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Mountain hares *Lepus timidus* and tourism: stress events and reactions

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Summary

1. Winter tourism in the European Alps has developed rapidly over the past few decades, leading to the expansion of ski resorts, growing numbers of visitors and a massive increase in snow sport activities such as free-ride skiing and snowboarding, backcountry skiing and snowshoeing. Wildlife is often disturbed by these largely unpredictable activities, and animals may have limited opportunities to adapt. Mountain hares *Lepus timidus* are affected by this increase in alpine tourism, but their physiological and behavioural reactions to tourist activity are still unknown.

2. We measured the levels of faecal glucocorticoid metabolites (GCM) in wild mountain hares living in areas that had no, medium or high levels of tourist activity during winter in 2011. Furthermore, we compared the changes in GCM excretion, behaviour and food intake of six captive mountain hares following predator challenge experiments from early to mid-winter.

3. Our field results showed that GCM excretion is positively correlated with increased tourism intensity. In the predator challenge experiments, hares spent less time resting and grooming (including re-ingesting faecal pellets) during and after the stress treatments. These stress events lead to higher energy demands due to flushing, increased GCM levels, and disrupted the energy intake that hares derive from faeces.

4. We conclude that mountain hares living in areas with frequent human winter recreational activities show changes in physiology and behaviour that demand additional energy in winter, when access to food resources is limited by snow.

5. *Synthesis and applications*. To bring down the frequency of stress threats for mountain hares, we recommend that managers keep forests inhabited by mountain hares free of tourism infrastructure and retain undisturbed forest patches within skiing areas. Other species such as black grouse *Tetrao tetrix* and/or capercaillie *Tetrao urogallus* are also likely to benefit from such management activities because they share similar habitat requirements with mountain hares.

Key-words: Alps, behaviour, cortisol, faeces, non-invasive, *Lepus timidus*, tourism

Introduction

Winter tourism in the European Alps has developed rapidly over the past few decades, leading to the expansion of ski resorts, growing numbers of visitors and a massive increase in snow sport activities such as free-ride skiing and snow-boarding, backcountry skiing and snowshoeing (Ingold 2005; Schweizer Alpen-Club 2012). Thus, in addition to predictable environmental conditions such as seasonal changes in climate and resource availability, wild animals must also cope with unpredictable levels of human disturbance (Wingfield & Romero 1999; Taylor & Knight 2003; Ingold 2005). Expansions in tourist activities that increase pressure upon biodiversity (Czech, Krausman & Devers 2000; Watson & Moss 2004; Arlettaz *et al.* 2007; Barja *et al.* 2007; Ellenberg *et al.* 2007) and lead to habitat loss and degradation can elicit costly behavioural responses in animals (Lott & McCoy 1995; Fernandez-Juricic & Telleria 2000; Sapolsky, Romero & Munck 2000;

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Maréchal *et al.* 2011). Even in the absence of behavioural reactions, the presence of humans may evoke a physiological stress response (Stillman & Goss-Custard 2002; Walker, Boersma & Wingfield 2005; Arlettaz *et al.* 2007; Thiel *et al.* 2008), with chronically elevated stress levels affecting metabolism, immune response, reproduction and/or survival (Boonstra *et al.* 1998; Sapolsky, Romero & Munck 2000; Sheriff, Krebs & Boonstra 2009; Clinchy *et al.* 2011). Both physiological and behavioural responses are often combined with extra energetic costs (Baltic *et al.* 2005), especially during winter when most wildlife species face an energy bottleneck. Nevertheless, the physiological and behavioural reactions of mountain hares *Lepus timidus* to tourist activities are still unknown.

Non-invasive methods for measuring steroid hormone metabolites in the faeces have become a widely accepted tool to assess the endocrine status of animals, especially free-ranging animals (Palme 2005; Sheriff *et al.* 2011). The advantage of such methods is that samples can be collected easily without any need to handle the animal. The methods are therefore appropriate for evaluating adrenocortical activity in wild animals.

In this study, we measured the levels of glucocorticoid metabolites (GCM) in mountain hares in areas with different tourist intensities during winter. We also investigated the influence of predator challenge experiments on GCM excretion, behaviour and food intake. Finally, we suggest management strategies for conserving mountain hare populations in the Alps.

Materials and methods

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To study the effect of different levels of tourism on mountain hares, we selected three sites in south-eastern Switzerland based on their proximities to one another and their tourist activities in 2011. The ski region Lagalp (46°25′N, 10°00′E, 2079–2905 m a.s.l.) represents an intensively (=high) used region with 227 ± 22 visitors per day on 1 km of ski trail; the ski region Minschuns (46°38′N, 10°19′E, 2075–2700 m a.s.l.) received moderate (=medium) use with 125 ± 6 visitors per day on 1 km of ski trail; and the Swiss National Park (46°39′N, 10°11′E, 1897–2201 m a.s.l.) is closed to tourism (=zero; not frequented) in the winter. The climate in the region is continental and comparable between all three sites. As measured over three decades at the Buffalora weather station at 1970 m a.s.l. (Aschwanden *et al.* 1996), the mean winter temperature for the region is −9·2 °C and the mean precipitation is 54 mm.

Faecal samples were collected over transects with a total length of 42·9 km (high = 18·0 km, medium = 18·6 km and zero = 6·3 km) and altitudinal differences of 900 m between January and March 2011 (outside the breeding season of mountain hare). We collected samples close to places with tourist activities (if available within 100 m of source), and the accessibility (danger of avalanches) was taken into consideration. We randomly searched for potential locations for faeces at each site (distinctive stones and trees, locations with mountain hare tracks), cleared them of all mountain hare faeces and marked them with GPS. Three nights later, plots were revisited and fresh samples (one sample consisted of a minimum of three pellets) were collected as recommended by Rehnus, Hackländer & Palme (2009).

In total, 132 faecal samples were collected (high = 33, medium = 46 and zero = 53). The altitude of each location and the type of the nearest tourist activity (‘ski’, ‘snowshoe’ and ‘cross-country skiing’) and its distance to the faeces were determined. As the mountain hare has been shown to be the only species of hare in these three study sites (Rehnus *et al.* 2010, 2013; D. Godli & J. Gross, personal communication), our sampled faeces could not have been confused with faeces from European hares, *Lepus europaeus*.

STRESS EXPERIMENTS

In general, humans as hikers in wildlife habitats are recognized as potential predators (Beale & Monaghan 2004). We used predator challenge experiments to investigate their potential effects on GCM excretion, behaviour and food intake in six mountain hares by comparing periods of stress and non-stress (for details see Table 1).

Animals were kept in aviaries (6–12 m^2) in a separate hall that was protected against all hare predators. Mean air temperature (in the morning) in the hall was 7·2 ± 0·3 °C (range 2–12 °C). We used a trained dog (without barking or whining) and a kite with a wingspan of 1·8 m as simulated terrestrial and avian predators. Both simulate natural predators of the mountain hare such as the fox *Vulpes vulpes* and the golden eagle *Aquila chrysaetos* (Thulin & Flux 2003). The hares in the stress aviaries were separated from those in the control aviaries by a dark green cloth and a 5-m corridor. The dog (walking and sniffing around the aviaries) or kite (flying over the aviaries) was taken to each stress aviary for 1–2 min every other day. To ensure habituation did not occur (Dallman & Bhatnagar 2001), stressors were used at various times throughout the day and the order of exposure was randomized. Control hares had no contact, visual or physical, with the stressors. Although they may have smelled the dog, control hares did not alter their behaviour during stress exposure (Sheriff, Krebs & Boonstra 2009). The same stressors were used throughout the experiment.

Fresh samples (with a minimum of five pellets) were collected each morning while cleaning the aviaries. On days with a predator challenge, additional samples were collected 8 hours after the simulation. Thus, samples collected after 8, 24 and 48 hours were available to estimate individual peaks of GCM levels after stress simulation (Rehnus, Hackländer & Palme 2009).

To detect the changes in relative amounts of a particular type of behaviour over the course of a day, we compared control and stressed hares over a 24-hour period. Activities were recorded by a video camera (Monacor IP65) that allowed observation during day and night. We observed each individual for four 24-hour periods, where 2 days were in the stress period (days with simulation) and two in the non-stress period. Usually records started early in the morning and ended at the same time the next day. As a result of randomized simulations during daytime, time between start of recording and initial simulation differed. Behaviour activities were analysed by the software CowLog (Hänninen & Pastell 2009). We classified the behaviour of hares based on a literature review (Schneider 1978; Hewson 1990a; Wolfe & Long 2002) as follows: Feeding (feeding activities at available food boxes and hay place), Canopy (hare under natural canopy in its

Table 1. Chronology of the stress experiment carried out on six mountain hares from October 2011 to January 2012

Date	Group*	Treatment	Procedure (Sample collection times)
October 13	1, 2		Moving to the experimental study site and blood sampling
October 13–23	1, 2	Acclimatization	Monitoring of GCM excretion (5 × 24 hours per week per hare), behaviour (2 × 24 hours per hare), food intake (2 days per week per hare), endoparasites (1× per week)
October 24–November 24	1	Predator challenge (random stressor at various times)	Monitoring of GCM excretion (5 × 24 hours per week and hare and an 8-hour sample per hare after threat), behaviour (2 × 24 hours per hare), food intake (2 days per week per hare), endoparasites (1× per week)
October 24–November 24	2	No stress simulations	Monitoring of GCM excretion (5 × 24 hours per week per hare), behaviour (2 × 24 hours per hare), food intake (2 days per week per hare), endoparasites (1× per week)
November 25	1, 2		Blood sampling
November 26–December 4	1, 2	Recovery	As above (acclimatization)
December 5–January 9	1	No stress simulations	As above
December 5–January 9	2	Predator challenge (random stressor at various times)	As above
January 10–30	1, 2	No stress simulations	As above
January 30	1, 2		Blood sampling

*Each group consisted of three mountain hares.

aviary), Resting (resting and sleeping in open areas), Moving (movements in open areas to/from canopy and/or to/from feeding places) and Grooming (grooming in open areas, coprophagy). In grooming, we also included potential re-ingestion activities, because coprophagy could not always be definitively distinguished from some grooming activities from the fixed camera images.

To investigate food intake (gross MJ per day) during different periods, we measured the food weight (mix of Provacca chips, standardized mountain hare mix including lucerne pellets and hay from alpine meadows) given to the hares before and after each 24-hour period (n = 118).

To ensure an adequate state of health for each hare during the experiment, we regularly checked faecal samples for endoparasites and took blood samples to check various health parameters (mineral nutrients, protein, creatinine, cholesterol, etc.). When a hare experienced a coccidial infection (each hare up to three times), we used Toltrazuril over three consecutive days. Faeces collected during periods of infection were not used for analysis because infection can increase the GCM levels (Sheriff *et al.* 2011).

ANALYSIS OF FAECAL CORTISOL METABOLITES

To measure faecal GCM, we used an 11-oxoaetiocholanolone enzyme immunoassay (EIA) previously shown as being suitable for evaluating adrenocortical activity in mountain hares (Rehnus, Hackländer & Palme 2009). Details of the extraction procedure and the EIA can be found elsewhere (Möstl *et al.* 2002; Rehnus, Hackländer & Palme 2009; Palme *et al.* 2013).

Data analysis

All statistical tests were conducted using R 2·13·1 (R Development Core Team 2010).

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Faecal samples were classified according to the intensity of tourism: high (Lagalp), medium (Minschuns) and zero (SNP). The Shapiro–Wilk normality test showed that the frequencies of visitors to the two study sites (February to March 2011) were normally distributed, and a t test was used to determine differences in frequencies. Influences on the GCM concentration were tested using variance analysis with the GCM concentration as a dependent variable and the site as a predictor variable. Differences between sites were evaluated with a Tukey test for *post hoc* testing. In the same way, we tested the potential influence of distance and type of activity (ski/snowboard, snowshoe and cross-country skiing) on GCM concentration.

STRESS EXPERIMENTS

To test the effect of stress simulation on GCM levels, behaviour classes and food intake, we compared two models, with and without the simulation, with likelihood-ratio tests and hare as a repeated measure. Before analysis, we evaluated linear mixed models by their residuals (including residual plots). We did not include temperature as a potential explanatory variable (Flux 1970; Rehnus *et al.* 2010) because it did not change significantly during experiments (t tests: t = 0·5387, d.f. = 195·21, P = 0·59).

To investigate the influence of the predator challenge experiments on GCM level, we initially determined individual delay times of GCM excretion. Individual differences were found in the peaks after simulation (8 and 24 hours after treatment). In further statistical analyses, we used only samples reflecting peak GCM production of individuals. Thus, the original sample size was reduced by 64% from 589 to 219 samples.

Results

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Concentrations of GCMs in faecal samples of mountain hares varied significantly across study areas ($F_{2,132}$ = 4·36, P = 0·01). As revealed by *post hoc* tests, faecal GCM values were higher (P < 0·05) at the site with high tourist activity than at the other two sites (Fig. 1). Within

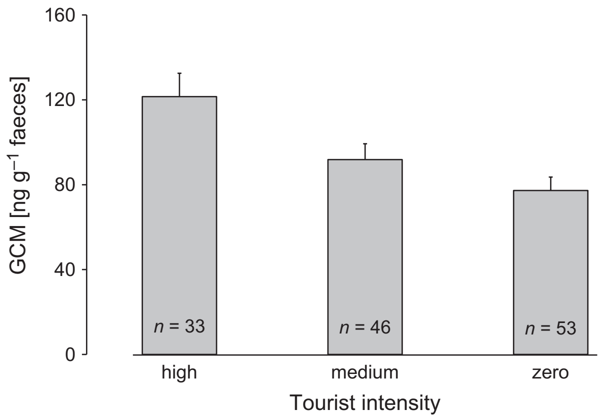

Fig. 1. Concentrations of faecal glucocorticoid metabolites (GCM, mean ± SE; $n = 132$) of mountain hares in areas with different levels of tourist activity in Switzerland in winter 2011. The Tukey test showed differences between the area with the highest activity and the areas with medium (t = 2·2364, $P = 0{\cdot}04$) and no tourist activity (t = 2·6901, $P = 0{\cdot}01$).

touristically frequented areas, frequencies of tourists were different (t test: t = −4·468, d.f. = 54·488, $P < 0{\cdot}001$) but GCM concentrations were not influenced by the type of activity ($F_{2,78} = 0{\cdot}01$, $P = 0{\cdot}96$) or by the distance of the activity to the site of collection of faeces ($F_{1,78} = 1{\cdot}81$, $P = 0{\cdot}17$).

STRESS EXPERIMENT

We found a significant influence of stress simulation on GCM levels (likelihood-ratio test: $\chi^2 = 8{\cdot}2878$, d.f. = 1, touristically = 0·01). GCM concentrations increased after simulation (mean ± SD: 67·2 ± 19·0 ng g^{-1}) compared with days without stress simulation (50·4 ± 12·5 ng g^{-1}). The maximum increase above baseline was up to fourfold (Table 2).

The predator challenge had a significant influence on the behaviour grooming (likelihood-ratio test: $\chi^2 = 4{\cdot}5672$, d.f. = 1, $P = 0{\cdot}03$) and resting ($\chi^2 = 3{\cdot}6526$, d.f. = 1, $P = 0{\cdot}05$), while moving ($\chi^2 = 0{\cdot}0375$, d.f. = 1, $P = 0{\cdot}85$), feeding ($\chi^2 = 0{\cdot}3392$, d.f. = 1, $P = 0{\cdot}56$) and canopy ($\chi^2 = 1{\cdot}4481$, d.f. = 1, $P = 0{\cdot}22$) did not differ. Grooming and resting decreased after simulation (Mean ± SD: grooming: 4·0 ± 2·3% and resting: 26·8 ± 14·2% of a 24-hour period) compared with days without the stressor (grooming: 5·4 ± 3·1%, resting: 32·4 ± 14·4% of a 24-hour period; Fig. 2).

We found a significant influence of stress simulation on food intake (likelihood ratio test: $\chi^2 = 53{\cdot}25$, d.f. = 1, $P < 0{\cdot}001$). Food intake increased after simulation (mean ± SD: 3·18 ± 0·29 MJ day^{-1}) compared with days without stress simulation (2·60 ± 0·36 MJ day^{-1}).

Table 2. Stress challenge: individual baseline and peak values (ng/g faeces; percentage increase) of faecal GCM concentrations after predator challenge (dog/kite) analysed by the 11-oxoaetiocholanolone EIA ($n = 219$)

Animal	Baseline (Mean ± SD)	After stress simulation: Maximum (ng g^{-1})	After stress simulation: % Increase
1	45 ± 11	160	354
2	49 ± 12	91	186
3	43 ± 13	72	167
4	41 ± 11	99	245
5	63 ± 9	97	152
6	53 ± 10	81	154

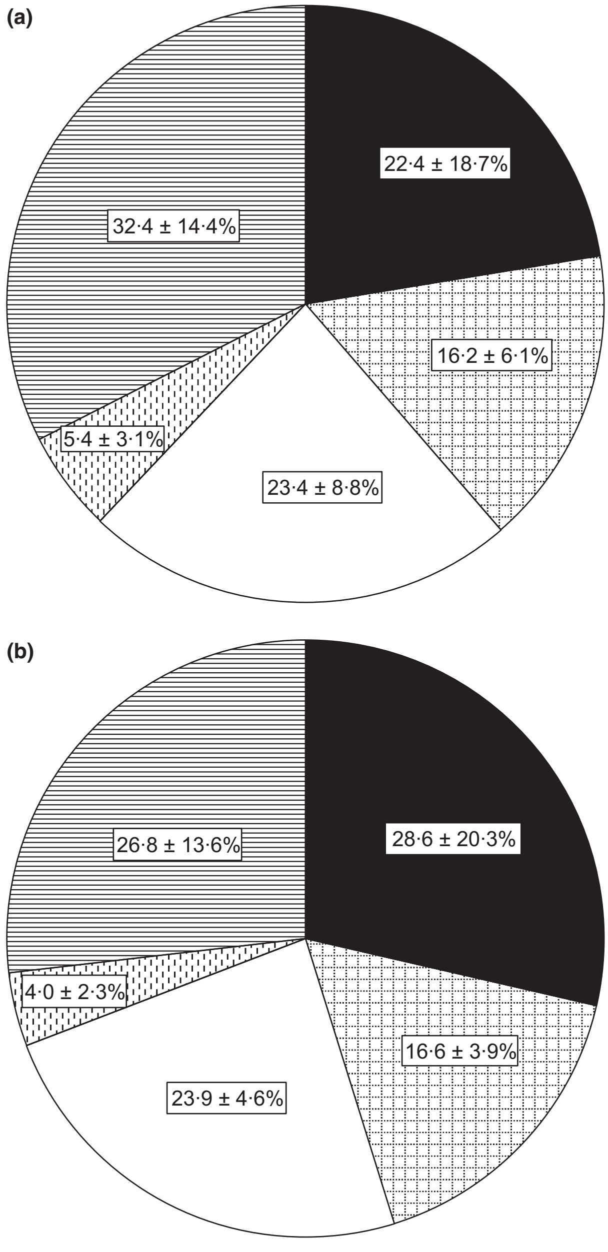

Fig. 2. Relative duration (mean ± SD) of each class of behaviour (clockwise: black = canopy, checked = feeding, white = moving, dotted = grooming, grey = resting) in a) control hares ($n = 12$) and b) stressed hares ($n = 12$).

Discussion

FIELDWORK

Our results showed that GCM excretion is positively correlated with increased tourist activity. This result is in accordance with findings from studies on other wildlife species. For example, black grouse *Tetrao tetrix* and capercaillies *Tetrao urogallus* had higher GCM levels due to increased human recreation activities during the winter (Arlettaz *et al.* 2007; Thiel *et al.* 2008, 2011) and birds flushed from their snow burrows showed increased concentrations of faecal corticosterone metabolites (Arlettaz *et al.* 2007). In red deer *Cervus elaphus* and wolves *Canis lupus* snow-mobile activity and glucocorticoid metabolites in the faeces were also positively correlated (Creel *et al.* 2002). Nevertheless, increased GCM levels should be interpreted with caution. The stress axis plays a key part in allowing animals to respond to changes and challenges in the face of environmental certainty and uncertainty (Boonstra 2013a), and as a consequence, life-history decisions (e.g. to reproduce, to grow or to put energy into storage) are implemented (Ricklefs & Wikelski 2002). On the one hand, short-term glucocorticoid secretion is related to the adaptive response of animals to stressors and is beneficial, because glucocorticoids facilitate energy mobilization and behavioural changes (Boonstra *et al.* 1998; Wingfield & Romero 1999; Arlettaz *et al.* 2007; Thiel *et al.* 2008). On the other hand, chronically elevated GCM secretion may lead to a pathological status (Munck, Guyre & Holbrook 1984; Stewart 2003) and may reduce both survival and reproductive success (Sapolsky 1992; Möstl & Palme 2002; Arlettaz *et al.* 2007; Ellenberg *et al.* 2007; Thiel *et al.* 2011; Sheriff *et al.* 2012), although no such increases in pathology were found in snowshoe hares *Lepus americanus* (Boonstra 2013b). Boonstra (2013b) discussed the possibility that an environment with high predation risk (elevated GCM levels in animals) leads to a decrease in reproductive success (Sheriff, Krebs & Boonstra 2009), while surviving offspring have higher vigilance and anti-predator behaviour. Thus, hares may make a trade-off between reproduction and survival (Boonstra 2013b). We interpret our results as a first indication of a higher risk of such a shift in mountain hares that are exposed to tourist activities.

STRESS EXPERIMENTS

Our predator challenges increased hares' GCM concentrations up to fourfold compared with baseline. Peaks were reached between 8 and 24 hours after treatment, depending on the individual hare, which is in line with previously reported results for the species (Rehnus, Hackländer & Palme 2009). Interestingly, we observed that the female hares failed to reproduce following our stress experiment, in agreement with the study by Sheriff, Krebs & Boonstra (2009) that found a link between elevated GCM levels and a decline in reproductive output of free-ranging snowshoe hares. We postulate that higher GCM levels during the winter may negatively affect the reproduction of wild mountain hares in the subsequent breeding season.

Under control conditions, hares behaved similarly to those in other studies (Hewson 1962; Lemnell & Lindlöf 1981; Wolfe & Long 2002). However, stress treatments lead to changes in the behaviour of wildlife (Lott & McCoy 1995; Fernandez-Juricic & Telleria 2000; Maréchal *et al.* 2011). Animals exposed to tourist activities tend to move and stay under the canopy (Treves & Brandon 2005). Similarly, during stress periods, our captive hares rested less in open areas (close to shelter resources) and stayed more under the canopy, leading to a reduction in grooming and resting times in open areas. Hares are well equipped to detect approaching predators visually and acoustically and to escape by running, and may therefore flee from predators they can see, with escape more likely than from those that are recognized by scent but unseen (Hewson 1990b). This behaviour reduces energy demands through the avoidance of direct contact with predators. Another way to escape predation is to move into areas of denser cover, although these are associated with a lower quality of food (Hik 1995). Furthermore, visual monitoring of humans (vigilance) and/or spending more time under the canopy may reduce hares' ability to detect predators or other threats.

Mountain hares and other leporids have been observed to re-ingest hard and soft faeces excreted during daytime rest (Hewson 1962; Flux 1970; Pehrson 1983; Hirakawa 1994, 1996; Thulin & Flux 2003). Such activities were significantly decreased after stress simulation in our captive hares. The interruption and prevention of coprophagy is associated with a disturbance in digestion and a higher risk of diarrhoea in domestic rabbits (Proto 1968; Laplace & Lebas 1977). Furthermore, the growth rate of rabbits was reduced when they were denied access to caecotrophes and feed conversion was reduced in comparison with rabbits given access to caecotrophes (Robinson, Cheeke & Patton 1985; Kamphues *et al.* 1986; Robinson *et al.* 1986; Phiny & Kaensombath 2006). Thus, stress events decrease the time hares spend in safe resting positions where they can re-ingest faecal pellets and reduce the energy hares derive from faecal pellets.

We found higher food intake after stress treatments (up to one fifth of the total daily food intake), which must be compensated from available food resources during other times. In our experiments, we provided food ad libitum. However, additional food resources are not always available during winter in the wild (Rehnus *et al.* 2013). Differences between available food and energy demands probably contribute to a reduced body condition of hares in the wild. Malnutrition and low temperatures interact strongly with predation to influence mortality (Keith *et al.* 1984). After predator challenges, we found higher GCM levels than in non-stressed periods, which can also lead to higher energy needs (Baltic *et al.* 2005).

During winter with limited food resources, wild animals minimize energy expenditure by reducing their spatial and temporal activity. The energy saving is disrupted by behavioural changes due to predation threats through movement from resting place to canopy, which can additionally increase energy demands. However, we did not find that the time used for feeding differs between days with and without treatments, as has been described for other species (Lott & McCoy 1995; Fernandez-Juricic & Telleria 2000). We assume that this discrepancy relates to the natural behaviour of hares, which mostly use open fields or grassland when active at night (Tapper & Barnes 1986) to minimize predation risk (Hik 1995).

The observed increase in food intake in captive hares can be explained by the direct energetic costs of flushing and increased GCM levels, as well as by indirect factors such as disruption of re-ingestion and the consequent loss of energy that hares derive from faeces. Such differences cannot be compensated by hares in the wild, which have limited access to additional food resources in winter. In addition, captive hares did not change their behaviour for searching for food to minimize the risk of predation.

MANAGEMENT IMPLICATIONS

The findings of our field study and stress experiments showed that human recreational activities in winter and simulated predator challenges lead to higher GCM levels and behavioural changes in mountain hares. Although further studies are needed, we recommend decreasing the frequency of stress threats for mountain hares, keeping forests inhabited by mountain hares free of tourism infrastructure and retaining undisturbed forest patches within skiing areas. The creation of new skiing areas should be avoided in mountain hare habitats, and existing sites should not be further developed. Regulations in areas where mountain hare habitats overlap with human winter recreational activities should stipulate that tourists stay on the marked trails. In areas with low connectivity to other populations of mountain hare or with low numbers of hares, trails should be closed or relocated to reduce the extent of disturbance. Other species such as black grouse and/or capercaillie are also likely to benefit from such management activities because they share similar habitat requirements with mountain hares.

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