Is wildlife inhabiting snow sport areas less fit than in undisturbed areas? A case study of the Alpine Black grouse

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Manuel Lingg

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Prof. Dr. Raphaël Arlettaz, Zoologisches Institut,
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Is wildlife inhabiting snow sport areas less fit than in undisturbed areas? A case study of the Alpine Black grouse

Manuel Lingg[1], Patrick Patthey[1], Philippe Christe[2] & Raphael Arlettaz[1,3,4]

[1] Zoological Institute, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH–3012 Bern, Switzerland.

[2] Institut d'Ecologie—Laboratoire de Zoologie et Ecologie Animale, Bâtiment de Biologie, Université de Lausanne, CH-1015 Lausanne, Switzerland

[3] Swiss Ornithological Institute, Valais Field Station, Nature Centre, CH–3970 Salgesch, Switzerland

[4] The Ecology Centre, University of Queensland, St Lucia, QLD 4072, Australia

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* Corresponding Author:
Raphael Arlettaz
Zoological Institute – Conservation Biology
University of Bern
Baltzerstrasse 6
CH–3012 Bern
Switzerland
Fax: +41 31 631 45 35
E-mail: raphael.arlettaz@students.unibe.ch

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Abstract

Outdoor winter recreations such as skiing and snowshoeing have recently spread and intensified in Alpine ecosystems. Human disturbance elicits behavioural modifications and physiological stress in wintering wildlife, representing a new growing conservation threat. We predicted a despotic distribution of phenotypes between highly disturbed and quasi natural habitats, with low quality individuals more likely to occur in disturbed, supposedly suboptimal areas. We tested whether parasite load and body condition (two measures of individual quality) of Black grouse, an emblematic species of Alpine timberline ecosystems, vary with respect to human disturbance. Firstly, faecal material was collected from 151 snow burrows at 26 sites that differed in regards to levels of winter disturbance (from undisturbed habitat to highly disturbed snow sport areas around ski resorts); for that purpose, parasite prevalence and intensity were estimated by counting in the droppings the density of *Capillaria* eggs, a nematode. Secondly, we derived indices for fluctuating asymmetry and body condition based on body measurements of 88 adult male Black grouse. Thirdly, we estimated, on transects along the timberline at each study site, the intensity of human disturbance through the density of ski lifts and the number of traces of skis, snowboards and snowshoes. The same transects were also used to estimate the density of lekking Black grouse males. Contrary to our expectations, Black grouse inhabiting disturbed winter sport areas had a superior body index and were less parasitized than individuals in more natural sites; this, however, was not reflected in a disturbance-specific pattern of fluctuating asymmetry. Finally, snow sports areas harboured fewer lekking Black grouse. Although birds occurring in winter sports areas are more stressed during winter (Arlettaz et al. 2007), they appeared in a relatively better physiological condition in spring than individuals inhabiting more natural, rather undisturbed areas. The results suggest that host abundance and male-male competition in spring (both higher in natural habitats) may be the principal determinants of bird's quality and health condition, therefore masking any potential direct effect of human disturbance on the distribution of phenotypes.

1. Introduction

Outdoor recreation is increasing in popularity worldwide, becoming a major conservation issue as it adds to other detrimental factors already affecting wildlife (Taylor & Knight, 2003). The actual impact of such activities is still poorly understood (Blumstein et al., 2005; Ficetola et al., 2007; Sutherland, 2007), but has recently been the focus of several research projects. Montane ecosystems, which have long remained vast untouched landscapes in winter, are becoming more affected by the tourism industry, especially by snow sports such as skiing, snowboarding and snowshoeing (Ingold, 2005). Wildlife occurring in disturbed areas is impacted indirectly by changes in habitat quality due to snow sports infrastructure (Rolando et al., 2007; Storch, 2007; Wipf et al., 2005) and directly by subtle stress-induced alterations of behaviour and physiology (Arlettaz et al., 2007; Baltic, 2005; Fowler, 1999; Lacy & Martins, 2003; Padgett & Glaser, 2003; Wirthner, 2006).

Animals wintering in montane ecosystems have to cope with a harsh climate and limited resource availabilities. They rely on a finely-tuned physiological balance, reducing their activity to a strict minimum. This renders them especially vulnerable to any changes in environmental conditions. Frequent human disturbance may disrupt energy budget and affect survival (Baltic, 2005; Bélanger & Bédard, 1990; Janczak et al., 2007; Wingfield, Breuner & Jacobs, 1997). Escape maneuvers are costly, whilst temporarily leaving shelter leads to detrimental exposure to adverse ambient temperatures in those animals relying on snow burrowing for sparing energy. Therefore, the capacity to maintain homeostasis is affected (Wingfield, Breuner & Jacobs, 1997), which translates into increased stress hormone production (Arlettaz et al., 2007; Carney & Sydeman, 1999; Fowler, 1999; Gutzwiller et al., 1998; Hofer & East, 1998; Mullner, Linsenmair & Wikelski, 2004). Severe chronic stress can further down-regulate the immune system, diminishing the defense readiness of the organism (Christe, Morand & Michaux, 2006; Navarro et al., 2004; Padgett & Glaser, 2003). This opens the way to parasite infestations, with anti-parasite strategies in turn incurring extra energy expenditures (Giorgi et al., 2001). Repeated disturbance in winter, as observed in areas devoted to snow sports, may thus select against low quality individuals (e.g. low body condition index) or force them to emigrate towards less disturbed areas. Alternatively, dominant individuals may settle in less disturbed, i.e. supposedly more optimal habitats, outcompeting subordinate birds that have then no other option than occupying suboptimal habitats affected by higher snow sports traffic. Either pattern would invariably lead to a despotic distribution of phenotypes.

We studied the impact, in terms of individuals' condition, of the winter tourism industry on Alpine wildlife, using the Black grouse (*Tetrao tetrix*) as a model species. Black grouse populations have undergone major declines over the past decades in Central and Western Europe (Storch, 2007). In the European Alps, Black grouse are bound to high-altitude timberline habitats. Areas devoted to snow sport recreations are still frequently inhabited, although at much lower density (Patthey et al., in review). Beside habitat type (i.e. natural vegetation community), snow sport infrastructure appears to be the principal determinant of Black grouse density (Wirthner, 2006). Snow sports installations (exclusively ski-lifts) alter and fragment the natural habitat matrix (Rolando et al., 2007; Storch, 2007; Wipf et al., 2005), increase mortality due to cable collisions (Watson & Moss, 2004), augment the frequency of disturbance by humans and predators (Storch & Leidenberger, 2003; Wittwer, 2007), with the latter eliciting elevated stress (Arlettaz et al., 2007; Baltic, 2005).

The aim of this study was to test empirically whether human disturbance in winter affects Black grouse condition to the extent that phenotypes redistribute themselves among patches of habitat in a despotic way. Namely, we predicted that stronger individuals would inhabit less disturbed, i.e. supposedly more suitable habitats, whereas weaker individuals would be rejected towards less suitable, more disturbed areas around snow sports areas. We compared parasite burdens (prevalence and intensity of a nematode; (Belleau, 2006) and body condition indices (body mass corrected for structural size; fluctuating asymmetry;(Brown, 1996; Stevenson & Woods, 2006) in birds stemming from areas with varying intensities of human disturbance, while controlling for other covariates such as bird population density.

2. Materials and Methods

2.1 Parasite load

2.1.1 Study sites

The study about parasite load was conducted at 26 sites in southwestern Switzerland, which had already been used for a research on Black grouse stress ecology (Arlettaz et al., 2007; Baltic, 2005). Half of the study sites were close to ski resorts, i.e. frequently disturbed by humans in winter, whilst the other sites were in undisturbed or less disturbed areas farther away from tourist resorts.

2.1.2 Parasites *Capillaria spp*.

We focused on *Capillaria spp*., a group of very thin, transparent intestinal nematodes. These hairworm parasites have either a direct life cycle, or a complex one which includes earthworms as intermediate hosts. The eggs of these nematodes are excreted with host's droppings, being then absorbed orally by a new host during foraging. The adult worms bore with their rostrum in the epithelial layer of the intestine and can inflame the intestinal wall. *Capillaria* species are among the most frequent endoparasites of Black grouse (Belleau, 2006). Actually, *Capillaria* spp. were the only parasites we could retrieve from the faecal samples collected in this study. In poultry, hairworms are known to cause diarrhoea, weakness, weight loss and a drop in egg production (Schneider, Boch & Supperer, 2006). They can also have a negative impact on the development and expression of sexual ornaments (Martinez-Padilla et al., 2007; Mougeot et al., 2007), affecting the mating and breeding successes of Black grouse cocks (Alatalo et al., 1996; Siitari et al., 2007).

2.1.3 Parasite intensity and prevalence

The *Capillaria* eggs present in the droppings were used to assess parasite loads (Seivwright et al., 2004). Faecal samples were collected from early January until end of March in 2005 and 2007. Isomursu et al. (2006) have documented a sex-biased infestation. Males are on average more parasitized, which has been attributed to both the immunosuppressive effect of male sex hormones and males' larger body size (Hoby et al., 2006; Isomursu et al., 2006). Unfortunately, our faecal samples could not be sexed based on dropping size, despite sexual size dimorphism. Also, tests with genetic markers failed (L. Fumagalli, pers. comm.). Our sample therefore consists only of droppings collected from snow burrows from which birds have been flushed by the observers, which allowed sex identification. Faecal samples were stored in a deep-freezer to avoid damages to the eggs.

Preliminary tests of different methods used for detecting and counting intestinal parasite eggs [sedimentation-flotation and McMaster methods (Kaufmann, 1996); Ovatec-Plus method, Dr. E. Graeub AG, performed according to manufacturers' manual] revealed that the most reliable technique regarding sensitivity and repeatability was the sedimentation-flotation-method (Lingg, unpublished report). We therefore opted for it.

The faecal material submitted to sedimentation-flotation was a random 5 g subsample of the droppings collected from an individual's snow burros. To separate nematode eggs from food remains, the droppings were first squeezed through a sieve into a cup of normal tap water. There the eggs sank down. Two ml of the precipitate were then poured into a test-tube. After filling up the tube with a $ZnCl_2$-solution (density: 1.3), a cover slip was placed on the top of the tube. As the eggs were now lighter than the solution, they arose to the cover slip. This process was accelerated by centrifuging the test-tubes at 1800 rpm for 5 min. Given that the eggs pasted underneath the cover slip, they could be counted by scanning the complete surface with a microscope. To gather information about (and control for) moisture of the faecal material beforehand, the remaining part of the sample was dried for 3 h at 70°C and then weighed. Initial drying of the whole sample would have destroyed the eggs by desiccation. Egg counts were used to estimate the prevalence (presence/absence, i.e. percentage of individuals infested at a given site) and intensity of the parasites (mean number of eggs per g of dry dropping mass; three replicates per individual; (Zander, 1998).

2.2 Individual condition

2.2.1 Study sites

In order to estimate patterns of body condition we used data available from Black grouse males captured in the same study area in 2002-2007: 12 sites were located close to ski resorts, whilst the remaining 12 sites were in low disturbed areas.

2.2.2 Body condition

Black grouse cocks were captured in winter and spring. In winter, a net was set above an occupied igloo and the bird was captured by flushing it from its snow burrow. In spring, the birds were mist-netted on leks at dawn. The captured birds were weighed and the lengths of both tarsi, both wings, both 1st primaries, middle and outer tail feathers and bill were measured. We distinguished two age classes (subadults and adults) according to the color, shape and length of the 1st primary feather (Klaus et al., 1990).The birds were also ringed and radio-tagged for a long-term study of population dynamics.

Body condition was estimated through an index that corrected body mass for individual structural size variation (Brown, 1996; Stevenson & Woods, 2006). Structural size is the nutrient-reserve independent size of an individual, where nutrient reserves are tissues that can by utilized by the animal prior to starvation. Incorporating this variation distinguishes more accurately between body nutrients that are utilizable (stores) and not utilizable (structural components; (Piersma & Davidson, 1991). In the case of the Black grouse, nutrient reserves are mainly stored in muscles and energy shortages are compensated for by catabolizing muscle proteins (Willebrand & Marcstrom, 1989). The residuals of a mass x structural size regression therefore served as a body condition index (Green, 2001; Schulte-Hostedde et al., 2005). However, because the mass of adult males continuously decrease from mid winter until late spring (Klaus et al., 1990), body mass had also to be corrected for a time effect: for that, we regressed body mass against capture date. The slope of this line was then used to calculate the average mass on the capture date. The residuals of the mass x size regression were calculated from a multivariate model that includes the corrected mass as the dependent variable and mean lengths of tarsus and 1st primary as separate predictors (Green, 2001). Repeatedly captured adults were only included once in the analysis. In this case the measurements of the first capture at adult age were used.

2.2.3 Fluctuating asymmetry

Small deviations from perfect morphological symmetry in bilateral traits are called fluctuating asymmetry (FA; (Brown, 1996; Palmer & Strobeck, 1986). Environmental stressors during the development of bilaterally symmetric traits can lead to asymmetric growth and FA is therefore an indicator of the conditions prevailing at the time when the trait was acquired (Swaddle & Witter, 1994). The FA of a trait is measured as the difference in size between left and right sides. If the linear correlation between the absolute difference (|L – R|) and the mean value (L + R)/2 is positive and significant, then the measurements need to be corrected for variation in size between birds. Otherwise the absolute asymmetry (|L – R|□□□) between left and right trait can be used (Rintamaki et al., 1997). Therefore we checked first if we had to use corrected or absolute values.□□□□

2.3 Despotic distribution of phenotypes

To test whether human disturbance leads to a despotic distribution of phenotypes, differences in the structural size between the study sites were investigated. We used the first principal component of a PCA obtained from mean tarsus and mean of 1st primary lengths as an index of structural size of the birds. The sample consisted of the same cocks as for the body condition analysis above.

2.4 Explanatory variables

Three categories of variables that may affect the state of health of Black grouse were used in the modelling so as to account more widely for other sources of environmental variation. The first category comprised variables expressing degrees of human disturbance, the second category characterized habitat typology and the third one depicted Black grouse density (Table 1).

2.4.1 Human disturbance

Human disturbance was estimated in three different ways, accounting for exposure to human disturbance (stress), snow sports infrastructure, and snow sports traffic outside ski resorts. An index of disturbance intensity was firstly derived from previous measures of the concentration of stress hormone metabolites in Black grouse droppings: Arlettaz et al. (2007) have shown that corticosterone levels correlate positively with the intensity of human disturbance in winter. Yet, this dataset could be used only for the analysis of parasite infestation because the information was not available from several capture sites in the present study. Secondly, an index for snow sports infrastructure was determined as the 1st factor of a principal component analysis obtained from measures of ski-lifts density derived at different spatial scales, in addition to the mean distance to ski-lifts of any reference pixel (Patthey et al., 2008; Wirthner, 2006). A high score means both a high density of snow sports infrastructure and a short distance thereto. Thirdly, the traffic of snow sports outside main ski resorts was calculated from the number of ski, snowboard and snowshoe traces recognized on aerial pictures of timberline habitats taken in 2004 and 2007 (Arlettaz et al., 2007; Baltic, 2005): all traces from snow sport activities (mostly skiing) in a 500 m radius around located igloos were counted and sites were classified in three categories (low traffic: 0-1 trace; moderate traffic: 2–11 traces; intense traffic: more than 11 traces).

2.4.2 Habitat typology

We classified sites according to the dominant tree cover in four categories: habitats consisting, namely, of pure larch, larch and stone pine, fir and spruce, as well as larch and spruce.

Additionally, we used two previously GIS-derived habitat indices, in the form of two factors of a principal component analysis, to describe vegetation communities which best explain Black grouse density (Wirthner, 2006). These two factors are thereafter called vegetation community I and II.

2.4.3 Black grouse density

Black grouse density was estimated in two ways. Firstly, we used counts of the number of displaying males on lekking places at Black grouse capture sites in 2005 (Patthey et al., in review). Again, however, this data was not available from all study sites. Thus, to estimate density for all study sites we had to use a GIS-model of Black grouse male density built in 2005. This model contains the snow sports infrastructure as well as the two habitat indices for vegetation communities described above (Wirthner, 2006). This density index shows a significant linear correlation with the snow sports infrastructure index (r_s= 0.153, n = 268, F = 49.56, p < 0.001) and both habitat indices (r_s = 0.4693, n = 268, F = 49.56, p < 0.001; r_s = 0.02922, n = 268, F = 9.096, p = 0.003; respectively).

2.5 Statistical analysis

A hierarchical model selection approach was used to rank the best models among all candidate models, applying the small-sample unbiased Akaike Information Criterion (AICc) as a correction (Burnham & Anderson, 1998; Johnson & Omland, 2004). Global candidate models for all six response variables were all seven possible combinations of the three explanatory categories described above. Within each category, submodelling procedures were applied for every response variable, with all the variables yielding the lowest AIC and a ΔAIC of 2 or less being retained for the subsequent global modelling. Sites were included in all models as a random effect so as to nest the individual samples (either individual condition measurements or parasite burdens) within the sites.

In the parasite infestation analysis, year and sex were included as fixed effects. To test for factors influencing parasite intensity, linear mixed models were used, applying a quasi-poisson distribution to account for data dispersion. For the analysis of the parasite prevalence, logistic mixed regression was used. The analyses of body condition index, FA and despotic distribution of phenotypes were undertaken with linear mixed models.

Model quality for parasite intensity, body condition and despotic distribution of phenotypes was assessed by a Spearman correlation test between observed and predicted values, with a resampling validation (n = 1000; (Vaughan & Ormerod, 2005). For parasite prevalence, a resampling validation (n = 1000) using true skill statistic (TSS) was used, as mean prevalence differed from 50% (Allouche, Tsoar & Kadmon, 2006).

To define the best explanatory main variable category from the seven global models for every response variable, model averaging was performed in each case, with the selection probability and the averaged estimates being determined for every category. If the 95% confidence intervals (95% CI) of the averaged estimates of the variables used for a category did not overlap with 0, the category was considered as having a significant impact on the response variable (Johnson & Omland, 2004).

For all statistical analyses we used the program R, version 2.4.1, with the library 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). The Body condition index and the FA were calculated using JMP in 5.1 (SAS institute Inc. 2001, Cary, NC, USA).

3. Results

A comparison among all potential submodels within the human disturbance category for every response variable revealed that the snow sports infrastructure index has in any case a higher explanatory power than stress level and snow sports traffic (ΔAIC > 2). Therefore, the human disturbance component of the global model in all six analyses includes only that principal factor. The comparison within the Black grouse density submodels revealed that the density index had in any case the lower AIC values (ΔAIC > 2) than the counts of the number of displaying males. Thus, in the following results of the global models, Black grouse density is always expressed by the density index. There was no consistent best explanatory variable within the habitat category submodels. Thus, depending on the response variable, different variables for habitat typology had to be incorporated.

Because the basic submodels (pseudo null models) already contained site and year (and sex in addition for parasite load), and model quality of these submodels was relatively good, the difference in model quality between the various candidate models remains small (Tables 2, 4 and 6).

3.1 Parasite load

The analysis is based on 42 male and 23 female faecal samples collected at 10 sites in 2005; and 61 male and 25 female samples obtained from 26 sites in 2007.

3.1.1 Prevalence

There was a significant effect of year on parasite prevalence over all seven global candidate models (mean $p < 0.001$, SD = 0.001), with 90% of sites (9 out of 10) harbouring at least one infected bird in 2005 vs. 27% in 2007 (7 out of 26). The effect of sex on parasite prevalence was not significant in the global candidate models (mean $p = 0.867$, SD = 0.061). The best global model among all candidate global models (AICc weight = 0.574) included only the habitat typology category (containing only the vegetation community I, according to the submodels), whereas the second best model (AICc weight = 0.180) combined the variables for human disturbance (snow sports infrastructure index) and habitat typology (vegetation community I) (Table 2). Global models with other combinations of category sets had lower probabilities to be the best model (AICc weights < 0.12; Table 2). TSS (True skill statistic) values of the bootstrap method for these two best models (TSS = 0.617 and 0.636, respectively, with standard deviation of 0.092 in both cases) indicate good model qualities.

The global model indicates that parasite prevalence is mainly explained by habitat typology, as shown by its high selection probability (0.913, Table 3) and an averaged estimate which does not overlap with 0. Mainly juniper shrubs have a positive effect on the parasite prevalence, whereas grass cover in open forest decreases parasite prevalence. The selection probability for human disturbance (0.292) and Black grouse density (0.209) were clearly lower and the 95% CI of their averaged estimates overlapped with 0 (Table 3).

3.1.2 Intensity

There was a significant effect of year on parasite intensity over all the seven global candidate models (mean $p < 0.001$, SD < 0.001), with droppings from 2005 containing more parasite eggs than in 2007 (2.23 vs. 0.611 eggs/g of dry faecal material) as well as an effect of sex (females being more parasitized than males; mean $p = 0.002$, SD = 0.002). For the habitat typology category the two vegetation community factors I and II were included in the global models. The best global model among all candidate global models (AICc weight = 0.621) combined the variables for human disturbance (snow sports infrastructure index) and Black grouse density (density index), whereas the second best model (AICc weight = 0.255) only included the variable for human disturbance (snow sports infrastructure index) (Table 2). Correlation coefficients of a resampling validation test between observed and predicted values were significant in these two best global models ($r_s = 0.904$ and 0.905, respectively; both $p < 0.0001$) indicating good model qualities. Global models with other combinations of variable sets had lower probabilities to be the best model (AICc weights < 0.11; Table 2).

The highest selection probability to be the best explanatory variable had the variable for the human disturbance category (snow sports infrastructure index) (0.990) (Table 3). Birds living within or close to ski resorts had lower parasite intensities than birds living in natural areas (averaged estimate: –0.1046; 95% CI: –0.2483 and

0.0390). Black grouse density and habitat typology had a lower selection probability (0.727 and 0.119 respectively; Table 3).

3.2 Body condition

The analysis of body condition index and FA was restricted to adult males (n = 88, from 24 sites) because the sample sizes for females (n = 28, from 12 sites) and subadult males (n = 33, from 14 sites) were too small. Cocks living within or close to ski resorts lost significantly less weight between winter and late spring than males from natural areas (linear regression t-test; R^2(adj) = 0.3312, DF = 99, F = 17.83, p = 0.0215, Fig. 1).

3.2.1 Body condition index

Data on mass, mean lengths of tarsus and 1st primary were available from 84 adult males from 24 sites. There was no significant effect of year of capture on the body condition index in all seven candidate global models (mean p = 0.255, SD = 0.022). Only vegetation community II was included for habitat typology. Clearly, the best model among all candidate models (AICc weight = 0.824) combined the variables for human disturbance (snow sports infrastructure index) and Black grouse density (density index), whereas the second best model (AICc weight = 0.126) only included the single variable for human disturbance (snow sports infrastructure index; Table 4). Correlation coefficients of a resampling validation test between observed and predicted values were significant in these two best models (rs = 0.750 and 0.783, respectively, with both p < 0.05), indicating good model qualities. Models with other combinations of variable sets had lower probabilities to be the best model (AICc weights < 0.02; Table 4).

Model averaging revealed that the selection probability to be the best explanatory variable was highest for the snow sports infrastructure index of the human disturbance category (0.967; Table 5). Birds living in more disturbed areas tend to have a higher body condition index than birds living in more natural areas. With an averaged estimate of 4.218 (95% CI: 0.586 and 7.850) it does not overlap with 0. The averaged estimates for habitat and Black grouse density do overlap with 0 (Table 5).

3.2.2 Fluctuating asymmetry: tarsi

Lengths of left and right tarsus were available from 86 adult males stemming from 24 sites. There was no significant linear correlation between the absolute difference between the left and right tarsus and the mean tarsus length (F-test, DF = 85, $p = 0.957$). Thus, the absolute asymmetry value was used. There was no effect of year of capture on tarsus FA over all the seven candidate global models (mean $p = 0.51$, SD = 0.009). There was no clear pattern in the model ranking and model quality was low (Table 4). Black grouse density (0.475) and human disturbance (0.440) had a slightly higher selection probability than habitat typology (0.280) (Table 5), but all 95% confidence intervals for the averaged estimate overlap with 0.

3.2.3 Fluctuating asymmetry: external tail feathers

Data on left and right tail feather lengths was available from 74 adult male Black grouse at 24 sites. There was again no significant linear correlation between the absolute difference between the left and right tail feathers and the mean tail feather length (F-test, DF = 73, $p = 0. 266$). Thus, the absolute asymmetry was used. Year of capture had no significant effect on tail fluctuating asymmetry in the seven candidate global models (mean $p = 0.134$, SD = 0.008). In habitat category, vegetation community I and II were both included. Human disturbance and Black grouse density had a slightly higher selection probability than habitat category, but 95% CI of the averaged estimate overlapped with 0 (Tables 4 and 5).

3.3 Despotic distribution of phenotypes

The same 84 males as in the body condition analysis were used here. Vegetation community I and II were both included from the habitat category. The effect of the year of capture was not significant in the candidate global models (mean $p = 0.138$, SD = 0.005). The best model among all candidate models (AICc weight = 0.468) only included the human disturbance category (snow sports infrastructure index), whereas the second best model (AICc weight = 0.389) only included Black grouse density (density index) (Table 6). Correlation coefficients of a resampling validation test between observed and predicted values were significant in these two best models ($r_s = 0.805$ and 0.802, respectively; both $p < 0.05$,) indicating good model qualities. Models with other combinations of variable sets had lower probabilities to be the best model (AICc weights < 0.1; Table 6).

Model averaging revealed that the selection probability to be the best explanatory variable was highest for human disturbance (0.574; Table 7). With an averaged estimate of 0.058 and 95% CI of −0.128 and 0.245, it does overlap with 0 however. The averaged estimates for habitat and Black grouse density with a selection probability of 4.95 and 0.044 respectively, also overlap with 0 (Table 7).

4. Discussion

Although snow sport recreational activities in general are believed to affect wildlife physical condition (Arlettaz et al., 2007; Baltic, 2005; Bélanger & Bédard, 1990; Fowler, 1999; Janczak et al., 2007; Lacy & Martins, 2003; Padgett & Glaser, 2003; Wingfield, Breuner & Jacobs, 1997), the present study of the Black grouse in the Swiss Alps could not confirm that view. Actually, Black grouse living in snow sports areas did not differ, from a purely structural body size viewpoint (the phenotype distribution approach used here), from birds in less disturbed, more natural areas. Contrary to our expectations, the former even appeared to be in better condition (better body condition indices and lower parasite intensities). We believe that there are three different scenarios which may explain this apparently paradoxical situation. The first series of explanations is merely methodological, the other two are biological.

Firstly, there may be some typical drawbacks inherent to the methods applied. Although the usage of a body condition index seems to be widely accepted (Brown, 1996; Green, 2001; Stevenson & Woods, 2006), relying on fluctuating asymmetry as an indicator of fitness is still controversial (Bergstrom & Reimchen, 2005; Lens et al., 2002; Van Dongen, 2000). In Black grouse it has yet been demonstrated that asymmetric tarsi determine a subordinate position on the lek arena, which in turn impacts negatively on the mating success (Rintamaki et al., 1997). We observed no differences in fluctuating asymmetry of tarsi and external tail feathers between Black grouse males living in snow sports areas compared to individuals living in less disturbed areas, which would support the idea of a non-despotic distribution of phenotypes between areas with different levels of human disturbance. Then, although we purposely focused on the intestinal parasite most frequently found in Black grouse (Belleau, 2006), we may have missed other sorts, less numerous parasites exerting a larger impact on fitness (Belleau, 2006; Höglund, Alatalo & Lundberg, 1992; Holmstad, Jensen & Skorping, 2008; Isomursu et al., 2006). Finally, our estimate of parasite prevalence (percentage of sites within either disturbed or natural study sites with presence of at least one parasitized bird) must have been affected by the small sample size available from snow sports areas.

Secondly, the phenotypes can still be distributed among habitats in a despotic way, as indirectly suggested by the body condition analysis, this in the absence of a significant pattern yielded by the phenotypic approach (structural body size). However, contrary to our expectations, only the strongest individuals (e.g. harbouring an effective immune system) would be able to survive next to ski resorts. This is again reflected in birds inhabiting disturbed areas having a higher body condition index and lower parasite intensities. Such a distribution could be achieved through death or systematic emigration of the weakest. As migration events could not be documented for males in the study population (unpublished data), the former hypothesis would be more likely.

Thirdly, and this is probably the main lesson from the present study, local Black grouse density may itself determine both birds' condition (through an intense intraspecific competition for access to e.g. crucial food resources) and parasite load (enhanced horizontal transmission). In this respect, the magnitude of density-dependent mechanisms could simply mask any slighter difference due to human disturbance. As regards body condition, the opposite, relative seasonal change observed in the mass of our cocks between winter and spring (Fig. 1) can be indicative of such an operating mechanism. Male Black grouse usually put on weight during winter, reaching a maximum weight in January, then progressively lose weight throughout late winter and spring until the end of the lekking season (Klaus et al., 1990; Willebrand & Marcstrom, 1989). Our results suggest that adult males living within or close to ski resorts lose proportionally less weight during this period than males from natural areas (Fig. 1). As we could also establish that areas around snow sport resorts support less lekking Black grouse (which furthermore rarely aggregate in groups; Patthey et al, in review) winter survivors in ski resorts may simply lose comparatively less weight because of a lower sexual competitive pressure exerted by other lekking cocks. Note that the impact of weight loss on the mating success of cocks is presumably low (Rintamäki et al., 2001) and can apparently be rapidly compensated for when food supply is sufficient (Willebrand & Marcstrom, 1989). Black grouse density can also have an impact on horizontal parasite transmission, which largely depends on host abundance (Zander, 1998). In Black grouse, parasites' free-living stages would naturally be more prone to transmission within natural, undisturbed areas because of a higher Black grouse density. Our results furthermore show a significant dependence of parasite prevalence upon habitat type, which suggests that egg transmission is facilitated by certain vegetation conditions as proposed by (Roberts et al., 1992). In our case it seems that juniper shrubs facilitate egg transmission, whereas grass cover in open forest apparently hampers it. There is, however, the methodological aspect of prevalence analysis raised above which may affect the outcome of the modelling. The real impact of infestations by *Capillaria* varies greatly not only according to host density, but also in relation to season and year.

Parasite intensities reach a trough during winter months, probably due to low accessibility of the eggs under the snow cover, i.e. low ingestion/contamination risk (Klaus et al., 1990). An effect of year on parasite prevalence and intensity was especially strong in this study. This is likely a consequence of between-year variation in weather conditions which greatly impact on the free-living larval stages (Altizer et al., 2006; Stromberg, 1997).

The disturbance elicited by snow sports activities affects wintering Black grouse in a rather non-intuitive way. Birds of apparently better physical condition (smaller parasite burden and better body condition) survive at low density in highly disturbed areas. Although individuals inhabiting snow sports areas have been shown to suffer from elevated stress (Arlettaz et al., 2007), they in turn probably face less intrasexual competition during the courtship period due to lower density of displaying cocks.. This study does not imply that winter human disturbance, especially around snow sport facilities, exerts no impact on Alpine Wildlife. Actually, the approaches used here to measure health state and physical condition of Black grouse (parasite burdens, body condition indices and fluctuating asymmetry) may be too sensitive to density-dependence mechanisms. Any effect of disturbance would thus simply have been masked by these overwhelming mechanisms. What remains certain is that wildlife in Alpine timberline ecosystems suffers from severe reductions in population density. Whether this is due to the stress caused by a growing snow sports traffic (Arlettaz et al., 2007), other corollary effects such as enhanced predation (Patthey et al. in review), or a combination thereof still remains to be elucidated.

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7. Tables

Table 1. Summary description and availability of variables used as fixed effects in the models. The variables were classified in three main categories: human disturbance, habitat typology and Black grouse density.

Category	Variable	Description	available for following analysis
Human disturbance	Stress index	Average corticosterone level per site in 2004 (Arlettaz et al. 2007)	parasite load
	Snow sports infrastructure index	1^{st} PC of density and distance to ski lifts (Patthey et al. in review)	parasite load / body condition / despotic distribution
	Snow sports traffic 2004	Number of ski traces counted from aerial pictures taken in 2004	parasite load / body condition / despotic distribution
	Snow sports traffic 2007	Number of ski traces counted from aerial pictures taken in 2007	parasite load / body condition / despotic distribution
Habitat typology	Vegetation community I	PCA factor obtained from various habitat variables (Patthey et al. in review)	parasite load / body condition / despotic distribution
	Vegetation community II	Other PCA factor obtained from various habitat variables (Patthey et al. in review)	parasite load / body condition / despotic distribution
	Forest type	Main forest type in habitat	parasite load / body condition / despotic distribution
Black grouse density	Number of lekking males	Number of displaying males along transects in 2005	parasite load / body condition / despotic distribution
	Density index	1st PC of Snow sport infrastructure index, Vegetation community I and Vegetation community II (Patthey et al. in review)	parasite load / body condition / despotic distribution

Table 2. Model ranking for all candidate global models of parasite prevalence (a, Generalized Linear Mixed Models) and parasite intensity (b, Linear Mixed Models) in Black grouse faecal material collected at 26 study sites in the Swiss Alps. k: number of model parameters; $\Delta \mathrm{AIC}_c$: differences in corrected Akaike Information Criterion scores; AIC_cw: AIC_c weights; Mean TSS: mean of true skill statistics of a bootsrap method (n = 1000); SD: standard deviation of TSS bootstrap. Mean r_s: mean of Spearman Rank Correlation coefficients of a resampling validation test (n = 1000) between observed and predicted values; SD r_s: standard deviation of Mean r_s; $p < 0.05$ of 1000: number of p-Value < 0.05 of 1000 resampling validation tests.

a) Parasite prevalence		k	Δ AICc	AICc w	Mean TSS	SD
1	Habitat typology	5	0.00	0.574	0.617	0.092
2	Human disturbance + Habitat typology	6	2.32	0.180	0.636	0.092
3	Habitat typology + Black grouse density	6	3.22	0.115	0.619	0.094
4	Human disturbance + Habitat typology + Black grouse density	7	5.12	0.044	0.636	0.092
5	Human disturbance	5	5.50	0.037	0.604	0.091
6	Human disturbance + Black grouse density	6	5.82	0.031	0.627	0.089
7	Black grouse density	5	6.80	0.019	0.609	0.085
	Pseudonullmodel	4	4.60	0.057	0.590	0.084

b) Parasite intensity		k	Δ AICc	AICc w	Mean rs	SD rs	p < 0.05 of 1000
1	Human disturbance + Black grouse density	6	0.00	0.621	0.904	0.027	1000
2	Human disturbance	5	1.78	0.255	0.905	0.025	1000
3	Human disturbance + Habitat typology + Black grouse density	8	3.65	0.100	0.903	0.026	1000
4	Human disturbance + Habitat typology	7	7.50	0.015	0.904	0.026	1000
5	Black grouse density	5	9.48	0.005	0.904	0.026	1000
6	Habitat typology	6	10.30	0.004	0.902	0.027	1000
7	Habitat typology + Black grouse density	7	14.00	0.001	0.902	0.026	1000
	Pseudonullmodel	4	6.58	0.023	0.905	0.025	1000

Table 3. Selection probability and estimates with 95% confidence intervals (CI) of the averaged models obtained from all variables or groups of variables for a) parasite prevalence and b) parasite intensity. Human disturbance: snow sports infrastructure index; Black grouse density: density index; Habitat typology: vegetation community I and II. See text for more details.

	Variable category	Variable	Selection probability	Estimate	lower CI	upper CI
a)	Parasite prevalence					
	Habitat typology	Vegetation community I	0.913	0.3956	0.0195	0.0687
	Human disturbance	Snow sports infrastructure index	0.292	-0.0205	-0.0931	0.0522
	Black Grouse density	Density index	0.209	-0.0194	-0.1076	0.7717
b)	Parasite intensity					
	Human disturbance	Snow sports infrastructure index	0.990	-0.1046	-0.2483	0.0390
	Black grouse density	Density index	0.727	-0.1468	-0.5213	0.2278
	Habitat typology	Vegetation community I	0.119	-0.0400	-0.2379	0.1579
		Vegetation community II	0.119	-0.0189	-0.1170	0.0792

Table 4. Model ranking of all candidate global models (Linear mixed Models) to explain a) body condition index, b) fluctuating asymmetry in tarsi and c) fluctuating asymmetry in external tail feathers in Black grouse at 24 study sites in Switzerland. k: number of model parameters; Δ AIC$_c$: differences in corrected Akaike Information Criterion scores; AIC$_c$w: AIC$_c$ weights; Mean r_s: mean of Spearman Rank Correlation coefficients of a resampling validation test (n = 1000) between observed and predicted values; SD r_s: standard deviation of Mean r_s; $p < 0.05$ of 1000: number of p-Value < 0.05 of 1000 resampling validation tests.

		Model description	k	Δ AIC$_c$	AIC$_c$ w	Mean r_s	SD r_s	$p < 0.05$ of 1000
a)	Body condition index							
	1	Human disturbance + Black grouse density	5	0.00	0.824	0.750	0.175	932
	2	Human disturbance	4	3.76	0.126	0.783	0.177	929
	3	Black grouse density	4	7.68	0.018	0.807	0.150	960
	4	Habitat typology	5	8.40	0.012	0.795	0.149	960
	5	Human disturbance + Habitat typology + Black grouse density	7	8.50	0.012	0.784	0.130	976
	6	Human disturbance + Habitat typology	6	9.92	0.006	0.793	0.148	962
	7	Habitat typology + Black grouse density	6	11.09	0.003	0.795	0.138	964
		Pseudo null modell	3	6.18	0.038	0.818	0.132	976
b)	Fluctuation asymmetry (tarsi)							
	1	Black grouse density	4	0.00	0.340	0.514	0.310	580
	2	Human disturbance	4	0.20	0.308	0.487	0.325	527
	3	Habitat typology	6	1.23	0.184	0.553	0.185	743
	4	Human disturbance + Black grouse density	5	3.09	0.072	0.525	0.301	605
	5	Habitat typology + Black grouse density	7	4.54	0.035	0.581	0.202	761
	6	Human disturbance + Habitat typology	7	4.67	0.033	0.559	0.183	760
	7	Human disturbance + Habitat typology + Black grouse density	8	5.03	0.028	0.603	0.177	838
		Pseudo null modell	3	-2.58	1.234	0.528	0.316	605
c)	Fluctuation asymmetry (external tail feathers)							
	1	Human disturbance	4	0.00	0.456	0.820	0.154	964
	2	Black grouse density	4	0.69	0.323	0.837	0.136	974
	3	Human disturbance + Black grouse density	5	3.09	0.097	0.823	0.145	973
	4	Habitat typology	5	3.52	0.078	0.829	0.136	974
	5	Human disturbance + Habitat typology	6	5.90	0.024	0.813	0.161	958
	6	Habitat typology + Black grouse density	6	6.94	0.014	0.831	0.149	967
	7	Human disturbance + Habitat typology + Black grouse density	7	8.34	0.007	0.826	0.139	969
		Pseudo null modell	3	-2.03	1.257	0.841	0.116	989

Table 5. Selection probability and estimates with 95% confidence intervals of the averaged model of all variables or groups of variables for a) body condition index, b) fluctuating asymmetry in tarsi and c) fluctuating asymmetry in external tail feathers. Human disturbance: snow sports infrastructure index; Black grouse density: density index; Habitat typology: vegetation community I and II. See text for more details.

a)	Variable category	Variable	Selection probability	Estimate	lower CI	upper CI
a)	Body condition index					
	Human disturbance	Snow sports infrastructure index	0.967	4.218	0.586	7.850
	Black grouse density	Density index	0.856	7.702	-3.143	18.546
	Habitat typology	Vegetation community II	0.033	0.339	-4.227	4.904
b)	FA (tarsi)					
	Black grouse density	Density index	0.475	0.019	-0.067	0.106
	Human disturbance	Snow sports infrastructure index	0.440	0.001	-0.022	0.024
	Habitat typology	Vegetation community I	0.280	0.038	-0.092	0.168
		Vegetation community II	0.280	-0.011	-0.074	0.052
c)	FA (tail feathers)					
	Human disturbance	Snow sports infrastructure index	0.584	0.010	-0.032	0.052
	Black grouse density	Density index	0.442	-0.006	-0.089	0.077
	Habitat typology	Vegetation community I	0.123	0.002	-0.013	0.017
		Vegetation community II	0.123	0.000	-0.009	0.008

Table 6. Model ranking of all candidate models (Linear mixed Models) to explain despotic distribution of phenotypes (structural size) in Black grouse at 24 study sites in Switzerland. k: number of model parameters; Δ AIC_c : differences in corrected Akaike Information Criterion scores; AIC_cw: AIC_c weights; Mean r_s: mean of Spearman Rank Correlation coefficients of a resampling validation test (n = 1000) between observed and predicted values; SD r_s: standard deviation of Mean r_s; p < 0.05 of 1000: number of p-Value < 0.05 of 1000 resampling validation tests.

	Model description	k	Δ AICc	AICc w	Mean rs	SD rs	p < 0.05 of 1000
1	Human disturbance	4	0.00	0.468	0.805	0.179	949
2	Black grouse density	4	0.37	0.389	0.802	0.174	957
3	Human disturbance + Black grouse density	5	3.09	0.100	0.788	0.176	945
4	Habitat typology	6	5.38	0.032	0.729	0.168	946
5	Human disturbance + Habitat typology	7	8.72	0.006	0.746	0.151	969
6	Habitat typology + Black grouse density	7	9.01	0.005	0.738	0.163	949
7	Human disturbance + Habitat typology + Black grouse density	8	12.92	0.001	0.745	0.152	963
	Pseudo null model	3	5.21	0.037	0.822	0.170	961

Table 7. Selection probability and estimates with 95% confidence intervals of the averaged model of all variables or groups of variables for the despotic distribution of phenotypes (structural size). Human disturbance: ski index; Black grouse density: density index; Habitat: vegetation community I and II.

Variable category	Variable	Selection probability	Estimate	lower CI	upper CI
Human disturbance	Snow sports infrastructure index	0.574	-0.058	-0.245	0.128
Black grouse density	Density index	0.495	0.022	-0.282	0.326
Habitat typology	Vegetation community I	0.044	-0.037	-0.232	0.017
	Vegetation community II	0.044	0.001	-0.093	0.094

8. Figures

Figure 1: Variation of body mass of Black grouse cocks (n = 102) in relation to capture day and human disturbance (48 males stem from ski resorts and 54 from undisturbed areas; Patthey et al., in review). Male Black grouse captured in natural areas lose significantly more weight (-1.4 gram per day) from late winter to late spring than males living within or close to ski resorts (-0.7 gram per day).