lifts within different radii. It can thus be seen as a compound index of ski lift density and winter sport activities (SKI LIFTS). Finally, the mean PC-1 pixel value was calculated for each census transect.

Hunting pressure

In some Alpine cantons of Switzerland, black grouse cocks can still be hunted during late autumn, outside federal and cantonal game reserves. To obtain a spatial estimate of hunting pressure, the area within a community territory (the smallest administrative unit) was restricted both to the altitudinal belt occupied by black grouse (1400–2300 m a.s.l.) and to the area subjected to hunting, excluding game reserves. The mean harvests for 2000–2004 (long-term cumulative effect) and for only 2004 (short-term effect) were attributed to these areas. On the basis of the geo-referenced maps, we calculated the harvest density within circular buffer radii similar to the procedure used for SKI LIFTS. Principal component analyses were run with the five resulting variables. The first principal component from each analysis (2000–2004, 96% of variance; 2004, 95% of variance) was retained for the following analyses. These two components were positively correlated to harvest densities and were used as indices of hunting pressure (HUNTING). Mean pixel values of the resulting PC-1 maps were extracted for each transect.

MODELLING BLACK GROUSE ABUNDANCE

We used a Generalized Linear Model procedure, with Poisson error distribution and a log link function (McCullough & Nelder 1989) to model black grouse abundance as a function of habitat typology, ski lift density and hunting pressure:

$$\log(p) = \beta_0 + \beta_1 X_1 + ... + \beta_N X_N,$$

where p is the abundance, X_N the Nth predictor and β_N is the Poisson regression coefficient. We followed an information-theoretic

Table 1. Summary of the model selection procedure for predicting Alpine black grouse abundance. The seven candidate models (see the combinations of X) include the following descriptors: habitat type (HABITAT), ski lifts and winter sport activities (SKI LIFTS), and hunting pressure (HUNTING). The models are ranked according to Akaike's Information Criterion (AIC$_c$) and their weights (w_i). k indicates the number of parameters in the model

SKI LIFTS	HABITAT	HUNTING	k	ΔAIC$_c$	w_i
X	X		4	0·00	0·872
X	X	X	6	3·91	0·123
X			2	11·05	0·003
	X		3	14·36	0·001
X		X	4	14·85	0·001
	X	X	5	16·05	0·000
		X	3	27·03	0·000
0·999*	0·996*	0·124*			

*selection probability (see Material and methods for details).

approach (Burnham & Anderson 1998; Johnson & Omland 2004) and predefined seven candidate models (Table 1), resulting from the combinations of the three main groups of predictors: HABITAT, SKI LIFTS and HUNTING. Models were ranked according to Akaike's Information Criterion, corrected for small samples (AIC$_c$), AIC$_c$ differences (ΔAIC$_c$) and Akaike weights (w_i). We used a two-stage process (e.g. Johnson *et al.* 2005). First, we selected the best set of predictors within the HABITAT group of variables. Among all possible combinations of PC-1 to PC-5, we retained the predictors that had ΔAIC$_c$ < 2, compared to the best sub-model (i.e. the best model within the group of predictors; Burnham & Anderson 1998). Secondly, we integrated these sets of predictors, where appropriate, into the seven candidate models. Our approach allowed the number of predictors to be reduced and the most likely explanatory predictors selected. This also avoided testing all possible combinations of predictors, which would have dramatically increased the number of candidate models at the second stage. We estimated the relative importance of each group of predictors by summing the AIC$_c$ weights for each group across all models that contained that group of predictors. According to Burnham & Anderson (1998), this sum corresponds to a selection probability. Finally, we used a model-averaging approach to estimate coefficients and 95% confidence intervals (CI) for each predictor into a final, general model (Burnham & Anderson 1998). The predictive performance of the final model was evaluated with a Spearman's rank correlation test (r_s) (e.g. Potts & Elith 2006), coupled with a randomization procedure (Vaughan & Ormerod 2005). This procedure had to be adopted, first, because our sample size would have been too small ($n = 30$ sites) to reasonably cross-validate our model; and secondly, because there is no other similar abundance data for other sites in the Swiss Alps, rendering it impossible to validate with an external data set. Thus, we generated 1000 bootstrap samples of equal size to the original data set by random sampling with replacement. For each bootstrap sample, we recalculated the model coefficients. We used these and the original data set to predict black grouse abundance and to estimate the correlation between the predicted and observed abundance. We also computed the mean and standard deviation of the Spearman's rank correlation tests. This method simulates the use of independent data to evaluate the predictive performance of the original model (Vaughan & Ormerod 2005). We considered the correlation to be significant if the Spearman's tests were statistically significant ($P < 0.05$) more than 950 times from the 1000

bootstrap repeats (Manly 1997). Homosedasticity and normality were determined based on residuals.

CONSTRUCTING LARGE-SCALE ABUNDANCE MAPS

The habitat typology section of the black grouse abundance model was based on precise data collected in the field. Such detailed habitat maps do not exist across the entire study area, contrary to the self-constructed GIS HUNTING and SKI LIFTS maps. It was therefore not possible to directly and spatially extrapolate the relationships between local bird abundance and habitat type to the entire study area. In order to construct predictive abundance maps, we had to find GIS surrogates for the HABITAT principal components. First, we extracted monthly indices of vegetation productivity (NDVI, see Pettorelli *et al.* 2005) from three LANDSAT-5 satellite images taken in April, May and August 1998. In subsequent analyses, we retained the first principal component obtained through a PCA conducted on these three NDVI data sets. Secondly, for each of the three monthly satellite images, we ran a separate PCA using six reflectance wavelengths in the visible (blue, green, red), near-infrared, shortwave, and thermal infrared sections of the electromagnetic spectrum, again retaining PC-1 from each seasonal analysis, for use in subsequent analyses. Another PCA was finally carried out on these three monthly principal components, in order to integrate the information obtained throughout the season. We then used a vector-based habitat data base (Swisstopo, Wabern, Switzerland) to calculate the density of isolated trees, bushes, open forests and closed forests, in circular buffers, using the same buffer radii as for the other predictors (see above) and likewise, the first factor(s) of a PCA applied to these density maps were retained for further analyses. Then, we performed stepwise (forward and backward) linear regression to model surrogates of the HABITAT PCs. The independent variables were the GIS habitat predictors created previously and their associated quadratic terms. Here, we used stepwise modelling instead of model averaging, since we wanted to obtain a simple model and, additionally, we were not interested in the model composition (Whittingham *et al.* 2006). We used R^2 to assess whether a given model had sufficient predictive power to be considered reliable.

A post-development abundance map for the period following the construction of the ski resorts, based on present-day habitat typology (main vegetation communities only change over the very long term in the Alps) was generated by applying the black grouse abundance model using the HABITAT surrogates, as well as the SKI LIFTS and HUNTING maps. Similarly, a final pre-development abundance map (i.e. in the theoretical absence of ski lifts and related winter sport activities) was created using the abundance model; this time, however, the overall SKI LIFTS predictor was held constant, using the average value obtained from the natural sites. This approach was used to predict the effect of winter tourism development on black grouse abundance, whilst accounting for other covariates.

We used ArcGIS 9·1 (Environmental Systems Research Institute, California), IDRISI32 (Clark Labs) and Biomapper (Hirzel, Hausser & Perrin 2002) software for GIS analyses. Statistical analyses were performed using the statistical package R (version 2·4·0, R Core Team 2006).

Results

MODEL SELECTION

Between one to 20 black grouse cocks (average ± SD: 5·6 ± 4·2) were observed along the 30 transects. During the first stage of the model selection process, two HABITAT predictors (HABITAT PC-2 and PC-5) substantially explained the black grouse abundance pattern within this predictor group. These were retained for the second stage of modelling and integrated in the seven subsequent candidate models. These two predictors were not correlated with the SKI LIFTS predictor ($r_s = -0·10$, $P = 0·60$ and $r_s = 0·10$, $P = 0·62$, respectively). Neither were the two HUNTING pressure indices (i.e. the long-term cumulative and the short-term effect) correlated with the SKI LIFTS predictor ($r_s = -0·29$, $P = 0·13$ and $r_s = -0·32$, $P = 0·09$, respectively), showing that ski resorts and natural sites did not differ regarding hunting pressure and habitat typology.

Among the set of candidate models, SKI LIFTS and HABITAT variables were the most likely ecological correlates of black grouse abundance (selection probabilities of 0·999 and 0·996, respectively; Table 1). In comparison, the probability of linking HUNTING predictors with black grouse abundance was lower (0·124). The most parsimonious model consists of a combination of SKI LIFTS and HABITAT predictors ($w_i = 0·87$; Table 1), with a good predictive power, as shown by the significant correlation between observed and predicted abundance ($r_s = 0·54 ± 0·08$, $P < 0·05$).

BLACK GROUSE ABUNDANCE MODEL

In the averaged model, both HABITAT PC-2 and PC-5 were positively correlated with black grouse abundance. We ranked raw habitat variables by combining (not shown) their loadings with the Poisson regression coefficients (Table 2); high proportion of mixed *Rhododendron–Vaccinium* shrubs, open young forest with grass-Ericaceae, open old forest with grass, *Alnus* forest and open old forest with grass-Ericaceae were associated with high black grouse abundance. Among these habitat variables, mixed *Rhododendron–Vaccinium* shrubs clearly had a stronger effect. On the contrary, a high proportion of other habitat types, but mainly of rocks and scree, *Rhododendron-Vaccinium* and pasture, *Juniperus* and pasture, open young forest with grass and *Juniperus* shrubs decreased the likelihood of high black grouse abundance.

The covariate SKI LIFTS PC-1 had a negative effect on black grouse abundance, meaning that a higher density of ski lifts and a shorter distance to them lowered the abundance of black grouse (Table 2). According to their PC loadings, higher ski lift densities within radii of 500 to 1000 m have a stronger negative effect than a higher ski lift density close to the transect (250 m; Table 2).

The two HUNTING predictors were not correlated with black grouse abundance, as their coefficients overlapped with zero (0·0041, 95% CI: −0·0058 – 0·0139; −0·0045, CI: −0·0142 – 0·0053, respectively). Moreover, the HUNTING predictors had a low model selection probability (Table 1).

Thus, we predicted black grouse abundance as a function of the SKI LIFTS predictor by holding the HABITAT predictors constant at their mean value, and without considering any effect of HUNTING. Mean predicted black grouse abundance in natural sites was 6·6 cocks 1·5 km^{-1} linear transect along the timberline vs. 4·2 in ski resorts (Fig. 1).

Table 2. The SKI LIFTS and the two HABITAT variables derived from a principal component analysis, included in the averaged Poisson regression model of black grouse abundance. Proportion of the variance accounted for by the principal component is indicated between brackets. Loadings are the correlation coefficients of each original variable onto the principal components (PC). SKI LIFTS PC-1 is composed of five densities of ski lifts (calculated in circles of 250, 500, 750, 1000 and 1500 m radii; r is for radius) and the minimum distance to the nearest ski lift

SKI LIFTS PC-1 (80%)		HABITAT PC-2 (14·6%)		HABITAT PC-5 (9·3%)	
Variable	Loading	Variable	Loading	Variable	Loading
Density r250	0·81	*Juniperus* shrub	–0·37	Rocks, scree	–0·36
Density r500	0·94	Open old forest with Ericaceae	–0·28	Pasture with *Juniperus*	–0·35
Density r750	0·97	Dense *Alnus viridis* forest	–0·27	Pasture with *Rhododendron, Vaccinium*	–0·34
Density r1000	0·96	Open young forest with Ericaceae	–0·23	Open young forest with grass	–0·23
Density r1500	0·90	Open young forest with grass	–0·16	Alpine pasture	–0·16
Distance	–0·51	Rocks/scree	–0·14	Open old forest with grass, Ericaceae	–0·14
		Pasture with *Rhododendron, Vaccinium*	–0·11	Open young forest with Ericaceae	–0·08
		Alpine pasture	–0·10	Open old forest with grass	–0·05
		Pasture with *Juniperus*	–0·03	*Juniperus* shrub	–0·03
		Mixed *Rhododendron–Vaccinium* shrub	0·05	Open young forest with grass, Ericaceae	0·03
		Open old forest with grass	0·37	Open old forest with Ericaceae	0·05
		Open young forest with grass/Ericaceae	0·39	Dense *Alnus viridis* forest	0·42
		Open old forest with grass/Ericaceae	0·55	Mixed *Rhododendron–Vaccinium* shrub	0·59
Poisson regression coefficient	–0·051		0·171		0·244
SE	0·014		0·075		0·072
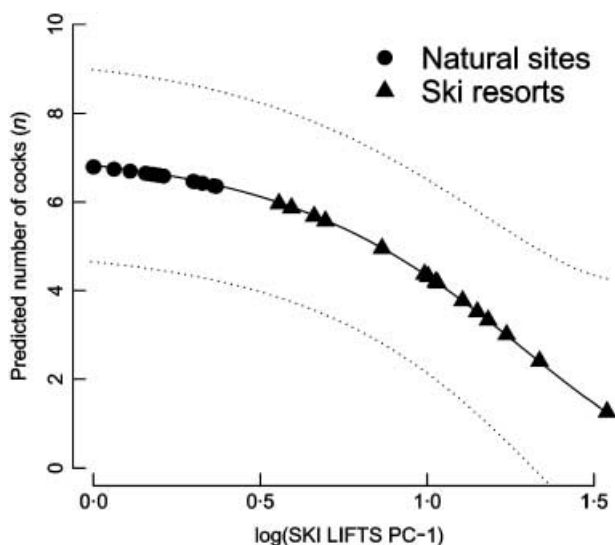
Fig. 1. Predicted Alpine black grouse abundance relative to ski lifts and winter sport activity with 95% confidence limits. Abundance was allowed to vary with the ski lifts and winter sport activity index (SKI LIFTS PC-1), while HABITAT covariates were held at their mean values. Predictions are based on the averaged model.

This would translate to a 36% mean reduction of abundance within ski lift areas, compared to natural sites. Based on this result and on the relationship between the SKI LIFTS index and our site classification into ski resorts or natural sites (Fig. 1), we estimated that 20% of the potential range of black grouse in our study area is already moderately affected by winter sports close to ski facilities [Fig. 1; 0·5 < log (SKI LIFTS PC-1) < 1; with abundance of cocks reduced by ~18%]. The proportion of the area already under high pressure is

24% [Fig. 1: log (SKI LIFTS PC-1) > 1, ~49% reduction in abundance]. This leaves 56% of the potentially suitable area for black grouse currently unaffected by winter recreation linked to ski resorts. Extrapolating from these figures, we can estimate that the development of ski lifts and related winter sport activities, has contributed to a 15% reduction of the whole Valais black grouse population (56% × 0% + 20% × 18% + 24% × 49%).

BLACK GROUSE ABUNDANCE MAP

It was possible to find adequate GIS surrogates for the HABITAT predictors selected in the final averaged model (Supporting Information Table S2). The linear regression between the HABITAT predictors and their GIS surrogates showed good predictive power (HABITAT PC-2 = 1·00 ± 0·18 × HABITAT PC-2 GIS surrogate, $P < 0.0001$, $R^2 = 0.49$; HABITAT PC-5 = 1·00 ± –0·09 × HABITAT PC-5 GIS surrogate, $P < 0.0001$, $R^2 = 0.80$). Post-development and pre-development abundance maps constructed for a major ski resort in the European Alps gives a visual representation of the negative impact of ski lifts and related winter sport on activities black grouse (Fig. 2).

Discussion

This study provides the first quantitative evidence that ski lifts and related outdoor winter sports negatively impact on a key alpine indicator species on a large scale. Our model suggests that black grouse abundance is approximately 36% lower in ski resort sites than in natural areas, after accounting for the effect of habitat type, given that grassy shrubland with
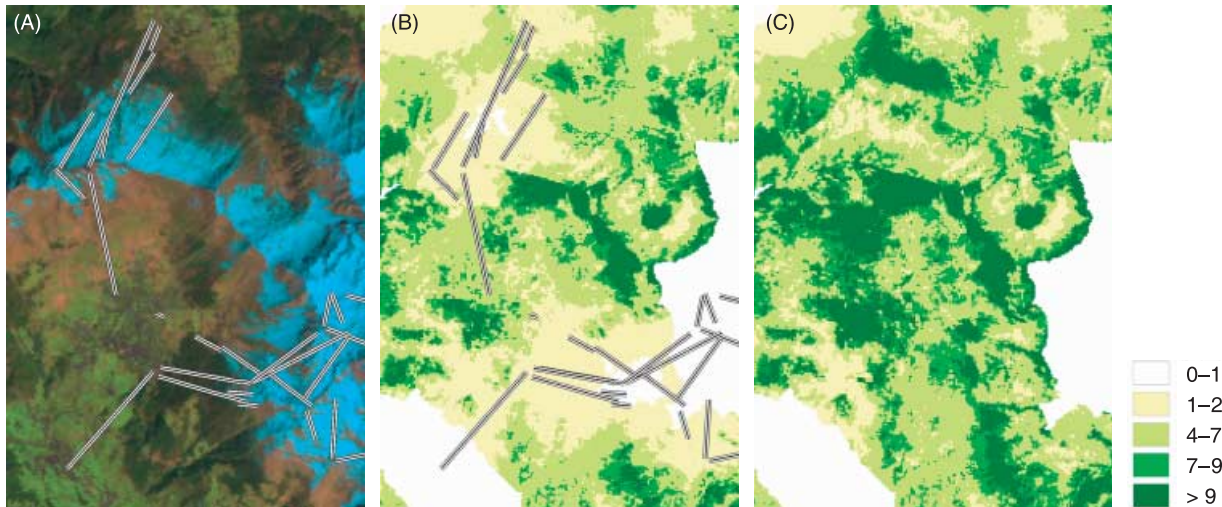
Fig. 2. Illustration of the effect of ski lifts and winter sports activity on relative spatial abundance of black grouse in the ski resort of Verbier, Valais. (A) Satellite view: blue, snow cover; dark green, closed forests; dark red, shrubland; light green, pasture; violet, built areas. (B) Current abundance map (post-development, i.e. after the construction of the ski resort). (C) Pre-development abundance map: theoretical distribution in the absence of ski lifts. Lines depict aerial ski lift cables. In B and C, colour gradient indicates the predicted number of cocks per horizontal transect of 1·5 km. The negative effect of ski lifts on relative abundance is recognizable: the average pixel value is 5·1 ± 2·8 cocks for the current situation and 6·9 ± 3·0 cocks for the pre-development situation.

scattered trees is the most favoured habitat type (N. Signorell *et al.* unpublished data). Modification of native vegetation on ski runs has been shown to reduce faunal species richness up to 100–200 m from the ski runs (Wipf *et al.* 2005; Rolando *et al.* 2007). Ski resorts also affect threatened wildlife on a much broader scale, predominantly within 500–1000 m distance, and up to 1500 m from ski lifts (this study). Influences at a larger scale cannot be ruled out as 1500 m was our greatest radius. Our estimation suggests that ski facilities and the related winter sport activities may induce a 15% decrease in the carrying capacity of the entire black grouse population in Valais. We have to stress here that this estimate is very conservative, as it only accounts for the impact of outdoor winter sports close to ski resorts. Actually, Arlettaz *et al.* (2007) have shown that rapidly spreading, free-riding winter sports such as ski mountaineering, evoke a stress response in black grouse well beyond the boundaries of the marked snow fields of ski resorts.

The negative effect of ski lifts and related winter sport activities on black grouse abundance is probably due to a combination of different factors: (i) habitat destruction or alteration (Ingold 2005); (ii) higher predation rate caused either by habitat fragmentation, which increases foraging opportunities for predators (Storch, Woitke & Krieger 2005), or by deposition of food remains, which may enhance predator density (Storch & Leidenberger 2003; Wittwer *et al.* unpublished data); (iii) increase of direct disturbance by humans inducing higher stress levels (Arlettaz *et al.* 2007; Thiel *et al.* 2008) and extra energetic, compensatory costs (Baltic 2005); finally, (iv) additional mortality due to collisions with cables (Miquet 1986). At this stage, we still do not know which factor(s) contribute most to lowering black grouse density in the Alps. In a recent study from England, Baines & Richardson (2007) did not detect any difference

in fecundity or summer flushing distance between varying experimental disturbance treatments, which would possibly infer an effect of predation. However, English black grouse do not face such harsh winters as their Alpine relatives; they are also less exposed to human disturbance from recreational activities (e.g. no skiing facilities). Refined investigations are thus required in the Alps to disentangle these various factors. We recommend that winter disturbance intensity should be measured through an assessment of the actual winter sport traffic, instead of relying on a crude ski lift density index, as in this study.

Our results confirm former views that both young and old open forest stands, with a wide Ericaceae-grass cover represent preferred black grouse habitat in the European Alps (Swenson & Angelstam 1993; Storch 2007; Pearce-Higgins *et al.* 2007; N. Signorell *et al.* unpublished data). Common habitat features across species' range seem to be richly structured, semi-open habitats with scattered trees, within a matrix dominated by a mosaic of shrubs and grasses.

We did not find any significant link between hunting pressure and black grouse abundance. It seems therefore likely that at the scale of our study area, hunting is principally a trigger of compensatory mortality (Zbinden *et al.* 2003), where harvesting is relatively low (104–187 cocks shot yearly in our study area (3000 km^2), with an unknown black grouse population size). These results contrast with the past situation in the UK, where hunting mortality was observed to be locally additive (Baines & Lindén 1991). Although the current hunting regime had no discernable effect on black grouse abundance, at least compared to other more decisive factors, such as habitat type and presence of ski lifts, it would be interesting to see whether, and if so, how, hunting affects local survival and population dynamics. This holds especially for

areas where harvesting is intensive, such as in highly accessible areas, namely ski resorts. The development of individual-based capture–recapture models (using marked birds) could provide decisive insights and lead to the development of spatially explicit hunting plans adapted to the local geographic context.

Conservation implications

Given the great number of ski resorts in the European Alps, a negative impact of ski lifts and related recreational activities on black grouse is likely to be widespread. According to our estimation, a quarter to a half of the potentially suitable black grouse habitat in Valais is potentially affected. This does not include human disturbance outside the main ski resorts, caused mostly by the rapid spread of free-riding winter sports (Arlettaz *et al*. 2007).

Clear guidelines for species conservation can be drawn from our results. First, alpine vegetation is often severely damaged by both skiing and the preparation of ski runs (Wipf *et al*. 2005): shrubs, small trees and grass cover are reduced in height and density in order to smooth the ski runs (although this may also restrict natural shrub encroachment following abandonment of traditional grazing practices). In addition, road networks are generally more dense, to facilitate access and maintenance of the facilities (Ingold 2005). The conservation or restoration of a patchy shrub–grass vegetation cover should be promoted along ski runs and roads along the timberline. Where the preservation of a vegetation mosaic is not possible or where damage is already too severe, restoration methods such as safe-site islands, that is, small undisturbed patches of native plants (Urbanska 1997), grass seeding (Bayfield 1996) and transplants of native grass (Fattorini 2001), may be applied to help accelerate the recolonization process of the native vegetation. In areas where closure of vegetation and bush encroachment have occurred after the abandonment of summer pastures (Laiolo *et al*. 2004), forestry measures should be considered, such as tree-thinning and removal of dense bush cover. Alternatively, extensive farming practices, such as grazing, should be promoted (Storch 2007).

The present study could not identify the proximate mechanisms that affect black grouse abundance. These are likely to be embedded within our general index of ski lifts and winter sport activities, which mostly impact on local black grouse abundance. Previous studies, however, have shown that black grouse have to cope with a more pronounced stress challenge within ski resorts and ski mountaineering areas, compared to natural, undisturbed sites (Arlettaz *et al*. 2007). Additionally, repeated flushing events induce an immediate stress response (Arlettaz *et al*. 2007), as well as extra energetic costs linked to compensatory feeding in disturbed birds (Baltic 2005). The creation of specific wintering preserves within ski resorts may therefore improve the survival of black grouse, potentially leading to an increase in their local abundance. Our pre-development abundance map (abundance of black grouse in the theoretical absence of ski lifts and related winter recreation) offers the opportunity to locate suitable sites (e.g. Doherty *et al*. 2008), providing vegetation conditions are not too degraded. In these refuges, human access should be banned or severely restricted throughout the winter. Our spatial abundance model may also serve as a tool for creating or modifying ski lift routes, so that their impact on wildlife is minimized. Alternative ski lift routes may be evaluated by virtually modifying the landscape and assessing the effect on black grouse abundance (e.g. Johnson *et al*. 2005). In addition, virtual modification of habitat typology could also be tested. The comparison of these scenarios, or of pre-development maps with maps of winter sport activities, should enable zones of potentially high human-wildlife conflict to be recognized, and sustainable, wildlife-friendly management of ski resorts to be promoted. Nevertheless, we recommend creating new abundance maps based directly on raw GIS data (without referring to surrogates) to delineate the spatial distribution of black grouse abundance. The main reason for basing our modelling on habitat surrogates was to allow the impact of our groups of predictors on the abundance of black grouse to be tested independently. This was the only way to evaluate different scenarios of habitat management in a biologically meaningful way.

Based on our results, we predict that regions of the Alps where black grouse habitat is suboptimal (shrub encroachment, closure of forest stands, etc.) such as at the periphery of the species' Alpine distribution, and which also harbour extensive ski resorts, will experience severe declines in their black grouse population (Zbinden *et al*. 2003). In more central locations, where populations are more stable, further declines are to be expected if the winter tourism industry continues to expand, which seems very likely (Arlettaz *et al*. 2007). Although further research is needed to identify the main mechanism(s) involved in the decline of black grouse populations, the mitigation measures listed above, which aim to increase local carrying capacity, should be implemented at an early stage. If so, they are likely to benefit key indicator species and other elements of biodiversity within the Alpine timberline ecosystems.

References

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R. & Jenni-Eiermann, S. (2007) Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proceedings of the Royal Society, Series B*, **274**, 1219–1224.

Baines, D. & Lindén, H. (1991) The impact of hunting on grouse population dynamics. *Ornis Scandinavica*, **22**, 245–246.

Baines, D. & Richardson, M. (2007) An experimental assessment of the potential effects of human disturbance on Black Grouse *Tetrao tetrix* in the North Pennines, England. *Ibis*, **149** (Suppl. 1), 56–64.

Baltic, M. (2005) *Impact of human disturbance on Alpine wildlife in winter: stress, activity and energetics in the endangered black grouse* Tetrao tetrix. Inaugural dissertation, Universität Bern, Bern, Switzerland.

Bayfield, N.G. (1996) Long-term changes in colonization of bulldozed ski pistes at Cairn Gorm, Scotland. *Journal of Applied Ecology*, **33**, 1359–1365.

Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A. & Garity, S.C. (2005) Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, **42**, 943–953.

Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference*. Springer-Verlag, New York.

Caizergues, A. & Ellison, L.N. (2002) Natal dispersal and its consequences in black grouse *Tetrao tetrix*. *Ibis*, **144**, 478–487.

Doherty, K.E., Naugle, D.E., Walker, B.L. & Graham, J.M. (2008) Greater sage-grouse winter habitat selection and energy development. *Journal of Wildlife Management*, **72**, 187–195.

Fattorini, M. (2001) Establishment of transplants on machine-graded ski runs above timberline in the Swiss Alps. *Restoration Ecology*, **9**, 119–126.

Hirzel, A.H., Hausser, J. & Perrin, N. (2002) *Biomapper 3·0*. Laboratory for Conservation Biology, University of Lausanne, Lausanne, Switzerland.

Ingold, P. (2005) *Freizeitaktivitäten im Lebensraum der Alpentiere*. Haupt, Bern, Switzerland.

Jackson, D.A. (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology*, **74**, 2204–2214.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A. & Mulders, R. (2005) Cumulative effects of human developments on arctic wildlife. *Wildlife Monographs*, **160**, 1–36.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101–108.

Klaus, S., Bergmann, H.H., Marti, C., Müller, F., Vitovic, O.A. & Wiesner, J. (1990) *Die Birkhühner*. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany.

Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, **41**, 294–304.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007) Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, **44**, 185–195.

Manly, B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd edn. Chapman & Hall, London.

Marchand, P.J. (1996) *Life in the Cold*, 3rd edn. University Press of New England, Hanover, NH, USA.

McCullough, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, New York.

Miquet, A. (1986) Premiers résultats d'une enquête sur la mortalité du Tétras lyre par percussion dans les câbles. *Bulletin mensuel de l'Office National de la Chasse*, 33–36.

Mullner, A., Linsenmair, K.E. & Wikelski, M. (2004) Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation*, **118**, 549–558.

Pearce-Higgins, J.W., Grant, M.C., Robinson, M.C. & Haysom, S.L. (2007) The role of forest maturation in causing the decline of Black Grouse *Tetrao tetrix*. *Ibis*, **149**, 143–155.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**, 503–510.

Potts, J.M. & Elith, J. (2006) Comparing species abundance models. *Ecological Modelling*, **199**, 153–163.

R Development Core Team (2006) ʀ: *A Language and Environment for Statistical Computing*. ʀ Foundation for Statistical Computing, Vienna, Austria.

Reisigl, H. & Keller, R. (1999) *Lebensraum Bergwald*, 2nd edn. Spektrum Akademischer Verlag, Heidelberg, Germany.

Rolando, A., Caprio, E., Rinaldi, E. & Ellena, I. (2007) The impact of high-altitude ski-runs on alpine grassland bird communities. *Journal of Applied Ecology*, **44**, 210–219.

Storch, I., ed. (2007) *Grouse: Status Survey and Conservation Action Plan 2006–2010*. IUCN, The World Pheasant Association, Gland, Switzerland.

Storch, I. & Leidenberger, C. (2003) Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. *Wildlife Biology*, **9**, 301–308.

Storch, I., Woitke, E. & Krieger, S. (2005) Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. *Landscape Ecology*, **20**, 927–940.

Sutherland, W.J. (2007) Future directions in disturbance research. *Ibis*, **149**, 120–124.

Swenson, J.E. & Angelstam, P. (1993) Habitat separation by sympatric forest grouse in Fennoscandia in relation to boreal forest succession. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **71**, 1303–1310.

Taylor, A.R. & Knight, R.L. (2003) Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications*, **13**, 951–963.

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R. & Jenni, L. (2008) Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. *Journal of Applied Ecology*, **45**, 845–53.

Urbanska, K.M. (1997) Restoration ecology research above the timber line: colonization of safety islands on a machine-graded Alpine ski run. *Biodiversity and Conservation*, **6**, 1655–1670.

Vaughan, I.P. & Ormerod, S.J. (2005) The continuing challenges of testing species distribution models. *Journal of Applied Ecology*, **42**, 720–730.

Walker, B.L., Naugle, D.E. & Doherty, K.E. (2007) Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management*, **71**, 2644–2654.

Watson, A. & Moss, R. (2004) Impacts of ski-development on ptarmigan (*Lagopus mutus*) at Cairn Gorm, Scotland. *Biological Conservation*, **116**, 267–275.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, **75**, 1182–1189.

Williams, R., Lusseau, D. & Hammond, P.S. (2006) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation*, **133**, 301–311.

Wipf, S., Rixen, C., Fischer, M., Schmid, B. & Stoeckli, V. (2005) Effects of ski piste preparation on alpine vegetation. *Journal of Applied Ecology*, **42**, 306–316.

Zbinden, N., Salvioni, M. & Stanga, P. (2003) *La situazione del fagiano di monte* Tetrao tetrix *nel Cantone Ticino alla fine del ventesimo secolo*. Schweizerische Vogelwarte/Stazione ornitologica svizzera and Dipartimento del territorio, Ufficio della caccia e della pesca e Sezione forestale del Cantone Ticino, Bellinzona, Switzerland.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of habitat types as characterized in the field

Table S2. Composition of the GIS HABITAT surrogates

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.