# Spreading free-riding snow sports represent a novel serious threat for wildlife

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Stress generated by humans on wildlife by continuous development of outdoor recreational activities is of increasing concern for biodiversity conservation. Human disturbance often adds to other negative impact factors affecting the dynamics of vulnerable populations. It is not known to which extent the rapidly spreading free-riding snow sports actually elicit detrimental stress (allostatic overload) upon wildlife, nor what the potential associated fitness and survival costs are. Using a non-invasive technique, we evaluated the physiological stress response induced by free-riding snow sports on a declining bird species of Alpine ecosystems. The results of a field experiment in which radiomonitored black grouse (*Tetrao tetrix*) were actively flushed from their snow burrows once a day during four consecutive days showed an increase in the concentration of faecal stress hormone (corticosterone) metabolites after disturbance. A large-scale comparative analysis across the southwestern Swiss Alps indicated that birds had higher levels of these metabolites in human-disturbed versus undisturbed habitats. Disturbance by snow sport free-riders appears to elevate stress, which potentially represents a new serious threat for wildlife. The fitness and survival costs of allostatic adjustments have yet to be estimated.

**Keywords:** stress ecology; conservation biology; species protection; alpine ecosystems; human disturbance; winter snow sports

## 1. INTRODUCTION

Wild animals have to cope not only with predictable characteristics of the environment such as seasonal changes in climate and resource availability, but also with a variety of unpredictable events, including human disturbance, which have tended to be on the increasing side in most ecosystems worldwide (Wingfield & Romero 1999; Taylor & Knight 2003; Ingold 2004). All disturbance factors have the potential to cause stress responses and can result in the activation of the hypothalamo–pituitary–adrenocortical axis. This hormonal cascade results in an increase in glucocorticoid production (Silverin *et al.* 1997; Wingfield *et al.* 1997; Romero *et al.* 2000; Taylor & Knight 2003). Glucocorticoid production has shown to enable rapid physiological and behavioural adjustments to otherwise unpredictable changes in the environment. Animals will be able to react more efficiently to adverse circumstances, thereby minimizing their exposure to stress and increasing their chances of survival and a progressive return to 'normal' life (Hofer & East 1998). The sum of these adaptive processes actively maintaining viability during the stabilization process of basic vital functions (homeostasis) to change is described as allostasis (McEwen & Wingfield 2003). The latter authors have provided the most comprehensive conceptual framework to stress ecology to date. An allostatic load (stress) is *per se* not dangerous or maladaptive, as it primarily consists of behavioural and physiological processes that enable an organism to cope with alterations in its environment. However, if stress persists or is repeated over time, an animal may at some point face allostatic overload (McEwen & Wingfield 2003), which in turn may affect it physiologically and induce a variety of detrimental symptoms (Hofer & East 1998). These detrimental symptoms may eventually lead to reduced individual fitness and, if stressful events affect many members of a population repeatedly, to a progressive population decline (Müllner *et al.* 2004).

Populations of wild animals already classified as vulnerable as a result of global environmental changes and local habitat alterations now face new potential threats brought about by the expansion of the tourist industry (McClung *et al.* 2004; Watson & Moss 2004; Walker *et al.* 2005). The popularization of extreme sports impels more and more people to trespass out of the marked boundaries of the ski slopes and onto protected land. Little or no consideration is given to the fate of alpine wildlife by the promoters of these new alpine ski activities (Ingold 2004).

In the European Alps, where most winter outdoor tourist activities aggregate from across the continent, several wild animal species are currently undergoing alarming decline. For instance, the International Union for the Conservation of Nature suggests that the decline in the alpine black grouse (*Tetrao tetrix*), an emblematic
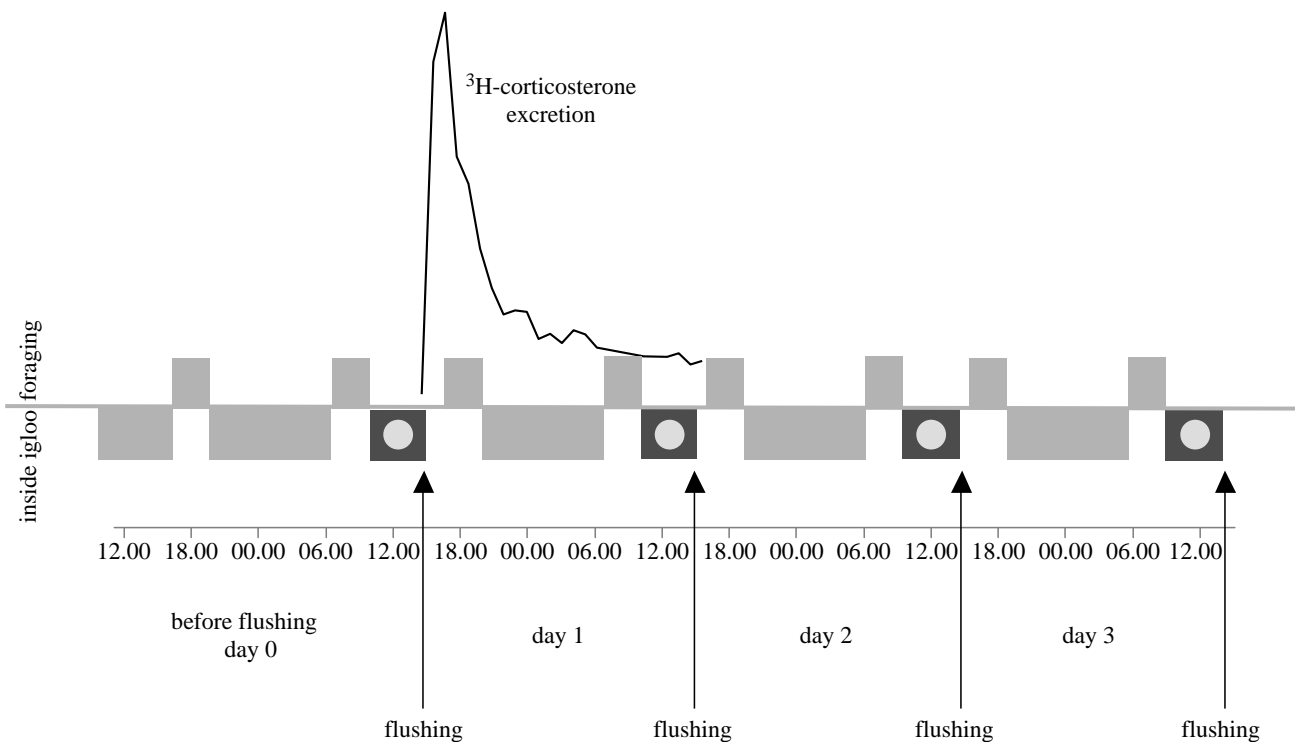
Figure 1. Sampling design during the flushing experiment. The light grey-shaded blocks show the approximate average duration of dawn and dusk foraging bouts (above the *x*-axis, which depicts time) and of igloo resting (below the same axis) in our three free-ranging, experimentally disturbed birds. The arrows depict approximate time of flushing and faeces collection. The dark grey blocks marked with a circle indicate the period during which faecal material collected for the analysis was deposited inside snow burrows. Black line: temporal pattern of a corticosterone excretion curve (redrawn from Baltic *et al.* 2005) after injection of $^3$H-corticosterone, as retrieved from the droppings excreted in a chronological sequence by four black grouse in captivity. After a peak within 1–3 h after administration, the concentrations of corticosterone metabolites progressively decreased to almost baseline levels after 24 h.

species of upland and boreal ecosystems, is linked to the spreading and intensification of winter sports. Black grouse can to some extent survive in fragmented habitats among ski resorts; however, free-riding skiers and snowboarders are increasingly threatening resting birds, inadvertently flushing them from their snow burrows. Ski lifts, installed mostly around the timberline zone (1800–2300 m altitude), have also led to primary black grouse habitat deterioration (Storch 2000).

Roosting in igloos is a crucial antipredator (Spidsø *et al.* 1997) as well as energy-saving strategy for alpine black grouse (Marjakangas *et al.* 1984), enabling them to cope with adverse weather conditions such as low winter temperatures (Marchand 1996). Flushing grouse from igloos not only elicits abrupt escape flights, but also provokes costly 'outdoor' exposure, affecting the birds' fine-tuned winter energetic balance (Marjakangas *et al.* 1984; Marchand 1996). It is still poorly understood whether human winter disturbance evokes a physiological stress response (an allostatic load)—with associated energetic expenditures—leading to an increase of circulating glucocorticoids, and whether repeated disturbance may lead to a chronic stress state (an allostatic overload of type I, McEwen & Wingfield 2003).

To answer these questions we monitored corticosterone levels, the main avian glucocorticoid reflecting adrenal activity, in black grouse population of the Swiss Alps. The concentration of the metabolites of this stress hormone was measured from faecal material, i.e. non-invasively and retrospectively (Möstl & Palme 2002; Millspaugh & Washburn 2004; Baltic *et al.* 2005; Touma & Palme 2005).

In winter, the birds spend most of their time buried in their igloos (more than 80% of their time in this study, figure 1). Moreover, black grouse burrow two igloos per day, i.e. one new igloo after each feeding session. Most of the faecal material is therefore deposited in igloos where natural conditions such as shade and temperature remaining below 0°C prevent degradation of hormones and their metabolite by-products by enzymes, bacteria and sun's radiation (Baltic *et al.* 2005).

In a field experiment, we actively flushed radiotagged black grouse from their snow burrows once a day, during four consecutive days, and collected droppings from igloos for the assessment of faecal corticosterone metabolites. This procedure enabled us to test whether stress increased after initial disturbance, and whether there was an additive effect over the course of the experiment. We then compared the hormone metabolite concentrations from 32 sites (SW Switzerland) that showed varying degrees of disturbance by free-riders, testing the hypothesis that overall stress load was higher in habitats frequently visited by skiers and snowboarders.

## 2. MATERIAL AND METHODS

### (a) *Field experiment*

Three black grouse males were mist netted at leks, nearby two ski resorts in the southwestern Swiss Alps (Verbier 46°06 N, 07°15 E and Les Diablerets 46°20 N, 07°07 E) in May 2002. They were tagged with 16 g neck-laced radio transmitters equipped with an activity sensor (Holohil Systems Ltd, Carp, Canada), under licences of the Swiss Federal Office for the

Environment, and Wildlife and Game services of Valais and Vaud. The birds' habitat consisted of upper subalpine coniferous forest patches that were not regularly visited by humans despite the vicinity of ski pistes. Non-simultaneous field experiments were carried out between 19 February and 21 March 2003, i.e. more than eight months after radio-tagging and before the onset of the lekking season which starts in the last decade of April in the Alps. The radiomonitored birds were sedentary year round, moving no more than 500 m away from their initial capture site. In winter, black grouse show a classical bimodal activity pattern with two periods of feeding at dusk and dawn, and resting inside snow burrows for the rest of the day, at least as long as snow conditions are appropriate (Pauli 1974; Pulliainen 1981). In our experimental birds, feeding bouts lasted on average 2 h 7 min ($\pm$17 min s.d., $n=3$) and 2 h 17 min ($\pm$18 min s.d., $n=3$) in the morning and at dusk, respectively (four days of data collection per bird, figure 1). All our black grouse burrowed a new igloo after each feeding session. The experiment consisted of flushing a bird from its snow igloo on four consecutive days between 14:00 and 15:00 (average of daily mean$\pm$s.d.: 14:28$\pm$49 min, $n=3$; figure 1), and collecting all defaecated droppings from its igloo. The droppings were transported in liquid nitrogen and then stored in a deep freezer at $-22°C$ until analyses.

The faecal material in each igloo consisted of 2–36 droppings ($n=182$ droppings in total), all deposited between the return from the early morning feed (09:05$\pm$26 min) and the time of flushing (see above). Average time of faecal deposition was 5 h 35 min ($\pm$57 min; range: 4 h 25 min to 7 h; figure 1). Peak corticosterone excretion in the droppings occurs 1–3 h after exposure to stress (Baltic *et al.* 2005). Previous experiments with captive black grouse (Baltic *et al.* 2005) have also shown that a stressful event (e.g. flushing) does not significantly add to the concentrations of measured corticosterone metabolites 17–24 h after the event. The faecal samples collected in the afternoon were therefore likely to mirror the physiological state of the birds during the morning. This is further justified by the fact that both the transit of food items through the digestive track and the defaecation rate are rapid in herbivorous–frugivorous birds, especially when the diet is rich in fibre (Klasing 2005), as is the case for the black grouse. It is important to note that the content of caeca, easily recognizable by its pasty aspect, was not included in the collected material as it is known to contain hemicellulose and other plant material usually retained for 12 h or more before once-daily excretion (Klasing 2005). Also, all our birds showed a normal bimodal activity outside burrows, i.e. no bird skipped a feeding session as may be observed under extreme adverse weather conditions (Marchand 1996). The shortest overnight stay in an igloo observed among our birds was 10 h 30 min, which is more than the time usually needed for complete excretion of faecal material from the last feeding session (Klasing 2005). For all these reasons, it is most probable that droppings collected at the time of flushing were remains from the morning feed rather than the previous evening's, and that the corticosterone levels reflected potential morning stress levels (see also the curve in figure 1).

As weather conditions varied during the experiments and could also have affected hormone levels (Romero *et al.* 2000; Raouf *et al.* 2006), ambient temperature had to be accounted for in our statistical analysis. Faeces collected on the first initial flushing event (day 0) were used as our control (or reference baseline) as they were excreted prior to any experimental (and natural) disturbance (i.e. flushing); the three subsequent days represent our treatment measurements (days 1–3).

### (b) *Comparative study*

Faecal samples ($n=132$) for the comparison of faecal corticosterone metabolites among habitats with various degrees of human disturbance were collected between January and March 2004 from 32 sites (on average, 4.1$\pm$ 0.2 (s.e.) igloo samples per site) spread across the south-western Swiss Alps, over an area of approximately 5000 km$^2$. The average ($\pm$s.e.) distance among collecting sites was 31.9$\pm$0.8 km. As seasonal hormonal changes may affect a bird's physiological state, we accounted for the sampling date in our statistical treatment. Levels of disturbance by skiers and snowboarders were estimated by counting the number of ski and snowboard traces within a 500 m radius around each sampled black grouse igloo. For accuracy, traces were counted on aerial pictures taken during a one-off flight four days after a snow fall in March 2004. The sites were then categorized according to three levels of disturbance: null or very limited (0–1 ski trace; 7 sites); moderate (2–11 traces; 13 sites); and high (more than 11 traces; 12 sites). This design defined a gradient ranging roughly from natural habitats (category 1), through ski mountaineering zones (category 2), to intensive ski resorts areas (category 3).

### (c) *Laboratory analyses of corticosterone metabolites*

Faecal corticosterone metabolites were quantified by a cortisone enzyme immunoassay, which was first established to measure glucocorticoid metabolites in chicken (Rettenbacher *et al.* 2004), and then validated for black grouse (Baltic *et al.* 2005). Droppings were desiccated (3 h at 70°C), homogenized, and 0.5 g random aliquots were extracted in 5 ml of 60% methanol. These aliquots were diluted 1 : 10 in the assay buffer (pH 7.5) and submitted to the enzyme immunoassay procedure (Rettenbacher *et al.* 2004; Baltic *et al.* 2005). For the flushing experiment, each dropping was analysed separately in order to collect information about the within-sample variation (i.e. among faecal pellets collected from one igloo). In the comparative approach among habitats with various degrees of disturbance, 4–10 random subsamples per igloo sample were analysed, and we used the sample median for subsequent statistical treatment. The coefficient of variation within an igloo was 11%.

### (d) *Statistical analysis*

We used linear mixed models for the analyses of both datasets. Owing to unequal sample sizes among categories, we did not use standard maximum likelihood estimations but the method of residual maximum likelihood estimation (Payne *et al.* 1993). For the analysis of the field experiment, we considered the factors individual and the interaction of individual and day (categorical) as random terms (Maindonald & Braun 2003). Average daily ambient temperature—calculated from the values recorded every 30 min with thermistors located at the birds' habitats—day (continuous), as well as its quadratic term were considered as a fixed term. The latter was used to test for a possible curvilinear increase of faecal corticosterone metabolites during the course of the experiment. The residuals of the overall model were normally distributed (Anderson–Darling test, $A^2=0.70$, $p>0.10$). The analysis of the comparative study required a nested design, with the factor disturbance

level (treatment) as the fixed term and the collection site as the random term. We adjusted for a possible seasonal change in corticosterone levels by including the date as a fixed factor in the model. Faecal samples (i.e. igloos) were nested (random term) within study sites. The residuals of the overall model were normally distributed (Anderson–Darling test, $A^2 = 0.43$, $p > 0.15$). Given that the analysis of the faecal samples from the flushing experiments was carried out in Vienna, whereas the faecal material collected for the comparative analysis was analysed in Sempach (Switzerland), we present percentage values on the graph (figure 2) due to common rule discrepancies among hormone laboratory settings and standardization procedures (Joyce *et al.* 1981; Romero 2004; D. Thiel & S. Jenni-Eiermann 2006, personal communication). All statistical analyses were performed with GENSTAT v. 5.41 (Payne *et al.* 1993). Absolute values are available as electronic supplementary material.

## 3. RESULTS

In the field experiment, concentrations of faecal corticosterone metabolites increased continuously from days 0 to 3 of the experiment (figure 2a), with day being a significant factor (Wald test, $\chi_1^2 = 4.0$, $p = 0.046$), but not its quadratic term ($\chi_1^2 = 1.2$, $p = 0.273$) nor ambient temperature ($\chi_1^2 = 3.2$, $p = 0.074$). Using the model restricted to significant factors, with only day as the fixed term (Wald test, $\chi_1^2 = 3.8$, $p = 0.05$), we estimated that faecal corticosterone metabolite concentrations increased daily by an average of 20%, which corresponds to a total increase of 60% between days 0 and 3 of the experiment.

In the comparative analysis, faecal corticosterone metabolite concentrations differed significantly between habitats with various levels of human impact (Wald test, $\chi_1^2 = 10.1$, $p = 0.006$; figure 2b); there was also a significant effect of the factor site, reflecting some variation among sites within a given habitat category (likelihood ratio test: $\chi_1^2 = 5.6$, $p = 0.017$), as well as a seasonal effect (Wald test, $\chi_1^2 = 14.8$, $p < 0.001$). Pairwise *post hoc* comparisons showed that birds in disturbed habitat had significantly higher concentrations of faecal corticosterone metabolites (approx. 12–17% more) than habitats with null or very limited human disturbance (contrast test: $\chi_1^2 = 9.6$, $p = 0.002$), whereas faecal corticosterone metabolite concentrations did not differ between habitats with moderate versus high human disturbance (contrast test: $\chi_1^2 = 0.5$, $p = 0.48$).

## 4. DISCUSSION

Combining experimental and comparative data, this pilot study indicates that disturbances caused by free-ride skiing and snowboarding appear to be an additional stress factor for a threatened species of the Alpine fauna. Our faecal samples were defaecated in igloos after early morning feeding bouts. Given the delay time of peak corticosterone metabolite excretion in the droppings (1–3 h; Baltic *et al.* 2005; figure 1), the collected droppings reflected the physiological state of the birds that same morning. As disturbance by snow sports is uncommon at dawn and our experiments were conducted in the afternoon, our estimates are the reflection of baseline adrenocortical activity rather than the acute flushing stress response. The values recorded here can therefore be considered as conservative estimates.
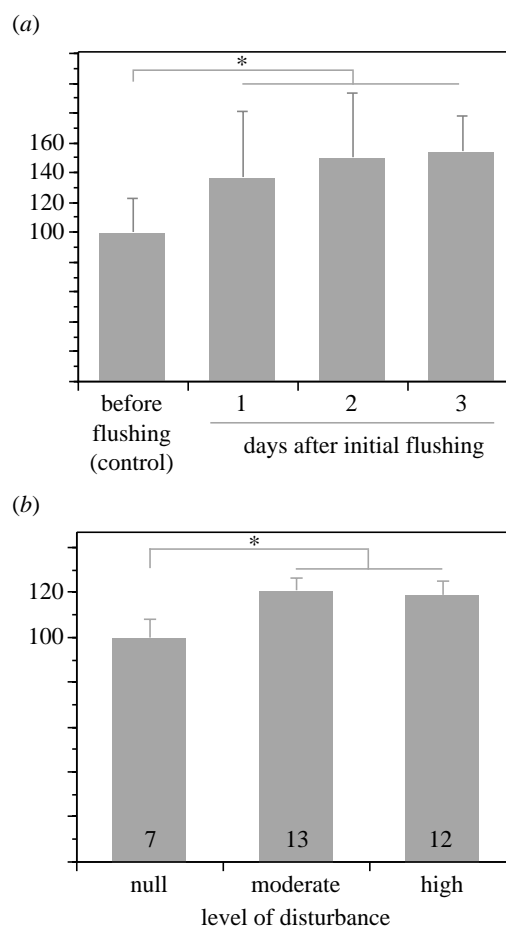
Figure 2. Stress level faced by wild free-ranging black grouse, measured as the relative concentration of faecal corticosterone metabolites (mean + s.e., in nmol $kg^{-1}$ of dry material) in droppings collected from individual snow burrows. Data are presented as percentage, with the mean value of the control reference set at 100% (i.e. day before initial flushing in the experiment, or habitat with null or limited disturbance in the comparative approach). (a) Results of a disturbance experiment with three radiomonitored males that were experimentally flushed in winter, once a day over four successive days. Faecal corticosterone metabolite levels increased significantly from control day 0 throughout to day 3 of experiment (linear mixed model), stemming mainly from a difference between the control and the experimental days ($\chi_1^2 = 7.9$, $p = 0.005$), and not from differences among experimental days ($\chi_2^2 = 0.3$, $p = 0.86$); (b) Faecal corticosterone metabolite concentrations in the droppings collected from 32 sites spread across SW Switzerland (totalling 132 igloo samples) with various levels of disturbance by skiers and snowboarders (sample size at column foot), after correction for a seasonal effect. Stress hormone concentrations differed significantly between sites with no or limited human disturbance versus sites with either moderate or high disturbance; the latter two categories did not differ between each other. $^* p < 0.05$.

Our results are further conservative in the sense that the disturbance we measured was restricted to one single flushing per individual bird and day. We know, however, that black grouse can potentially be disturbed several times a day if their rests happen to be too close to ski resorts or ski mountaineering routes. Repeated disturbances, if occurring over successive days, may actually generate a durable allostatic load (chronic stress). Our comparative analysis showing an increase of faecal corticosterone metabolites along the disturbance gradient

appears to support this hypothesis. It now remains to be demonstrated whether allostatic adjustments entail long-lasting negative behavioural and physiological effects (allostatic overload). Further studies and, in particular, experiments carried out over a longer period of time are necessary to evaluate whether physiological adaptations to repeated disturbance are plausible in the midterm (Walker *et al.* 2006).

Black grouse are facing increasing disturbance during the winter, not only affecting them by the extra physiological costs that sudden escape flights incur, but also by the fact that they face other costs and risks which may add to allostatic adjustments. First, every time they exit their snow burrows they have to thermoregulate more intensively as they do no longer benefit from the temperature buffer of igloos. This factor might become especially critical at low ambient temperatures. Second, when they leave their igloos after disturbance, the grouse either rest on trees for a while or immediately start snow burrowing elsewhere, making them more conspicuous to predators (Spidsø *et al.* 1997). All these factors, either acting alone or in addition to one another, are ultimately likely to affect the birds' winter energetic balance, physiological condition, immunological competence, reproductive ability and survival (Sapolsky 1992; Hofer & East 1998). Future investigations ought now to quantify the implications of disturbance by free-riding snow sports upon wildlife fitness and survival, i.e. to determine whether disturbance causes allostatic overload *sensu* McEwen & Wingfield (2003). The next necessary step will be to define tolerance thresholds towards spreading and intensifying winter outdoor sports, so as to mitigate any detrimental human-induced impact and to promote secure wintering zones for wildlife.

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