 doi: 10.1111/j.1365-2664.2008.01465.x

Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach

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Summary

1. Human outdoor recreational activities are increasing and have a significant impact on wildlife. There are few methods suitable for investigating the response of rare and endangered species to human recreational activities, although the impact can be assessed at various scales by measuring both physiological and behavioural responses to disturbance.

2. Capercaillie *Tetrao urogallus* are suffering strong population declines throughout central Europe. We examined the effects of ski tourism on capercaillie habitat use and adrenocortical activity, measured non-invasively in droppings.

3. During three winters, 2003–06, we radio-tracked 13 capercaillie. In the southern Black Forest in Germany, we sampled 396 droppings of these and additional individuals before and after the start of the ski season. We tested whether the intensity of human winter recreational activities affected home range location and habitat use, and we identified those factors influencing the concentration of corticosterone metabolites (CM) in droppings.

4. Capercaillie used habitats subject to ski tourism. Although the latter did not affect home range location, capercaillie preferred undisturbed forests within their home ranges and avoided areas with high recreation intensity in the ski season. Faecal CM levels of individuals in areas with low recreation intensity were significantly lower than those in areas with moderate or high recreation intensity during the entire study period.

5. We conclude that ski tourism affects both habitat use and endocrine status in capercaillie, with potential negative consequences on body condition and overall fitness.

6. *Synthesis and applications.* This study demonstrates the relevance of studying wildlife responses at various temporal and spatial scales, and the value of using multiple methods applied to the same individuals to monitor the impact of human recreational activities on a free-ranging species. In order to protect capercaillie populations, we recommend that managers keep forests inhabited by capercaillie free from tourism infrastructure and retain undisturbed forest patches within skiing areas.

Key-words: corticosterone, grouse, habitat selection, human disturbance, stress ecology, winter tourism

Introduction

Human outdoor recreational activities are of increasing conservation concern and are one of the main causes of the decline of all threatened and endangered species in the USA (Czech 2000). In order to investigate the impact of such activities on free-ranging species, we need to know how animals respond to the presence of humans before assessing the evidence for a link between the effect of human disturbance and population declines.

The response of free-ranging animals to human presence has been studied extensively. Animals may respond to the appearance of humans with anti-predatory behaviour (Beale

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& Monaghan 2004). Human presence can cause animals to interrupt feeding behaviour, flee or abandon preferred habitats temporally or permanently (Fernandez-Juricic & Telleria 2000). Such direct behavioural responses can affect predation risk, energy intake and energy expenditure of the animal (Cassirer, Freddy & Ables 1992) and thus have direct fitness costs (Amo, Lopez & Martin 2006). As a physiological response to stressors, glucocorticoids are secreted into the blood (Sapolsky, Romero & Minck 2000) as part of a mechanism to adjust the behaviour and physiology of an animal to prevailing environmental conditions (Wingfield & Romero 1999). Chronically elevated and prolonged high levels of corticosterone can be physiologically harmful to individuals, affecting immune function, growth, reproduction and survival (Sapolsky, Romero & Minck 2000). Thus high corticosterone concentrations may indicate that an animal is stressed, even if obvious behavioural changes cannot be detected (Walker, Boersma & Wingfield 2005). Conversely, not every behavioural response to the presence of humans leads to a physiological stress response (Müller *et al.* 2006). Animals in a critical body condition (e.g. starving in winter) may show only weak behavioural reactions to humans (Stillmann & Goss-Custard 2002). Studies investigating the effects of human recreational activities on animals usually focus on either behavioural (Stalmaster & Kaiser 2004) or physiological responses to humans (Wasser *et al.* 1997) and therefore can be misleading. Only a few studies have simultaneously measured behavioural and physiological responses to human recreational activities (Walker, Boersma & Wingfield 2005; Walker, Boersma & Wingfield 2006).

The assessment of the response of rare and endangered free-ranging species to human recreational activities is particularly difficult because few methods are available. Experimental disturbance and other invasive methods should be avoided. The capture of individuals is often restricted because of their conservation status or low capture success rates. However, measuring stress hormone levels in droppings is an appropriate non-invasive method of evaluating the endocrine status of rare and endangered species (Goymann 2005; Touma & Palme 2005).

In this study, we investigated both habitat use as a behavioural response and faecal concentrations of corticosterone metabolites (CM) as a physiological response of capercaillie *Tetrao urogallus* L. to human winter recreation activities. Many populations of capercaillie in Europe have been extirpated or declined rapidly within the last few decades (Storch 2000a). Human disturbance together with habitat deterioration and forest fragmentation are the main potential causes of population decline (Storch 2000b). The only study investigating the response of capercaillie to human recreational activities suggests that capercaillie cannot adapt to off-trail disturbances (Thiel *et al.* 2007a). Studies assessing capercaillies' physiological responses to humans and how they respond to on-trail disturbances are lacking but are needed urgently for effective management plans and conservation strategies.

The level of winter sport activity and the introduction of new outdoor sports (e.g. snow shoeing) has increased drastically during the last decade and affects essential habitats or retreats for a number of rare and shy species, such as black grouse *Tetrao tetrix* and chamois *Rupicapra rupicapra*. Human recreational activities in winter could be particularly harmful to capercaillie because they are energetically constrained by their dependence on low-quality conifer needles as food (Klaus *et al.* 1989). Body condition at the end of winter has been shown to affect reproduction success of the related rock ptarmigan *Lagopus mutus* (Moss & Watson 1984).

Materials and methods

STUDY AREA AND STUDY SPECIES

We conducted the study in the forest-dominated mountain range of the southern Black Forest in south-western Germany (47°51′N, 07°58′E). The study area (2812 ha) consisted of capercaillie habitat in two study plots (plot A and plot B; see Appendix S1 in the supplementary material), with altitudes ranging from 900 to 1400 m. The study plots were separated by a steep valley of 5 km width with unsuitable habitat. Plots were demarcated by altitude (> 900 m), paved roads or treeless pastures. The hilltops and valley bottoms were covered with patchy forests and interspersed with pasture. The forests were managed and used intensively for various recreation activities, and were dominated by Norway spruce *Picea abies* (49%), European silver fir *Abies alba* (19%) and common beech *Fagus sylvatica* (22%; Suchant, Baritz & Braunisch 2003). The winter climate in the area is temperate with high precipitation (2000 mm year^{-1}). The area is snow-covered from November/December–April, with a snow depth of 0·5–3 m. Recreation activities in the snow-free season are mainly hiking and mountain biking, and in winter cross-country skiing, downhill skiing (only in the upper part of study plot A; see Appendix S1 in the supplementary material) and hiking. Backcountry and free-riding skiing were frequent in the down-hill skiing area between ski-runs in the upper part of study plot A (see Appendix S1 in the supplementary material). The intensively used cross-country ski-tracks, with up to 1000 visitors a day (R. Roth, personal communication), near a tourist lodge in study plot A (see Appendix S1 in the supplementary material) and a biathlon shooting stand in study plot B (see Appendix S1 in the supplementary material), were mainly confined to forest roads or were situated in unforested areas. Intensive ski tourism starts between early and late December, when the snow depth allows the preparation of ski-runs. Before the ski season starts, only a few hiking tourists visit the study area. The ski season ends with the snow melt in early spring (March/April).

In the entire Black Forest (7000 km^2), during the last 30 years, the highly endangered capercaillie population has declined rapidly by about 65%, to 220 males. They persist in isolated fragments of just 510 km^2 (Braunisch & Suchant 2006). The study area was located within the core population of the southern Black Forest and is currently inhabited by about 60 individuals.

RADIO-TRACKING AND HABITAT USE

In September–October 2003 and 2004, seven capercaillie males and eight females were caught in walk-in ground-nets set in bilberry *Vaccinium myrtillus*-rich forest patches, where capercaillie prefer to search for food (Storch 1993a). There was no bias in age or sex ratio and all were healthy individuals. Males are twice the size of females and were equipped with a 40–69-g backpack radio-transmitter;

Table 1. Number of bearings collected during the pre-ski and ski seasons for seven radio-tracked capercaillie males and eight females, and the size of their home ranges (minimum convex polygon, MCP, in ha), during the pre-ski and ski season for birds with more than 22 bearings per period. Individuals with 22 bearings or less (1–22) were not included in statistical analyses. Bearings were taken over 72 different days during the pre-ski season and over 147 different days in the ski season

	Number of bearings		Home range (MCP, ha)	
Individuals	Pre-ski	Ski	Pre-ski	Ski
Male 1	27	(5)	59	–
Male 2	23	25	141	22
Male 3	30	31	185	137
Male 4	41	63	171	125
Male 5	49	95	208	245
Male 6	51	102	548	219
Male 7	(17)	0	–	–
Female 1	29	0	179	–
Female 2	39	26	79	66
Female 3	45	(21)	130	–
Female 4	45	67	134	58
Female 5	(9)	69	–	128
Female 6	43	65	118	71
Female 7	52	96	367	104
Female 8	(6)	(14)	–	–

females were fitted with a 25–40-g backpack transmitter (model GPI, Titley Electronics Ltd, Ballina, Australia; model A1540, Atstrack Advanced Telemetry Systems Inc., Isanti, MN; and model PTT-100, Microwave Telemetry Inc., Columbia, MD). Transmitters were <4% of the birds' body mass and had no noticeable effect on behaviour. We tested for a possible effect of wearing a transmitter on CM levels but none was detected (see below). During the winters 2003/04–2005/06, between 1 November and 31 March birds were located by 'homing in' (Kenward 2001) using a three-element hand-held antenna. Eight birds were tracked during one winter only, seven birds in either two or three winters. To minimize disturbance, most bearings were taken from forest roads or ski-tracks at <1 km distance. The forest canopy was relatively open with many leafless deciduous trees, access was easy and the spatial activity of capercaillie in winter low (Storch 1993b). All bearings were accurate and could be included in the analyses.

We defined two time periods because the area and intensity of human recreational activity changed over the course of the winter. The 'pre-ski season' started on 1 November (early winter with leafless deciduous trees, low snow cover) and lasted until the first heavy snow fall, when ski tourism began, usually in December. The 'ski season' started with the first day of ski tourism (when the number of tourists increases suddenly from almost zero to >1000) until 31 March, when the habitat use of capercaillie changes because of early lekking behaviour. In both periods, ecological and climatic conditions remain similar, with temperatures mostly <0 °C and capercaillie utilizing their winter habitats. In the ski season we could follow only 10 individuals because three were predated (male 1 and females 1 and 3) and one individual dispersed at the beginning of the study period (female 5; Table 1). All birds with more than 22 radio-locations per time period were included in the analyses. The time between two consecutive radio-locations ranged between 4 hours and 25 days (median 1 day).

Home ranges were determined by the minimum convex polygon method (MCP; GIS software ArcView 3·2) separately for the two time periods, pre-ski and ski season (Table 1). The extents of the study area and home ranges were calculated by excluding non-forested areas and very steep slopes >40°, which were unsuitable habitat for capercaillie; no radio-locations were recorded in such habitats.

Capercaillie prefer flat snow-rich mountain ridges and hilltops, and avoid steep slopes (Klaus *et al*. 1989; Graf *et al*. 2005). As a measure of habitat quality, we used the steepness of the slope with two categories (SLO1 = 0–10°, SLO2 = 10–40°, based on 50 × 50-m grid cells; DEM, Land Survey Office of Baden-Wuerttemberg, AZ:2851·9/3). We treated the intensity of recreation, and thus the potential of human disturbance, as another component of habitat quality. We defined three classes of recreation intensity. All forested areas without human presence during the winter (e.g. inaccessible areas and away from any ski-tracks) were digitized as REC1 (low recreation intensity). All regularly used tourism infrastructure in forests, such as ski-tracks, ski-lifts, ski-runs, hiking trails, roads, the tourist lodge and the biathlon shooting stand, with a buffer of 50 m, were digitized as REC3 (high recreation intensity; see Appendix S1 in the supplementary material). A previous study had revealed a 90-percentile flushing distance of 50 m (752 flushing events; Thiel *et al*. 2007a) between capercaillie and an off-trail hiker. All habitats that did not fall in one of the two categories were classified as areas with moderate recreation intensity (REC2). All GIS analyses for the habitat use study were conducted with GIS software ArcGis 9·1.

As the recreation intensity classes did not reflect the same intensities in both time periods, we defined them separately except for REC1. REC1 was associated with no or very low recreation intensity in both time periods. During the pre-ski season, $REC2_A$ accounted for off-trail recreation activities with a low intensity level, $REC2_B$ in the ski season for off-trail recreation activities with a moderate intensity level. $REC3_A$ during the pre-ski season included the area of all on-trail recreation activities within a buffer of 50 m, mostly forest roads with only a few hikers. In the ski season, $REC3_B$ included on-trail recreation activities within a 50-m buffer along all intensively used ski-tracks, ski-runs and hiking trails with several hundred recreationists per day.

SAMPLING OF DROPPINGS

All droppings were sampled from 1 November to 31 March in 2003/04 and 2004/05 in the same study area. We located transmitter-equipped capercaillie every 3–5 weeks to sample their fresh droppings. In addition, fresh droppings from capercaillie without transmitters were collected by walking along contour lines crossing forests and searching for droppings by eye on the surface of the snow (Thiel *et al*. 2007b). When searching for droppings of capercaillie without transmitters, the same location was visited only three times per winter. We determined the sex of the capercaillie from the size of the intestinal droppings, i.e. the dropping diameter of males is >10 mm, and that of females <8 mm (K. Bollmann, unpublished data). As home ranges of capercaillie in winter are small (Storch 1993b; Table 1), the droppings were spatially clumped. We only sampled fresh droppings and considered droppings from the same sex within a circle of 300 m (28·3 ha) as originating from the same individual, because at low densities capercaillie only occasionally aggregate in flocks (Klaus *et al*. 1989). Therefore we assigned each dropping of an individual without a transmitter to a 'potential individual', as an approach to prevent pseudoreplication in statistical analyses. Moreover, all repeated sampling of droppings from the same location were treated as originating from the same potential individual. As we only sampled fresh droppings and we knew at the time of sampling where the transmitter-equipped birds were located, we could avoid unintentionally sampling droppings from transmitter-equipped birds. We sampled 5–15 droppings at each location (= 1 dropping sample).

For each dropping sample, we determined the following predictor variables for the analyses: RADIO (without or with transmitter), INDIVIDUAL (potential individual for birds without a transmitter or individual transmitter-equipped bird), SEX (male or female), SEASON (pre-ski or ski season) and minimum daily temperature, TEMPMIN, from the nearest meteorological station (DWD Deutscher Wetterdienst) corrected for altitude by 0·6 °C per 100 m. Ambient temperature is known to affect energy metabolism, food intake, dropping production and therefore steroid measurements (Goymann *et al.* 2006). Furthermore, we determined the type of droppings, DROPTYPE, in three categories (night-roost droppings, droppings excreted during foraging, and droppings excreted during walking or day roosting on the ground; see definitions in Thiel *et al.* 2007b). Caecal droppings were not sampled because their different composition of micro-organisms affects enzymatic steroid metabolism (Klasing 2005). Each dropping sample was assigned to a slope category, SLOPE, (SLO1, SLO2) and a recreation intensity class, RECREATION (REC1–3). In total, we obtained 106 dropping samples from 14 transmitter-equipped individuals (n = 2–19 per individual, from all individuals except female 1; Table 1). The 290 droppings from birds without a transmitter were assigned to 53 potential individuals (n = 1–14 per potential individual) according to the method described above. All samples were stored at –23 °C until analysis. We did not have to be concerned about diet composition as a determinant of glucocorticoid metabolite concentration (Goymann 2005) because in winter capercaillie feed exclusively on conifer needles (Klaus *et al.* 1989), particularly on Norway spruce needles in the southern Black Forest (Lieser 1996). Other factors that might affect faecal CM, such as sex (Touma *et al.* 2003) and temperature (Goymann *et al.* 2006), were included as factors in our model. Sampling was restricted to winter before the reproduction period started, therefore life-cycle stage was held constant (Huber, Palme & Arnold 2003). The age and storage of droppings (Millspaugh & Washburn 2004) was not a concern because collection took place when temperatures were <0 °C and CM was stable (Thiel, Jenni-Eiermann & Palme 2005).

CM MEASUREMENTS

The faecal concentration of CM reflects the level in the plasma and can therefore be used to biomonitor the endocrine status (Touma & Palme 2005). Glucocorticoids are metabolized in various organs and therefore droppings contain a mixture of several different metabolites with a wide range of polarities. Because glucocorticoid metabolism is often species- and sometimes even sex-specific (Palme *et al.* 2005), a careful physiological validation of any method to measure faecal CM must be undertaken (Touma *et al.* 2003). We measured CM in droppings after extraction (60% methanol) with a previously described cortisone enzyme immunoassay (EIA), detecting steroids with a 3,11-dioxo structure (Rettenbacher *et al.* 2004). This EIA has been proven to measure corticosterone metabolites reliably in capercaillie droppings (Thiel, Jenni-Eiermann & Palme 2005). CM levels in capercaillie droppings remain stable for at least 21 days as long as the ambient temperature is <9 °C, which was the case throughout our study period; time of day does not influence faecal CM level (Thiel, Jenni-Eiermann & Palme 2005).

Because we were interested in measuring the potential long-term effects of recreation intensity on the baseline corticosterone, we wanted to eliminate potential short-term effects of other stressors, such as predator appearance. Moreover, because of differences in corticosterone metabolite concentrations between droppings (Baltic *et al.* 2005), probably caused by the pulsed excretion of corticosterone by the bile (K. Klasing, personal communication), we collected and homogenized the 5–15 droppings per individual and sampling location to obtain a mean concentration of these metabolites over a longer time span.

STATISTICAL ANALYSES

We used mixed models (residual maximum likelihood analysis, REML; Patterson & Thompson 1971) to test whether individual home range size varied with the number of bearings per individual (BEARINGS) or with season (SEASON). INDIVIDUAL was included as a random effect, BEARINGS, SEASON and its interaction term as fixed effects.

We combined the categories of the two habitat classifications (REC and SLO), resulting in six habitat types: REC1SLO1, REC1SLO2, REC2SLO1, REC2SLO2, REC3SLO1 and REC3SLO2. To test whether habitat use by capercaillie was influenced by recreation intensity, we applied compositional analysis (Aebischer, Robertson & Kenward 1993) using an Excel macro (Smith 2005) for two types of analyses.

First, we compared the composition of the six habitat types in the home ranges with the availability of the habitat types in the entire study area. This was done for the pre-ski and ski season periods separately, to test whether the home ranges of capercaillie were preferentially located in areas of particular habitat types.

Secondly, we compared habitat use within each home range, as revealed by the composition of the habitat types from the telemetry locations, with availability (habitat composition of the corresponding home range). For both periods separately, we tested whether capercaillie preferred or avoided certain habitat types within their home ranges.

Following Aebischer, Robertson & Kenward (1993), we substituted missing values by a small proportion (0·001%) for available but unused habitat types; 1000 iterations for randomizations were used. For each compositional analysis of capercaillie habitat use, Wilk's lambda (λ) and randomized P-values were reported.

We used REML to identify factors affecting CM levels. Data from all years were pooled, and data from birds with and without transmitters were analysed in the same model, because we tested for any effects of year and of wearing a transmitter by the variable RADIO. The model contained all six predictor variables as fixed effects and the variable INDIVIDUAL as a random effect. Furthermore, we included the three interaction terms SEX × SEASON, SEX × RECREATION and SEASON × RECREATION because we expected them to be biologically relevant. Non-significant interaction terms were omitted from the final model. We used GenStat for Windows version 7·3 (Payne 2003) for the analysis.

Results

HABITAT USE

Areas with intensive human activity (the tourist lodge, ski-runs and biathlon shooting stand) were used during the pre-ski season but mainly avoided in the ski season (see Appendix S1 in the supplementary material). In contrast to ski-runs, areas with cross-country ski-tracks were used during both the pre-ski and ski seasons. During the pre-ski season, capercaillie were more evenly distributed in the study area than in the ski season, when capercaillie locations were more aggregated in certain areas (see Appendix S1 in the supplementary material). In the ski season, 50% of 84 locations in areas with high recreation intensity ($REC3_B$) occurred on days with only a few skiers because of snowfall and storm. Compared with an expected frequency of 25% (proportions of days with low recreation activity when birds were radio-tracked), this shows that capercaillie used $REC3_B$ areas in the ski season when recreationists were mostly absent.

Home range size, as determined by telemetry in nine birds, differed significantly with SEASON (Wald χ^2_1-probability = 0·006) and was not influenced by the number of bearings (Wald χ^2_1-probability = 0·940). Home ranges during the pre-ski season were larger than in the ski season for all individuals except for male 5 (Table 1). The location of the home ranges did not change between the two periods; 75 ± 5·3% (mean ± SE, $n = 9$) of the home range area in the ski season was already part of the home range area before the ski season started. Hence capercaillie did not markedly relocate or change their home range with the start of the ski season, except for male 1. During the pre-ski season, this male used forests with ski-runs and ski-lifts. With the beginning of the ski season, it relocated to an area 2700 m away with moderate recreation intensity, $REC2_B$ (cross-country skiing area), by crossing a valley 1500 m wide. After 3 weeks this bird returned near to its previous location but in a forest with low recreation intensity (REC1), where it was predated by a red fox *Vulpes vulpes*.

In a next step, we analysed, at the individual level, whether the composition of the six habitat types (combination of slope and recreation intensities) in the home ranges differed from the habitat composition of the entire study area. During the pre-ski season, capercaillie home range composition did not differ from the composition of the study area (Wilk's λ = 0·618, χ^2 = 5·777, randomized P = 0·539; Fig. 1a). In the ski season, habitat composition of capercaillie home ranges differed only slightly from availability in the study area (Wilk's λ = 0·138, χ^2 = 19·841, randomized P = 0·045) and there were no significant differences between habitat types (Fig. 1b).

On a smaller spatial scale, we analysed whether habitat use, as revealed by the locations within home ranges, differed from the habitat composition of the corresponding individual home ranges. During the pre-ski season, capercaillie preferred areas with moderate recreation intensity, $REC2_A$, to REC1 and $REC3_A$, independent of slope (Wilk's λ = 0·252, χ^2 = 16·539, randomized P = 0·018; Fig. 2a). In the ski season, capercaillie significantly preferred undisturbed areas, REC1, to highly disturbed areas, $REC3_B$, independent of slope (Wilk's λ = 0·1522, χ^2 = 18·824, randomized P = 0·046; Fig. 2b).

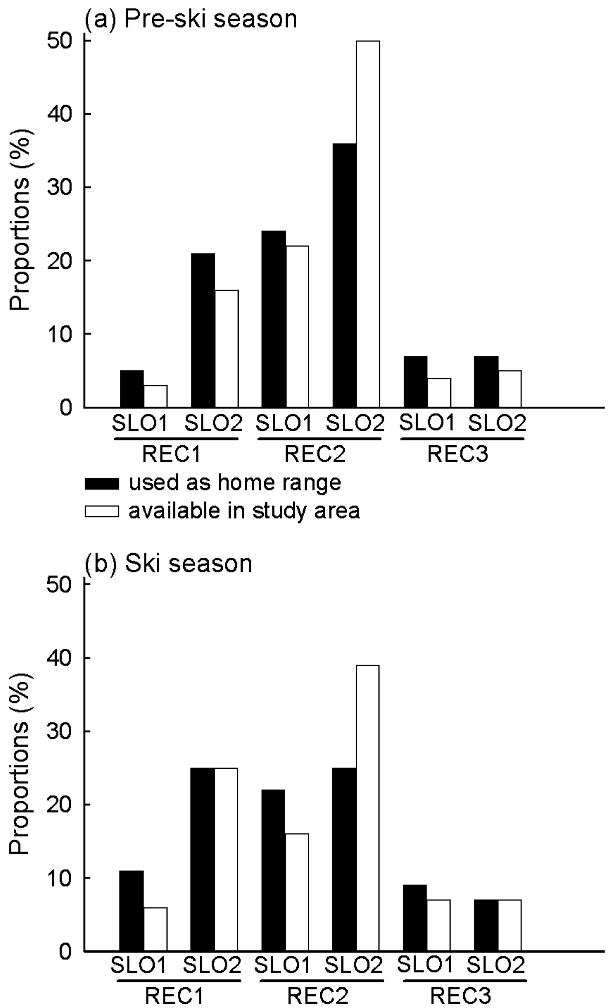

Fig. 1. Proportions of six habitat types of recreation intensity classes [REC1, no/low recreation intensity; REC2, off-trail recreation activities with low (during the pre-ski season) or moderate (in the ski season) intensity level; REC3, on-trail recreation activities within a buffer of 50 m] and habitat slope categories (SLO1, 0–10°; SLO2, 10–40°) of capercaillie winter home ranges compared with the availability in the entire study area during the (a) pre-ski season and (b) ski season. There were no significant differences between use and availability of the six habitat types.

STRESS HORMONE ANALYSES

Five out of seven variables (SEX, SEASON, TEMPMIN, DROPTYPE and RECREATION) contributed significantly to explaining the variation in CM level (Table 2). Males (predicted mean ± SE, 45·0 ± 2·4 ng g dropping^{-1}) exhibited generally higher faecal CM levels than females (37·7 ± 2·3 ng g dropping^{-1}; Fig. 3). The CM level during the pre-ski season (34·6 ± 3·1 ng g dropping^{-1}) was significantly lower than in the ski season (48·6 ± 1·9 ng g dropping^{-1}; Fig. 3). The CM level increased with decreasing minimum daily temperatures (Table 2). The CM level from night-roost droppings (41·3 ± 1·4 ng g dropping^{-1}) was lower than those excreted during foraging (44·0 ± 1·5 ng g dropping^{-1}) and during walking or day roosting on the ground (49·5 ± 2·5 ng g dropping^{-1}). In both periods, CM levels of capercaillie were lower in areas with low (REC1) compared with moderate (REC2) recreation intensity (Fig. 3).

Table 2. Dependence of the concentration of CM in capercaillie droppings ($n = 396$) on various predictor variables analysed in a multivariate linear REML model with the individual bird INDIVIDUAL as the random effect. Effects ± SE were calculated considering a reference value of zero for RADIO (no), SEX (male), SEASON (pre-ski season), DROPTYPE (night roosting), SLOPE (0–10°) and RECREATION (low). None of the two-way interaction terms was significant

Independent variables	Effect ± SE	Wald statistics	d.f.	*P*
Constant	31·49 ± 4·65			
RADIO (yes)	2·86 ± 3·01	0·23	1	0·63
SEX (female)	−7·82 ± 2·59	11·37	1	< 0·001
SEASON (during)	13·61 ± 3·25	10·66	1	0·001
TEMPMIN	−0·57 ± 0·23	9·50	1	0·002
DROPTYPE		7·25	2	0·027
Foraging	−1·02 ± 2·68			
Day roosting/walking	5·30 ± 2·68			
SLOPE (10–40°)	−3·09 ± 2·14	3·18	1	0·074
RECREATION		17·91	2	< 0·001
Moderate	9·96 ± 2·88			
High	8·89 ± 2·88			

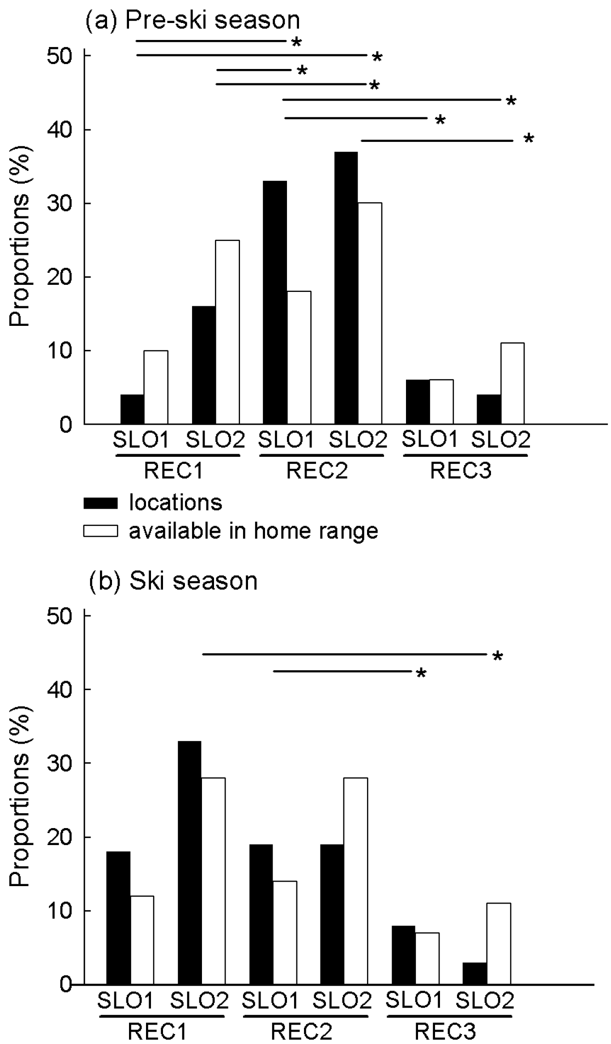

Fig. 2. Proportion of the six habitat types (see Fig. 1 for explanation) used within home ranges (locations) compared with the composition of their individual home ranges during (a) the pre-ski season and (b) the ski season. *($P < 0·05$, compositional analysis) indicates significant differences between habitat types connected by a line.

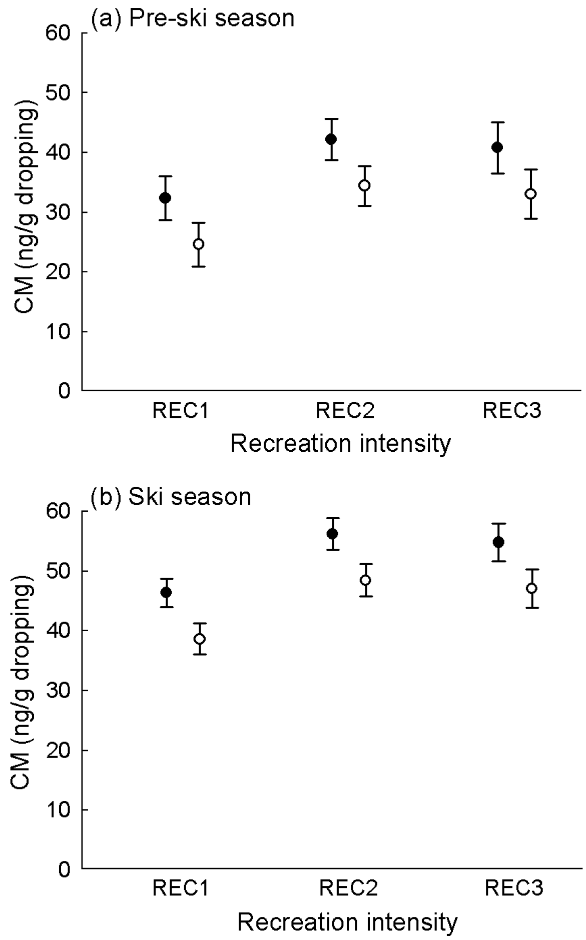

Fig. 3. Predicted means (± SE) of the REML analysis (Table 2) of concentrations of CM in capercaillie droppings ($n = 396$) of males (filled circles) and females (open circles) for three recreation intensity levels during (a) the pre-ski season and (b) the ski season.

CM levels of capercaillie in areas with REC2 did not differ from those with high recreation intensity, REC3 (Fig. 3). Faecal CM levels of capercaillie with or without a transmitter did not differ. SLOPE did not contribute to explaining the variation in CM level. Analysis of the 106 droppings from the 14 individually known radio-tracked birds without the variable RADIO revealed that the same variables were significant except for SEX ($P = 0·456$) and DROPTYPE ($P = 0·466$). RECREATION had by far the largest impact of all variables ($P = 0·002$, effect size 13·2 for REC2 and 11·0 for REC3).

Discussion

METHODOLOGICAL APPROACH

This study has demonstrated the importance of measuring both physiological and behavioural responses of marked individuals in order to evaluate their susceptibility to human recreational activities. In addition, by investigating habitat use at two spatial and two temporal scales we could assess the scale at which capercaillie modify their behaviour in response to winter tourism. Had we focused on a specific scale or only investigated either the physiological or the behavioural response, we may have drawn the wrong conclusions. Several studies have shown that, under certain circumstances, animals do not, or only weakly, respond behaviourally to disturbances because this would be too costly, although they are stressed (Frid & Dill 2002; Stillmann & Goss-Custard 2002). Thus the reliability of studies focusing only on behavioural responses can be limited or misleading. Therefore a physiological measure of stress from the same individuals provides important additional information with which to evaluate possible responses to human disturbance. However, a physiological measure of stress does not provide information on behavioural reactions and the precise circumstances under which human presence has an impact on the animal, information which is needed for mitigation measures. This calls for a combination of methods.

The capercaillie/winter tourism system was particularly appropriate for this methodological approach because the large body size and longevity of capercaillie allowed the use of heavy and long-lived transmitters to follow the birds for up to three consecutive winters. In addition, snowy conditions increased the efficiency of finding sufficient droppings for powerful statistical analyses, and frost kept the corticosterone metabolites stable. Therefore this methodological approach is most appropriate for studying species that can be radio-tracked over a long period and where droppings can be collected in an environment that stabilizes stress hormone metabolites.

HABITAT USE

This study revealed that winter tourism affected habitat use at a small spatial scale within home ranges, that capercaillie preferred disturbance-free forest patches and that areas with tourism infrastructure were only used when tourists were absent. The decrease in home range size with the start of the ski season could be related to the concomitant increase in snow depth. With this increase, foraging on ground vegetation becomes impossible and birds are restricted to low-quality conifer needles, which is likely to reduce their spatial activity (Gjerde & Wegge 1987). However, the preference of capercaillie in the ski season for areas with low human recreational intensity within their home ranges is unlikely to be caused by snow depth or food availability, because capercaillie in our study area mainly fed on the superabundant and spatially evenly distributed Norway spruce (Lieser 1996). An effect of predators is also possible, but data on this were not available.

STRESS HORMONES

We found a physiological response in capercaillie to human recreation during the pre-ski and ski seasons at a small spatial scale (between individuals) and at a landscape scale (between home ranges). These findings seem to be robust because the increase of faecal CM level appeared in both sexes, both seasons and for birds with and without transmitters. The physiological response of capercaillie to winter tourism was more pronounced and obvious than the behavioural response; droppings on hiking trails with a low frequency of tourists during the pre-ski season showed higher CM levels compared with areas away from any human presence. In accordance with our findings, faecal glucocorticoid metabolites in wolves *Canis lupus* and pine marten *Martes martes* were higher in areas used by humans, and day-to-day variation in these levels in elk *Cervus elaphus* paralleled variation in the number of snowmobiles (Creel *et al*. 2002; Barja *et al*. 2007).

Higher levels of faecal CM in males than females is similar to a study on chickens using the same EIA (Rettenbacher *et al*. 2004). This may indicate a different metabolism of corticosterone (Goymann 2005; Touma & Palme 2005), a difference in steroid-binding plasma globulins (Breuner & Orchinik 2002) or reflect sex-specific differences in plasma corticosterone levels indicating that males are more stressed than females. Thiel *et al*. (2007a) have suggested a higher susceptibility of capercaillie males to human recreational activities when reporting longer flushing distances as a response to an off-trail hiker.

The strong effect of season on CM level (higher CM levels in the ski season than in the pre-ski season) could be caused either by the higher recreation activity in the ski season or by environmental changes. With the increase of snow depth, capercaillie change their forage from energy-rich and easily digestible bilberries on the forest ground to low-quality conifer needles in trees. This change in food could be stressful, leading to increased faecal CM levels. Low temperatures, occurring more frequently in the ski season than the pre-ski season, may also result in an increase in CM levels. However, the effect of season on CM level is not because of a correlation of season with temperature, as the significance of season remained the same even when we first corrected for temperature by changing the order of the predictor variables in the REML analysis.

THE IMPORTANCE OF REFUGES

Several reasons can be offered to explain why capercaillie used skiing areas despite the possible negative consequences, and why the effect of winter recreation on capercaillie habitat use was spatially scale-dependent. Habitat selection of capercaillie and skiers are similar. Winter tourism in the southern Black Forest is restricted to the highest snow-rich altitudes, mostly dominated by flat and gently sloped coniferous forests with low tree density. These forests are the last high-quality capercaillie habitat in the region (Braunisch & Suchant 2006). Capercaillie may remain within disturbed areas because they cannot find alternative suitable habitat nearby, a situation also found in Malaysian plovers *Charadrius peronii* on tourist beaches (Yasué & Dearden 2006). It is possible that frequent or long-distance movements in response to human recreation may be too costly or too risky, decreasing body condition and increasing predation risk. Capercaillie probably use skiing areas only when undisturbed refuges are also available within their home ranges. Forest patches that are inaccessible to humans might provide a visual and acoustic shield from recreation activities in adjacent areas.

The question is whether the avoidance of tourist areas within home ranges and high stress hormone levels indicate adverse effects of winter tourism on capercaillie. It is well known that chronically elevated corticosterone levels have negative impacts on physiology, immune system and behaviour (Sapolsky, Romero & Minck 2000), although we do not know whether the CM levels observed in this study were at a detrimental level. Juvenile hoatzins *Opisthocomus hoazin* living at ecotourist-exposed sites had a lower body mass and higher mortality and showed a stronger increase in corticosterone levels to experimental stress compared with individuals at undisturbed sites (Müllner, Linsenmair & Wikelski 2004).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We conclude that areas with frequent human winter recreational activities are suboptimal capercaillie habitat. We recommend that the creation of new skiing areas should be avoided and that existing sites should not be developed further in or adjacent to capercaillie habitats. In areas where capercaillie habitat overlaps with human winter recreational activities, management plans should ensure that forest patches without human access are interspersed as refuges, and off-trail activities in capercaillie core areas should be prevented. Regulations should stipulate that tourists stay on the marked trails. Wherever possible, trails in capercaillie core areas should be closed or relocated to reduce the extent of disturbance, and thus increase suitable capercaillie habitat. Hazel grouse *Bonasa bonasia*, black grouse and other species are also likely to benefit from such management activities because they share similar habitat requirements with capercaillie and are probably affected similarly by disturbance from human winter recreational activities (Arlettaz *et al.* 2007).

Acknowledgements

We thank Dölf Egenter, Samuel Ehrenbold, Judith Ehrlacher, Christoph Grütter, Jonas Kleyer, Christof Elmiger, Ruedi Meier, Peter Nyffeler, Uli Querner, Matthias Ritschard, Tobias Roth, Thomas Sattler, Andreas Schmidt and Conny Thiel-Egenter for their assiduous fieldwork. We are especially grateful to the foresters Wolfgang Ebser and Claudio Röhmer-Litzmann, who supported this study with valuable help and access in the field. We thank Peter Berthold, Wolfgang Fiedler and Rudi Suchant, who made it possible to realize this study in the Black Forest. Marc Kéry supported us with statistical analyses, and Beat Naef-Daenzer with radio-tracking techniques. For helpful comments on this manuscript, we thank Christian Marti, Gernot Segelbacher Philip Tipping, Niklaus Zbinden, Mai Yasué and an anonymous referee. D. Thiel was financially supported by the International Council for Game and Wildlife Conservation CIC and the Janggen-Pöhn-Foundation. Catching and radio-tracking of capercaillie were carried out under the permit of the Regierungspräsidium Freiburg, Baden-Württemberg (Freiburg; no. 0–9213·21, höhere Naturschutzbehörde).

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Received 14 February 2007; accepted 15 January 2008
Handling Editor: Des Thompson

Supplementary material

The following supplementary material is available for this article.

Appendix S1. Locations of radio-tracked capercaillie in the southern Black Forest during the pre-ski season and ski seasons.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2008.01465.x
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