Negative impact of tourist resort settlement on reproductive success of Alpine wildlife: a case study of the Black grouse *(Tetrao tetrix)*

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Abstract

1. Alpine ecosystems have faced a dramatic increase of tourism and related recreational activities over the last decades. Tourist activities and related infrastructures may negatively affect population dynamics of wildlife due to landscape modifications, increasing human disturbance and predation pressure.

2. The aim of this study was to test whether predator abundance and predation pressure, combined with human disturbance, are higher in sites with than without tourist resort settlement and whether these factors impact on the breeding success of an emblematic wildlife species, the Black grouse.

3. Our results show (I) that corvids are more abundant at the sites which are most frequently used by tourists, with extended infrastructures for recreational activities; (II) that tourist resort settlement negatively impacts on Black grouse reproductive success both directly through human disturbance and indirectly through predation.

4. Human disturbance, especially close to tourist resorts should be minimized during the critical breeding season. This could be achieved if tourists stay on marked hiking trails and avoid entering sensitive breeding habitat. Also, the deposition of human food remains around tourist stations and huts should be minimized to prevent further support for generalist predators that impact on Black grouse reproductive success.

Key words: tourism, human disturbance, predation, artificial nests, breeding success, *Tetrao tetrix*

1. Introduction

Alpine ecosystems are facing an increase of tourism and related recreational activities since decades (Wüthrich 2001, Ingold 2005). Skiing, snowboarding and snow-shoeing in winter as well as hiking, biking and hang-gliding in summer attract an increasing number of people to mountain ranges worldwide. To promote these activities, numerous infrastructures have been built in several upland regions. The effects of this increase of the tourism industry and of outdoor recreation on nature and wildlife are complex, highly variable and/or remain still poorly understood (Miller et al. 2001, Reimers et al. 2003, Finney et al. 2005, Baines & Richardson 2007, Langston et al. 2007, Sutherland 2007). Humans may influence wildlife population dynamics by reducing habitat quality (Storch 2000, Vistnes et al. 2004), disturbing the animals (Creel et al. 2002, Kerley et al. 2002, Taylor & Knight 2003, Reimers et al. 2003, Baltic 2005, Johnson et al. 2005, Arlettaz et al. 2007), if not through an alteration of interspecific interactions (Storch & Leidenberger 2003, Marzluff & Neatherlin 2006). Human-generated habitat degradation, loss and fragmentation are of primary conservation concern (Kurki et al. 2000, Storch 2000, Vistnes et al. 2004, Rolando et al. 2007). In the Alps, habitat quality decreases due to the installation of ski resorts (Rolando et al. 2007). Farmland intensification is a threat locally (Bignal & McCracken 1996, Britschgi et al. 2006), whilst the progressive abandonment of traditional farming practices, such as cattle grazing and meadow mowing, is an additional threat elsewhere (Bignal & McCracken 1996, Blanco et al. 1998, Storch 2000).

Direct human disturbance through trendy sports is a new serious source of problems, resulting in elevated stress (Creel et al. 2002, Arlettaz et al. 2007), extra energetic expenditures and costly behavioural adaptations (Fortin & Andruskiw 2003, Reimers et al. 2003, Baltic 2005), if not desertion of otherwise suitable habitats (Vistnes & Nellemann 2001, Taylor & Knight 2003, Johnson et al. 2005).

Snowsport infrastructures and tourists may offer attractive resources for Alpine wildlife. Cliff-nesting birds such as Alpine choughs (*Phyrrocorax graculus*) and Snow finches (*Montifringilla nivalis*) use buildings for nesting, whilst predators such as red foxes (*Vulpes vulpes*) and corvids profit from left food remains. Storch & Leidenberger (2003) showed that carrion crows (*Corvus corone*) and magpies (*Pica pica*) are exclusively observed at huts and that jays (*Garrulus glandarius*) occur more frequently in hut areas, whilst they are absent in areas rarely visited by humans. Tourist activities and infrastructures seem thus to positively influence the distribution and abundance of mobile opportunistic and generalist predators, which may lead to an increase in bird nest predation rate, particularly as regards ground-nesting birds. In the Cairngorms massif in Scotland, crow predation on ptarmigan (*Lagopus mutus*) eggs and chicks even led to local extinction near tourist stations. It further reduced ptarmigan breeding success as well as dampened its population cycles in the wider surroundings (Watson & Moss 2004).

Similar processes may affect other species occurring in Alpine ecosystems. The Black grouse *(Tetrao tetrix)*, an emblematic tetraonid species inhabiting the timberline zone has faced dramatic population declines in Western and Central Europe (Klaus et al. 1990, Storch 2000), including some peripheric populations in the Alps (Klaus et al. 1990, Hess 2000). Changes in land use (expansion of ski resorts and deterioration of traditionally occupied habitats after the abandonment of mountain pastures) have been suggested as major factors of decline in Alpine regions (Meile 1982, Storch 2000, Zbinden & Salvioni 2003). Wirthner (2006) showed that local density of displaying Black grouse cocks is much lower in ski resorts than in sites less exposed to human pressure. However, no difference in survival of cocks was found in anthropized vs. natural sites (Patthey et al. 2006). This suggests that another mechanism than site-specific male mortality is involved, such as lower carrying capacity, lower female survival, lower reproductive output or higher chick mortality.

Here we test whether reproductive output is affected in first line in anthropized habitats. More specifically, we first compare predator abundance and predation rate on artificial grouse nests between ski resorts and more natural sites. Second, we compare breeding success between anthropized and natural sites. We finally model the relative impacts of predation pressure and human disturbance on nest predation rate and reproductive output of Alpine Black grouse.

2. Material and Methods

2.1 Study area and study sites

The research was conducted in two regions: in Valais and Vaud (South-Western Switzerland), and in Haute-Savoie, Savoie, Isère and Hautes-Alpes (France). The study area in Switzerland is characterized by warm and dry summers and cold, relatively wet winters. Fifteen anthropized study sites (≥ 2-3 skilifts each) and 15 natural study sites (outside ski resorts, no skilift) were chosen and investigated on ± 1.5 km long survey transects (mean = 1.53 km, sd = 0.24) along the timberline zone, the main habitat of the Black grouse. The main criterion for selecting these 30 sites was the possibility to observe cocks along the transect from the opposite side of the valley (Wirthner 2006). The study area in France has similar conditions as the Swiss area but precipitation is more abundant. Here, 10 anthropized and 10 natural study sites, where Black grouse are monitored by the Observatoire des Galliformes de Montagnes (OGM) were chosen based on the same criterion as in Switzerland and were also investigated on ± 1.5 km long survey transects (mean = 1.58 km, sd = 0.15).

2.2 Black grouse abundance

Since leks of displaying Black grouse males are known to attract females (Hovi 1994) we controlled for a possible correlation between reproductive output and local density of Black grouse males. The abundance of Black grouse cocks was estimated from censuses of the spring density of lekking males. In Switzerland, the study sites were censused twice between mid April and the end of May 2006. The visit sequence was randomised among anthropized and natural sites. All Black grouse cocks present in a habitat belt along the survey transect (100 m below and 200 m above the timberline) were located from the opposite side of the valley (Wirthner 2006).

In France, the surveys were conducted by the Observatoire des Galliformes de Montagnes (OGM). Eight sites were censused three times in May 2006 whereas 12 sites were censused three times in May of previous years (1997 [n = 1], 1998 [n = 1], 2003 [n = 1], 2004 [n = 3] and 2005 [n = 6]). Here, all Black grouse cocks present in the habitat belt along the survey transects were located either when walking along the transect or from an observation point on the site (Y. Magnani, pers. comm.). For surveys of 1997 – 2005, the number of observed cocks was corrected for the survey year (Y. Magnani, unpublished data). For all Swiss and French study sites, the maximum number of simultaneously observed cocks in one of the two or three daily surveys, respectively, per transect was our estimate of local Black grouse cocks abundance.

2.3 Predation pressure

2.3.1 Predator abundance

We estimated the abundance of predators by direct observations (birds) and faecal counts (mammals) only at the Swiss sites. Corvids are reported as the main avian predators on eggs of large ground-nesting birds such as Black grouse (Andrén 1992, Baines et al. 2004, Storch et al. 2005): carrion crow (*Corvus corone*), raven (*Corvus corax*), magpie (*Pica pica*), Eurasian jay (*Garrulus glandarius*). We mapped corvid observations during 5 visits along transects in June (n = 2), July (n = 2) and August (n = 1). Time of the day (morning vs. afternoon) for visits to a given site was alternated due to potential fluctuations of detection probability. The mean sum of observed corvids per site corrected for observation duration and transect length was our estimate of avian predator abundance.

In the Alps, the most abundant mammalian generalist predator is the red fox (*Vulpes vulpes*), which is easily attracted by settlements because of human food remains (Storch & Leidenberger 2003). Several studies have established fox predation upon eggs of artificial grouse nests (Thiel 2002, Baines et al. 2004, Svobodova et al. 2004). Other predators on ground nests are pine marten (*Martes martes*), beech marten (*Martes foina*), badger (*Meles meles*), stoat (*Mustela erminea*), red squirrel *(Sciurus vulgaris;* Storch 2005, Svobodova et al. 2004) and domestic dogs *(Canis familiaris;* S. Mettaz, pers. comm.). Due to problems of detectability and determination of the faeces of some species, we only recorded scats of red fox and domestic dogs. In every study site a ± 1.5 km long scat transect (mean = 1.58 km, sd = 0.34) along hiking trails was determined that more or less paralleled the Black grouse census transect (Sadlier et al. 2004). During 3 visits in July (n = 2) and August (n = 1) scats of red fox and domestic dogs were distinguished by their shape and size (Bang and Dahlström 1986). To avoid repeated recordings of the same scats we removed the encountered droppings. The mean number of fox scats and the mean number of dog scats per site corrected for the length of the scat transect were our estimates of fox and dog abundance, respectively.

2.3.2 Predation rate

We investigated predation rate on Black grouse nests based on an experimental approach with artificial nests, this at every study site in Switzerland. Artificial nests do not experience the same predation rates as natural nests (Willebrand & Marcström 1988) and there are many potential biases associated with their use (Major & Kendal 1996, Zanette 2002). However, it is acknowledged that artificial nest experiments sufficiently reflect relative (not absolute) predation rates or local predator assemblages if the experiment is well designed (Major & Kendal 1996, Wilson et al. 1998).

At every site 13 artificial nests were placed regularly within potential Black grouse breeding habitats (Open forest with grass/Ericacea cover, *Rhododendron-Vaccinium* shrubs and pasture, *Juniperus* shrubs and pasture; Klaus et al. 1990, N. Signorell, pers. comm.) along the ± 1.5 km long transect at the timberline. The distance between nests was at least 100 m. Ten nests consisted of three small brown eggs of domestic hens (with natural egg content), but 3 additional nests consisted of one wax filled egg (for the identification of possible predators through biting marks) plus two natural brown eggs. Positions of nests with wax eggs were selected randomly among all the nests along the transect. The eggs were handled with gloves exclusively, so as to avoid the transmission of human scent. They were put in small ground depressions in the cover of the *Rhododendron* or *Juniperus* shrubs. The wax filled eggs were fixed with a string and a nail to prevent predators from carrying them away. We controlled for the nest concealment with a horizontally placed 20 x 20 cm checkerboard with 16 evenly spaced black and white squares (5 x 5 cm each; Higgins et al. 1996). Nests were placed at locations where 8 to 12 squares were covered by vegetation when viewed from 1 m upright (Manzer et al. 2005). The number of eggs per nest visible from 1 m upright was noted. The nests were installed from June 16th to 24th, i.e. during incubation peak (Klaus et al. 1990). Two to three study sites could be installed on the same day. The sequence of visits was randomised among anthropized and natural sites and, the sites were visited in the same order during successive controls after 9, 18, 36 and 48 days. A nest was considered as predated, if at least one egg was missing or damaged. We identified predators of wax filled eggs (birds vs. mammals) by tooth or beak marks left on the wax surface. The proportion of predated nests after 48 days per site was our estimate of predation pressure on Black grouse nests.

2.4 Productivity

We estimated Black grouse reproductive success with the use of trained pointing dogs and their conductors in 20 out of the 30 study sites in Switzerland and in 20 study sites in France. Ten anthropized and 10 natural study sites were chosen randomly in each country. The counts were conducted between August 18th and September 7th. Every site was controlled once according to a standardised searching method along the ± 1.5 km long transect. Black grouse were searched inside a belt within a flight distance of 125 m below and 125 m above the transect line. A pair of an anthropized and a natural site was surveyed on the same day and time of the day (morning vs. afternoon) for visits was alternated among pairs. Pointing dog controls in France were conducted by the Observatoire des Galliformes de Montagnes (OGM). In Switzerland, supervision was done by our research group. The number of observed Black grouse males, females and chicks and the coordinates of their location were recorded. The number of chicks per study site was our estimate of Black grouse yearly local productivity.

2.5 Human disturbance

2.5.1 Summer

Tourist pressure

In Switzerland tourist pressure was estimated by the number of persons counted along the same trails within the study plots which were used for recording the scats. Five surveys were carried out in June (n = 2), July (n = 2) and August (n = 1). The sequence of the visits was randomised and the time of the day (morning vs. afternoon) was alternated due to possible daily fluctuations in presence of visitors. The mean number of observed visitors per survey corrected for observation duration and transect length was our estimate of human disturbance. In France, no surveys for estimating the number of persons within the study plots could be carried out.

Hiking path and road network

In order to further estimate tourist pressure in Switzerland and France, we calculated (I) the density of the hiking path and road network and (II) the distance between the transect line along which the nests were installed and/or the chicks were counted and the nearest hiking path and road. Based on vectorial maps of hiking paths and roads we created several hiking path and road density grid maps at a resolution of 25 m (ArcGIS 9.0; Spatial analyst tool). Because we ignore up to which distance hikers can disturb Black grouse, density maps within a radius of 250, 500, 750, 1000 and 1500 m were calculated. For each transect line a mean pixel value per radius increment (5 resulting variables) was calculated as the average hiking path and road density value among all pixels within that radius, respectively. In addition, the Euclidean mean distance between the transect lines and the nearest hiking paths and roads were calculated, respectively, resulting in one hiking path and one road distance variable. Similarly, the hiking path density and road density variables for the artificial nest locations as well as the Euclidean distance between the nest locations and the nearest hiking paths and roads were calculated for the Swiss study sites.

2.5.2 Winter

Snowsport infrastructures (skilifts)

The density of skilifts and the distance between the transect lines and the nearest skilifts was used as an estimate of winter human pressure to Black grouse, both for Switzerland and France. Five skilift density variables (from 250 – 1500 m radius) and one skilift distance variable (Euclidean mean distance between the transect line and the nearest skilifts) were calculated in the same way as for the hiking path and road network. Similarly, the 5 skilift density variables and the skilift distance variable were calculated for the artificial nest locations in Switzerland.

2.5.3 Hunting pressure

We had to control for possible indirect effects of hunting, because in Switzerland and France cocks are still hunted. We thus used the density of game reserves and the distance between the transect lines and the nearest game reserve as an estimate of hunting pressure for each study site in Switzerland and France. We used a vectorial map containing game reserves within study areas in Switzerland and France as polygons, and calculated 5 game reserve density variables (from 250 – 1500 m radius) and one game reserve distance variable (Euclidean mean distance between transect line and nearest game reserve) with a similar procedure as described above. To reduce the number of variables and variable interdependency a Principal Component Analysis (PCA) on the above 6 variables (5 density variables plus one distance variable) for hiking paths, roads, skilifts and game reserves was performed. The number of PC factors retained for the analysis was determined by the broken-stick method (Jackson 1993).

2.6 Habitat typology

Finally, we controlled for possible habitat effects by distinguishing 14 different habitat types, that encompass all extant habitats present in the study area (Wirthner 2006). In autumn, we stepped out all transects in Switzerland and France and took GPS coordinates at each habitat type boundary along the transect, this in order to estimate the local proportion of each habitat type. On these 14 raw variables a PCA was performed that resulted in factors summarizing the habitat typology.

2.7 Statistical analysis

To test for factors influencing predator abundance we computed Generalized Linear Models (Poisson distribution, log link function) for all Swiss sites with indices for corvid, fox and a combination of fox and dog abundance as the response variables. Explanatory variables included human disturbance in summer and winter, and habitat characteristics.

In the artificial nest predation experiment in Switzerland, we tested for the effects of predator abundance, human disturbance (summer and winter), habitat typology and egg visibility (as a control variable for nest concealment).

Generalized Linear Mixed-Effects Models were used (binomial distribution, logit link function). To account for the nested design of our experiment, we treated predation on artificial nests within a study site as random effect (random intercept) and the other explanatory variables as fixed effects. Additionally, we compared the proportion of predation of real egg vs. wax egg clutches by a χ^2 test.

Factors impacting on productivity were analysed separately for Switzerland and France. Generalized Linear Models (Poisson distribution, log link function) were performed with the number of Black grouse chicks per study site as response variable. Explanatory variables included predator abundance, human disturbance (summer and winter disturbance, as well as hunting pressure), habitat typology and Black grouse cocks abundance as regards the Swiss analysis. For the data of France the same explanatory variables were used except for predator abundance and tourist pressure which were not available for these study sites.

A model selection approach was used to rank the best models among candidate models based on a priori hypotheses (Burnham & Anderson 1998), i.e. the effects of the explanatory variables on predator abundance, predation rate and productivity, respectively. The competing models for the predation rate were ranked according to the Akaike Information Criterion (AIC) and those for predator abundance and productivity were ranked according to the corrected "small sample unbiased" Akaike Information Criterion (AIC_c) because we had to account for the small sample size of the latter two analyses. AIC and AIC_c weights were used for model selection (Johnson 2004). Prior to fit the models, correlations between explanatory variables were tested (Spearman rank correlation): there were no close linkages (all $r < 0.7$) between the explanatory variables which could thus all be used for modelling. For the model selection procedure, the best model within a set of explanatory variables (predator abundance, summer disturbance, winter disturbance, hunting pressure, habitat typology) was selected. Then the variables of the best models for every set were combined to select the best models with combined variable sets. Model quality was finally assessed by Spearman correlation tests between observed and predicted values for Poisson Linear Models and Kappa statistics for logistic regressions (Allouche 2006).

For the calculations based on raster maps we used a geographical information system (GIS) application (ArcGIS 9.0, Spatial analyst tool, Environmental Systems Research Institute, California). The PCAs were run with the program JMP 5.1. For all the other statistical analyses we used the program R version 2.4.1 including the package lme4 for the Linear Mixed-Effects Models (R: A Language and Environment for Statistical Computing, R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria, 2006).

3. Results

3.1 Summarizing information from explanatory variables

Using Principal Component Analyses (PCA) we concentrated the information from the explanatory variables into a few factors. As regards human summer disturbance at the Swiss study transects, namely the hiking path and road network variables, the first two principal components explained 94.4% and 93.9% of the variance, respectively. For winter sport infrastructures the first two factors explained 98.4%, whereas for hunting pressure the first two factors explained 98.1% of the variance. The first two factors of habitat typology explained 41.2% of the variance; henceforth they are referred to as vegetation I and vegetation II. As regards PCA on the habitat features at the study transects in France, similar proportions of the variances were explained by the first two factors (hiking path network 94.1%, road network 95.3%, skilifts 96.6%, hunting pressure 94.9 % and habitat typology 40.5%). Regarding habitat features around the artificial nests, the first three factors of the PCA on the hiking path network explained 94.5% of the variance (67.8, 21.3 and 5.4%, for factors 1-3, respectively).

In all cases, loadings of the first factors were positively correlated with the density variables. For instance, the first factor of the PCA on the hiking path network was positively correlated to the five hiking path density variables. Therefore we further used first principle components as surrogates of density variables (e.g. hiking path density refers to the first factor of the PCA on the hiking path network). In contrast, loadings of the second principle components were in all cases positively correlated to the distance between study transects or nest location and the infrastructure features. We therefore used second principle components as variables for distance (e.g. distance to hiking path refers to the second factor of the PCA on the hiking path network). Regarding nest predation rate analysis, the loadings of the third factor of the PCA on the hiking path network was also positively correlated to the distance between nests and hiking paths, and we therefore used this third component as another variable for distance to hiking paths. Here, distance to hiking path I refers to the second principle component and distance to hiking path II to the third principle component.

3.2 Predator abundance

In our estimation of corvid abundance, only observations of carrion crows and ravens were finally taken into account, because magpies and Eurasian jays were observed only very rarely (3 times). As regards corvids, the best model (AIC_c weight = 0.304) among the set of candidate models included variables belonging to the set of summer disturbance, whereas the second best model (AIC_c weight = 0.199) combined variables of the summer and winter disturbance sets (Table 1). Models with other combinations of variable sets had lower probabilities to be the best model among the candidates (AIC_c weights < 0.14; Table 1). Correlation coefficients between observed and predicted values of corvid abundance for these two best models were significant ($r_s = 0.538$, $n = 30$, $p < 0.01$; $r_s = 0.559$, $n = 30$, $p < 0.01$, respectively) indicating good model qualities.

In the best model tourist pressure had a positive effect whilst distance to hiking paths had a negative effect (Table 2). There is thus a positive association between corvid abundance and the presence of tourists and hiking paths (Fig. 1).

In the second best model in addition to the two variables of the best model (tourist pressure and distance to hiking path) winter snow sport infrastructures (skilift density) had a positive effect (Table 2). Therefore, this model shows a positive association between corvid abundance vs. the presence of tourists, hiking paths and skilifts.

Among the candidate models no set of variables could explain patterns of fox abundance and the combination of fox and dog abundance. In both sets of candidate models the best model was the null model without any variable (AIC_c weight = 0.210 and 0.249, respectively). Moreover, the other models did not show any correlation between observed and predicted values ($r_s = 0.214$, $n = 30$, $p = 0.26$, $r_s = 256$, $n = 30$, $p = 0.17$, respectively).

3.3 Predation rate

After 48 days, 10% (n = 30/300) of artificial nests with real eggs and 17% (n = 15/88) of artificial nests with wax eggs showed signs of predation. The proportion of predation of real egg clutches vs. wax egg clutches did not differ significantly ($\chi^2 = 3.3$, df = 1, $p = 0.08$). Predators often removed all eggs of a real egg clutch. Only in 7 cases signs of predators were left, such as broken shells. In contrast, beak and tooth marks on predated wax eggs allowed to identify avian (n = 1) vs. mammalian (n = 5, probably fox or marten) predators. In addition, in 9 wax eggs tooth marks of small mammals, probably rodents were recognized. The tooth marks of rodents were found exclusively around the holes through which the wax eggs had been filled. Hence, we assumed that rodents were not able to crack intact egg shells and therefore we tested for a difference in the proportion of rodent vs. fox/marten or corvid predation of real eggs and wax eggs, which was significant ($\chi^2 = 22.5$, df = 1, $p < 0.01$). Because of this significant difference and because mammal predators have been shown to be more attracted by the odour of wax eggs compared to real eggs (Major & Kendal 1996), the nests with wax eggs were eventually excluded from further analyses.

The best model (AIC weight = 0.629) among the set of candidate models to explain predation pressure incorporated nest concealment, predator abundance and human summer disturbance, whereas the second best model (AIC weight = 0.243) added habitat characteristics (Table 3). All other single or combinatory models had lower AIC weights (< 0.09; Table 3). The Kappa value for the best two models (mean of Kappa from permutation tests = 0.629 and 0.604, respectively) indicated good model qualities. In the best model, corvid and fox abundance had positive effects on the nest predation risk (Table 4). The relationship between predator abundance and nest predation is shown in Fig. 2. Distance to hiking path I and II, i.e. second and third factors of the PCA on the hiking path network, had opposite effects (Table 4). However, the negative estimate of distance to hiking path II had more explanatory power due to a relatively smaller standard error than distance to hiking path I (Table 4). This suggests a trend for lower nest predation risk farther away from hiking paths. Egg visibility, included as control variable for nest concealment had a positive effect on predation risk. In the second best model the same five variables of the latter model showed similar trends (Table 4), but vegetation I, i.e. first factor of the PCA on the habitat typology, was also incorporated. The estimate of vegetation I, however, had a large standard error suggesting low explanatory power.

3.4 Productivity

In only 5 out of the 20 study sites in Switzerland, 1 to 12 (mean = 1.05, sd = 2.78) Black grouse chicks were counted. The best model and the second best model (AIC_c weight = 0.608 and 0.136, respectively) included human summer disturbance, hunting pressure and Black grouse cocks abundance (Table 5). Other single or combinatory models had lower probabilities to be the best model (AIC_c weights ≤ 0.10; Table 5). Correlation coefficients between observed and predicted values for number of chicks were significant in these two best models ($r_s = 0.665$, $r_s = 0.697$, $n = 20$, $p < 0.01$, respectively) indicating good model qualities.

In the best model tourist pressure had a negative effect (Table 7) showing a tendency for a negative association between number of tourists and reproductive output (Fig. 3). Hiking path density and distance to hiking paths had negative effects too, whereas distance to roads had a positive effect (Table 7). The last variable, distance to game reserves had a negative effect. Additionally, Black grouse cocks abundance had a positive effect on the number of chicks in the second best model (Table 7). In summary, the combination of variables in the best two models therefore show a tendency for a negative association between tourist pressure, the presence of hiking paths as well as roads and reproductive output. Additionally, a positive association between the presence of game reserves and reproductive output, and a positive association between Black grouse cocks abundance and reproductive output was suggested by these best two models.

In France, in 13 out of the 20 study sites 1 to 13 (mean = 3.9, sd = 12.7) Black grouse chicks were counted. The best model (AIC_c weight = 0.671) incorporated winter sport infrastructures and habitat typology (Table 6). Other single or combinatory models had lower probabilities to be the best model (AIC_c weights < 0.12; Table 6). The correlation coefficient between the observed and predicted value of number of Black grouse chicks was significant ($r_s = 0.499$, $p < 0.05$), suggesting a good model quality. In this model skilift density and distance to skilift showed a negative association between presence of skilifts and reproductive output (Table 8). Vegetation index I, i.e. the first factor of the PCA on habitat typology, had a negative effect suggesting additional effects of habitat structure and composition on reproductive output (Table 8).

4. Discussion

This study quantifies for the first time the negative cumulative effects of direct and indirect impacts of tourist resort settlement on nest predation risk and productivity of Black grouse in the Alps. We showed that corvids are more abundant at the sites which are most frequently used by tourists and we could link the higher abundance of predators to a higher nest predation risk Black grouse face at sites with extended infrastructures for recreational activities. Further, we showed that elevated tourist pressure and dense hiking path and road networks negatively impact on Black grouse productivity.

Reproductive success is a critical determinant of Black grouse population dynamics (Ellison & Magnani 1985, Klaus et al. 1990, Ludwig et al. 2006). Populations are on the increase after nice summers (i.e. relatively warm and dry weather), because this enhances chicks survival (Klaus et al. 1990, Summers et al. 2004, Hannon & Martin 2006, Ludwig et al. 2006): chicks heavily depend on arthropod food (Ponce 1992) for optimal growth during their first weeks of life (Hannon & Martin 2006), with arthropod availability being reduced during adverse weather (Zbinden & Salvioni 2004). Our study further suggests that increased human recreational activities have the potential to negatively affect chicks, through direct disturbance by humans and increased predation pressure by corvids as predicted by Storch & Leidenberger (2003).

More carrion crows and ravens occurred at sites frequented by tourists in winter and summer. This confirms findings of Storch & Leidenberger (2003) and Watson & Moss (2004) of a significant positive relationship between corvid abundance and availability of cabins and huts. Corvids benefit from human food remains around tourist stations and at picnic places, both in summer and winter. Additionally, tourist resorts with associated infrastructures fragment the landscape (Ingold 2005), which further increases local predator abundance, such as corvids, due to edge effects (Andrén et al. 1992, Watson & Moss 2004). Higher corvid abundance at tourist resorts caused elevated predation risk for artificial nests. This is in agreement with Watson & Moss (2004) and Manzer et al. (2005) who showed that grouse nests succeed more likely in sites with lower corvid abundance. Andrén et al. (1992) and Storch et al. (2005) also documented higher nest losses in fragmented landscapes.

Although foxes are opportunistic feeders readily attracted to tourist stations (Capt & Stalder 1988), we could not establish a direct link between their occurrence and the presence of tourists and the infrastructure density indices (skilifts, hiking path and road network). Our estimate of carnivore abundance through scat counts may be inappropriate. Although estimation of fox abundance is difficult (Webbon et al. 2004, Sadlier et al. 2004), casual observations during our field work suggest a rather homogeneous distribution across sites. However, fox abundance increased the predation risk of our experimental clutches, which confirms nest predation by foxes (Svobodova et al. 2004, Storch et al. 2005). The absence of effects of dog presence, which dramatically increases with tourist pressure, is difficult to interpret. It might be that dogs are not so attracted by artificial clutches. In contrast to wild predators dogs are not depending on food recourses at these sites.

In our experiment the predation rate on artificial nests with real eggs was 10 -50% lower than predation rates recorded in similar experiments elsewhere (Thiel 2002, Summers et al. 2004, Svobodova et al. 2004, Storch et al. 2005). Possible reasons might be a higher nest concealment in our experiment compared to others (Summers et al. 2004, Storch et al. 2005) and/or the use of one wax egg in every artificial clutch in the studies by Thiel et al. (2002), Summers et al. (2004) and Svobodova et al. (2004). The odour of wax filled eggs is likely to attract more predators than natural eggs (Major & Kendal 1996). This was also suggested in our experiment indicated by a higher predation rate on artificial nests with wax eggs (difference 7%). Finally it should be mentioned that predation rates on real nests are assumed to be 40% higher than on artificial nests. (Klaus et al. 1990, Willebrand & Marcström 1988). This is because predators may locate nests due to the behaviour and odour of breeding hens (Major & Kendal 1996, Zanette 2002). Our estimates would therefore be extremely conservative in regards to actual predation pressure.

Black grouse productivity in Switzerland was low at sites frequented by tourists, i.e. where hiking path and road network was large. Moreover, productivity appeared to be higher in or close to game reserves and was positively correlated with local Black grouse cocks density. This confirms the views by Langston et al. (2007) that human disturbance negatively impacts on breeding birds. Direct human disturbance may lead to stress (Arlettaz et al. 2007) and extra energetic costs for chick-rearing hens (Hüppop 1995) and hence may lead to reduced performance of hens and chicks (McClung et al. 2004). These results contrast with findings of Baines & Richardson (2007) who did not detect any difference in fecundity of Black grouse between experimental disturbance treatments in England. However, we think that their experimental approach is hardly comparable to our study because in England Black grouse do not face as harsh winter climate (no need to stay in snow burrows as an energy saving strategy) as in the Alps and are less exposed to human disturbance from recreational activities (no skiing facilities, less dense road and path networks). Another important difference is a lower predation pressure due to systematic predator controls in England, which increases reproductive output as shown by Summers et al. (2004).

Although only males are hunted in Switzerland, hunting pressure had a negative impact on reproductive output. Reduction of lek size by hunting may disturb the mating system (Baines & Lindén 1991) and have profound effects on population dynamics (Klaus et al. 1990, Hovi et al. 1994, Rintamäki et al. 1998), especially in a species where males are as sedentary as in Black grouse with no dispersal in that sex at all (Höglund et al. 1999). These symptoms were observed in our study: productivity correlated positively with cocks density.

In contrast to the results for Switzerland, results for France show that productivity was low where skilift density was high, which suggests that winter sport infrastructures and/or disturbance has larger impacts in France. Furthermore, reproductive output depended on the habitat typology at the French study sites. These differences between two close geographic regions show that models fitted to data from one area cannot be extrapolated straightforwardly, since there might be considerable variability between study areas due to the complexity of the underlying system. We can conclude, however, that human resort settlement has negative impacts on Black grouse population dynamics.

4.1 Implications for conservation

The main conclusion of this study is that tourist resort settlement decreases Black grouse reproductive output, presumably through direct human disturbance and indirectly through an increased predation risk by corvids and carnivores. Higher nest predation and low reproductive output in areas disturbed by humans probably negatively affect population dynamics and could be one mechanism explaining why local density of Black grouse is lower close to ski resorts (Wirthner 2006).

For conservation management, corrective measures are necessary. Restriction of summer tourist activity to trails and roads and/or the partial closure of trails in main breeding habitat would be a first option. Disturbance by hikers or mountain bikers during the critical breeding season would then be diminished and reproductive output enhanced. To which extent these zones could overlap with winter reserves must be further evaluated (Arlettaz et al. 2007).

Given that the nesting success of Black grouse is negatively related to corvid abundance, control of carrion crows and ravens should be envisioned, according to what could be achieved in England (Baines et al. 2004, Summers et al. 2004). For the Alps, the best way to reduce corvid density would be to deprive them from additional human-generated food resources. In particular, deposition of food remains around tourist stations and Alpine cabins must be minimized. As the Black grouse is an emblematic species of habitats in the Alps, these measures would probably benefit other ground-breeding bird species suffering from a higher predation pressure than in more natural conditions.

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Tables

Table 1. Model ranking of the sets of candidate models (Generalized Linear Models) to explain corvid abundance at 30 study sites in Switzerland. *k*: number of model parameters; $AIC_c\Delta_i$: differences in Akaike Information Criterion scores; $AIC_c w_i$: AIC_c weights; r_s: Spearman Rank Correlation coefficients between observed and predicted values; p: p-values of r_s.

	Model description	*k*	$AIC_c\,\Delta_i$	$AIC_c\,w_i$	r_s	p
1	Summer disturbance	4	0.00	0.304	0.538	0.002
2	Summer disturbance + winter disturbance	5	0.84	0.199	0.559	0.001
3	Summer disturbance + habitat typology	5	1.59	0.137	0.415	0.023
4	Null model	2	1.71	0.129		
5	Habitat typology	3	2.91	0.071	0.237	0.207
6	Summer disturbance + winter disturbance + habitat typology	6	3.21	0.061	0.530	0.003
7	Winter disturbance	3	3.23	0.060	0.130	0.495
8	Winter disturbance + habitat typology	4	4.15	0.038	0.241	0.199

Table 2. Coefficients and standard errors (SE) of the variables included in the best two models for estimating corvid abundance [1) best model, 2) second best model]. Distance to hiking path: PC factor 2 of a Principal Component Analysis (PCA) on the hiking path variables; Skilift density: PC factor 1 of a PCA on the skilift variables; NA: variable not retained during model selection procedure.

	1) Summer disturbance		2) Summer + winter disturbance	
	estimate	SE	estimate	SE
Intercept	-2.3383	0.5366	-2.5763	0.5851
Tourist pressure	0.1241	0.0430	0.1494	0.0471
Distance to hiking path	-1.1761	0.4570	-1.3913	0.4842
Skilift density	NA	NA	0.2196	0.0940

Table 3. Model ranking of the set of candidate models (logistic mixed-effects models) to explain predation on artificial nests at 30 study sites in Switzerland. *k*: number of model parameters; AICΔ_i : differences in Akaike Information Criterion scores; AICw_i: AIC weights; Kappa: Kappa statistic value.

	Model description	*k*	AICΔ_i	AICw_i	Kappa
1	Nest concealment + predation pressure + summer disturbance	8	0.0	0.629	0.629
2	Nest concealment + predation pressure + summer disturbance + habitat typlogy	9	1.9	0.243	0.604
3	Nest concealment + summer disturbance	6	4.0	0.085	0.654
4	Nest concealment + summer disturbance + habitat typology	7	6.0	0.031	0.596
5	Nest concealment + predation pressure	5	10.5	0.003	0.519
6	Null model	3	11.3	0.002	0.482
7	Nest concealment	4	11.4	0.002	0.521
8	Nest concealment + predation pressure + habitat typology	7	12.1	0.001	0.509
9	Nest concealment + winter disturbance	5	12.8	0.001	0.558
10	Nest concealment + habitat typology	5	13.1	0.001	0.500

Table 4. Coefficients and standard errors (SE) of the variables included in the best two models estimating predation on artificial nests [1) best model, 2) second best model]. Distance to hiking path I and II: PC factors 2 and 3 of a Principal Component analysis (PCA) on the hiking path variables, respectively; Vegetation I: PC factor 1 a PCA on the habitat variables; NA: variable not retained during model selection procedure.

	1) Nest concealment + predation pressure + summer disturbance		2) Nest concealment + predation pressure + summer disturbance + habitat typology	
	Estimate	SE	Estimate	SE
Intercept	-4.6311	0.9347	-4.6080	0.9407
Corvid abundance	1.3093	0.5482	1.3532	0.5654
Fox abundance	0.8589	0.3830	0.8241	0.3933
Distance to hiking path I	0.4300	0.2082	0.4281	0.2080
Distance to hiking path II	-1.4939	0.4676	-1.4723	0.4698
Vegetation I	NA	NA	-0.0602	0.1917
Egg visibility	0.3075	0.2724	0.3065	0.2747

Table 5. Model ranking of the set of candidate models (Generalized Linear Models) to explain reproductive output (number of chicks) at 20 study sites in Switzerland. *k*: number of model parameters; $AIC_c\Delta_i$: differences in Akaike Information Criterion scores; $AIC_c w_i$: AIC_c weights; r_s: Spearman Rank Correlation coefficients between observed and predicted values; p: p-values of r_s.

	Model description	*k*	$AIC_c\Delta_i$	$AIC_c w_i$	r_s	p
1	Summer disturbance + hunting pressure	7	0.00	0.608	0.665	0.001
2	Summer disturbance + Black grouse abundance	8	3.00	0.136	0.697	<0.001
3	Summer disturbance + hunting pressure + winter disturbance	8	3.73	0.094	0.694	<0.001
4	Summer disturbance	7	5.13	0.047	0.651	0.002
5	Summer disturbance + hunting pressure + predation pressure	8	5.71	0.035	0.665	0.001
6	Summer disturbance + hunting pressure+ habitat typology	8	5.73	0.035	0.665	0.001
7	Summer disturbance + hunting pressure + Black grouse abundance	8	5.76	0.034	0.665	0.001
8	Summer disturbance + predation pressure	7	9.83	0.004	0.662	0.001
9	Summer disturbance + habitat typology	8	9.84	0.004	0.619	0.004
10	Summer disturbance + winter disturbance	8	10.89	0.003	0.651	0.002
11	Winter disturbance + hunting pressure	4	22.71	0.000	0.375	0.104
12	Black grouse abundance	3	23.33	0.000	0.292	0.212
13	Hunting pressure	3	26.54	0.000	0.314	0.177
14	Hunting pressure + habitat typology	4	27.00	0.000	0.351	0.129
15	Winter disturbance	3	32.30	0.000	0.254	0.280
16	Winter disturbance + habitat typology	4	33.35	0.000	0.367	0.112
17	Habitat	3	43.43	0.000	0.248	0.291
18	Predation pressure	3	43.51	0.000	0.026	0.914
19	Null model	2	44.70	0.000		

Table 6. Model and ranking of the set of candidate models (Generalized Linear Models) to explain reproductive output (number of chicks) at 20 study sites in France. *k*: number of model parameters; $AIC_c\Delta_i$: differences in Akaike Information Criterion scores; $AIC_c w_i$: AIC_c weights; r_s: Spearman Rank Correlation coefficients between observed and predicted values; p: p-values of r_s.

	Model description	*k*	$AIC_c\,\Delta_i$	$AIC_c\,w_i$	r_s	p
1	Winter disturbance + habitat typology	5	0.00	0.671	0.499	0.025
2	Winter disturbance + habitat typology + hunting pressure	6	3.59	0.111	0.471	0.036
3	Winter disturbance + habitat typology + summer disturbance	6	4.05	0.088	0.538	0.014
4	Winter disturbance + habitat typology + Black grouse abundance	6	4.10	0.086	0.521	0.019
5	Habitat typology	3	8.78	0.008	0.418	0.067
6	Summer disturbance + habitat typology	4	8.79	0.008	0.396	0.084
7	Winter disturbance + hunting pressure	5	8.92	0.008	0.355	0.124
8	Black grouse abundance + habitat typology	4	9.65	0.005	0.342	0.140
9	Winter disturbance	4	10.14	0.004	0.370	0.108
10	Winter disturbance + hunting pressure + summer disturbance	6	10.76	0.003	0.413	0.070
11	Hunting pressure + habitat typology	4	11.23	0.002	0.341	0.141
12	Summer disturbance + habitat typology + hunting pressure	5	12.41	0.001	0.396	0.084
13	Winter disturbance + Black grouse abundance	5	13.26	0.001	0.387	0.092
14	Winter disturbance + summer disturbance	5	13.66	0.001	0.378	0.100
15	Hunting pressure	3	23.43	0.000	0.184	0.438
16	Black grouse abundance	3	23.44	0.000	0.215	0.363
17	Summer disturbance	3	23.65	0.000	0.024	0.921
18	Summer disturbance + hunting pressure	4	24.99	0.000	0.178	0.454
19	Null model	2	26.27	0.000		
20	Summer disturbance + hunting pressure + Black grouse abundance	5	26.92	0.000	0.265	0.258

Table 7. Coefficients and standard errors (SE) of the variables included in the best two models estimating reproductive output in Switzerland [1) best model, 2) second best model]. Hiking path density: PC factor 1 of a Principal Component analysis (PCA) on the hiking path variables; Distance to hiking path: PC factor 2 of the PCA on the hiking path variables. The same nomenclature applies to Road density index, Distance to road and Distance to game reserve. NA: variable not retained during model selection procedure.

	1) Summer disturbance + hunting pressure		2) Summer disturbance + Black grouse abundance	
	Estimate	SE	Estimate	SE
Intercept	-3.3662	2.7256	-5.0809	2.1921
Tourist pressure	-1.5908	1.0604	-2.0447	0.7492
Hiking path density	-2.2881	1.5622	-2.9930	1.0698
Distance to hiking path	-0.8381	0.7765	-0.3890	0.5076
Road density	NA	NA	0.5201	0.2665
Distance to road	2.9758	1.5829	2.1018	1.0965
Distance to game reserve	-1.7861	1.0586	NA	NA
Abundance of Black grouse cocks	NA	NA	0.2208	0.0979

Table 8. Coefficients and standard errors (SE) of the variables included in the best model estimating reproductive output in France. Skilift density: PC factor 1 of a Principal Component analysis (PCA) on the skilift variables; Distance to skilift: PC factor 2 of a PCA on the skilift variables; Vegetation I: PC factor 1 of a PCA on the habitat variables.

	1) Winter disturbance + habitat typology	
	Estimate	SE
Intercept	1.1009	0.2515
Skilift density	-0.1321	0.0907
Distance to skilift	0.3828	0.2541
Vegetation I	-0.3783	0.2043

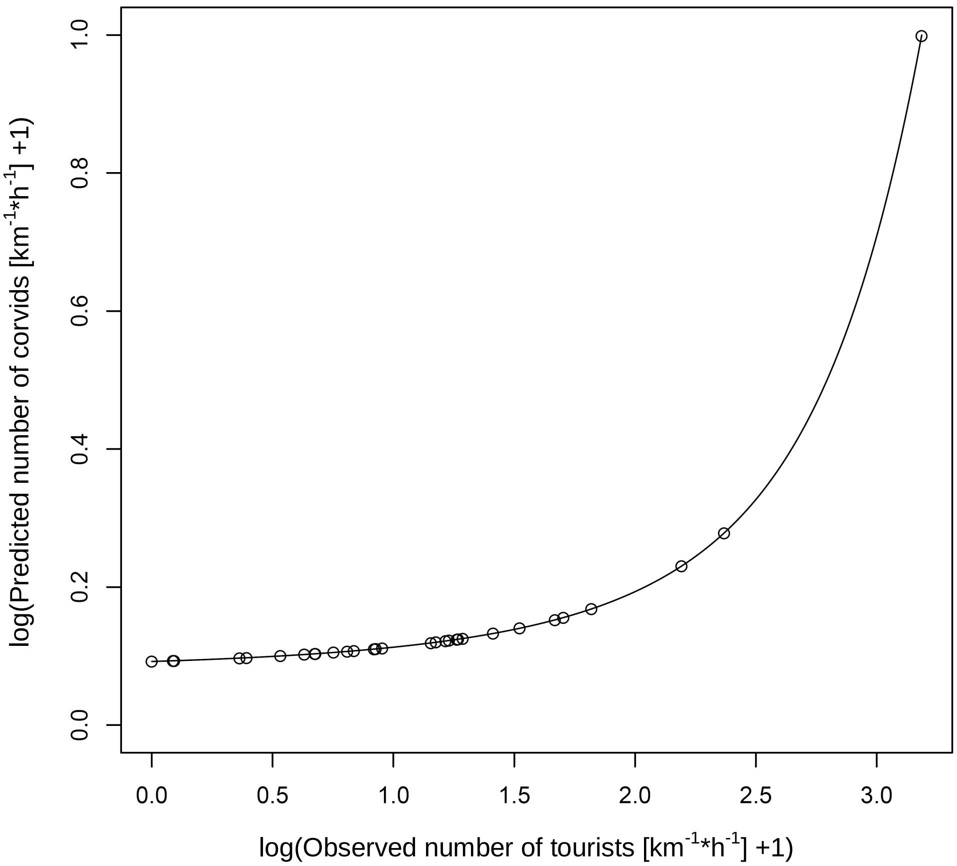
Figures

Figure captions

Figure 1. Relationship between corvid abundance and tourist pressure predicted from the best model drawn from study sites in Switzerland (Table 1). Corvid abundance was allowed to vary with tourist pressure while the other variable included in the model (distance to hiking paths; Table 2) was fixed at its mean value.

Figure 2. Probability of predation on artificial nests relative to corvid abundance predicted from the best model drawn from study sites in Switzerland (Table 3). Probability of predation was allowed to vary with corvid abundance while other variables included in the model (fox abundance, distance to hiking paths I and II, egg visibility; Table 4) were fixed at their mean values.

Figure 3. Correlation between Black grouse reproductive output (number of Black grouse chicks) and tourist pressure predicted from the best model drawn from study sites in Switzerland (Table 5). The number of chicks was allowed to vary with tourist pressure while other variables included in the model (hiking path density, distance to hiking paths, distance to roads, distance to game reserves; Table 7) were fixed at their mean values.



log(Predicted number of corvids [km^{-1}*h^{-1}] +1)
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
log(Observed number of tourists [km^{-1}*h^{-1}] +1)

Figure 1

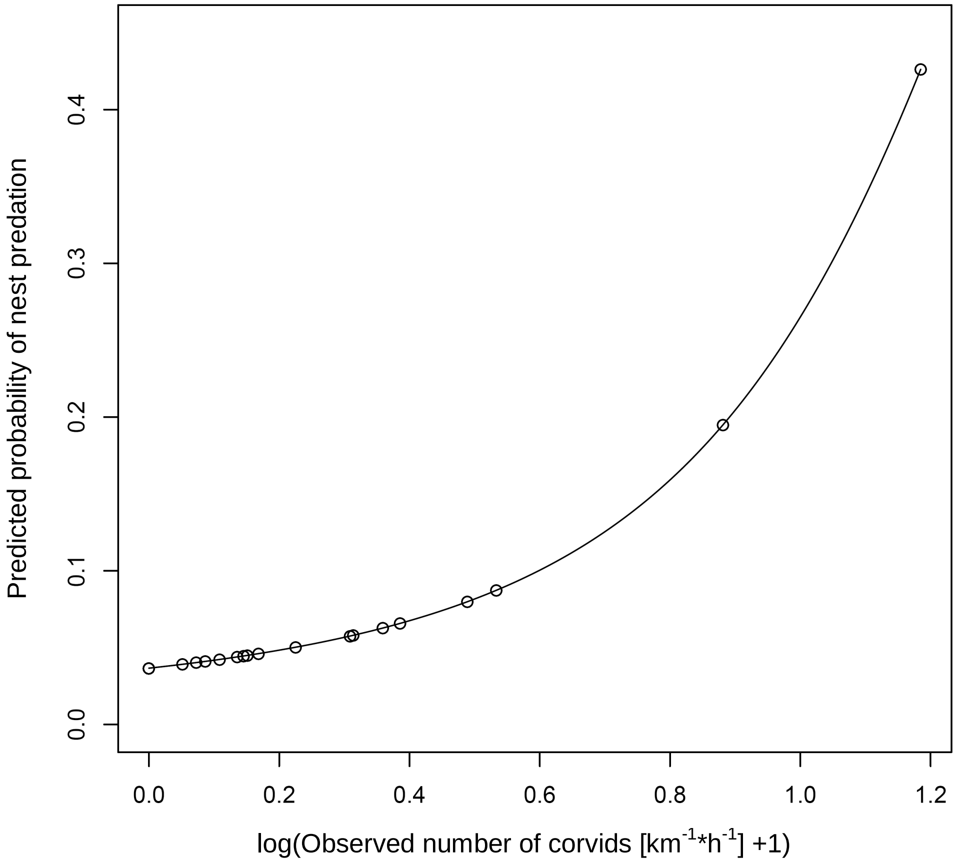

Predicted probability of nest predation
0.0
0.1
0.2
0.3
0.4
0.0
0.2
0.4
0.6
0.8
1.0
1.2
log(Observed number of corvids [km^{-1}*h^{-1}] +1)

Figure 2

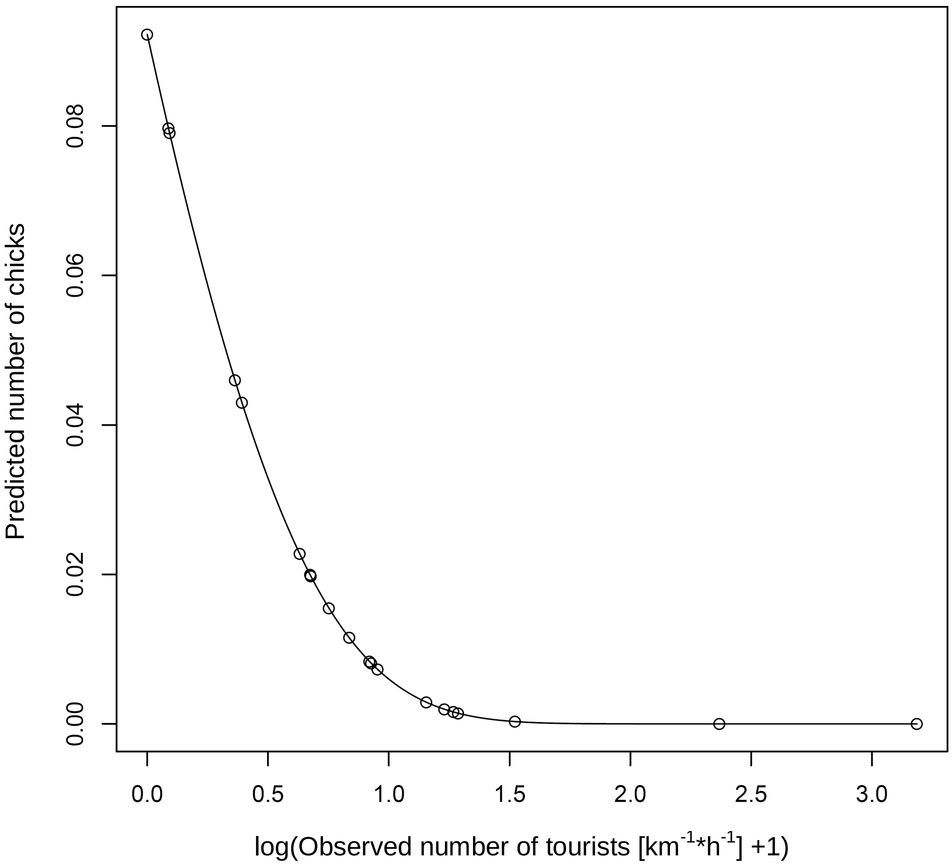
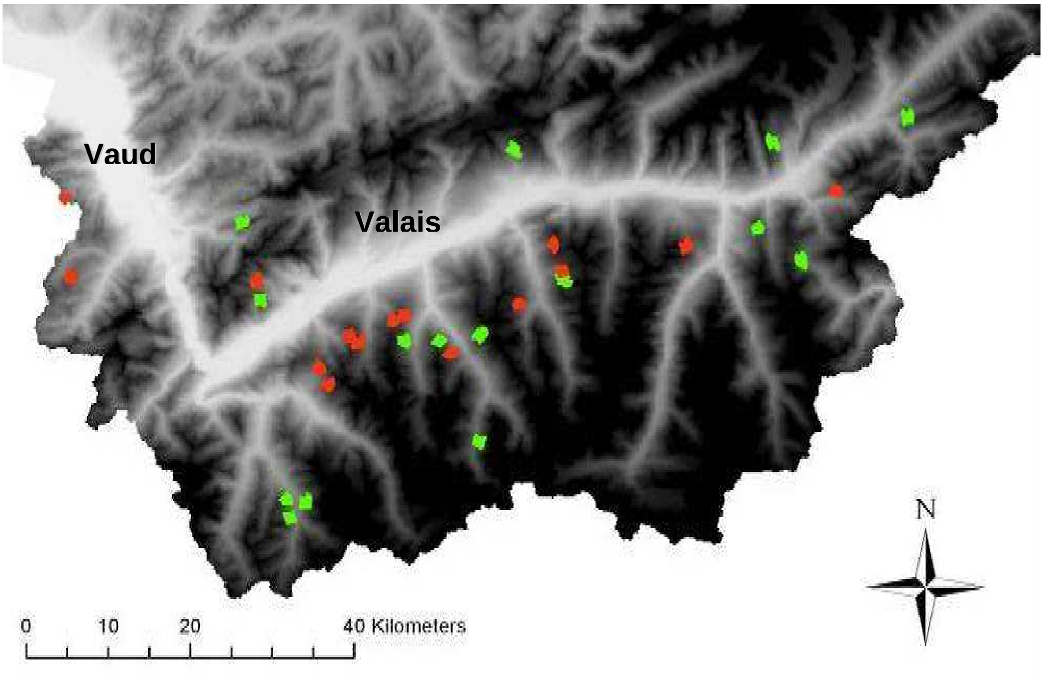

Predicted number of chicks
0.00
0.02
0.04
0.06
0.08
0.0
0.5
1.0
1.5
2.0
2.5
3.0
log(Observed number of tourists [km^{-1}*h^{-1}] +1)

Figure 3

Appendices

Appendix 1a. Number of predated artificial nests and observed Black grouse chicks in 15 natural (N) and 15 anthropized (A) sites (site type) in the Alps of Valais and Vaud, Switzerland. At each study site 10 artificial nests with real eggs and 3 artificial nests with wax eggs were installed. Nests with real eggs: number of predated artificial nests with real eggs after 48 days; Nests with wax eggs: number of predated artificial nests with wax eggs after 48 days; Chicks: number of observed chicks during a pointing dog control.

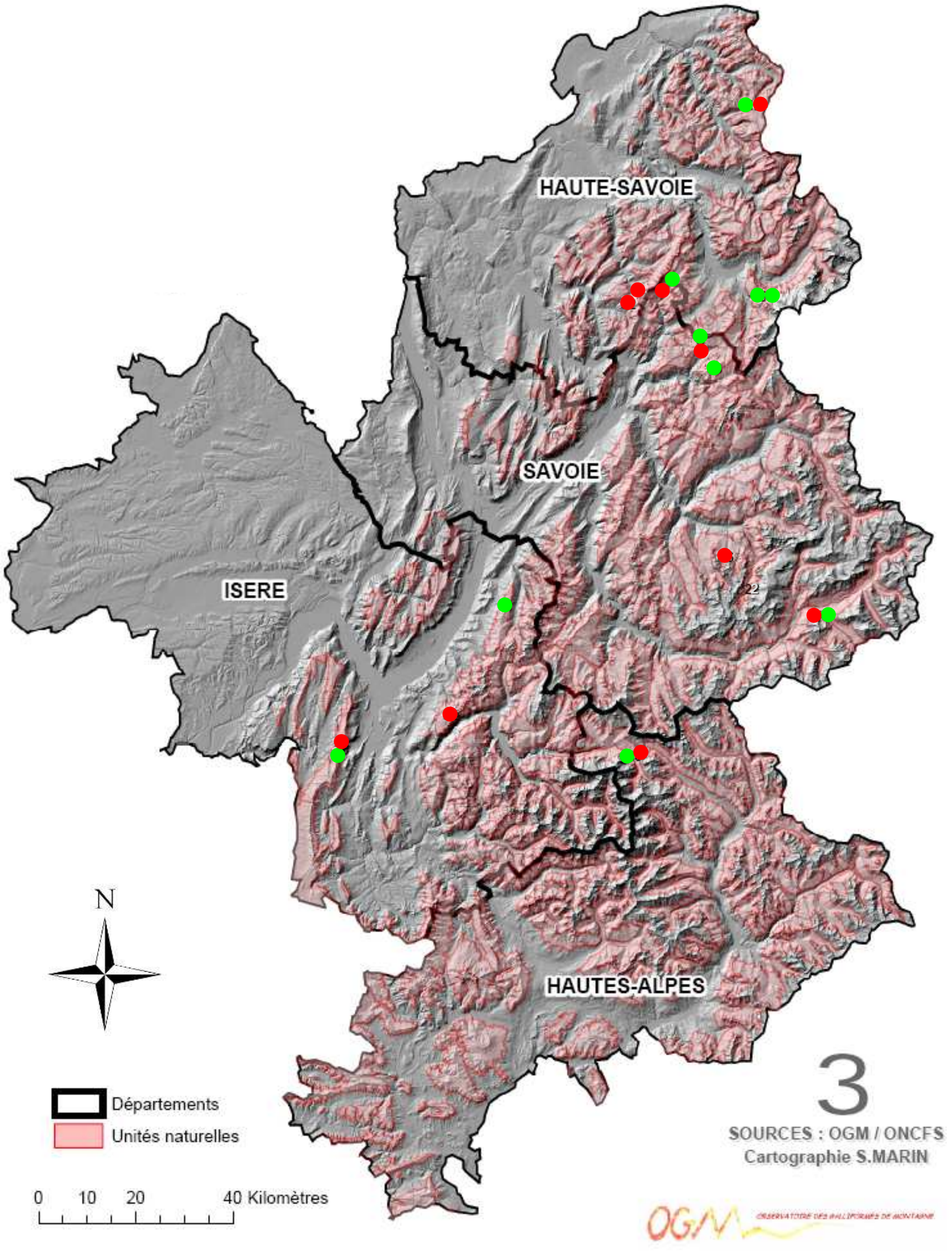
	Study site	Location	Site type	Nests		Chicks
				real eggs	wax eggs	
1	Belalp	Alpe Bäll	N	0	0	0
2	Simplon Süd	Nideralp	N	1	2	-
3	Montana	Bevron	N	0	1	-
4	Arolla	La Tsa	N	2	0	4
5	Binntal	Eggerhorn	N	0	0	12
6	Bourg St. Pierre	Les Arpalles	N	0	0	-
7	Bourg St. Pierre	Tsanlotset	N	1	0	0
8	Bourg St. Pierre	Azerin	N	0	1	0
9	Visperterminen	Gebidum	N	1	2	0
10	Gryon	Les Planards	N	2	0	0
11	Vald d'Heremence	Les Barmettes	N	0	0	-
12	Ovronnaz	Fratier	N	0	0	0
13	Hérens	Vendes	N	2	0	-
14	Hérens	Eison	N	1	1	2
15	St. Luc	Montagne du Touron	N	1	0	0
16	Bürchen	Moosalp	A	0	1	0
17	Champoussin	Pertuis	A	3	1	1
18	Thyon	Thyon east	A	0	0	-
19	Thyon	La Combire	A	1	0	-
20	Torgon	Les Frontanettes	A	1	0	-
21	Rosswald	Abeweid	A	0	0	-
22	Siviez	Les Marenda	A	0	2	0
23	Ovronnaz	Bougnone	A	1	0	0
24	Verbier	Les Attelas	A	5	1	0
25	Nendaz	Dent de Nendaz	A	1	1	0
26	Hérens	Combetta	A	0	0	2
27	St. Luc	Prarion	A	1	0	0
28	Grimentz	Bendolla	A	0	0	0
29	Anniviers	Alpage Chandolin	A	0	1	0
30	Verbier	Le Vacheret	A	6	1	-



Appendix 1b. Location of the 15 natural (green) and 15 anthropized (red) sites in the Alps of Valais and Vaud, Switzerland (Appendix 1a).

Appendix 2a. Number of observed Black grouse chicks in 10 natural (N) and 10 anthropized (A) sites (site type) in the Alps of the Departments of Haute-Savoie (74), Savoie (73), Isère (38) and Haute-Alpes (05), France. Chicks: number of observed chicks during a pointing dog control.

	Study site	Location	Department	Site type	Chicks
1	Mont de Granges	Châtel	74	N	0
2	Tricot I	St.-Gervais-les-Bains	74	N	0
3	Tricot II	St.-Gervais-les-Bains	74	N	13
4	Aravis-Nord	Megève	73	N	2
5	Nôtre Dame de Bellecombe	Le Planay	73	N	8
6	Hauteluce	Hauteluce	73	N	12
7	Lanslebourg	Lanslebourg	73	N	5
8	La Ferrière d'Allevard	Theys	38	N	0
9	La Grande Moucherolle	Lans-en-Vercors	38	N	6
10	Villar d'Arène	Col du Lautaret	05	N	4
11	Mont de Granges	Châtel	74	A	10
12	Aravis Nord	La Clusaz	74	A	0
13	L'Etale	La Clusaz	74	A	0
14	Aravis Nord	Megève	73	A	0
15	Hauteluce	Les Saisies	73	A	4
16	St. Bon-Tarentaise	Courechevel 1850	73	A	1
17	Lanslebourg	Termignon	73	A	2
18	Chamrousse	Chamrousse 1650	38	A	8
19	La Grande Moucherolle	Lans-en-Vercors	38	A	0
20	Villar d'Arène	Col du Lautaret	05	A	3



Appendix 2b. Location of the 10 natural (green) and 10 anthropized (red) sites in the Alps of the Departments of Haut-Savoie (74), Savoie (73), Isère (38) and Haute-Alpes (05), France (Appendix 2a).

Appendix 3. Typology of Black grouse habitats mapped along census transects in the study areas. Artificial nests were installed in main breeding habitat types (3, 6, 10 or 11).

	Habitat type
1	*Alnus* forest
2	Open young forest with grass cover
3	Open young forest with grass/Ericacea cover
4	Open young forest with Ericacea cover
5	Open old forest with grass cover
6	Open old forest with grass/Ericacea cover
7	Open old forest with Ericacea cover
8	Mixed *Rhododendron -Vaccinium* shrubs
9	*Juniperus* shurbs
10	*Rhododendron -Vaccinium* and pasture
11	*Juniperus* and pasture
12	Typical alpine pasture
13	Rocks and scree
14	Flatted skipists with pasture/scree cover

Appendix 4. Explanatory variables used for the analyses of predator abundance, predation pressure and productivity.

Variable categories	Variables
Predation pressure	Corvid abundance
	Fox abundance
	Dog abundance
Summer disturbance	Tourist pressure
	Hiking path density (PC factor 1)
	Distance to hiking path I (PC factor 2)
	Distance to hiking path II (PC factor 3)
	Road density (PC factor 1)
	Distance to road (PC factor 2)
Winter disturbance	Skilift density (PC factor 1)
	Distance to skilift (PC factor 2)
Hunting pressure	Game reserve density (PC factor 1)
	Distance to game reserve (PC factor 2)
Habitat typology	Vegetation I (PC factor 1)
	Vegetation II (PC factor 2)
Black grouse abundance	Abundance of Black grouse cocks
Nest concealment	Egg visibility

Appendix 5. Eigenvectors of the Principal Component Analyses (PCA) run to reduce variable number in model selection procedures for predator abundance models and reproductive output models for the study transects at the study sites in Switzerland. The retained factors were selected via the broken-stick method.

	PC factor 1	PC factor 2
Hiking path variables		
Explained variance	74.68%	19.67%
mean distance to hiking paths	-0.178	0.820
hiking path density radius 250 m	0.396	-0.381
hiking path density radius 500 m	0.465	-0.015
hiking path density radius 750 m	0.461	0.134
hiking path density radius 1000 m	0.455	0.213
hiking path density radius 1500 m	0.419	0.346
Road variables		
Explained variance	82.56%	11.29%
mean distance to roads	-0.380	0.432
road density radius 250 m	0.406	-0.377
road density radius 500 m	0.436	-0.188
road density radius 750 m	0.442	0.025
road density radius 1000 m	0.428	0.307
road density radius 1500 m	0.349	0.736
Skilift variables		
Explained variance	89.57%	8.84%
mean distance to skilifts	-0.315	0.938
skilift density radius 250 m	0.421	0.171
skilift density radius 500 m	0.425	0.209
skilift density radius 750 m	0.427	0.174
skilift density radius 1000 m	0.428	0.134
skilift density radius 1500 m	0.421	0.007
Hunting variables		
Explained variance	91.39%	6.74%
mean distance to game reserves	-0.343	0.939
game reserve density radius 250 m	0.418	0.186
game reserve density radius 500 m	0.422	0.165
game reserve density radius 750 m	0.424	0.148
game reserve density radius 1000 m	0.424	0.136
game reserve density radius 1500 m	0.413	0.130
Habitat variables		
Explained variance	23.60%	17.56%
1 *Alnus* forest	0.138	0.391
2 + 5 open young/old forest with grass cover	0.515	0.244
3 open young forest with grass/Ericacea cover	-0.192	-0.014
4 open young forest with Ericacea cover	-0.321	-0.154
6 open old forest with grass/Ericacea cover	0.303	-0.132
7 open old forest with Ericacea cover	0.128	-0.451
8 mixed *Rhododendron -Vaccinium* shrubs	-0.332	0.315
9 + 11 *Juniperus* shurbs/*Juniperus* and pasture	-0.018	-0.496
10 *Rhododendron -Vaccinium* and pasture	-0.288	0.408
12 typical alpine pasture	0.503	0.121
13 rocks and scree	-0.143	-0.126

Appendix 6. Eigenvectors of the Principal Component Analyses (PCA) run to reduce variable number in model selection procedures for reproductive output models at the study sites in France. The retained factors were selected via the broken-stick method.

	PC factor 1	PC factor 2
Hiking path variables		
Explained variance	81.50%	12.57%
mean distance to hiking paths	-0.320	0.757
hiking path density radius 250 m	0.405	-0.388
hiking path density radius 500 m	0.439	0.063
hiking path density radius 750 m	0.438	0.217
hiking path density radius 1000 m	0.434	0.290
hiking path density radius 1500 m	0.400	0.376
Road variables		
Explained variance	87.55%	7.75%
mean distance to roads	-0.409	0.090
road density radius 250 m	0.402	0.417
road density radius 500 m	0.420	0.364
road density radius 750 m	0.427	0.176
road density radius 1000 m	0.429	-0.173
road density radius 1500 m	0.360	-0.790
Skilift variables		
Explained variance	87.61%	9.01%
mean distance to skilifts	-0.317	0.927
skilift density radius 250 m	0.414	-0.034
skilift density radius 500 m	0.431	0.112
skilift density radius 750 m	0.432	0.177
skilift density radius 1000 m	0.428	0.207
skilift density radius 1500 m	0.415	0.229
Hunting variables		
Explained variance	82.65%	12.25%
mean distance to game reserves	-0.346	0.594
game reserve density radius 250 m	0.378	0.582
game reserve density radius 500 m	0.424	0.377
game reserve density radius 750 m	0.444	0.081
game reserve density radius 1000 m	0.437	-0.123
game reserve density radius 1500 m	0.411	-0.381
Habitat variables		
Explained variance	22.17%	18.34%
1 *Alnus* forest	-0.223	0.381
2 + 5 open young/old forest with grass cover	0.014	-0.080
3 open young forest with grass/Ericacea cover	0.447	-0.065
4 open young forest with Ericacea cover	-0.277	-0.248
6 open old forest with grass/Ericacea cover	0.297	0.404
7 open old forest with Ericacea cover	-0.041	0.580
8 mixed *Rhododendron -Vaccinium* shrubs	-0.384	0.042
9 + 11 *Juniperus* shurbs/*Juniperus* and pasture	0.456	-0.191
10 *Rhododendron -Vaccinium* and pasture	-0.256	-0.290
12 typical alpine pasture	-0.123	-0.359
13 rocks and scree	0.384	-0.171
14 flatted skipist with pasture/scree cover	0.020	0.043

Appendix 7. Eigenvectors of the Principal Component Analyses (PCA) run to reduce variable number in model selection procedures for predation rate models for the nest locations at the study sites in Switzerland. The retained factors were selected via the broken-stick method.

	PC factor 1	PC factor 2	PC factor 3
Hiking path variables			
Explained variance	67.75%	21.34%	5.43%
mean distance to hiking paths	-0.176	0.767	0.593
hiking path density radius 250 m	0.374	-0.457	0.537
hiking path density radius 500 m	0.467	-0.053	0.348
hiking path density radius 750 m	0.472	0.156	0.032
hiking path density radius 1000 m	0.463	0.258	-0.184
hiking path density radius 1500 m	0.417	0.329	-0.451
Roads variables			
Explained variance	77.26%	12.78%	
mean distance to roads	-0.391	0.321	
road density radius 250 m	0.387	-0.479	
road density radius 500 m	0.439	-0.208	
road density radius 750 m	0.447	0.027	
road density radius 1000 m	0.432	0.335	
road density radius 1500 m	0.344	0.715	
Skilift variables			
Explained variance	80.63%	10.57%	
mean distance to skilifts	-0.321	0.822	
skilift density radius 250 m	0.380	0.416	
skilift density radius 500 m	0.433	0.282	
skilift density radius 750 m	0.442	0.147	
skilift density radius 1000 m	0.443	0.026	
skilift density radius 1500 m	0.416	-0.223	
Hunting variables			
Explained variance	89.36%	7.39%	
mean distance to game reserves	-0.337	0.936	
game reserve density radius 250 m	0.413	0.210	
game reserve density radius 500 m	0.425	0.185	
game reserve density radius 750 m	0.427	0.154	
game reserve density radius 1000 m	0.427	0.122	
game reserve density radius 1500 m	0.413	0.079	
Habitat variables			
Explained variance	23.60%	17.56%	
1 *Alnus* forest	0.138	0.391	
2 + 5 open young/old forest with grass cover	0.515	0.244	
3 open young forest with grass/Ericacea cover	-0.192	-0.014	
4 open young forest with Ericacea cover	-0.321	-0.154	
6 open old forest with grass/Ericacea cover	0.303	-0.132	
7 open old forest with Ericacea cover	0.128	-0.451	
8 mixed *Rhododendron -Vaccinium* shrubs	-0.332	0.315	
9 + 11 *Juniperus* shurbs/*Juniperus* and pasture	-0.018	-0.496	
10 *Rhododendron -Vaccinium* and pasture	-0.288	0.408	
12 typical alpine pasture	0.503	0.121	
13 rocks and scree	-0.143	-0.126	