High-quality habitats and refuges from tourism reduce individual stress responses in a forest specialist

Sascha Rösner[A,B,C,]* iD, Dana G. Schabo[C] iD, Rupert Palme[D] iD, Tomáš Lorenc[E,G], Emily Mussard-Forster[B], Roland Brandl[A] and Jörg Müller[B,F] iD

For full list of author affiliations and declarations see end of paper

*Correspondence to:
Sascha Rösner
Department of Biology – Animal Ecology,
Philipps-Universität Marburg,
Karl-von-Frisch-Straße 8, Marburg 35043,
Germany
Email: sascha.roesner@uni-marburg.de,
mail@sascharoesner.de

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ABSTRACT

Context. The assessment of suitable habitat for a species is often evaluated based merely on where the species is most abundant. However, a variety of environmental factors such as temperature, resources and human disturbances might force animals to avoid otherwise high-quality habitats. Additionally, individuals' capacities to cope with such factors – as reflected in physiological stress responses – may also contribute to avoidance. Combining measures of stress response of individual animals with habitat suitability models may contribute essential insights to the development of species conservation plans. **Aims.** We used a landscape-level approach to assess whether habitat quality, abiotic factors and human disturbance affect the physiological stress response of a forest specialist, the capercaillie (*Tetrao urogallus*), and to what extent these relationships are determined by variation between individuals. **Methods.** We applied a non-invasive approach by collecting 1096 droppings across the entire species range in two adjacent national parks spanning the border between the Czech Republic and Germany. We measured faecal corticosterone metabolites (FCMs) to evaluate the physiological stress response. To test the influences of temperature, habitat quality, season and sex, as well as forest management and tourism intensity on FCM levels, we used generalised additive mixed effect models (GAMMs). The same models were applied for a reduced subset of randomly selected samples that were attributed to individuals via DNA profiling using 10 microsatellite loci. This approach allowed us to control for possible individual differences (through repeated measures within individual genotypes). **Key results.** Both models revealed decreasing FCM levels with increasing habitat quality and showed no relationship between increasing forestry intensity and FCMs. When accounting for individual identity, we found a significant positive effect from increasing tourism intensity, although this relationship was not significant in the full dataset. **Conclusions.** Our results highlight three conclusions for the conservation of capercaillie: (1) high-quality habitats reduce stress levels; (2) tourism-free refuge areas are important, and (3) individuality appears to be a strong determinant of response to environmental factors. **Implications.** Generalising management recommendations from observations for single individuals to an entire population may be inappropriate.

Keywords: conservation, faecal corticosterone metabolites, field endocrinology, genotyping, recreation, stress ecology, *Tetrao urogallus*, Tetraonidae.

Introduction

Reproduction, survival and ultimately the distribution of species are mainly driven by the availability and distribution of suitable habitats (e.g. Morris 2003; Griffen and Norelli 2015; Boyce *et al.* 2016). Consequently, ecologists, conservationists and wildlife managers often assess the availability and quality of habitats as a surrogate for evaluating the status of threatened species and communities (van Horne 1983; Johnson 2007; Mosser *et al.* 2009; Grünkorn *et al.* 2014; Immitzer *et al.* 2013; Plummer *et al.* 2020). Potentially suitable habitats are often predicted and evaluated by habitat models (Storch 2002;

Buchanan *et al.* 2011; Teuscher *et al.* 2011) or habitat suitability indices (Jacquin *et al.* 2005; Burgman *et al.* 2001). In fact, estimates of abundance of focal species in a given set of habitats are often used as simple indicators of habitat quality (Morris 2003; Bock and Jones 2004; Johnson 2007; Homyack 2010; Kajtoch *et al.* 2012; but see Adamik 2005), based on the assumption that under an 'ideal free distribution' (see Fretwell and Lucas 1970), free-ranging animals actively select habitats of high quality and avoid habitats of low quality (Morris 2003; Johnson 2007).

Several studies have shown that abundance measures alone might be a misleading indicator for habitat quality (van Horne 1983; Mosser *et al.* 2009) because a variety of abiotic and biotic factors may decouple the positive abundance–habitat quality relationship (see van Horne 1983). There is evidence that individuals even aggregate in poor habitats if competition, predation risk or parasitism rates are high in resource-rich, high-quality habitats (Stanko *et al.* 2006; Johnson 2007; Mosser *et al.* 2009; Kajtoch *et al.* 2012; Seibold *et al.* 2013). Moreover, human disturbance can alter the spatial activity and distribution of a species (Harju *et al.* 2011; Meager *et al.* 2012) and can lead to displacement of vertebrates from their core activity areas (Borkowski *et al.* 2006; Coleman *et al.* 2003). Such a pattern was found for capercaillie, where the start of the snow sport season significantly affected their behaviour, with increased flushing distances observed in both sexes (Thiel *et al.* 2007). In addition, human activity affects the spatial distribution of capercaillie, leads to decreased activity-range sizes and forces birds to aggregate in higher abundances outside their original activity areas (Thiel *et al.* 2008; Mollet and Thiel 2009).

Consequently, direct measures of species fitness and performance – for example, in terms of body condition – should be part of habitat quality assessments to draw sound conclusions for conservation management of focal species (Johnson 2007; Griesser *et al.* 2007; Mosser *et al.* 2009). However, assessing appropriate fitness parameters on large spatial scales remains challenging. The assessment of physiological stress responses is a promising proxy for an individual's condition as it mirrors the individual's reaction to environmental factors (Sheriff *et al.* 2011; Dickens and Romero 2013). Multiple studies have described such stress responses in both domestic livestock and wildlife as a consequence of environmental changes; for example, medical treatment, translocation of individuals or the presence of predators (Scheuerlein *et al.* 2001; Acevedo-Whitehouse and Duffus 2009; Angelier and Wingfield 2013). In these studies, the physiological stress response was assessed by measuring glucocorticoid metabolite concentrations (Möstl and Palme 2002; Palme 2019). Glucocorticoids are among the front-line hormones by which animals respond to stressful situations and are closely linked to adrenocortical activity (Möstl and Palme 2002). In general, maintaining high glucocorticoid levels is energetically costly and thus influences other physiological processes, impacting overall performance, survival or reproduction (Walker *et al.* 2005; Johnson 2007; Goutte *et al.* 2011). A range of approaches have been used to integrate physiological stress response measures to acquire direct measures of an individual's condition in relation to environmental factors and human impact (i.e. field endocrinology, conservation physiology, see Wikelski and Cooke 2006; Thiel *et al.* 2008; Homyack 2010; Coppes *et al.* 2018; Palme 2019), with the aim of rapidly assessing the conservation status of focal species and supporting management decisions (Wikelski and Cooke 2006; Homyack 2010; Sheriff *et al.* 2011; Rehnus *et al.* 2014).

In this context, non-invasive measures of the physiological stress response (e.g. of faecal corticosterone metabolites; FCMs), are especially valuable for elusive and endangered species (Homyack 2010; Sheriff *et al.* 2011). Thus, evaluating adrenocortical activity of a species is a promising approach to improve classic measures of habitat quality using mere abundance data.

Endocrine responses to different stressors show high inter-individual variability, owing to phenotypic plasticity, sex, life history or habituation of individuals to stressors (Dickens and Romero 2013; Blas 2015). Individual differences in coping with stress have been associated with distinct behavioural traits known as animal personalities (Carere *et al.* 2010; Wolf and Weissing 2012; Merrick and Koprowski 2017). Such behavioural traits include, for instance, explorative behaviour (i.e. resource use; Fidler 2011; Serrano-Davies *et al.* 2017), activity/space use (Hawkes 2009) or habitat selection (Merrick and Koprowski 2017) and have been linked with individual fitness (Sih *et al.* 2004) and demographic parameters (Anthony and Blumstein 2000). When using faecal samples to assess stress responses in a species (Anthony and Blumstein 2000), it is important to avoid pseudo-replication of measurements – and thus biased conclusions – by unknowingly treating several samples from the same individual as being from separate individuals (Biro and Dingemanse 2009; Biro 2013). Individual identification via DNA profiling from faecal samples used for FCM analysis is one way to avoid such pseudo-replication.

In this study, we combined landscape-level field sampling with an endocrinological approach in two adjacent national parks, Šumava National Park (Czech Republic) and the Bavarian Forest National Park (Germany), to evaluate the impact of habitat quality, abiotic factors, human disturbance and variation between individuals on the physiological stress response of the endangered Western capercaillie (*Tetrao urogallus*). The capercaillie is highly sensitive to human disturbances. It is a forest specialist umbrella species for highly structured forest ecosystems (Storch 2002). Previous work developed habitat suitability models for different regions across the species' distributional range (see Braunisch and Suchant 2007; including our study area; Teuscher *et al.* 2011), as well as baseline information and techniques to

measure physiological stress responses in terms of FCM levels (see Thiel *et al.* 2005). Consequently, the capercaillie is an ideal model species for applying field endocrinology to advance models of habitat suitability. Here, we tested the relationship between (1) habitat quality derived from a habitat suitability model developed in the study area (Teuscher *et al.* 2011, 2013), (2) abiotic and individual factors affecting species performance (e.g. minimum daily temperature, season, sex) (Thiel *et al.* 2005; Coppes *et al.* 2018) and (3) the intensity of forestry (e.g. Klaus 1991; Wasser *et al.* 1997) and tourism activities (Thiel *et al.* 2007, 2008, 2011; Coppes *et al.* 2017) to measures of FCMs obtained from droppings non-invasively collected in the field. We repeated the analyses for a random subset of samples that were DNA-profiled (using microsatellite genotyping) to identify individuals, enabling us to account for possible effects of differences between individuals on the above-mentioned relationships.

Specifically, we tested the following hypotheses: (1) Capercaillie exhibit decreased FCM levels with increasing habitat suitability; (2) Capercaillie exhibit higher FCM levels at low temperatures – that is, under harsh conditions – and males show higher levels than females, (3) Capercaillie respond with increased FCM levels to both increasing forestry and tourism activity and (4) the above patterns are affected by individual differences.

Material and methods

Study area

Our study was conducted in a Central European low mountain range located in the tri-national borderland of Austria, Czech Republic, and Germany (ca. 119 000 ha, Fig. 1). This area – the Bohemian Forest – comprises one of the largest
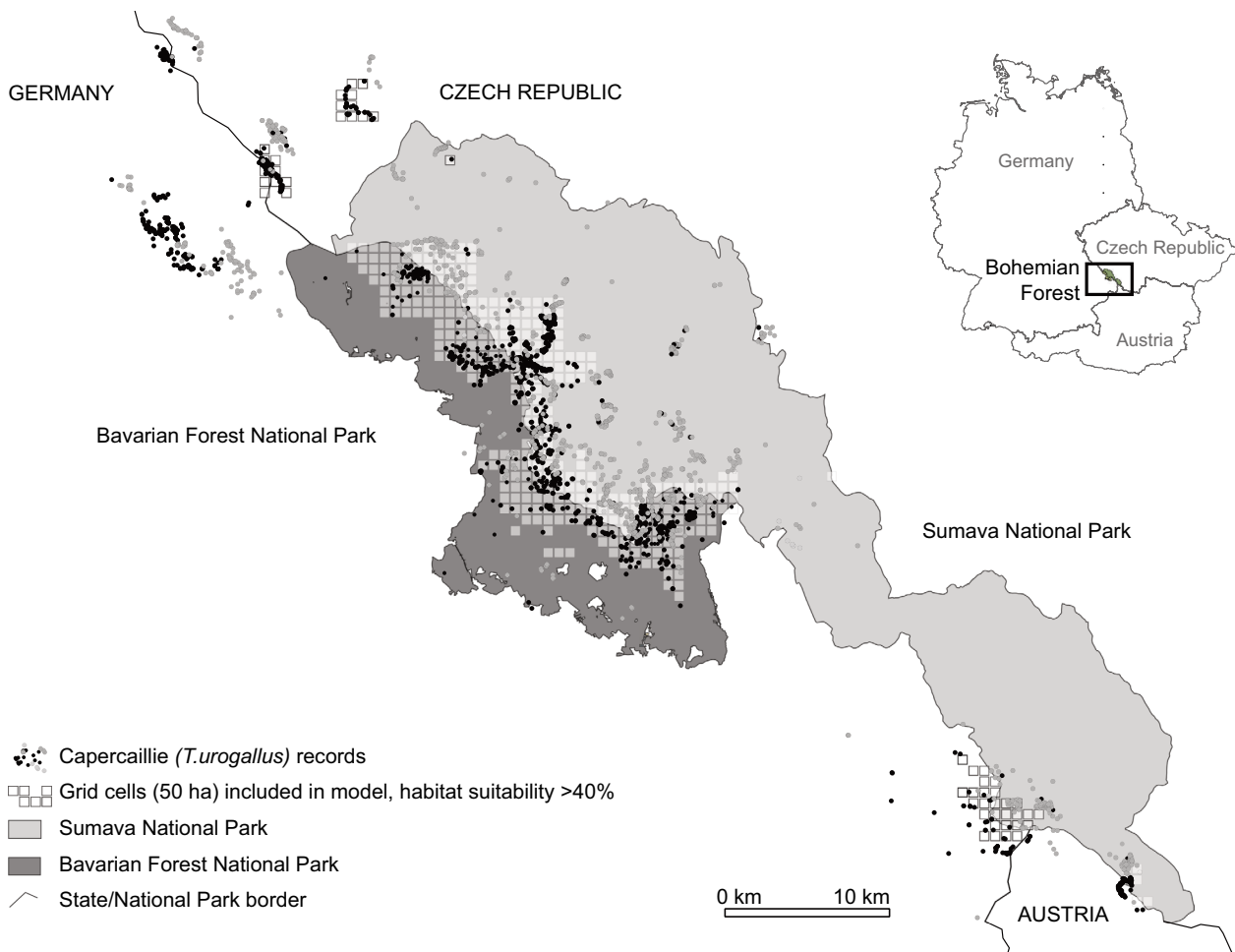

Fig. 1. Map of the study area covering Šumava National Park (Czech Republic, light grey) and Bavarian Forest National Park (Germany, dark grey) and adjacent landscape protection areas. Points indicate the distribution of all capercaillie (*Tetrao urogallus*) samples between 2006 and 2017. Grid cells (*N* = 348; 50 ha) indicated capercaillie habitats with suitability values >40% in correspondence to the habitat model by Teuscher *et al.* (2011).

protected forest systems in Central Europe (93 410 ha) and includes the Bavarian Forest National Park (24 368 ha, Germany, 49°00′N 12°40′E), Šumava National Park (69 039 ha, Czech Republic, 49°06′45″N 13°08′09″E) and the adjacent protected landscape areas of Austria, Czech Republic, and Germany (Fig. 1). Elevations range from 650 m to 1420 m a.s.l. (Bässler *et al.* 2009). The local climate is characterised by mean annual temperatures ranging from 3.8°C to 8.4°C and average annual rainfall between 1295 mm and 1771 mm (Bässler 2004). At low elevations, snow cover is present about 100 days per year and at high elevations for up to 200 days per year (Heurich and Neufanger 2005).

The montane forests are naturally dominated by Norway Spruce (*Picea abies*), interspersed with European Beech (*Fagus sylvatica*) and Mountain Ash (*Sorbus aucuparia*; (Walentowski *et al.* 2004). The ridge of the mountain massif (approx. 90 km in length) comprises large swathes of standing and fallen dead wood of Norway Spruce caused by multiple wind throws and repeated outbreaks of the spruce bark beetle (*Ips typographus*) over the last 20 years (Lehnert *et al.* 2013; Beudert *et al.* 2015; Thorn *et al.* 2016). Large patches are today covered with young spruce re-growth of different successional stages (Teuscher *et al.* 2011; Lehnert *et al.* 2013).

Both, private and state foresters on both sides of the border carry out forestry activities in the region. Forestry practices – including bark beetle mitigation activities – differ on either side of the border due to historical and political differences as well as diverse management policies and forest structures (Teuscher *et al.* 2011; Thorn *et al.* 2016). Within the protected areas of both national parks, forestry is generally limited to respective state authorities. Due to the bark beetle outbreaks of recent decades (see Müller and Job 2009; Lehnert *et al.* 2013), mitigation practices (see e.g. Thorn *et al.* 2016) have been implemented to protect private forests bordering the parks. Management includes selective and/or clear-cutting of infected trees and debarkation (Thorn *et al.* 2016) by means of forestry machinery such as harvesters and forwarders.

Tourism is an important economic sector for the surrounding region of the study area (Job *et al.* 2008). Tourist activities inside the national parks and surrounding protected landscape areas mainly comprise of hiking, biking, as well as alpine and cross-country skiing and snowshoeing. The fall of the 'Iron Curtain' and the subsequent establishment of transboundary tourist trails resulted in a boost of touristic activities particularly in the core area of the two national parks, and hence in the focal species' distribution range (see Job *et al.* 2008; Teuscher *et al.* 2011; Rösner *et al.* 2014a). The Bavarian Forest National Park area counted about 1 100 000 tourists in 2019 (Bayerisches Landesamt für Statistik 2020) and the Šumava National Park between 1 100 000 and 1 300 000 annual visitors (Trebicky and Čihař 2006).

Focal species and local population

The western capercaillie (*T. urogallus*, L. 1758) is a forest-dwelling grouse species inhabiting coniferous and mixed coniferous-deciduous forests from Scandinavia to eastern Siberia (del Hoyo *et al.* 1994; Glutz von Blotzheim *et al.* 1994; Storch 2001; Mikoláš *et al.* 2017). It is the world's largest grouse species and exhibits strong sexual dimorphism, with males weighing around twice as much as females (males, 3300–4300 g vs females 1440–1500 g; de Juana and Kirwan 2019). Capercaillie exhibit strong territoriality, with males defending their lek sites during the mating season. Strong individual differences in mating behaviour are well known in the species (Wegge and Larsen 1987; Storch 1997; Wegge *et al.* 2003). Mating starts at the end of March. Whereas individuals are solitary during spring and summer, they form flocks of 2–10 individuals from late autumn throughout winter (Bauer *et al.* 2005).

In central Europe, the core area of the species distribution is restricted to the European Alps (Storch 2001; Storch 2007). Only a few small populations persist in low mountain ranges with elevations above 900 m a.s.l. (e.g. Vosges and Fichtel Mountains; Storch 2001; Mollet *et al.* 2003). In central Europe only the Black Forest (Storch 2001; Storch 2007) and Bohemian Forest (Rösner *et al.* 2014b) populations are known to exceed the minimum viable population size of 470 individuals (Grimm and Storch 2000); in accordance to the species-specific stochastic population model with an extinction risk below 1% in 100 years following (Grimm and Storch 2000). Almost 40 years ago, the Bohemian Forest population had severely declined to only around 100 birds as recorded in 1985 (Scherzinger 2003; Rösner *et al.* 2014b). Authorities then established breeding and release programs to supplement the local population (Scherzinger 2003; Rösner *et al.* 2014b). In previous studies, we DNA-profiled (using microsatellite genotyping) to identify and count individual from droppings and used multiple density estimators to calculate population sizes and estimated the current population at approximately 500–600 birds in the study area (Rösner *et al.* 2014b; Becka and Rösner 2019).

The capercaillie is considered an umbrella species for forest-dwelling avifauna (Suter *et al.* 2002; Pakkala *et al.* 2003) because it mainly inhabits natural coniferous forests (Storch 2001; Segelbacher and Piertney 2007, but see Alda *et al.* 2013) with specific space and habitat requirements and is highly sensitive to disturbance (Storch 2002). As such, it is among the focal species under conservation management by the authorities of both national parks. Most importantly for our non-invasive hormone measurement approach, an enzyme immunoassay (*EIA*) previously developed for chickens (Rettenbacher *et al.* 2004) has been successfully validated for our focal species, including the species-specific laboratory procedure for measuring FCM concentrations (Thiel *et al.* 2005; Palme 2019).

Data collection and field work

In a citizen science approach, a team of around 70 volunteers (hunters, wildlife enthusiasts, ornithologists, rangers, students, laypersons etc.) collected capercaillie droppings at the landscape level. After volunteer recruitment, we trained all participants via seminars, workshops, and field training sessions to guarantee reliable data collection. For systematic fieldwork, we adopted a previously established grid system with 50-ha cells used for forest inventories, development of habitat models and other fieldwork in the national parks (Teuscher *et al.* 2011; Teuscher *et al.* 2013). The 50-ha grid system matched both the scale of average activity ranges of the focal species (550 ha, see Storch 1995) and the spatial resolution needed for management implementation at the landscape level in both national parks (see Teuscher *et al.* 2011).

Collection of droppings

DNA quality and FCM levels in droppings are strongly affected by storage temperature and age (Thiel *et al.* 2005; Murphy *et al.* 2007). Thus, we mainly collected droppings during the cold season when samples were preserved on snow. Samples collected during snow-free periods were only used if they were very fresh and wet with a high probability of having originated that same day. Samples were collected in two field campaigns: campaign 1 from October 2009 to May 2010 (with late snow at high elevations in May of that year) and campaign 2 from October 2010 to April 2011. Dropping collection took place in the known distribution of the capercaillie in the study area, roughly above 800 m a.s.l. (Teuscher *et al.* 2011). The search area covered 358 grid cells and approximately 22 000 ha (Rösner *et al.* 2014*a*). Each grid cell was searched at least twice. Parallel transects of around 10 m distance were walked with a team of volunteers recording all fresh droppings (2–3 days after fresh snowfall in winter and wet droppings in summer). Fresh dropping samples were kept cool during fieldwork until further processing in the lab following best practice guidelines established previously (Thiel *et al.* 2005). Samples were frozen at −20°C at the end of each day's fieldwork. Known lek sites were only visited once between March and April to avoid pseudo-replication and minimise disturbance (compare Thiel *et al.* 2008). Groups of droppings were collected when there was little doubt that they originated from a single capercaillie; for example, when they were situated around single feeding places or alongside individual tracks on fresh snow (see Thiel *et al.* 2008; Rösner *et al.* 2014*b*). Hence, our 'samples' consisted of one to a maximum of around seven droppings from a presumed single bird. Each sample was labelled with an individual identifier number (ID), GPS information, date and time. To cover important stages in the species breeding ecology, samples were categorised into two seasons, winter (15 October–15 April, after breeding and before mating) or summer (16 April–14 October, mating and breeding season), for further analyses.

In total, within a period of 14 months, our team of volunteers collected droppings across 252 different 50-ha cells covering elevations from 747 m to 1423 m a.s.l. The records were distributed across almost the entire study area and included 1439 samples (Fig. 2). Some samples missing location data were excluded from the data set, resulting in $n = 1096$ samples for further analyses.

FCM analysis

For analysis of FCM levels, we used one fresh dropping per sample ($n = 1096$). Further processing followed Thiel *et al.* (2005). In short, we used 0.5 g of fresh dropping material, which was extracted with 5 mL of 60% methanol (Thiel *et al.* 2005, 2011) before an aliquot was analysed in a cortisone enzyme immunoassay (Rettenbacher *et al.* 2004; see Thiel *et al.* 2005 for details). Extraction and analysis of FCM were performed at the University of Veterinary Medicine, Vienna, Austria. Concentration measures were provided in nanograms FCMs per gram of fresh dropping weight [$ng \times g^{-1}$].

Genotyping

To identify individuals from the dropping and thus control for possible inter-individual differences in response to potential stress drivers, we DNA-profiled a random subset of 550 samples using 10 microsatellite loci. We aimed for equal sex representation (275 from each) in the subset based on dropping diameter measured in the field (Thiel *et al.* 2008). Furthermore, we sampled at least one dropping from each of the 252 sampled grids to ensure sampling across the entire study area. For DNA-profiling, we extracted DNA from fresh droppings using the QIAamp Stool Kit (Qiagen) with a modified extraction protocol based on Jacob *et al.* (2009). Extracted DNA was purified by repeated washing and removing polymerase chain reaction (PCR) inhibitors (InhibitEX and specific buffers, Qiagen). Samples were genotyped at 10 microsatellite loci designed for capercaillie using the established primer pairs TUD1, TUD3, TUD5, TUD6, TUD7, TUT2, TUT3, and TUT4 (Segelbacher *et al.* 2000) and BG15 and BG18 (Piertney and Höglund 2001). DNA was amplified by polymerase chain reaction (PCR) following the published multiplex protocol by Jacob *et al.* (2009) and run on an ABI 3730 Sequencer (Applied Biosystems). Allele scorings were done using GeneMapper v. 4.0 (Applied Biosystems). We used Micro-Checker software (van Oosterhout *et al.* 2004) to detect null alleles. Further, we used PEDANT ver. 1.0 (Johnson and Haydon 2006) to estimate the rate of genotyping error per allele due to allelic dropout and false alleles.

Samples were only retained in the analysis if allele scoring was consistent over three consecutive runs of one single dropping sample at a minimum of nine loci. This means
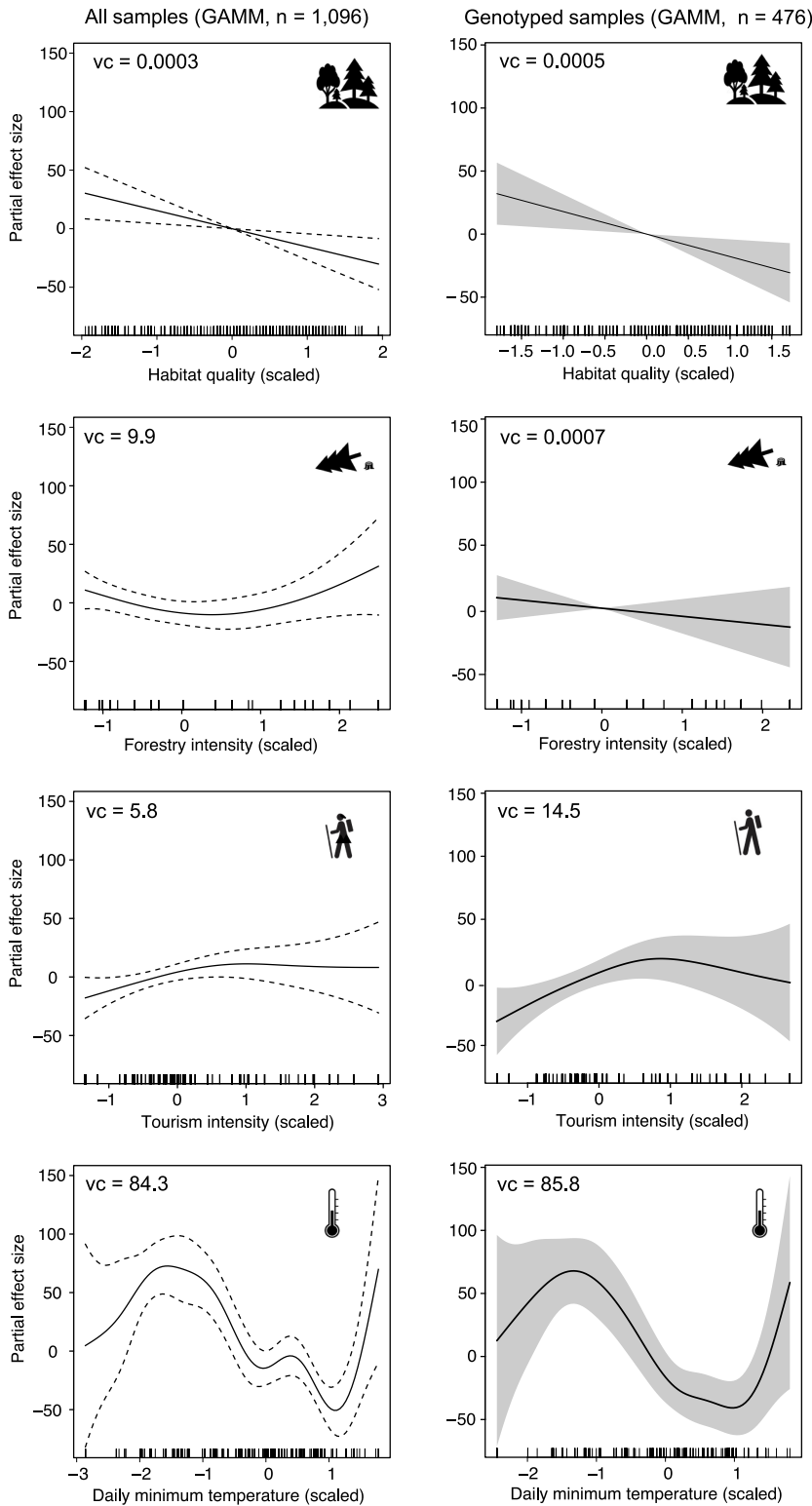
Fig. 2. Partial effect plots showing results from GAMM models relating faecal corticosterone metabolite (FCM) levels (ng/g dropping) as a function of the environmental predictor variables with smoothed terms for habitat quality, forestry intensity, tourism activity and daily minimum temperature. Variance components associated with each smoothed term are shown in the upper left corner of the boxes. The left column shows the GAMM model for $n = 1096$ samples and grid cell as random effect; the right column shows results of the model with a subset of $n = 476$ samples of genotyped individuals with grid cell and genotype as random effects. Dashed lines (left) and grey areas (right) indicate the 95% confidence intervals conditional on the estimated smoothed parameters of the model. Estimated variance components (vc) are depicted for each smoothed term.

that samples where more than one allele repeatedly failed to amplify (allelic dropouts) were excluded. To estimate the 'probability of identity' (PID), we calculated the average probability of two individuals sharing the same multilocus genotype (Lacy and Sherman 1983) using GenAlEx v. 6.4 (Peakall and Smouse 2006). Results revealed a PID of $P = 5.5 \times 10^{-9}$. Hence, we assumed each genotype represented an individual bird (see Rösner *et al.* 2014b).

This approach resulted in 476 genotyped samples, covering 195 unique multilocus genotypes; hereafter 'individuals'.

Sex identification

To verify the field-assigned sex for the subset of 195 individuals revealed by multilocus genotyping, one sample per individual was analysed using chromosome-specific markers (P2 and P8) following published protocols (Griffiths et al. 1998). PCR amplifications were run twice for each sample (for laboratory details see Rösner et al. 2014b). This revealed $n = 163$ female and $n = 32$ male individuals in the subset and allowed us to test the accuracy of sex assignments in the field for all successfully genotyped samples ($n = 476$) using accuracy tests (R package rfUtilities, ver. 2.1.5). The overall accuracy field-assigned sex was 87% ($n = 476$).

Human disturbance: forestry and tourism intensity

We assessed human disturbance in terms of forestry (i.e. bark beetle mitigation) and touristic activity (i.e. intensity of human presence; tourism) per grid cell across the entire study area in the years 2009 and 2010, coinciding with the time of fieldwork for the sampling of droppings. We provided topographic enquiry maps (1:25.000) corresponding to management units used in forestry and national park administrations to rangers, foresters, hunters and other local experts. We asked three to five participants per grid cell to evaluate the level of intensity for the two disturbance types on a four-level scale: 0 – zero intensity of forestry or tourism activities in the cell, 1 – low intensity of forestry or tourism activities, 2 – mid-level intensity of forestry or tourism activities, and 3 – intense forestry or tourism activities. Forestry activities, e.g. logging in the context of bark beetle mitigation activities, were evaluated as one estimate per grid cell per person, thereby evaluating the intensity of forestry across the last 5 years. Summer and winter tourism were evaluated separately and afterwards summed to retrieve a year-round assessment with values from 0 to 6 for the analysis. Multiple intensity scores for the same grid-cell as provided by at least three different people (see above) were later averaged resulting in a single score (see also Rösner et al. 2014a). All data were entered and mapped using ArcGIS v. 9.2.3 (ESRI, Redlands, Ca. USA).

Habitat suitability

In a previous study, we established a habitat suitability model for the capercaillie for the entire region, based on abundance data. In short, elevation a.s.l., lying deadwood, clear cut areas and a certain amount of young coniferous stands were identified to be key factors determining habitat suitability (for details, see Teuscher et al. 2011, 2013). Habitat

suitability values (0–100%) were extracted from Teuscher et al. (2011) for each grid cell of the established 50 ha grid in this study.

Climatic conditions

It is known that temperature is a decisive factor for the distribution of capercaillie (Teuscher et al. 2011, 2013). To obtain temperature values, we assigned each grid cell to the nearest of three climate stations maintained by the National Park administration of the Bavarian Forest and assigned the daily minimum temperature in °C of the date of sampling to the grid. Values were corrected for elevation a.s.l. of the according grid cell with 0.6°C difference per 100 m difference in elevation.

Data analysis

The response of FCM levels to habitat, abiotic, sex and human disturbance was analysed using generalised additive mixed models (GAMM) with thin plate regression splines. We included habitat quality, daily minimum temperature, intensity of forestry, intensity of tourism, sex, season (winter vs summer) as well as sampling campaign (campaign 2, campaign 1) as model predictors (Table 1). We did two separate analyses, one for the entire dataset of all samples ($n = 1096$) and one for the subset representing known individuals ($n = 476$); that is, treating multiple samples from the same individuals as repeated measures. In both models, habitat quality, forestry intensity, tourism intensity and daily minimum temperature at time of sampling were added as smooth terms (see Table 1), and sex, season, and sampling campaign as parametric predictors. In the model for the dataset of all samples, grid cell was included as random effect. In the model for the dataset of 476 genotyped samples, grid cell and genotype were included as random effect. Continuous predictors were scaled to zero mean and unit variance. Variance components were calculated for the predictors (smoothed terms). Model calculations and extraction of variance components of the smoothed terms (function gam.vcomp) were performed with GAMM4 ver. 0.2–5 (Wood and Scheipl 2017) and R ver. 3.6.0 (R Core Team 2019).

Results

Physiological stress response

Across all samples ($n = 1096$), mean FCM levels were 149 ng × g^{-1} ± 125 ng × g^{-1} dropping (hereafter mean in ng × g^{-1} ± s.d. in ng × g^{-1}; range; range: min 3.0 – max. 1640). FCM levels decreased with increasing habitat quality for both the model with all samples as well as the model with genotyped individuals only (Table 2, Fig. 2). The

Table 1. List and description of the response variable (FCMs, in italics) and predictor variables used in Generalised Additive Mixed Models (GAMM) in capercaillie (*Tetrao urogallus*).

	Variable	Description	Unit	Range	Mean ± s.d.	Data structure
FCMs	*Stress load*	*Physiological stress response*	*ng/g (faeces)*	*3–1640*	*149.0 ± 124.5*	*Continuous*
Habitat	Habitat suitability	Region-specific habitat suitability derived from Teuscher *et al.* (2011), resolution: 50 ha grid cells	%	0.0–1.0	0.50 ± 0.23	Continuous
Raster grid	Raster ID	Name of 50 ha raster cells	−	n.a.	n.a.	Categorial
Human disturbance	Forestry intensity	From 0 (zero intensity) to 3 (high intensity) per grid cell	−	0.0–3.0	0.99 ± 0.81	Continuous
	Tourism intensity	From 0 (zero intensity) to 6 (high intensity) per grid cell	−	0.0–6.0	1.88 ± 1.41	Continuous
Climate	Minimum temperature	Daily minimum temperature on the day of dropping collection derived from nearest climatic station and corrected for elevation	°C	−14.0 − +7.7°C	−0.67°C ± 4.69	Continuous
	Season	Summer (16. April − 15. October) or winter (16. October − 15. April)	−	Summer/winter	n.a.	Categorical
	Field campaign	First or second field campaign of data sampling (cold season 2009/2010 and 2010/2011)	−	First, second	n.a.	Categorical
Individual	Genotype	Genotype specifying true individuals in reduced dataset (n = 476)		1.0–1096	n.a.	Categorical
	Estimated sex	Sex of the individual, m = male, f = female, estimated through relative dropping size for dataset of dropping samples		f, m	n.a.	Categorical
	Genetic sex	Sex of the individual, m = male, f = female, determined by sex specific chromosome markers for dataset of genotyped individuals		f, m	n.a.	Categorical

estimated proportion of the total variability attributed to habitat quality was relatively low (<1%) in both models (Fig. 2). We further found a phase pattern with highest physiological stress response at low temperatures as well as at high minimum daily temperatures in both models (Table 2, Fig. 2). The estimated variance component for temperature explained most of the total variability (>84%) in both models (Fig. 2). FCM levels were significantly lower during winter (144 112) than during summer (234 ± 257) and lower during the second field campaign (142 ± 101) than during the first (155 ± 140) in both models (Table 2). Male individuals showed a significantly higher FCM level (157 ± 131) than female individuals (130 ± 106).

FCM levels showed no clear relationship with forestry intensity in either the model with all samples (n = 1096; estimated variance component 9.9%) or the model with genotyped samples; that is, including individual as a random effect (n = 476, estimated variance component <1%, Table 2, Fig. 2). In the full model, tourism intensity was also not associated with FCM levels (estimated variance component 5.8%, Table 2, Fig. 2). However, using individual as a random effect, we found a significant increase in FCM levels with increasing tourism intensity (Fig. 2). Here the estimated variance component explained 14.5% of the total variability (Fig. 2).

Discussion

Our landscape-level approach revealed the lowest FCM levels of capercaillie in high-quality habitat. Further, FCM concentrations were highest both at low minimum daily temperatures as well as at high minimum daily temperatures and were significantly lower during winter than during summer. Males showed higher FCM levels than females. We did not find a relationship between forestry intensity and FCMs. However, we found a positive association between FCM levels of individuals and increasing tourism intensity.

Sex

Concurring with our expectations, male capercaillie had higher FCM levels than females. These findings are in line with previous work on capercaillie (Thiel *et al.* 2008; Coppes *et al.* 2018) as well as on other vertebrate species, including birds (Weingrill *et al.* 2004; Palme 2019). Such patterns most probably reflect sex-specific differences in behaviour and physiology, e.g. enhanced competition between territorial males during the breeding season (Moss *et al.* 2008; Thiel *et al.* 2011). In line with this, the seasonal pattern with higher FCM levels in summer than in winter is probably also linked to the start of the mating season in April in the study area. During this time, capercaillie males

Table 2. Generalised additive mixed model results explaining faecal corticosterone metabolite (FCM) levels.

Model with all samples					Model with genotyped individuals				
Sample size		n = 1096					n = 476		
	Estimate	s.e.	t value	P-value		Estimate	s.e.	t value	P-value
Intercept	320.1	18.34	12.54	<0.0001***	Intercept	238	24.1	9.85	<0.0001***
Season (winter)	−96.7	18.5	−5.20	<0.0001***	Season (winter)	−97.4	23.2	−4.20	<0.0001***
Sex (estimated, male)	29.1	7.90	3.70	<0.001***	Sex (estimated, male)	24.8	13.0	1.91	0.0565
Sampling campaign (year)	−24.8	9.70	−2.60	<0.05*	Sampling campaign (year)	−21.1	13.9	−1.52	0.1295
Approx. sign. of smooth terms:	Ed.f.	Ref.d.f.	F	P-value		Ed.f.	Ref.d.f.	F	P-value
s(scale(Habitat quality))	1.00	1.00	7.68	0.006**	s(scale(Habitat quality))	1.00	1.00	6.80	0.0094**
s(scale(Forestry intensity))	2.23	2.23	1.82	0.131	s(scale(Forestry intensity))	1.00	1.00	0.88	0.350
s(scale(Tourism intensity))	1.92	1.92	1.87	0.111	s(scale(Tourism intensity))	2.21	2.21	2.80	0.048*
s(scale(daily minimum temperature))	6.68	6.68	11.0	<.0001***	s(scale(daily minimum temperature))	4.78	4.78	7.86	<.0001***
R-sq.(adj) = 0.14					R-sq.(adj) = 0.18				
lmer.REML = 13.50					lmer.REML = 5.84				
Scale est. = 12.47					Scale est. = 12.2				
n = 1096					n = 476				

Left: Model covering all n = 1096 samples and grid cell as random effect. Right: Model with n = 476 genotyped individuals and grid cell and genotype as random effects. Predictors and their explanations are given in Table 1.
lmer.REML, restricted maximum likelihood of the linear mixed effect model with random effect (lmer).

are generally more stressed given that they vigorously defend their territories at lek sites and display intensively to attract females (Klaus *et al.* 1989).

Temperature and season

The highest stress response in our study was found in cold temperatures as well as at lowest minimum daily temperatures (late winter, early spring). This is consistent with previous work showing that during periods of low temperatures, capercaillie feed on conifer needles, which represent a low-caloric energy source (Linden 1984; Andreev 1991; Klaus *et al.* 1989; Lindsay *et al.* 2020). With limited daylight hours during this period of the year, it is difficult to acquire enough energy to maintain a good body condition. Consequently, overall activity is usually reduced (Storch 1993). During such harsh periods of the year the metabolic rate needs to increase to initiate foraging and to mobilise energy stores – processes which include elevated corticosterone levels, resulting in the high FCM levels also found here (Harvey *et al.* 1984; Astheimer *et al.* 1995; but see Wingfield *et al.* 1995). High FCM levels at high minimum daily temperatures in late April again correspond to the beginning of the mating season during which capercaillie are generally more stressed, particularly males (Klaus *et al.* 1989).

Habitat quality

We found that habitat quality is not only an important predictor of distribution and abundance of capercaillie (Teuscher *et al.* 2011), but is also of major importance for stress responses, with lower stress responses found in high-quality habitats. This concurs with previous work showing that capercaillie prefer undisturbed forest areas associated with lower FCM levels (Thiel *et al.* 2011). Such large and undisturbed forest areas provide young spruce re-growth of different successional stages (Teuscher *et al.* 2011) as well as high food availability in terms of Bilberry *Vaccinium myrtillus* and other important and nutrient-rich food sources. Thus, high-quality habitat provides optimal conditions for animal fitness and is thus important for population health at the landscape scale. However, according to our results, disturbance from human activities should be incorporated into habitat suitability models in the future.

Human disturbance

We found higher tourism intensity invokes a stronger physiological stress response of capercaillie. This adds to previous work showing that tourism activities reduce the frequency of occurrence (Rösner *et al.* 2014a), have an impact on habitat use (Coppes *et al.* 2017) and particularly in winter evoke a physiological stress response in capercaillie (Thiel *et al.* 2008, 2011). Given that tourism activities reduce the local occurrence of capercaillie (Rösner *et al.* 2014a) and effectively reduce their habitat (Coppes *et al.* 2017), general habituation in capercaillie seems unlikely (Powell 2013). Nevertheless, it has been shown that capercaillie individuals differ considerably in their physiological response

to human disturbances measured as recreational infrastructure densities with elevated FCM levels at the home range scale (Coppes *et al.* 2018). The present study supports these findings based on findings from an entire, unfragmented landscape scale.

Individual tolerance of human presence or even individual habituation to human activities has been shown in several bird species (Arlettaz *et al.* 2007; Kitchen *et al.* 2011; Gaudet and Somers 2014). Such differences in coping with stress have been linked to distinct behavioural traits such as breeding performance (Bókony *et al.* 2009) and individual personalities (Carere *et al.* 2010; Wolf and Weissing 2012; Merrick and Koprowski 2017). Our study also indicates such a difference in individual susceptibility of birds to tourism: the effect that an increased tourism intensity evokes stronger stress response was detectable only when controlling for individuals (see Fig. 2). Repeated measures of single, well-habituated individuals may have blurred this negative effect of tourism in the model for the total sample set. This idea is supported by data from a repeatedly 're-sampled' capercaillie cock whose droppings were found only in an area of very high human intensity (a highly frequented trail close to a mountain peak with a mountain hut) and showed relatively low FCM levels. Further, this entire area (covering almost 450 ha) was not used by other capercaillie (no other individuals' droppings were found in this area; see Rösner *et al.* 2014a). Measuring the stress response of the same individuals at different timepoints can provide important information for assessing the response of wildlife to environmental and human disturbances. Thus, assessing the reproductive status of potentially habituated individuals within the population would be a pivotal future step towards assessing the potential long-term consequences of tourism for the status of the species.

Besides direct negative effects of human presence and activities, such as disturbance through noise (Francis and Barber 2013), indirect effects might also contribute to higher physiological stress responses of capercaillie. The presence of trails and changes in vegetation structure through tourism activity may alter the detectability of approaching predators and thus predation pressure (Borkowski *et al.* 2006; Dowd 2010), which is among the key factors determining FCM levels (Thiel *et al.* 2011). Predation pressure may be higher close to trails (Dowd 2010), and thus, tourism activities may alter the 'landscape of fear' (see Laundré *et al.* 2010). Potential fitness and reproductive consequences are unknown. However, elevated physiological stress response to tourism may lead to reduced fitness as even stress-tolerant birds show lower reproductive rates (Strasser and Heath 2013). Ultimately, this may also lead to an avoidance of high-quality habitat (Coppes *et al.* 2017; Rösner *et al.* 2014a). Thus, tourism activities appear to be an important factor when assessing species distribution and population health on a landscape scale.

Contrary to our prediction, the birds in our study did not show elevated FCM levels in response to higher forestry intensity. This contrasts with previous studies demonstrating a physiological stress response to forestry activities in other prominent species such as male Northern Spotted Owls (*Strix occidentalis caurina*) (Wasser *et al.* 1997). Given that our study area is predominantly in national parks and landscape protection areas, forestry activities in our study area include only short-term interventions such as mitigation of bark-beetle outbreaks (bordering private forests or in designated development areas) or in the case of wind throws. This causes short-term moderate disturbance, which may be more tolerable than period-wise high-intensity forestry in private or commercial forests. Moreover, the natural small-scale disturbances caused by bark beetles open up habitat in dense spruce stands of the Bohemian Forest and thus create highly structured habitat suitable for capercaillie, which may counteract the potential negative effect of human disturbance (Storch 2001).

Conclusions

Taken together, our findings add to previous work showing that environmental conditions such as habitat quality, temperature and season, as well sex of individuals are determining factors in the physiological stress response in capercaillie. Moreover, accounting for individual differences in the stress response at the landscape level revealed that human impact in terms of tourism intensity elevated FCMs of this highly sensitive forest specialist. These findings highlight that beyond solely focusing on undisturbed and high-quality refuge areas, species conservation management should consider differences among individuals across the population (identified by DNA profiling of droppings as done here), when making management recommendations. This is particularly important because generalising from observations of single animals to entire populations – as is often done in conservation practice – may be inappropriate.

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Author affiliations

[A]Department of Biology – Animal Ecology, Philipps-Universität Marburg, Karl-von-Frisch-Straße 8, Marburg 35043, Germany.

[B]Bavarian Forest National Park, Freyunger Straße 2, Grafenau 94481, Germany.

[C]Department of Biology – Conservation Ecology, Philipps-Universität Marburg, Karl-von-Frisch-Straße 8, Marburg 35043, Germany.

[D]Department of Biomedical Sciences, University of Veterinary Medicine, Veterinärplatz 1, Vienna 1210, Austria.

[E]Šumava National Park and Protected Landscape Area, Sušická 399, Kašperské Hory 34192, Czech Repulic.

[F]Department Animal Ecology, Julius-Maximilians University Würzburg, Fabrikschleichach, Am Hubland, Würzburg 97074, Germany.

[G]Present address: Loretská 869, Horažďovice 341 01, Czech Repulic.