Effects of recreation disturbance on foraging patterns and habituation potential of Alpine wildlife:

a case study of black grouse, an endangered species of timberline ecosystems

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Human disturbance by outdoor snow-sports induces compensatory foraging in a key indicator species of alpine ecosystems

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Summary

1. Free-ranging animals have evolved various strategies to cope with environmental variability and to maintain physiological homeostasis. Increasing outdoor recreation generates novel human-wildlife conflicts which potentially induce energetically costly behavioural and physiological responses in animals. Energy losses can be compensated for by increasing energy intake, decreasing energy expenditures or monopolizing fat reserves. Yet, animals with an already finely-tuned ecophysiology, e.g. species of boreo-alpine biomes, seem to be particularly at risk.

2. We investigated the activity patterns of a vulnerable key indicator species of timberline ecosystems, the alpine black grouse (*Tetrao Tetrix*). We first tested whether there was any time overlap in the activities of black grouse (foraging) and snow-sport practitioners (skiers and snowboarders); second, whether exposition to winter outdoor recreation causes extension of foraging duration in response to disturbance (e.g. inadvertent flushing from snow burrows).

3. Generalized linear mixed effects models and a model selection approach were used to rank the predictors of recreation disturbance and environment characteristics that could potentially influence the foraging patterns of cocks and hens in winter.

4. Compared to little disturbed, natural sites, cocks in anthropized areas prolonged their daily foraging activity by feeding earlier and longer in the evening, increasing the probability of encounters with snow-sports traffic in their habitat. No effect could be evidenced for hens. This suggests that black grouse males in anthropized sites may be obliged to compensate for energy losses (caused by human disturbance) by increasing food intake, which can only be achieved by augmenting feeding duration.

5. We recommend creating wildlife winter refuges within and around ski resorts so as to limit agonistic interactions between snow-sports people and black grouse and to provide quiet foraging opportunities for black grouse in the close proximity to humans.

290 words

Key words: Foraging patterns, disturbance *Tetrao tetrix,* Winter recreation, Winter sports

Introduction

Wildlife has evolved various strategies to cope with the natural challenges posed by environmental variation, such as harsh climatic conditions that limit resource availability. Wild animals must also adapt to more recent alterations of the environment, for instance habitat fragmentation and climate change (Walther et al. 2002; Root et al. 2003; Ingold 2005; Ferraz et al. 2007). The recent, rapid development of winter recreation such as skiing, snowshoeing, or back-country skiing represents an additional threat for wildlife (Creel et al. 2002; Arlettaz et al. 2007; Patthey et al. 2008; Thiel et al. 2008). The unpredictable disturbance generated by people trespassing out of marked boundaries of ski slopes affects species which are already rendered vulnerable by scarce food resources and a finely-tuned energy balance during the cold season. Not surprisingly, sportspeople are thus often assimilated to predators by wildlife (Frid & Dill 2002; Beale & Monaghan 2004). Upon detection of human presence, animals' heart rate usually starts to increase (Wilson et al. 1991) whereas the release of stress hormones can be triggered (McEwen & Wingfield 2003; Ellenberg et al. 2006). These adaptive physiological responses already induce additional energetic expenditures for the organism (Hofer & East 1998; von der Ohe & Servheen 2002). If humans come closer, a typical behavioural response of wildlife is to flee (Baines & Richardson 2007; Thiel et al. 2007). Such escape manoeuvres represent a further impairment of the energy balance. McEwen & Wingfield (2003) have proposed a conceptual framework to understand the ecophysiological processes of anthropogenic disturbance upon wildlife. Any behavioural and physiological responses induced by perturbations of the environment represent an allostatic load for the organism, which is the additional energy necessary to keep a balanced physiological state, or homeostasis. This is principally an adaptation to deal with change and is thus per se neither dangerous nor maladaptive insofar as the required extra energy needed for compensating losses is available in the organism and/or the environment. Sometimes, however, the disturbance increases in intensity or duration, potentially leading to a situation of allostatic overload: not enough extra energy can now be extracted from the organism and/or the environment to compensate for the additional energy requirements, which leads to a dangerous physiological imbalance (McEwen & Wingfield 2003). This may in turn affect survival (Müllner, Linsenmair & Wikelski 2004), reproductive abilities (Watson & Moss 2004; Langston et al. 2007) and eventually population size (Müllner, Linsenmair & Wikelski 2004; Patthey et al. 2008). Maintaining homeostasis may therefore be crucial for long-term population persistence. In order to compensate for energy losses, an animal organism can monopolize its fat stores, reduce its energy consumption by limiting activity, and/or increase foraging time. Not all species, however, have these three possibilities. For instance, animals which do not constitute body fat reserves and thus already have a tight activity and energy budget have only compensatory feeding as an option. Any extension of foraging activity in such species would therefore indirectly inform about the actual impact of anthropogenic disturbance.

This study examines the effect of winter recreation disturbance on foraging patterns of Alpine black grouse (*Tetrao tetrix)*, an emblematic, indicator bird of timberline ecosystems, the habitat where most outdoor snow-sports activities concentrate in the European Alps. In this massif, local population declines have been attributed to spreading and intensifying winter sports (Storch 2007). Black grouse show a bimodal daily activity rhythm in winter, with two periods of foraging in the early morning and late afternoon (Marjakangas, Rintamäki & Hissa 1984). Between foraging sessions, black grouse rest in self-excavated snow burrows – if snow conditions allow –, therefore reducing predation risk, and energy losses thanks to the temperature buffer in the igloo (Marjakangas, Rintamäki & Hissa 1984). Arlettaz et al. (2007) have established that black grouse cocks show increased concentrations of stress hormone (corticosterone) metabolites in winter if they are repeatedly flushed from their snow burrows, or occur in areas with moderate and high levels of anthropogenic disturbance. At this stage, however, it is not known if and how black grouse compensate for the extra energy expenditures provoked by disturbance. As black grouse do not, or cannot, store fat reserves (Willebrand & Marcström 1989), we would expect extra foraging to be the only option available to them. We therefore investigated the foraging patterns of black grouse at sites with different levels of winter recreation disturbance. More specifically, we hypothesized i) that black grouse in disturbed areas have longer foraging bouts than black grouse in sites with no or little anthropogenic disturbance, which would provide evidence for allostatic adjustments in the former habitat; ii) that black grouse in highly disturbed sites shift their foraging periods to times when no humans are present in their habitat (earlier onset of foraging at dawn, later end of foraging at dusk). This information would prove essential to understand the ecophysiology of wintering alpine wildlife and to adapt management policies for these declining birds in and around ski resorts.

Materials and Methods

Study sites

The study was carried out between January and March 2004 and 2008 at 10 different study sites with different levels of human activity, ranging from natural areas with no or limited recreation to crowded ski resorts. Study sites are situated in the Alps of the cantons of Valais and Vaud (southwestern Switzerland, 46°10′ N, 7° 24′ E) within an elevation belt between 1400 and 2300 m altitude. Study sites consist of upper sub alpine coniferous forest patches intermixed with open grassland and/or *ericacea-juniperus* shrubland (Klaus et al. 1990). The climate is sub continental to continental, with cold, rather wet winters and warm dry summers (Reisigl & Keller 1999). In winter, skilift installations usually open at 9h00 and close between 16h15 and 16h45.

Fieldwork

Black grouse were captured from snow burrows (during winter) or with mistnets at leks (during Spring) between 2002 and 2007. They were tagged with 16 g neck-laced radio-transmitters equipped with an activity sensor (Holohil Systems Ltd, Carp, Canada) under licences from the Swiss Federal Office for the Environment and the Wildlife and Game services of Valais and Vaud. Activity patterns could be reconstructed from radio signals recorded – through a stationary omni directional aerial positioned on a vantage point overlooking birds’ habitat – using receivers' data loggers (TR-5, Telonics, Mesa, Arizona). They registered the duration and repetition rate of activity signals (several thousand records per bird and day), along with date and time and were placed in hermetic boxes burrowed in snow to keep their temperature as constant as possible and protect them from precipitation. The location of a bird was estimated every second day by triangulation using an H-antenna (White & Garrott 1990). We attempted to register radio-monitored birds at least four days each, although this was not always possible due to some topographical and technical limitations.

Activity patterns and response variables

In order to obtain daily foraging patterns, which were comparable between birds and days, we had to standardise activity curves obtained from radio-signals (Baltic 2005). The day was divided in 10 min period intervals. For each 10 min period we counted the absolute number of activity signals. By dividing those 10 min figures by the total number of data recorded per day, we obtained relative curves of signal pulse rates, i.e. activity curves (Fig. S1, S for supplementary material). Every single 10 min interval above a 4% threshold of the relative daily activity as well as any cluster of three or more 10-min intervals above 1% activity in a row were considered as indicating activity. These thresholds were set based on visual observations of radio-tracked birds, performed in parallel to automatic signal recording, which showed that behaviour could simply be coded in a dichotomic way, by distinguishing activity from resting (Baltic, 2005, Patthey et al., in prep., Fig. S1). Through these visual observations we could also assess that activity consisted almost exclusively of foraging. Morning and evening foraging bouts could easily be separated for all birds through a typical bimodal curve, with peaks before 11h and after 14h30. Infrequent activity sequences between 11h and 14h30 occurred in 16 birds during a total of 27 days (i.e. during <41% of bird*days) and represents < 7% of total activity; as they did not concern foraging they were referred to as additional activity. We calculated the duration of morning and evening foraging bouts, and whole day activity (the latter also including additional activity in the middle of the day), as well as start and ending times of foraging bouts, based on our 10 min time slots. Since sunrise and sunset times influence start and ending times of morning and evening foraging (Marti 1985), we subtracted sunrise and sunset official astronomic time from the start and ending times, respectively. The above mentioned variables were our response variables for estimating activity budgets.

Winter recreation disturbance predictors

We estimated winter recreation trough two variables. First we calculated a skilift index for every bird location. The skilift index is the first principal component (PC-1) of a PCA performed on GIS skilift maps; it correlates positively with skilift density and negatively with distance to the next skilift (Patthey et al. 2008). Second, we approximated daily ski traffic. We counted the number of ski traces in a 500 m radius from a birds location. If ski traces were to numerous to count or a ski slope passed in this 500 m radius we took the number of daily passages on skilifts linked with this ski slope. The latter data was provided by the ski resorts. To assess a potential quadratic relationship between foraging patterns and recreation disturbance we calculated as well the quadratic term of the disturbance predictors by creating one linear and one quadratic orthogonal variable. Table S1 summarizes the descriptors and their characteristics.

Natural predictors

The natural predictor which was considered to influence birds' behaviour was the minimum ambient temperature on the day before the activity (Baltic 2005). Temperature data were delivered by the Meteo station Evolène-Villaz (46°07'N / 07°24' E, 1823 m altitude), which is in the core of the study area. For males, but not for females, we tested for a year effect as data for males were collected in several years (Table S1).

Statistical analysis

We used general linear mixed effects models to model activity patterns of black grouse as a function of natural predictors and winter recreation disturbance. Males and females were analysed separately as response could vary between sexes. Individual was considered as a random effect in order to avoid pseudoreplication. We applied an information-theoretic approach (Burnham & Anderson 1998; Johnson & Omland 2004) and used the Akaike information criterion corrected for small sample size to rank our models. Minimum daily temperature, and also year for the males, were included in every model. Residuals were checked for normality. The response variable end time of evening foraging had to be transformed for the males to reach normality [(value + minimum value)^2].

First step of model selection

In a first step, we added the winter recreation disturbance predictors skilift index, skilift index^2, ski traffic and ski traffic^2 – separately – to the natural predictors. We retained the set of predictors in the model with a ΔAICc < 2 (Tables S2 & S3). If several models had a ΔAICc < 2 they were all retained.

Second step of model selection

In a second step the model/s including the best recreation disturbance predictor was compared with the basal model that included only the natural predictors. Models were ranked according to their ΔAICc and AIC weight (w_i, which represents the probability that a model is true out of a given set of models). The models with a ΔAICc < 2 were retained and averaged into a unique final model (Table 1, see also Table S4).

Model validation

The performance of the final models was evaluated with a Spearman's rank correlation test (r_s) (Potts & Elith 2006), coupled with a randomization procedure (Vaughan & Ormerod 2005). We adopted this procedure, first, because our sample size would have been too small (n = 14 males and 8 females) to reasonably cross-validate our models; and secondly, because there exists no other similar, independent dataset in the Swiss alps enabling true validation. Thus, we generated 1'000 bootstrap samples of equal size as the original dataset by random sampling with replacement. For each bootstrap sample, we estimated the correlation between the predicted and observed values. We computed the mean and standard deviation of the Spearman's rank correlation tests. This method simulates the use of independent data to evaluate the predictive performance of the original model (Vaughan & Ormerod 2005). We considered the correlation to be significant if the Spearman's tests were statistically significant more than 950 times from 1000 bootstrap repeats ($P < 0.05$; Manly, 1997).

Predicting activity and foraging patterns in relation to anthropogenic disturbance

We predicted (mean ± 95% CI) of activity durations and start respectively ending times of foraging bouts according to winter recreation (ski traffic or skilift index) using the same randomisation as for the model validation part. For each bootstrap sample we estimated the model coefficients and predicted the activity patterns. The other variables in the model were hold constant at their mean values. We set year as 2008 since it contained most data. We computed the means of mean and CI predictions among bootstrap samples. To allow comparisons with previous results (Arlettaz et al. 2007; Patthey et al. 2008) we split birds into two categories according to the skilift index; birds in little disturbed areas where winter recreation has no or little effect on their abundance (log (skilift index) < 0.5, Patthey et al. 2008) from those living in highly disturbed sites where their abundance is low (log (skilift index) > 0.5). Similarly, ski traffic variable allowed to split birds into two categories:

birds in little disturbed sites facing a low number of passages of snow-sport people (the number of skis traces within a 500 m radius around a bird location was possible to be counted, i.e. below 12) and birds living in an highly used area by skiers (ski traffic corresponds to the number of snow-sport people transported by nearby skilifts). We then calculated the predicted mean values, as well as 95% confidence intervals, for every response variable for each winter recreation category.

To quantify the mean potential conflict time window between bird and humans we overlapped the mean opening/closing time of skilifts with the mean predicted start/end time of birds foraging periods. The maximal potential conflict time window was estimated by using the 95% confidence intervals limit of foraging sessions instead of its mean values.

All analyses were performed with the statistical package R (version 2.6.2, R Core Team 2008, nlme library)

Results

Our sample consists of 39 days of data recorded from 14 males (6 in 2004 and 9 in 2008) at seven study sites, and 26 days from eight females at four study sites in 2008.

Activity patterns of males

First step of model selection

In the first step of model selection, the best predictor of recreation disturbance for the whole day activity, as well as for morning and evening foraging sessions was ski traffic (Table S2 a-c). Regarding the start and end time of the morning foraging bouts, both the skilift index and ski traffic had a ΔAICc < 2 and were retained for the next step (Table S2 d-e). Concerning the start and end time of the evening feeding bouts, only the skilift index and its quadratic term were retained (Table S2 f-g).

Sec*ond step of model selection*

Compared with the basal model, the model including ski traffic as a predictor of winter anthropogenic disturbance (in addition to minimum ambient temperature and year as natural predictors) yielded the best fit for the response whole day activity with a weighted AICc of 0.87 (w_i, Table 1a). There was a significant trend (no overlap of the confidence intervals of the estimate with zero; Table 2a) towards increased foraging duration with increasing ski traffic (Fig. 1). The mean predicted whole day activity for birds in little disturbed sites was 130.9 min (95% CI: 115.6 –149.2). In contrast, the foraging duration of birds in highly disturbed sites amounted to 168.9 min (95% CI: 134.2 – 193.8). Therefore birds living next to ski resorts showed an average prolongation of whole day activity of 38 min (29%) compared to birds living farther away in less disturbed areas. This model performed well as shown by the significant correlation between observed and predicted foraging duration ($r_s = 0.86 \pm 0.002$, $P < 0.001$)

For the duration of evening foraging the basal model was slightly better than the model including ski traffic. However, it still had a w_i of 0.49 (Table 1b), indicating that both models have about the same chance to be appropriate. Therefore, an effect of ski traffic on evening foraging duration appears less clear than for the whole day activity. The predicted values for the final averaged model also showed a similar, although less pronounced trend of increased foraging duration with increasing ski traffic (Fig. 1), but this time confidence intervals of the estimate overlap zero (Table 2b). The predicted mean evening foraging duration for birds in little disturbed sites was 54.2 min (95% CI: 47.9 – 60.4) vs 64.0 min for birds in highly disturbed sites (95% CI: 49.2 – 78.8), which gives a 9.8 min (18%) difference. This model performed well as shown by a significant correlation between observed and predicted foraging duration ($r_s = 0.89 \pm 0.002$, $P < 0.01$)

For the duration of morning foraging the basal model performed better than the model including ski traffic, with a w_i for the latter of only 0.36 (Table 1c). Moreover, confidence intervals of the estimate of the final model overlap zero (Table 2c). As the predicted curve shows only a very slight trend of increased foraging activity with increasing ski traffic it is not shown in Fig. 1. Therefore, no clear pattern of the effect of winter recreation disturbance on the duration of morning foraging could be found, despite the fact that this model had a good predictive power (r_s = 0.80 ± 0.003, P < 0.01).

As regards the start and end time of morning foraging the final models did not include predictors of recreation disturbance (Table 1d, e), suggesting that this factor does not influence the foraging schedule.

The final models for start and end times of evening foraging included the skilift index and its quadratic term. AIC weights were 0.81 and 0.96, respectively (w_i, Table 1f, g). Averaged linear coefficient values combined with the quadratic effect (Table 2f, g) resulted in a trend towards an earlier start and early end time of evening foraging bouts with an increasing skilift index (Figure 2). The mean predicted start time of evening foraging in birds in little disturbed sites was 7.5 min before sunset (95% CI: -27.6 – 44.0). Birds occurring in highly disturbed sites started to forage as early as 85.6 min before sunset (95% CI: -134.5 – -33.2). The mean predicted end time of evening foraging was 48.4 min after sunset (95% CI: 43.0 – 64.3) in birds in highly disturbed sites, but 22.1 min after sunset (95% CI: 2.8 – 38.5) in birds in little disturbed sites. Birds within and around ski resorts thus, on average, started to forage 78.2 min earlier and ended 26.2 min earlier than birds not affected by traffic originating from skilifts. As the skilifts close on average 53 min before sunset, there is a mean time window of potential conflict between bird and human activities of 32 min, if considering the mean value of start time (mean predicted start time of evening foraging minus mean closing time of skilifts). If one refers to the more conservative lower 95% confidence interval of predicted start time of evening foraging the time window for potential conflict would increase to 81 min (Fig. 2). These models had a good predictive power as shown by the significant correlation between observed and predicted foraging start and end times (r_s = 0.84 ± 0.003, P < 0.01; r_s = 0.79 ± 0.003, P < 0.01)

Females

Averaged models for all response variables included only the natural predictors. Therefore no effect could be found of recreation disturbance on whole day activity, morning and evening foraging durations, as well as on foraging schedules (Table S4a-g).

Discussion

This research establishes that black grouse cocks increase the duration of foraging activity (Fig. 1), mostly by anticipating their evening feeding session (Fig. 2) in relation to an increasing ski traffic across their habitat. This suggests that compensatory feeding may be a physiological response to disturbance by outdoor snow-sports, i.e. a way to compensate for the energy losses invoked by anthropogenic disturbance. Cocks occurring within or close to ski resorts showed a 38 min augmentation of daily foraging time (+29%) compared to birds inhabiting less disturbed areas. This confirms recent experimental findings by Patthey et al. (in prep.). A marked extension of foraging bouts appears to be the ultimate solution adopted by black grouse to survive in highly-disturbed areas. The mechanism behind this is probably a dramatic increase in energy demand by the organism following frequent disturbance (e.g. inadvertent flushing by passing-by skiers when birds rest in their igloos), potentially leading to a situation of allostatic overload ("stress"; Arlettaz et al. 2007). A compensation in the evening would also be consistent with the outcome of the experiments carried out by Patthey et al. (in prep.): black grouse use the next available opportunity, after disturbance by humans during the day, to replenish their energy stores. Note that the predicted later start and ending time of evening activity in sites with a very high skilift index (increases on the right end of the curve in Fig. 2) are probably artefactual because our sample for very high values of the skilift index consists of only two birds.

At this stage, it remains unclear whether black grouse actually are able to fully compensate for all energy losses, i.e. if they can through compensatory feeding easily avoid a situation of allostatic overload ("stress", Arlettaz et al. 2007; Patthey et al., in prep.). Arlettaz et al. (2007) have shown that concentrations of corticosterone (birds' stress hormone) metabolites in areas with moderate and high disturbance by outdoor snow-sports did not differ between each other, whilst concentrations observed in both were much higher than in natural, undisturbed areas. This pattern can be explained if black grouse in highly disturbed sites systematically suppress their stress response to ensure the maintenance of all necessary vital functions. This suggests chronic stress in birds within and around ski resorts (Arlettaz et al. 2007), a view recently confirmed by Patthey et al. (in prep.) who could show that birds with high initial baseline concentrations of corticosterone metabolites could not increase further their gluco-corticoid production and thus diminish instead of increasing the excretion of the stress hormone. It is thus very likely that birds inhabiting anthropized areas such as ski resorts face an allostatic overload of type I, which is another term for chronic stress (McEwen & Wingfield 2003). Black grouse in ski resorts therefore have no choice than extend foraging duration as much as they can, and the upper limit would be merely set by the volume of their crop and their long digestion transit time (Klaus et al. 1990). Supplementary foraging would therefore be compulsory and not just optional! In these conditions, it is not totally surprising that Patthey et al. (2008) found that black grouse density decreases dramatically with increasing winter disturbance.

Intriguingly, birds within or next to ski resorts started foraging ca 78.2 min earlier in the evening than birds in more natural areas. They also completed foraging, on average, 26.2 min earlier than their conspecifics inhabiting ski resorts. This is contrary to our hypothesis that birds could minimize interactions with humans by somewhat delaying the onset of evening feeding sessions until most skiers have left the ski slopes. Actually, most cocks sometimes started foraging when people were still skiing nearby, with a mean 32 min time window overlap between skiers' and black grouse activities. It is thus questionable whether humans (or at least skiers) are perceived as predators by black grouse (Beale 2004; Frid & Dill 2002). It may well be that the costs of feeding later on at dusk, when ambient temperatures drop and predators such as fox start to stray, are in reality higher than the detrimental effects resulting from human disturbance. Therefore, the marked time overlap in the activities of skiers and black grouse may represent a trade-off between the costs of feeding after sunset while confronted to predation risk and the costs of feeding while facing increased disturbance hazards. In addition, predation pressure in Alpine black grouse could be higher within and around ski resort areas than in more natural habitats as shown by (Storch & Leidenberger 2003; Wittwer et al. in prep). Further studies are necessary to elucidate the effects of recreation upon predator-prey relationships and demography.

No effect of winter recreation on foraging duration and time schedule could be evidenced in hens. This could be due either to a smaller sample size for females (n = 8 females vs 14 males), or to the fact that hens often have separated wintering and summering sites contrary to cocks which are strictly sedentary (Miquet 1988). They would thus be more likely to avoid areas where anthropogenic pressure is high in winter.

Management implications

Although the activity overlap between black grouse and skiers in the evening may result from the above described trade-off, it probably still represents a problem for the birds since they have low densities within and around ski resorts (Patthey et al. 2008). A solution would be to stop earlier the activity of skilifts close to main black grouse wintering habitat. By closing skilifts ca 80 min earlier than is usually the rule (lower confidence interval of evening foraging onset minus normal closing time) we could avoid this potential time overlap window. It is doubtful, however, whether this would be economically acceptable by ski infrastructure companies, especially during winter when days are naturally short. We thus better propose recommendations in line with Arlettaz et al. (2007) and Patthey et al. (2008), to create adequate winter refuges within and close to ski resorts to avoid risks of human-wildlife conflicts. Quiet zones would permit the birds to save essential energy and to forage undisturbed. The optimal spatial location and size of these winter refuges must still be investigated. BY GIS-mapping major conflict zones between outdoor winter sports and black grouse needs we could delineate the most promising areas for creating these winter refuges. These refuges will not only benefit black grouse but any other wildlife which may suffer from an excessive human presence in Alpine timberline ecosystems.

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References

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

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

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

Beale, C.M. & Monaghan, P. (2004) Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, **41**, 335-343.

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

Creel, S., Fox, J.E., Hardy, A., Sands, J., Garrott, B. & Peterson, R.O. (2002) Snowmobile activity and glucocorticoid stress responses in Wolves and Elk. *Conservation Biology*, **16**, 809-814.

Ellenberg, U., Mattern, T., Seddon, P.J. & Luna Jorquera, G. (2006) Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biological Conservation*, **133**, 95-106.

Ferraz, G., Nicols, J.D., Hines, J.E., Stouffer, P.C., Bierregaard Jr, R.O. & Lovejoy, T.E. (2007) A Large-Scale Deforestation Experiment: Effects of patch area and isolation on Amazon Birds. *Science*, **315**, 238-241.

Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, art. 11.

Hofer, H. & East, M.L. (1998) Biological Conservation and Stress. *Advances in the Study of Behavior*, **27**, 405-525.

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

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

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

Langston, R.H.W., Liley, D., Murison, G., Woodfield, E. & Clarke, R.T. (2007) What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*? *Ibis*, **149**(Suppl. 1), 27-36.

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

Marjakangas, A., Rintamäki, H. & Hissa, R. (1984) Thermal responses in the capercaillie *Tetrao urogallus* and the black grouse *Lyrurus tetrix* roosting in the snow. *Physiological Zoology*, **57**, 99-104.

Marti, C. (1985) Unterschiede in der Winterökologie von Hahn und Henne des Birkhuhns *Tetrao tetrix* im Aletschgebiet (Zentralalpen). *Der Ornithologische Beobachter*, **82**, 1-30.

McEwen, B.S. & Wingfield, J.C. (2003) The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, **43**, 2-15.

Miquet, A. (1988) Effets du dérangement hivernal sur les déplacements et la réproduction du tétras lyre *(Tetrao tetrix)*. *Gibier Faune Sauvage*, **5**, 321-330.

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

Patthey, P., Wirthner, S., Signorell, N. & Arlettaz, R. (2008) Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. *Journal of Applied Ecology*, **45**, 1704-1711

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

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

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Finger prints of global warming on wild animals and plants. *Nature*, **421**, 57-60.

Storch, I. (2007) Conservation status of grouse worldwide: an update. *Wildlife Biology*, **13**(Suppl. 1), 5-12.

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

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R. & Jenni, L. (2008) Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: A new methodological approach. *Journal of Applied Ecology*, **45**, 845-853.

Thiel, D., Ménoni, E., Brenot, J.F. & Jenni, L. (2007) Effects of recreation and hunting on flushing distance of capercaillie. *Journal of Wildlife Management*, **71**, 1784-1792.

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

von der Ohe, C.G. & Servheen, C. (2002) Measuring stress in mammals using fecal glucocorticoids: opportunities and challenges. *Wildlife Society Bulletin*, **30**, 1215-1225.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389-395.

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

White, G.C. & Garrott, R.A. (1990) *Analysis of Wildlife Radio-Tracking Data* Academic Press, Inc., San Diego.

Willebrand, T. & Marcström, V. (1989) Marrow, heart and body fat as indicators of Black Grouse *Tetrao tetrix* condition. *Ornis Scandinavica*, **20**, 49-52.

Wilson, R.P., Cilik, B., Danfeld, R. & Adelung, D. (1991) People in Antarctica - how much do Adéline penguins *(Pygoscelis adeliane)* care. *Polar biology*, **11**, 363-370.

Tables

Table 1: Ranking of candidate explanatory models for winter foraging activity of black grouse cocks (n = 14). A-g represent the different response variables. Two natural predictors (minimum temperature and year) as well as individual (random factor) were included in all models and are hence not shown. Models are ranked according to Akaike's Information Criterion (AIC_c) and its weights (w_i). k indicates the number of parameters in the model.

	Response variables	Winter recreation	k	AICc	ΔAICc	w_i
a)	Whole day activity	Ski traffic	5	404.17	0.00	0.87
		–	4	407.97	3.81	0.13
b)	Evening foraging	–	4	375.61	0.00	0.51
		Ski traffic	5	375.66	0.05	0.49
c)	Morning foraging	–	4	379.73	0.00	0.64
		Ski traffic	5	380.87	1.13	0.36
d)	Start morning foraging	–	4	409.88	0.00	0.83
		Ski traffic	5	413.99	4.12	0.11
		Skilift index	5	414.92	5.04	0.07
e)	End morning foraging	–	4	430.95	0.00	0.82
		Skilift index	5	435.13	4.18	0.10
		Ski traffic	5	435.60	4.64	0.08
f)	Start evening foraging	Skilift index+Skilift index²	6	452.60	0.00	0.81
		–	4	455.52	2.93	0.19
g)	End evening foraging	Skilift index+Skilift index²	6	819.17	0.00	0.96
		–	4	825.29	6.12	0.04

Table 2: Effect size of winter recreation on whole day activity, morning and evening foraging durations (min), as well as start and end time of evening foraging of 14 black grouse males in the Swiss Alps. Activity was recorded in sites showing different levels of human disturbance. Estimates and 95% confidence intervals (CI) are given for the predictors in the final averaged model for every response variable.

	Response variables	Winter recreation	Estimate	Lower CI	Upper CI
a)	Whole day activity	Ski traffic	2.16	0.91	3.40
b)	Evening foraging	Ski traffic	0.57	-0.73	1.87
c)	Morning foraging	Ski traffic	0.35	-0.65	1.35
f)	Start evening foraging	Skilift index	-146.65	-293.79	0.50
		Skilift index^2	297.86	153.70	442.03
g)	End evening foraging	Skilift index	149.37	84.70	193.52
		Skilift index^2	172.31	122.42	210.70

Figure legends

Figure 1: Predicted mean values and 95% confidence intervals of whole day activity (bold line) and evening foraging (thin line) of black grouse cocks in winter in function of winter recreation (ski traffic). Predictions and confidence intervals were obtained from re-sampling while keeping temperature constant at its mean and setting year to 2008 (i.e. the year with the larger sample size). Data distribution (sample days) is shown by the internal marks above the x-axis. Note that we have 24 and 15 sampled days for birds with a ski traffic value respectively below and above 12.

Figure 2: Predicted mean values and 95% confidence intervals of start time (thin line) and end time (bold line) of evening foraging in function of winter recreation. The ski lift index is on a log scale to allow comparison with Patthey et al. (2008). The grey-shaded area indicates the mean working time of ski lifts and thus the potentially conflictual time window between skiers and foraging black grouse. Predictions were made by holding the temperature constant at its mean and by setting the year to 2008 (i.e. the year with most data). Bird distribution is shown by the internal marks above the x-axis.

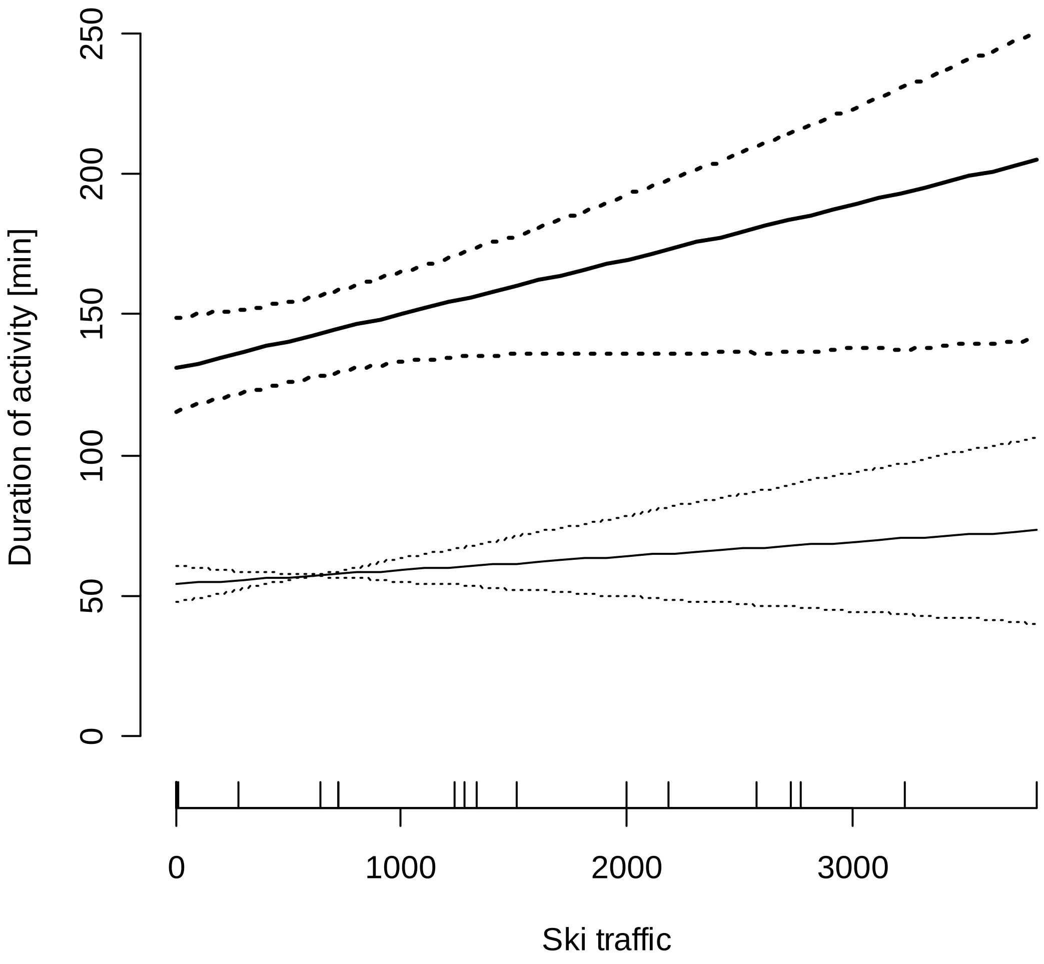

Duration of activity [min]
0
50
100
150
200
250
0
1000
2000
3000
Ski traffic

Fig.1.

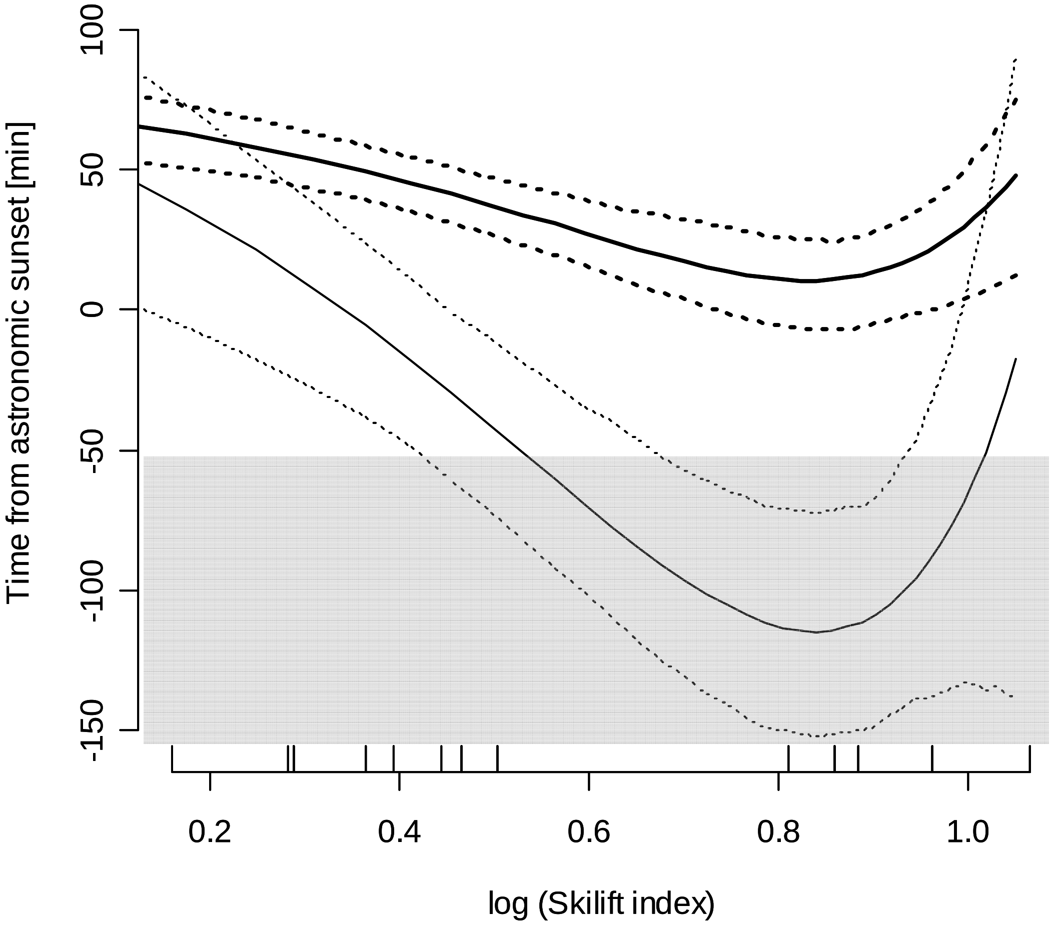

100
50
0
-50
-100
-150
Time from astronomic sunset [min]
0.2
0.4
0.6
0.8
1.0
log (Skilift index)

Fig.2.

Supplementary material

Table S1: Predictor variables used to characterize activity patterns of black grouse in winter.

Variable name	Levels	Definition
Individualizer	1...22	Birds individual tag frequency (MHz)
Sex	2	Male or female
Year	2	2004, 2008
Minimum temperatur	Continuous	Minimum ambient temperature of the previous day in ℃
Skilift index	Continuous	First principal component from ski lift density and distance
Skilift index^2	Continuous	Quadratic term of the previous variable
Ski traffic	Continuous	Number of ski traces in a 500 m radius from a birds location if the bird was far away from a skilift or number of passages on skilifts linked with slopes passing within a 500 m radius from a birds location
Ski traffic^2	Continuous	Quadratic term of the previous variable

Table S2: Selection process of the best winter recreation predictors explaining winter foraging patterns of 14 black grouse males (January – March 2004 and 2008). Two natural predictors (minimum temperature and year) as well as individual (random factor) were included in all models and are hence not shown. The different recreation disturbance predictors were added separately to the natural predictors. The predictor/s in the model/s with a ∆AICc below 2 were retained for the next step. Models are ranked according to Akaike's Information Criterion (AIC_c) and weights (w_i). k indicates the number of parameters in the model.

	Response variables	Winter recreation	k	AICc	∆AICc	w_i
a)	Whole day activity	Ski traffic	5	404.17	0.00	0.93
		Ski traffic + Ski traffic²	6	410.30	6.13	0.04
		Skilift index	5	411.55	7.38	0.02
		Skilift index + Skilift index²	6	417.68	13.52	0.00
b)	Evening foraging	Ski traffic	5	375.66	0.00	0.83
		Skilift index	5	380.28	4.62	0.08
		Ski traffic + Ski traffic²	6	381.15	5.49	0.05
		Skilift index + Skilift index²	6	382.15	6.49	0.03
c)	Morning foraging	Ski traffic	5	380.87	0.00	0.83
		Skilift index	5	384.68	3.81	0.12
		Ski traffic + Ski traffic²	6	386.75	5.88	0.04
		Skilift index + Skilift index²	6	391.00	10.14	0.01
d)	Start morning foraging	Ski traffic	5	413.99	0.00	0.58
		Skilift index	5	414.92	0.93	0.36
		Ski traffic + Ski traffic²	6	419.36	5.37	0.04
		Skilift index + Skilift index²	6	420.62	6.62	0.02
e)	End morning foraging	Skilift index	5	435.13	0.00	0.50
		Ski traffic	5	435.60	0.46	0.40
		Skilift index + Skilift index²	6	438.68	3.55	0.08
		Ski traffic + Ski traffic²	6	441.78	6.65	0.02
f)	Start evening foraging	Skilift index + Skilift index²	6	452.60	0.00	0.85
		Skilift index	5	456.87	4.27	0.10
		Ski traffic	5	458.70	6.11	0.04
		Ski traffic + Ski traffic²	6	463.27	10.67	0.00
g)	End evening foraging	Skilift index + Skilift index²	6	819.17	0.00	0.97
		Skilift index	5	826.83	7.66	0.02
		Ski traffic	5	829.86	10.69	0.00
		Ski traffic + Ski traffic²	6	834.78	15.62	0.00

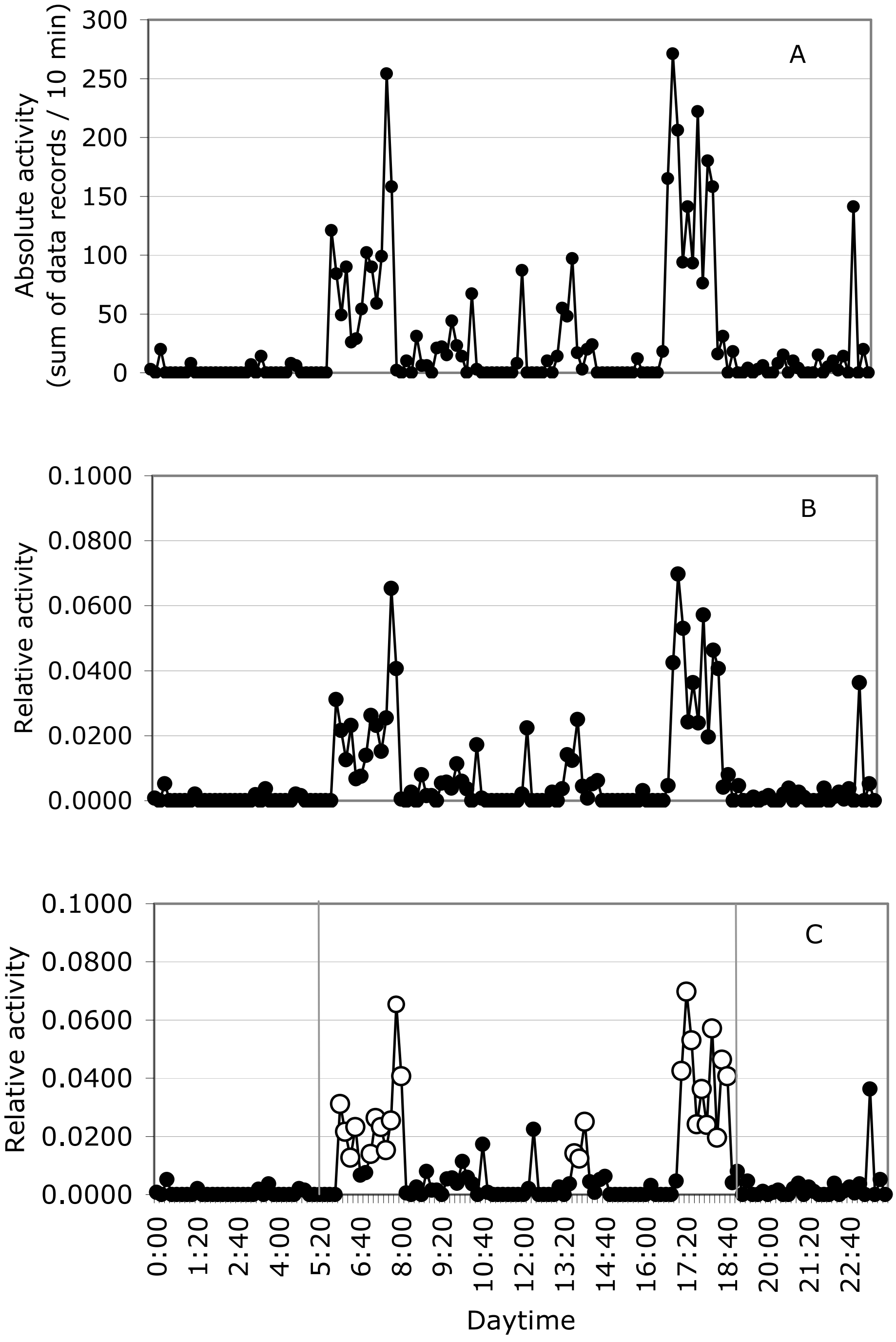
Table S3: Selection process of the best winter recreation predictors explaining winter foraging patterns of 8 black grouse females (January – March 2008). One natural predictor (minimum temperature) as well as individual (random factor) were included in all models and are hence not shown. The different recreation disturbance predictors were added separately to the natural predictors. The predictor/s in the model/s with a ∆AICc below 2 were retained for the next step. Models are ranked according to Akaike's Information Criterion (AIC_c) and weights (w_i). k indicates the number of parameters in the model.

	Response variables	Winter recreation	k	AICc	∆AICc	w_i
a)	Whole day activity	Ski traffic	4	284.79	0.00	0.31
		Skilift index	4	285.80	1.01	0.18
		Skilift index + Skilift index²	5	290.59	5.80	0.02
		Ski traffic + Ski traffic²	5	303.36	18.57	0.49
b)	Evening foraging	Skilift index	4	282.82	0.00	0.50
		Ski traffic	4	282.84	0.02	0.50
		Ski traffic + Ski traffic²	5	296.80	13.98	0.00
		Skilift index + Skilift index²	5	297.15	14.32	0.00
c)	Morning foraging	Ski traffic	4	268.67	0.00	0.60
		Skilift index	4	269.46	0.79	0.40
		Skilift index + Skilift index²	5	285.33	16.66	0.00
		Ski traffic + Ski traffic²	5	287.21	18.54	0.00
d)	Start morning foraging	Skilift index	4	271.22	0.00	0.84
		Ski traffic	4	274.61	3.39	0.16
		Passages + Passages²	5	287.70	16.48	0.00
		Skilift index + Skilift index²	5	289.36	18.13	0.00
e)	End morning foraging	Skilift index	4	305.27	0.00	0.52
		Ski traffic	4	305.46	0.19	0.48
		Skilift index + Skilift index²	5	322.44	17.16	0.00
		Ski traffic + Ski traffic²	5	324.11	18.84	0.00
f)	Start evening foraging	Skilift index	4	312.99	0.00	0.63
		Ski traffic	4	314.08	1.08	0.37
		Ski traffic + Ski traffic²	5	328.89	15.90	0.00
		Skilift index + Skilift index²	5	329.28	16.28	0.00
g)	End evening foraging	Ski traffic	4	291.74	0.00	0.53
		Skilift index	4	291.98	0.24	0.47
		Skilift index + Skilift index²	5	309.57	17.83	0.00
		Ski traffic + Ski traffic²	5	310.39	18.65	0.00

Table S4: Ranking of candidate explanatory models for winter activity of black grouse hens in the Swiss alps (n = 8). A-g represent the different response variables. One natural predictor (minimum temperature) as well as individual (random factor) were included in all models and are hence not shown. Models are ranked according to Akaike's Information Criterion (AIC_c) and its weights (w_i). k indicates the number of parameters in the model.

	Response variables	Winter recreation	k	AICc	ΔAICc	w_i
a)	Whole day activity	–	3	277.01	0.00	0.97
		Ski traffic	4	284.79	7.78	0.02
		Skilift index	4	285.80	8.79	0.01
b)	Evening foraging	–	3	273.52	0.00	0.98
		Skilift index	4	282.82	9.30	0.01
		Ski traffic	4	282.84	9.32	0.01
c)	Morning foraging	–	3	260.86	0.00	0.97
		Ski traffic	4	268.67	7.80	0.02
		Skilift index	4	269.46	8.60	0.01
d)	Start morning foraging	–	3	265.82	0.00	0.94
		Skilift index	4	271.22	5.41	0.06
e)	End morning foraging	–	3	296.13	0.00	0.98
		Skilift index	4	305.27	9.14	0.01
		Ski traffic	4	305.46	9.33	0.01
f)	Start evening foraging	–	3	306.16	0.00	0.95
		Skilift index	4	312.99	6.84	0.03
		Ski traffic	4	314.08	7.92	0.02
g)	End evening foraging	–	3	283.62	0.00	0.97
		Skilift index	4	291.74	8.12	0.02
		Ski traffic	4	291.98	8.35	0.01

Fig. S1. Example of an absolute activity curve (A), relative activity proportion curve (B) and activity budget curve (C) for one bird in Les Diablerets on 12th March (144 daily data points, i.e. 10 min periods); white circles in C represent feeding sequences. The two vertical lines show daylight interval boundaries.



A
Absolute activity (sum of data records / 10 min)
0
50
100
150
200
250
300
B
Relative activity
0.0000
0.0200
0.0400
0.0600
0.0800
0.1000
C
Relative activity
0.0000
0.0200
0.0400
0.0600
0.0800
0.1000
0:00
1:20
2:40
4:00
5:20
6:40
8:00
9:20
10:40
12:00
13:20
14:40
16:00
17:20
18:40
20:00
21:20
22:40
Daytime

Fig. S1.

Can wildlife habituate to disturbance by winter outdoor recreation: varying escape flight distances in a key indicator species of alpine ecosystems

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Summary

1. Spreading outdoor recreation increases the likelihood of human-wildlife conflicts, becoming a key conservation issue. This affects in particular species of boreo-alpine environments which have a finely-tuned winter physiological balance to cope with seasonal food shortage and low ambient temperatures. Any behavioural and physiological responses to disturbance may increase energy demand and elicit stress. Habituation to non-lethal stimuli could thus be advantageous. Yet, little is known about habituation of wildlife to anthropogenic disturbance in alpine ecosystems where the spreading of outdoor snow sports is rapid.

2. We investigated the behavioural response of a vulnerable key indicator species of timberline ecosystems, the alpine black grouse (*Tetrao Tetrix*), in reaction to different levels of disturbance by winter recreation and hunting pressure. A model selection approach, generalized linear mixed models and boot-strap resampling were used to identify and predict the effects of recreation disturbance intensity and hunting pressure upon flushing distances in black grouse cocks and hens.

4. In winter, males decreased flushing distances with increasing intensity of recreation. Hens showed a less clear response: they appeared to have lower flushing distances in both little-disturbed and highly-disturbed sites compared to moderately disturbed sites. Hunting pressure played a minor role. Summer flushing distance, in contrast, could not be correlated with our set of predictors, indicating that physiological bottlenecks concern only the winter period.

5. Male and female black grouse seemingly have the potential to habituate to the non-lethal human stimuli typical of highly-disturbed sites. As it is also in these sites that black grouse show higher concentrations of stress hormone metabolites, habituation may be a constrained, default outcome instead of a deliberate strategy by the birds.

6. *Synthesis and application*. Based on these results, we propose that wildlife winter refuges previously recommended to mitigate the effect of winter recreation upon black grouse integrate a 120 m broad buffer belt around their periphery; this corresponds to the upper 95% confidence interval of birds' flushing distance in the situation were birds showed the most sensitive reactiveness.

331 words

Key-words: AIC, flushing distance, human disturbance, hunting pressure, *Tetrao tetrix,* winter and summer recreation

Introduction

The last decades have seen a rapid development of summer and winter recreation activities such as skiing, snowshoeing, hiking, mountain biking and even ecotourism (Taylor & Knight 2003; Munns 2006; Sutherland 2007). For sensitive wildlife which has already to deal with habitat degradation and land-use changes, recreation potentially represents novel, additional threats that might impact upon animal behaviour (Baines & Richardson 2007; Thiel et al. 2007), physiology (Williams, Lusseau & Hammond 2006; Arlettaz et al. 2007) and demography (Müllner, Linsenmair & Wikelski 2004; Langston et al. 2007; Patthey et al. 2008). A direct consequence of tourist activity, particularly of off-road hiking or off-piste snow-sports free-riding is the disturbance of animals through flushing from their resting sites. Humans encountered by wildlife are usually recognized as predators (Frid & Dill 2002; Beale & Monaghan 2004). Already upon detection may a sudden physiological reaction be evoked, e.g. an augmentation of heart rate (Wilson et al. 1991) and / or an activation of the hypothalamo-pituitary-adrenal axis with the release of glucocorticoids (McEwen & Wingfield 2003; Ellenberg et al. 2006). Both represent energetically demanding processes for the organism (Hofer & East 1998; von der Ohe & Servheen 2002). Upon a predator's closer approach a prey can flee, hide or fight. Fleeing bears inherent costs: the direct energetic costs linked to escape manoeuvres and exposure to predators, and the indirect costs caused by reduced feeding activity and abandonment of good habitats (Frid & Dill 2002). From a physiological viewpoint, these costs increase allostatic load (McEwen & Wingfield 2003). Allostatic adjustments allow an organism to deal with changes in the environment; they are neither detrimental nor maladaptive, insofar as energy losses can be appropriately compensated. Yet, if energy intake does not suffice any more to perform any necessary physiological adjustments, the energy balance is disrupted and the organism faces a situation of allostatic overload, which is commonly referred to as detrimental stress (McEwen & Wingfield 2003). The various behavioural options available to an organism challenged in this way are thus eventually "evaluated" in terms of costs and benefits of different strategies. For instance, if the risk to get predated is assessed lower than the costs of fleeing, the animal will stay. Escape distance can therefore be seen as resulting from a trade-off between minimizing the costs of fleeing and maximizing the chance of survival (Ydenberger & Dill 1986; Lima & Dill 1990). Most studies about reaction of wildlife to anthropogenic disturbance have hypothesized longer escape distances in human-perturbed areas, with little consideration for habituation to human presence (MacArthur 1982; Bleich 1994; Steidl 2000; Ellenberg 2006; Thiel 2007). Based on the above rationale, however, phenomenon's of habituation would be expected in highly-frequented habitats because release of reactiveness to human presence would represent the best energy-saving and anti-predator response to a non-lethal stimulus (Frid & Dill 2002; Walker, Boersma & Wingfield 2006; Baudains & Lloyd 2007). This of course as long as humans actually are being recognized as non-lethal predators. In this respect, yet, any attempts to habituate could be easily annihilated if hunting still occurs. This is because humans will remain associated with dangerous predators (de Boer 2004). The literature about the influence of human disturbance or hunting pressure on wildlife abounds (Stankowich & Blumstein 2005; Sutherland 2007), but studies which have looked at these two aspects simultaneously are rare. Actually, only such combined investigations may permit to estimate the actual potential for habituation to recreation disturbance in threatened game species.

This paper examines the factors affecting escape flight (hereafter flushing) distances of alpine black grouse (*Tetrao tetrix*), an emblematic bird species inhabiting alpine timberline ecosystems where most outdoor winter and summer recreation occurs in the European Alps. This vulnerable key indicator species is currently declining in several parts of the Alps, which has been attributed mostly to spreading outdoor snow sports (Storch 2007). Despite these population decreases, black grouse cocks can still be hunted in several parts of the Swiss Alps, which questions about a possible additional impact of hunting.

Black grouse show a bimodal daily activity rhythm, more marked in winter, with two periods of foraging in early morning and late afternoon

(Marjakangas, Rintamäki & Hissa 1984; Klaus et al. 1990). They have a sensitive, very finely-tuned winter energy balance to cope with harsh environmental conditions. If snow conditions allow, winter resting sites are in self-excavated snow burrows, which limits predation risk and reduces energy expenditures through exposition to buffered ambient temperatures within the igloo (Marjakangas, Rintamäki & Hissa 1984). Disturbance by winter recreation, i.e. repeated flushing from igloos, evokes a stress response, as well as energy losses, followed by compensatory feeding (Arlettaz et al. 2007; Patthey et al. in prep; Schranz et al. in prep). In areas submitted to a marked tourist pressure such as ski resorts, black grouse seem to experience difficulties for maintaining their energy balance (homeostasis) and avoid allostatic overload, which may explain their low population density in human-impacted areas (Patthey et al. 2008). Habituation to human disturbance possibly represents a strategic option to limit any negative physiological consequences, but it can operate only if snow sport practitioners are effectively no longer considered as predators. Therefore we tested the following hypotheses in conjunction: i) black grouse in areas subjected to a high anthropogenic pressure flush at lower distances than black grouse in areas with no or limited human disturbance (all other factors being equal) because they habituate to human presence; and ii) black grouse in hunted sites (all other factors being equal) flush at longer distances than black grouse in game reserves where hunting is banned. The response of black grouse to experimental flushing will be investigated both in winter and summer, assuming that the effects must be pronounced in winter, when the energy balance is more difficult to achieve. This information will be crucial to develop sound conservation programmes for mitigating the impact of recreation upon vulnerable alpine wildlife, programmes which must absolutely account for the various sources of anthropogenic disturbance, namely winter recreation or hunting, and combination thereof.

Materials and Methods

Study sites

The study was carried out at 34 study sites with different levels of human disturbance and hunting pressure ranging from natural sites (no or limited winter sports disturbance, and game reserves) to highly disturbed sites (ski resorts and hunting areas). They are situated in the Alps of the cantons of Valais and Vaud (southwestern Switzerland, 46°10′ N, 7° 24′ E) within an elevation belt between 1400 and 2300 m altitude (Klaus et al. 1990; Patthey et al. 2008). Habitats consist of scattered upper sub alpine coniferous forest patches mixed with open grassland and / or ericacea-*juniperus* shrub. The climate is sub continental to continental, with cold, rather wet winters and warm dry summers (Reisigl & Keller 1999).

Fieldwork and environmental predictors

We captured a total of 173 black grouse from snow burrows in winter or with mistnets at leks in spring in 2002–2007. Birds were tagged with 16 g necklaced radio transmitters equipped with an activity sensor (Holohil Systems Ltd, Carp, Canada) under licences from the Swiss Federal Office for the Environment and the Wildlife and Game services of Valais and Vaud.

Winter flushing experiments were carried out between January and March 2004-2008. They consisted of approaching the birds for catching them from snow burrows and measuring escape distances. Igloos were localized visually from typical traces in the snow (Marti 1985) and approached slowly on skis, at a standardized speed of ca 0.4 m s^{-1}. The observer attempted to gently place a 2 x 2.5 m mist-net stretched between two up to 6 m long telescopic fishing rods directly on the snow surface above a suspected snow burrow. In case of a successful capture the flushing distance was therefore always below 6 m. Flushing distance was estimated at ± 0.5 m. Tagged individual birds were flushed only once. For untagged birds, however, we cannot completely exclude multiple flushings although this must remain scarce due to the number of study sites.

Summer flushings were carried out in 2005-2008 on radio-tracked birds according to a standardized experimental protocol. The experiments took place in late August and September, after the tourist summer peak and also to avoid disturbing brooding hens or hens with young chicks. Birds' precise location was obtained via triangulation and homing-in onto the animal (White & Garrott 1990). We walked slowly (speed of ca 0.4 m s^{-1}) towards a bird until it flushed, following a horizontal line of approach. Flushing distance was again estimated at ± 0.5 m.

Several predictors were recorded for every flushing event (Table S1). We determined 1) bird’s sex since flushing distances can be sex-specific as shown for other grouse species (Catt 1998; Thiel 2007); 2) bird group size as it could influence distance of detection of the experimentator (Burger & Gochfeld 1991); 3) the situation where a bird was resting (shrub in summer; tree or below snow surface in winter) because visibility influences flushing distance (de Boer 2004). Additional factors accounted for in the modelling were 4) study site, to avoid pseudo-replication; 5) year since environmental conditions can fluctuate from year to year; and 6) date as food supply and energy requirements are likely to vary within the season; 7) mean ambient temperature on the day before a flushing experiment and 8) cumulative average precipitation per month (for every month we summed the average precipitations of the months before starting by January and calculated the overall average. i.e. cumulative value for February = average January + average February / 2) to have a rough indicator of snow cover because both can influence bird’s response. Data were provided by the meteorological station of Evolène-Villaz, in the core of the study area (46°07’ N / 07° 24’ E, 1823 m). Any flushing location was also precisely located with GPS (9), while bird reference number (radio tag frequency) was noted (10). If a group of birds was flushed in a sequence we refer to the information from the first bird because that bird’s strategy had probably influenced the escape manoeuvre of the others.

Disturbance by recreation

To measure the intensity of recreation activity in winter (on-slope skiing and snowboarding, as well as free-riding activities such as ski mountaineering and snowshoeing) we followed two approaches. We first calculated a skilift index for every flushed bird. The skilift index is the first axis (PC-1) of a principal component analysis run using data from GIS skilift maps (Patthey et al. 2008). It correlates with skilift density and distance to skilift. We also assessed any potential quadratic relationship between flushing distance and recreation disturbance – under the hypothesis of longer flushing distances in moderately disturbed sites compared to little and highly disturbed sites by creating one linear and one quadratic orthogonal variable for the skilift index. In the predictive models, we used the criteria established by Patthey et al. (2008) to separate three levels of anthropogenic disturbance (log (skilift index) <0.5: low anthropogenic disturbance with natural black grouse abundance; 0.5-1: moderate disturbance with, on average, a 18% reduced black grouse abundance; >1: high disturbance with a 49% reduction in black grouse abundance). Second, off-piste, i.e. free-riding activities were quantified from aerial photographs taken during a one off-flight in late winter 2007 (Arlettaz et al. 2007). We counted the number of ski traces within a radius of 500 m around every flushing location, which gave a three-modal distribution of anthropogenic disturbance: low (0-3 ski traces), moderate (4-36 ski traces) and high (>36 ski traces). We shall refer to this predictor as ski traffic.

To measure the intensity of recreation activity in summer we counted the number of people walking along more or less horizontal walking paths (sorts of transects) crossing the habitat of radio-tagged black grouse. We had 18 such transects with an average (±SE) length of 1481.5 m (± 12.9). Counting's were performed 3 times on each transect once in June, July and August 2008, i.e. during the peak of tourist activity (Ingold 2005). They lasted for 45 min, starting once at 10h, 13h and 16h. The sequence of visits to transects was randomized, but always alternated between natural sites and ski resorts. The average number of hikers h^{-1} km^{-1} along a given transect was our index of summer recreation disturbance.

Hunting pressure

No statistics exist about precise location of hunted black grouse. We thus estimated hunting pressure merely thought the presence / absence of hunting reserves (hunting is banned on ca 42% of the study area; Arlettaz 1996).

Statistical analysis

Model selection

To account for the seasonal variation of environmental conditions and human disturbance, as well as expected sex-specific responses in black grouse, our modelling analysed separately both the two sexes and winter and summer data. For the summer model, we included mean ambient temperature of the previous day, group size and year as environmental predictors, but neither date nor place because all birds were flushed after the seasonal peak of tourist activity and because visibility is constant in summer as the birds always rest in Ericaceae-*Juniperus* shrub and under trees (Marjakangas, Rintamäki & Hissa 1984). As regards the winter model, we included: date and its quadratic term, group size, place, minimum ambient temperature of the previous day, year and precipitation (i.e. snowfall). Data from 2004 and 2008 had to be excluded from the analysis for the winter data due to a small sample size compared to the other years. Since there were only a few non-integer values for flushing distances we rounded all distances to the next integer value. This way we created a discrete response variable which was submitted to a generalized linear mixed effects modelling procedure, with a poisson error distribution and a log link function (MCCullough 1989). The models tested for the effect on flushing distance of the above described groups of predictors, in addition to winter and summer recreation disturbance and hunting pressure:

$$\log(p) = \beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n' + \beta_p + \varepsilon_r$$

where p is the flushing distance, X_n the N^{th} predictor, β_n the poisson regression coefficient and ε_r the random effect error term.

Due to overdispersion in the winter models for both cocks and hens (dispersion index of 2.30 and 1.60, respectively) the error distribution was specified as quasi-Poisson. We followed an information-theoretic approach (Burnham & Anderson 1998; Johnson & Omland 2004) and used the Akaike information criterion corrected for small sample size to rank models. A stepwise process (Johnson et al. 2005) was applied and we selected first the best set of environmental predictors among all possible combinations thereof. Then, the best recreation disturbance predictor was selected by adding every recreation predictor separately to the above selected environmental predictors. This step-wise procedure was necessary to reduce the number of candidate models which would otherwise have been dramatically inflated. The best predictors were defined as having a ΔAICc < 2 (Burnham & Anderson 1998). If several models had a ΔAICc < 2 we retained all their predictors for the next step. Finally, we fitted our five candidate models (Tables 1 & 2). Once ranked, we performed model averaging using all models with a ΔAICc < 2 , so as to build a final, general model (Burnham & Anderson 1998). In order to correct for pseudo-replication, study sites (winter model) and study sites plus individuals (summer model) were included as random factors in all models.

Model prediction and validation

The predictive performance of the final models was evaluated with a Spearman's rank correlation test (r_s, Potts & Elith 2006), coupled with a randomization procedure (Vaughan & Ormerod 2005). We adopted this procedure, first, because our sample size would have been too small (winter: n = 21 and 19 study sites for males and females, respectively; summer: 19 and 9 study sites, respectively) to reasonably cross-validate our models; and secondly, because there exists no other similar dataset which could enable validation with external data. Thus, we generated 1'000 bootstrap samples of equal size as the original dataset by random sampling with replacement. For each bootstrap sample, we recalculated the model coefficients. We used this and the original data set to predict flushing distances and to estimate the correlation between the predicted and observed values. We also computed the mean and standard deviation of the Spearman's rank correlation tests. This method simulates the use of independent data to evaluate the predictive performance of the original model (Vaughan & Ormerod 2005). We considered the correlation to be significant if the Spearman's tests were statistically significant ($P < 0.05$) more than 950 times from 1'000 bootstrap repeats (Manly 1997).

Results

In winter, we recorded 93 flushings of cocks at 21 study sites and 56 flushings of hens at 19 study sites. The summer samples consisted of 78 flushed cocks at 19 study sites and 21 hens at 9 study sites. The average (±se, range) flushing distance of cocks was 12 m (±1.8, 1-80) in winter, and 11.5 m (±1.2, 2-72) in summer. Females flushed in winter at 11.3 m (±1.6; 1-60), and, on average, at 8.1 m (±2.3; 2-53) in summer.

Model selection: winter

As regards the winter model for cocks, the selected environmental predictors were group size, year, minimum ambient temperature on the previous day, place, date and its quadratic term. For females, the retained predictors were place, date, its quadratic term and precipitation. Recreation disturbance was best explained by the skilift index as regards cocks and by ski traffic for hens (Table S2). These predictors were thus retained to fit the subsequent candidate models (Table 1a & b). All final averaged models, for both males and females, included the corresponding predictors of recreation disturbance. In contrast, hunting pressure was not retained in the final models obtained for both cocks and hens (Table 1a & b). Estimates and 95% confidence intervals of the predictors retained in the final models are given in Table 2a and b, for males and females, respectively. The model for males performed well as shown by its significant correlation between predicted and observed values (Spearman rank correlation test; males: r_s= 0.49 ± 0.003, $p < 0.01$) whereas for females the model performed less well although it was still acceptable (r_s = 0.51 ± 0.005, p = 0.055 ± 0.003).

Both cocks and hens flushed at longer distances when resting on trees than when resting in igloos. The date within the season had a slightly negative effect on flushing distance, whilst its quadratic term had a slightly positive effect. Males flushed at longer distances in 2006 and 2007 than in 2005, and also at longer distances when ambient temperature was high and the group size large. Finally, hens flushed at lower distance when there was a lot of precipitation (Table 2a & b).

The predicted flushing distance according to recreation disturbance (i.e. by holding the other predictors stable at their mean value) for cocks flushed from igloos (Fig. 1a) or from outside them (Fig. 1b) decreased with an increasing skilift index (skilift index shown on a log scale to allow comparison with Patthey et al. 2008). The mean (± 95% CI) predicted flushing distances calculated with respect to the three disturbance levels (Patthey et al. 2008; see also Material and Methods) are presented in Table 3.

Females resting outside vs inside igloos (Fig.2) flushed at almost equal distances at sites with low and high anthropogenic disturbance, but at much longer distances in moderately disturbed sites (mean predicted flushing distances and 95% CI for each category of ski traffic are given in Table 4).

Model selection: summer

The same process of model selection as above was applied for summer, on cocks and hens separately. Yet, the validation process (Spearman rank correlation tests between observed and fitted values) yielded no significant correlation; the summer models were therefore not reliable and discounted.

Discussion

This research constitutes one of the first attempts to jointly assess the impact of recreation disturbance and hunting pressure on flushing distance in alpine wildlife. We could first establish that flushing distance, in both black grouse cocks and hens, varies with the intensity of winter recreation activity (Figs. 1 & 2). The continuous decrease of flushing distance with increasing recreation disturbance in cocks might well reflect a process of habituation to non-lethal stimuli in high disturbed sites (Frid & Dill 2002) where human presence may no longer be assimilated to predation risk in this sex. A more contrasting pattern was observed in hens, however, which appear to be more sensitive in moderately disturbed sites, compared to sites with both low and high disturbance. Although the results for females must be interpreted with caution due to relatively imprecise estimates, this may point to some sex-specific differences regarding reactions to human disturbance. Since females are more likely to change their wintering habitats than males by more pronounced movements (Miquet 1988) they might encounter less interactions with humans than males. Therefore females who are in general less likely to be disturbed by humans because they have the opportunity to move to quieter areas in winter, may generally be more sensitive to anthropogenic disturbance than males. That they show the same reaction as cocks in highly-disturbed areas may result from the two sexes potentially being obliged to reduce allostatic overload. Actually, the recent finding that the concentrations of stress hormone (corticosterone) metabolites are equal in areas subjected to moderate and high disturbance by winter recreation, compared to little-disturbed areas (Arlettaz et al. 2007) seem to indicate that black grouse in (at least) highly-disturbed habitats may systematically suppress their stress response to ensure the maintenance of all necessary vital functions (allostatic overload type I; McEwen & Wingfield 2003), i.e. face a situation of chronic stress. A decrease of flushing distances in highly-disturbed sites may therefore similarly result from obligatory allostatic adjustments governed by the necessity to reduce to a strict minimum any energy losses and any fortuitous exposure to predators caused by escape manoeuvres. This would thus represent a kind of constrained instead of spontaneous «habituation» to human presence.

An effect of human disturbance on summer flushing distance was not found here, which can easily be explained by less constraining ambient temperature and less limiting food supply during the warm season (Stillman 2002). A smaller sample size can also be a handicap in the summer dataset.

This study could not demonstrate any effect of hunting on flushing distances: this predictor was not included in the best model. It is questionable, however, whether an effect of hunting, if marginal compared to the major impact of disturbance by winter recreation would have been detected at all. The occurrence of a minor, hidden effect of hunting is actually suggested by the inclusion of an interaction term recreation disturbance x hunting pressure in the second best model. Alternatively, it is possible that the hunting season (September-November) takes place so early during the cold season that black grouse did not assimilate at all humans to terrestrial predators when our experiments took place much later in the season, in January-March. This behavioural pattern would of course be totally inconsistent with the above-mentioned habituation hypothesis and leave little scope for population recovery through a more peaceful coexistence between humans and black grouse as suggested by Zeitler (pers. comm.). Finally, it is also possible that our hunting pressure index (presence/absence of game reserve) is too crude to appropriately quantify the actual hunting pressure (hunting effort per unit area) experienced by our study birds.

Management implications

This study provides support to the view that winter refuges have to be created within and around ski resorts in the Alps to protect wintering black grouse against human disturbance (Arlettaz et al. 2007; Patthey et al. 2008). It further enables providing precise figures about the optimal area for adequate winter refuges. Since in winter black grouse forage most of the time in groups and dig igloos in close vicinity from each other, these winter refuges must be slightly larger than the average bird's winter home range observed in the Alps (mean 11 ha; range: 4-18 ha; Ellison, Ménoni & Léonard 1989), let's say ca 18 ha to go for a conservative value. As a precautionary measure we propose to add a 120 m bright buffer belt around this focal area, 120 m being the upper 95% confidence interval of birds' flushing distance in the situation where birds showed the higher reactiveness to human disturbance in the present study (hens inside igloos in moderately disturbed areas, see Table 4). This would give an optimal winter refuge area of ca 40 ha. Since the optimal winter habitat for black grouse follows the timberline (Klaus et al. 1990), we propose to implement wildlife refuges along the timberline. These refuges encompass the best winter habitat of Black grouse when laid ca 150 m above and below the timberline (Klaus et al,. 1990) and including our buffer belt. Therefore we propose a size of 500 m high and 800 m long refuges. Such winter preserves will not only benefit black grouse but any other wildlife which may suffer from an excessive human presence in Alpine ecosystems.

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References

Arlettaz, R. (1996) Observations en Valais (Alpes suisses) de Gypaètes barbus (Gypaetus barbatus) issus de réintroduction: un premier bilan (1986-1995). *Nos Oiseaux,* **43**, 369-388.

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

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

Baudains, T.P. & Lloyd, P. (2007) Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation*, **10**, 400-407.

Beale, C.M. & Monaghan, P. (2004) Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, **41**, 335-343.

Bleich, V.C., R. T. Bowye, A. M. Pauli, M. C. Nicholoson, and R. W. Anthes. (1994) Mountain sheep (*Ovis canadensis*) and helicopter surveys: ramifications for the conservation of large mammals. *Biological Conservation*, **70**, 1-7.

Burger, J. & Gochfeld, M. (1991) Human distance and birds: tolerance and response distance of resident and migrating species in India. *Environmental Conservation*, **18**, 158-165.

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

Catt, D.C., D. Baines, N. Picozzi, R. Moss, and R. W. Summers. (1998) Abundance and distribution of capercaillie *Tetrao urugallus* in Scotland 1992-1994. *Biological Conservation*, **85**, 257-267.

de Boer, H.Y., van Breukelen, N., Hootsmans, M. J. M. and van Wieren, S. E. (2004) Flight distance in roe deer *Capreolus capreolus* and fallow deer Dama dama as related to hunting and other factors. *Wildlife Biology*, **10**, 35-41.

Ellenberg, U., Mattern, T., Seddon, P.J. & Luna Jorquera, G. (2006) Physiological and reproductive consequences of human disturbance in

Humboldt penguins: The need for species-specific visitor management. *Biological Conservation*, **133**, 95-106.

Ellenberg, U., Mattern, T., Seddon, P. J., Jorquera, G. L. (2006) Physiological and reproductive consequences of human disturbance in Humboldt penguins: The need for species-specific visitor management. *Biological Conservation*, **133**, 95-106.

Ellison, L.N., Ménoni, E. & Léonard, P. (1989) Déplacements d'adultes de tétras lyre (*Tetrao tetrix)* en automne et en hiver. *Gibier Faune Sauvage*, **6**, 245-260.

Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, art. 11.

Hofer, H. & East, M.L. (1998) Biological Conservation and Stress. *Advances in the Study of Behavior*, **27**, 405-525.

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

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

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

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

Langston, R.H.W., Liley, D., Murison, G., Woodfield, E. & Clarke, R.T. (2007) What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*? *Ibis*, **149** (Suppl. 1), 27-36.

Lima, S.L. & Dill, L.M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.

MacArthur, R.A., V. Geist, and R. H. Johnson. (1982) Cardiac and behavioural responses of mountain sheep to human disturbance. *Journal of Wildlife Management*, **46**, 351-358.

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

Marjakangas, A., Rintamäki, H. & Hissa, R. (1984) Thermal responses in the capercaillie *Tetrao urogallus* and the black grouse *Lyrurus tetrix* roosting in the snow. *Physiological Zoology*, **57**, 99-104.

Marti, C. (1985) Unterschiede in der Winterökologie von Hahn und Henne des Birkhuhns *Tetrao tetrix* im Aletschgebiet (Zentralalpen). *Der Ornithologische Beobachter*, **82**, 1-30.

MCCullough, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd edn. Chapman & Hall, New York.

McEwen, B.S. & Wingfield, J.C. (2003) The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, **43**, 2-15.

Miquet, A. (1988) Effets du dérangement hivernal sur les déplacements et la réproduction du tétras lyre *(Tetrao tetrix)*. *Gibier Faune Sauvage*, **5**, 321-330.

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

Munns, W.R.J. (2006) Assessing risks to wildlife populations from multiple stressors: Overview of the problem and research needs. *Ecology and Society*, **11**, article 23.

Patthey, P., Wirthner, S., Signorell, N., Arlettaz, R. (2008) Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. *Journal of Applied Ecology*, **45**, 1704-1711

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

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

Stankowich, T. & Blumstein, D.T. (2005) Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society. Series B, Biological sciences*, **272**, 2627-2634.

Steidl, R.J., and R. G. Anthony. (2000) Experimental effects of human activity on breeding Bald Eagles. *Ecological Applications*, **10**, 258-268.

Stillman, R.A., and J.D.Goss-Custard. (2002) Seasonal changes in the response of oystercacher *Haematopus ostralegus* to human disturbance. *Journal of Avian Biology*, **33**, 358-365.

Storch, I. (2007) Conservation status of grouse worldwide: an update. *Wildlife Biology*, **13** (Suppl. 1), 5-12.

Sutherland, W.J. (2007) Future directions in disturbance research. *Ibis*, **149** (Suppl. 1), 120-124.

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

Thiel, D., Ménoni, E., Brenot, J. F., and Jenni, L. (2007) Effects of recreation and hunting on flushing distances of Capercaillie. *Journal of Wildlife Management*, **71**, 1784-1792.

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

von der Ohe, C.G. & Servheen, C. (2002) Measuring stress in mammals using fecal glucocorticoids: opportunities and challenges. *Wildlife Society Bulletin*, **30**, 1215-1225.

Walker, B.G., Boersma, P.D. & Wingfield, J.C. (2006) Habituation of adult Magellanic Penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology*, **20**, 146-154.

White, G.C. & Garrott, R.A. (1990) *Analysis of Wildlife Radio-Tracking Data* Academic Press, Inc., San Diego.

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

Wilson, R.P., Cilik, B., Danfeld, R. & Adelung, D. (1991) People in Antarctica - how much do Adéline penguins *(Pygoscelis adeliane)* care. *Polar biology*, **11**, 363-370.

Ydenberger, R.C. & Dill, L.M. (1986) The economics of fleeing from predators. *Advances in the Study of Behavior*, **16**, 229-249.

Tables

Table 1. Model ranking to evaluate the factors influencing winter flushing distance in a) black grouse cocks and b) hens. The selected environmental variables were included in all candidate models (see Material and Methods and Table 2 for more detail) and are thus not shown in this table. Data were collected in winters 2005-2007 (cocks: n = 93 observations at 21 study sites; hens: n = 56 observations at 19 study sites). Models are ranked according to Akaike's Information Criterion (AIC_c) and their respective weights (w_i). k indicates the number of parameters in the model.

	Winter recreation		Hunting pressure	k	ΔAICc	w_i
a)	Skilift index		–	10	0.00	0.9171
	Skilift index	X[1]	game reserve	12	5.30	0.0648
	Skilift index		game reserve	11	7.93	0.0174
	–		–	9	14.26	0.0007
	–		game reserve	10	19.70	0.0000
b)	Ski traffic		–	8	0.00	0.9478
	Ski traffic		game reserve	9	5.80	0.0522
	Ski traffic	X[1]	game reserve	11	19.21	0.0001
	–		–	6	40.60	0.0000
	–		game reserve	7	43.68	0.0000

x: interaction between winter recreation and hunting pressure variables

Table 2: Effect size (estimates and 95% confidence intervals from the final, averaged model) of variables influencing flushing distances of a) black grouse cocks and b) hens in the Swiss Alps. Data were collected in 2005-2007. Variables are described in Table S1.

	Variables	Estimate	Lower CI	Upper CI
a)	Intercept	1.5145	-0.6317	3.4056
	Group size	0.1209	-0.0853	0.3093
	Year: 2006 *	0.5219	-0.0341	1.3849
	Year: 2007 *	0.7979	-0.2447	1.9646
	Place: outside igloo **	1.2657	0.7191	1.9363
	Temperature	0.0284	-0.0571	0.1116
	Julian date	-0.0232	-0.0637	0.1280
	(Julian date)²	0.0302	-0.1124	0.0606
	Skilift index	-0.0786	-0.2070	0.0630
b)	Intercept	2.4372	0.9253	4.0944
	Place: outside igloo **	1.0776	0.0292	1.7947
	Julian date	-0.0347	-0.0914	0.0586
	(Julian date)²	0.0428	-0.0539	0.1056
	Precipitation	-0.3215	-1.1073	0.2049
	Ski traffic: low disturbed sites ***	0.0724	-0.7580	1.0202
	Ski traffic: moderate disturbed sites ***	1.1051	-0.6681	2.5440

*compared to year: 2005; **compared to inside igloo; ***compared to highly disturbed sites

Table 3: Mean predicted flushing distance, with 95% confidence intervals, of black grouse cocks experimentally disturbed while resting a) outside and b) inside igloos in relation to winter recreation. Log (skilift index) < 0.5 represents low anthropogenic disturbance with high black grouse abundance; 0.5-1 represents moderate antropogenic disturbance with 18% reduced abundance; and >1 represents high antropogenic disturbance with 49% reduced black grouse abundance (Patthey et al. 2008). See also Fig. 1.

	Winter recreation level	Predicted mean flushing distance [m]	lower CI	upper CI
a)	Low	14.2	5.4	27.5
	Moderate	9.3	3.2	19.2
	High	6.0	0.8	20.7
b)	Low	3.9	1.5	7.2
	Moderate	2.5	0.9	4.9
	High	1.6	0.2	5.2

Table 4: Mean predicted flushing distance, with 95% confidence intervals, of black grouse hens experimentally disturbed while resting a) outside and b) inside igloos in relation to three levels of winter recreation (Ski traffic). Predicted flushing distances were obtained through bootstrap re-sampling.

	Winter recreation level	Predicted mean flushing distance [m]	lower CI	upper CI
a)	Low	15.6	5.7	33.2
	Moderate	48.3	7.5	120.2
	High	13.8	6.5	21.6
b)	Low	5.3	2.4	9.3
	Moderate	16.11	3.2	38.5
	High	4.8	2.1	7.8

Figure legends

Figure 1: Predicted flushing distance (with 95% confidence intervals obtained from bootstrap re-sampling) of black grouse cocks resting in winter a) inside and b) outside igloos in relation to intensity of winter recreation (n = 93 flushing events at 21 study sites). Other continuous predictors included in the best model were hold constant at their mean values. The year with the largest sample size (2005) served as a reference. Note that the skilift index is on a log scale to allow comparison with Patthey et al. (2008): Log (skilift index) < 0.5: little disturbed sites with normal, natural black grouse abundance: 0.5-1 moderately disturbed sites with 18% reduction in black grouse abundance; >1: highly disturbed sites with 49% reduction in black grouse abundance. The distribution of data points is indicated along the x-axis (lines looking inside).

Figure 2: Predicted flushing distance (with 95% confidence intervals) of black grouse hens resting in winter a) within (light grey bars) and outside (dark grey bars) igloos with respect to the intensity of winter recreation (n = 56 flushing events at 19 study sites). Other continuous predictors included in the best model were hold constant at their mean values. The year with the largest sample size (2005) served as a reference.

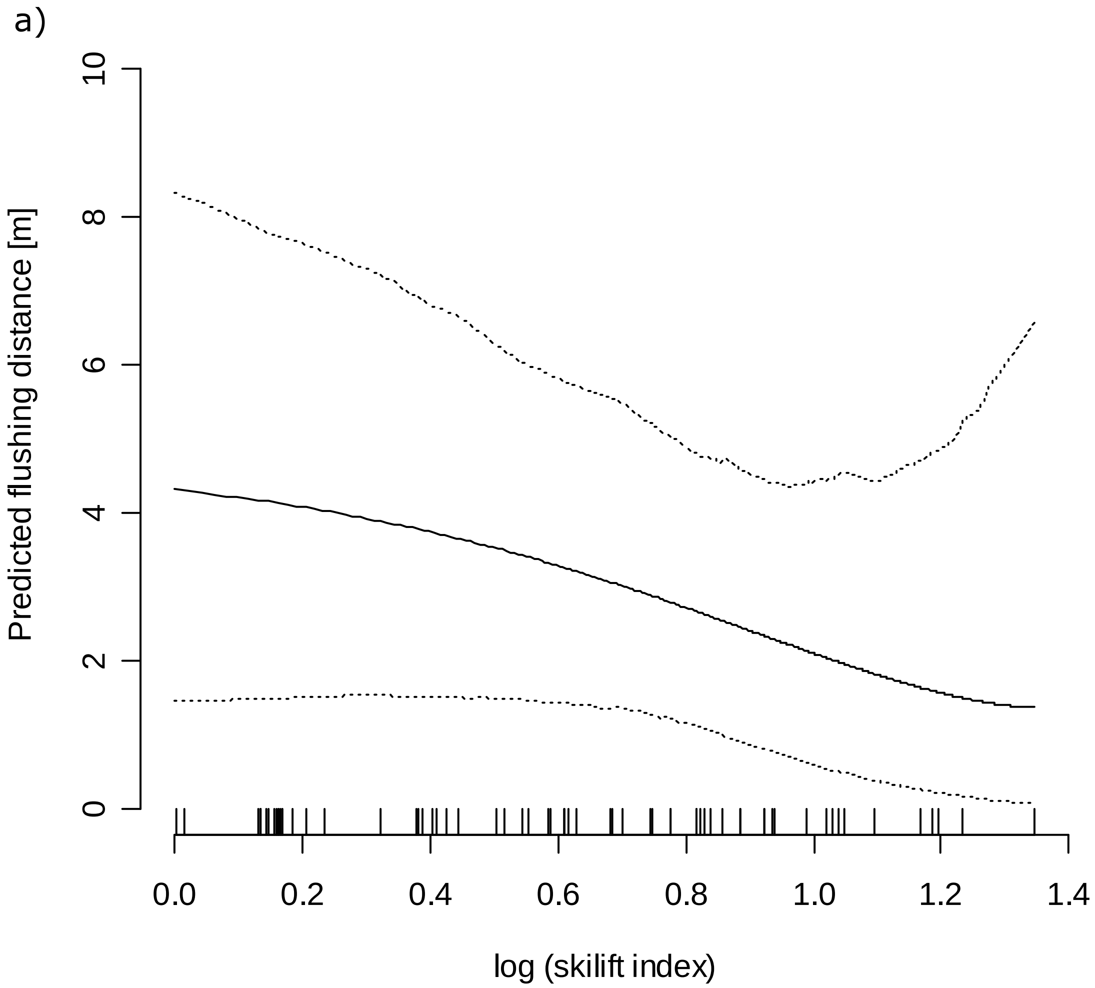
a)
10
8
6
4
2
0
Predicted flushing distance [m]
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
log (skilift index)

Fig.1a.

b)

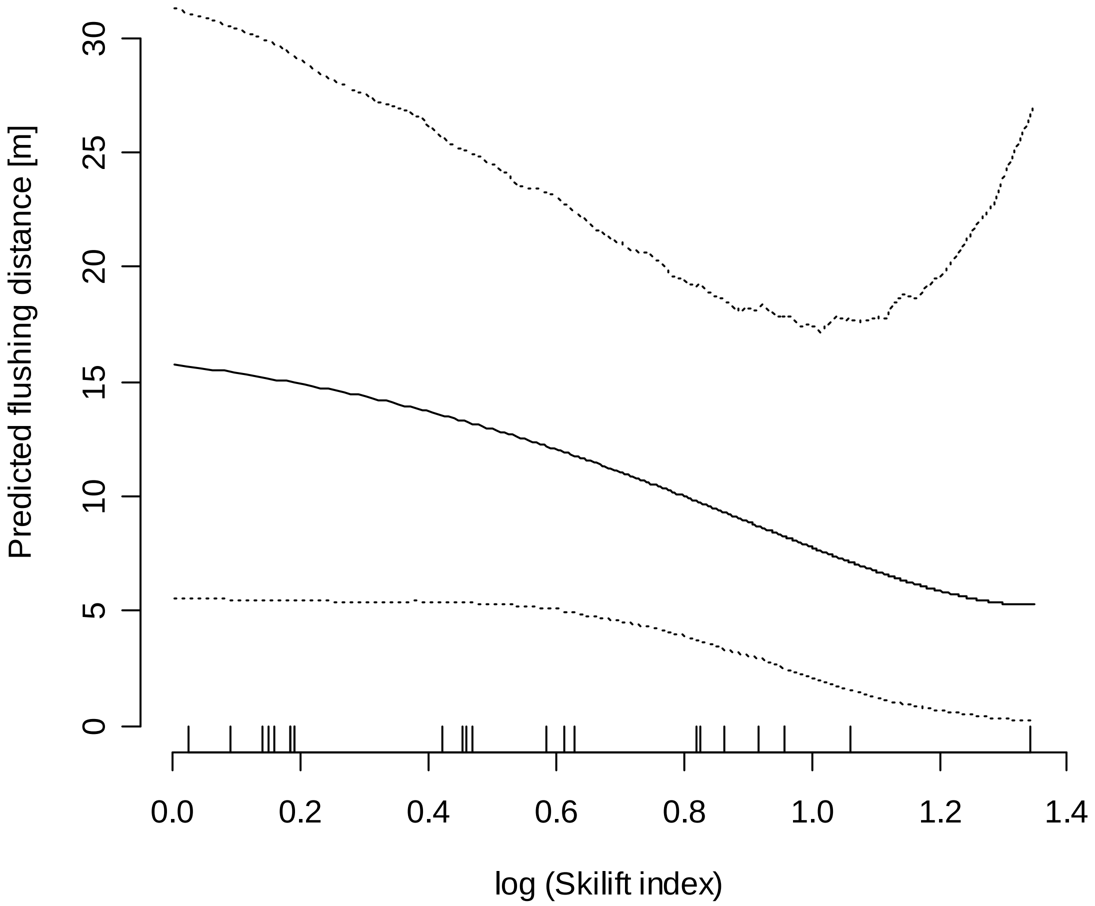
Predicted flushing distance [m]
0
5
10
15
20
25
30
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
log (Skilift index)

Fig.1b.

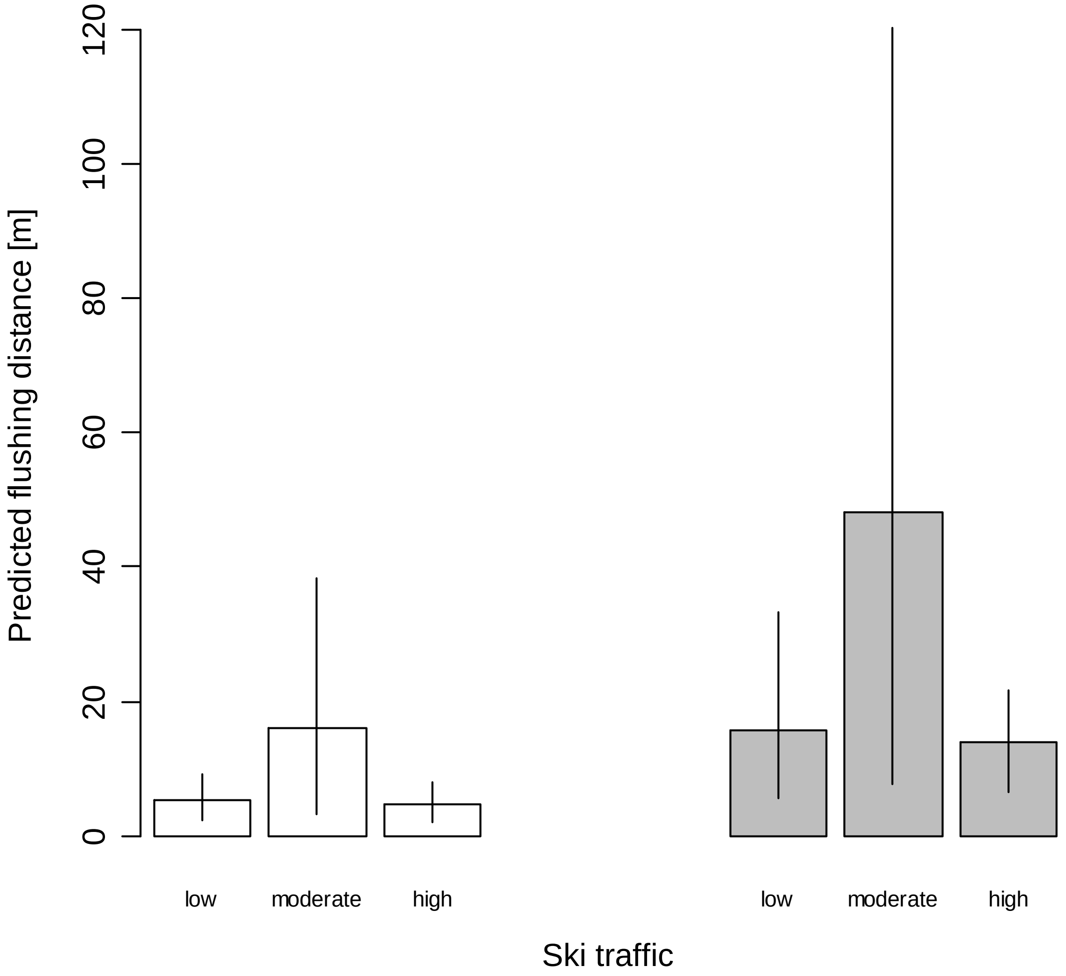
Predicted flushing distance [m]
0
20
40
60
80
100
120
low
moderate
high
low
moderate
high
Ski traffic

Fig.2

Supplementary material

Table S1: Predictor variables used to characterize flushing distances in Black grouse.

	Variable name	Definition
1)	Sex	Male or female
2)	Group size of birds	1 ,2, 3, 4...
3)	Place of bird	Winter: in igloo vs outside igloo / Summer: Under shrub vs on tree
4)	Study site	Name of study site
5)	Year	2004, 2005, 2006, 2007, 2008
6)	Date	Julian date
7)	Ambient temperature	Minimum ambient temperature one day before the flushing experiment in winter; average ambient temperature on same day as experiment in summer. Data provided from meteo station Evolène-Villaz (VS)
8)	Percipitation per month	Cumulative monthly averages (i.e. For cumulative value for February average January + average February / 2). Data provided from meteo station Evolène-Villaz (VS)
9)	Flushing location	Coordiantes of flushed bird
10)	Radiotag frequency	Bird's individualizer

Table S2: Selection process for the best predictors among winter recreation disturbance variables that explain winter flushing distances in black grouse a) cocks and b) hens. All environmental predictors (see Material and Methods and Table 2 for more detail) were included in the models and are thus not shown in this table; recreation disturbance predictors were added separately to these predictors. Predictor/s included in model/s with a ΔAICc<2 were retained in subsequent analytical steps (cocks: skilift index; hens: ski traffic). The sample comprises 93 flushing events at 21 study sites for cocks, and 56 flushing events at 19 study sites for hens. Models are ranked according to Akaike's Information Criterion (AIC_c) and their weights (w_i). k indicates the number of parameters in the model.

	Winter recreation	k	ΔAICc	w_i
a)	Skilift index	10	0.00	0.94
	Skilift index +skilift index²	11	5.53	0.06
	Ski traffic	11	16.13	0.00
b)	Ski traffic	8	0.00	1.00
	Ski lift index	7	45.78	0.00
	Ski lift index +ski lift index²	8	52.00	0.00