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RESEARCH ARTICLE

Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe

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Abstract Predators can create a "landscape of fear" that influences the spatial distribution of their prey. Understanding whether human activity similarly affects the distribution of species beyond habitat suitability is crucial but difficult to assess for conservation managers. Here, we assessed the effect of recreation and forestry activity on a threatened forest-dwelling umbrella species, the Capercaillie (*Tetrao urogallus*). We followed the citizen science approach on the landscape scale in the Bohemian Forest. We analyzed species data non-invasively collected through intensive fieldwork by volunteers and assessed human activity in the entire study area by analyzing expert questionnaires. The study area extends over 119,000 ha and harbors one of the largest relict populations of this grouse species in Central European low mountain ranges. Our statistical models revealed a negative impact of recreational activities on the intensity of habitat use of the birds within suitable habitats, thereby pointing toward a landscape of fear. The influence of forestry activity, in contrast, was not clear. In comparison to existing regional tourism impact studies, we were able to elevate the examination to the landscape scale. Our results underlined the relevance of recreation in limiting the species' habitat on an entire landscape and allow us to conclude that habitat managers should set aside well-defined zones without recreational activities to preserve the refuge of this umbrella species.

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Introduction

The habitat use of a species is driven not only by habitat suitability but also by interactions with other species. One such interaction affecting the spatial distribution and activity of a species is the avoidance of predators in a "landscape of fear" (Laundré et al. 2001). Such potential predators include human hunters, who may shape the spatial habitat use—and hence habitat quality—of game species (Tolon et al. 2009; Ciuti et al. 2012). Anthropogenic fear in wildlife can also cause behavioral responses, including avoidance of preferable habitat or changes in reproductive behavior (Frederick and Collopy 1989; van der Zee 1990; Fernández-Juricic 2002; Taylor and Knight 2003a, b). However, it has also been shown that some mammal species use humans to shield against carnivores (Berger 2007). Therefore, further research is needed to investigate the role of humans as suspected drivers on "landscapes of fear".

In Europe, the popularity of recreational sports is on the rise, and winter tourism is becoming an increasingly important economic factor for many previously remote and near-natural landscapes (Arlettaz et al. 2007; Thiel et al. 2008; Thiel et al. 2011; Zwijacz-Kozica et al. 2012). Summer activities, such as hiking and mountain biking, and novel activities, such as nocturnal snowshoeing and paragliding, pose special concerns (Taylor and Knight 2003b; Thiel et al. 2005; Summers et al. 2007). These activities are practiced also in or near areas established for the protection of biodiversity, e.g., national parks, where even quiet and non-consumptive recreation (e.g., nature-based tourism) may reduce the effectiveness of protected areas (Reed and Merenlender 2008). Therefore, human recreation is assumed to be one of the major contributors to loss of endangered species (Czech et al. 2000; Summers et al. 2007).

In addition to recreational demands, pressure remains on forests as sources of fuel, food, and raw materials. The increase in volume of coniferous forests in Europe has promoted several substantial disturbance events in the last decades, such as windstorms and bark beetle outbreaks (Seidl et al. 2011). This has intensified forest management and intervening measures, including the use of heavy logging machinery, even in remote and protected forests.

A fear effect of human activities on mountain forest species has been demonstrated at a local scale (e.g., Mollet and Thiel 2009; Braunisch et al. 2011; Thiel et al. 2011), but assessments at the landscape scale are rare due to the difficulty associated with the collection of activity data of human and focal species within forests (Braunisch et al. 2011). Nevertheless, the manner in which human activities may translate into a landscape of fear is a key question for all land-use managers and conservationists planning at the landscape scale (van der Zee 1990; Cole and Landres 1995; Knight and Cole 1995; Graf et al. 2005; González et al. 2006; Arlettaz et al. 2007; Graf et al. 2007; Erb et al. 2012).

Thiel et al. (2008) have demonstrated that radio-collared Capercaillie (*Tetrao urogallus*), an endangered forest habitat specialist (Scherzinger 2009), avoid humans temporally and spatially and have elevated stress hormone levels in winter sport areas (Mollet and Thiel 2009; Thiel et al. 2011). Despite the impacts of humans described in these findings, a "map of fear" has not yet been charted, probably owing to the difficulties in acquiring data on human activities and this elusive bird across entire populations. However, some studies have managed to acquire human activity patterns of high resolution in relation to habitat use of this grouse species. Rupf et al. (2011) have monitored winter sport activities by supplying hundreds of tourists with GPS loggers. Such data may help to mitigate conflicts between recreation and wildlife (Rupf et al. 2011).

In the Bohemian Forest, home of one of the largest Capercaillie relict populations in Central European low mountain ranges (Rösner et al. unpublished data), the fall of the Iron Curtain resulted in a boost in human activity, particularly the establishment and use of transboundary tourist trails in the core area of the species' distribution range (Job et al. 2008; Teuscher et al. 2011). Additionally, natural disturbance in terms of bark beetle outbreaks have called for mitigation activities with intensive logging (Lehnert et al. 2013), both in private forests and in the national parks of Šumava (Czech Republic) and the Bavarian Forest (Germany). In both protected areas, consequences for this species are unclear. Yet, studies carried out throughout Europe demonstrated that Capercaillie are affected by both, recreation and forestry activities

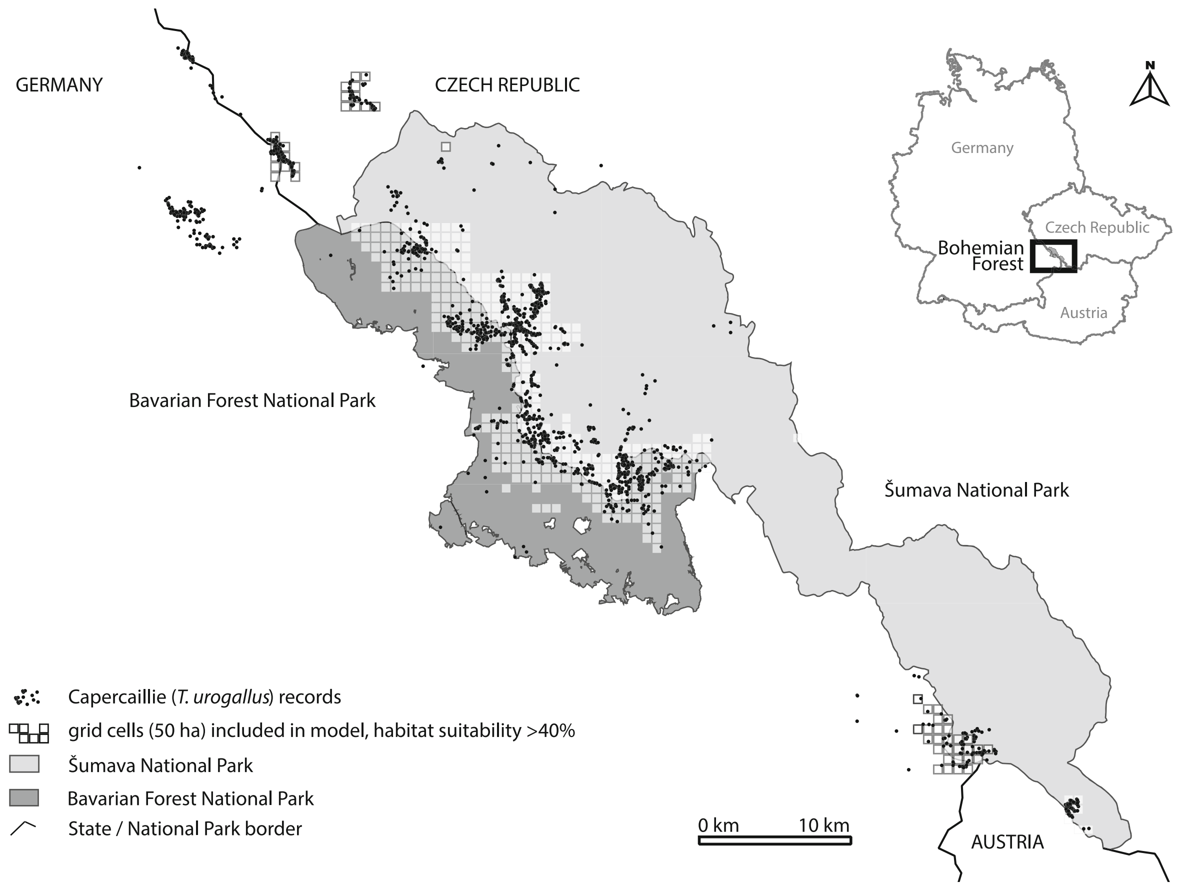

Fig. 1 Map of the study area in the Bohemian Forest. The Šumava National Park (Czech Republic) and Bavarian Forest National Park (Germany) are highlighted in *gray*. Points indicate the sample distribution of all Capercaillie (*Tetrao urogallus*) records between 2006 and 2011. Grid cells (N = 348; 50 ha) are from Teuscher et al. (2011) and show Capercaillie habitat suitability >40 % and are included in the model calculation summarizing 1,743 Capercaillie records

(Klaus 1991; Braunisch and Suchant 2007; Thiel et al. 2008). Therefore, we set out to determine using a citizen science approach whether Capercaillie activity patterns point toward a landscape of fear in this mountain massif.

Materials and methods

Study area

The study was conducted in the Bohemian Forest low mountain range, which extends over 85 km and covers ~119,000 ha of the borderland between the Czech Republic, Germany, and Austria. The area covers the transboundary Šumava National Park (69,039 ha, Czech Republic, 49°06′N 13°08′E) and Bavarian Forest National Park (24,368 ha, Germany, 49°00′N 12°40′E), as well as surrounding landscape protection areas (~20,000 ha, Fig. 1).

Below 1,100 m a.s.l., Norway Spruce (*Picea abies*), European Beech (*Fagus sylvatica*) and Silver Fir (*Abies alba*) are the most abundant tree species. Above 1,100 m, spruce prevails in montane forests with a small proportion of beech and Rowan (*Sorbus aucuparia*) (Walentowski et al. 2004). The highest elevations reach up to about 1,450 m a.s.l. The mean annual temperature is 3.8 °C, with an average rainfall of 1,800 mm, and snow cover is present up to 200 days per year (Bässler 2004).

In 2007, about 760,000 tourists visited the Bavarian Forest National Park, making it the most important attraction in the region (Job 2008; Job et al. 2008). In 2006, more than one million visitors were reported for Šumava National Park (Třebický and Cihar 2006). Singly and combined, these two areas constitute a significant source of existing and potential revenue to this transboundary region. Tourism in the region consists mainly of hiking and biking in summer and alpine and cross-country skiing and snowshoeing in winter.

Both private and state foresters on both sides of the border carry out forestry activities. Because of bark beetle outbreaks in recent decades (Lehnert et al. 2013), mitigation practices have been implemented to varying extents to protect adjacent private forests. Control measures on the Šumava side have been more extensive than on the Bavarian Forest side, although pressure from forest owners to eradicate the threat of the bark beetle is very strong on both sides. Management of outbreak areas includes selective removal or clear-cutting of infected trees and then decortication by means of heavy forestry machinery, such as harvesters and forwarders.

Focal species and population

For the last few decades, Capercaillie numbers in Central Europe have been declining owing to habitat loss and degradation. Local populations are often restricted to small and fragmented patches of forests at higher altitudes and persist in small population sizes of <200 birds (Storch 2000; Storch 2007), placing them below the approximate minimum viable population size of about 500 (Grimm and Storch 2000). Human disturbance may have contributed significantly to this decline (Thiel et al. 2005).

Systematic recording of Capercaillie occurrence in the Bavarian Forest revealed a population decline from ~250 individuals in 1945 to only 16 birds remaining in the Bavarian Forest National Park in 1984/1985 (Scherzinger 2003). In response to this rapid decline, a breeding program was established between 1985 and 2000, and ~1,300 individuals were released from captivity. Today, this region harbors one of the largest remnant populations in Central European low mountain ranges (Rösner et al., unpublished data).

In the study area, Capercaillie inhabits high montane forests dominated by Norway Spruce with interspersed European Beech and Mountain Ash (Teuscher et al. 2013). Above 950 m a.s.l., severe windthrows and bark beetle (*Ips typographus*) infestation have resulted in large patches of standing and fallen dead wood with interspersed young spruce second growth (Teuscher et al. 2011; Teuscher et al. 2013; Lehnert et al. 2013). These patches cover hundreds of hectares and occur over the entire area (Lausch et al. 2012). Forestry practices differ strongly within the Capercaillie habitats, depending on factors such as ownership, country, and type of management zone within the national parks (Müller et al. 2010).

Data collection and sampling

Capercaillie were sampled and recorded year-round by a group of approximately 70 people. Following a citizen science approach (see Dickinson et al. 2010), laypersons, nature enthusiasts, hunters, foresters, rangers, and non-professional ornithologists took part in our study. In preparation of the survey, we trained volunteers in seminars, workshops, and field trainings to guarantee accurate fieldwork. We then used an existing habitat model based on data from 2000 to 2005 and used predictions for conditions in 2008 (Teuscher et al. 2011). This model provides landscape-wide habitat suitability values derived from 29 environmental predictor variables acquired from aerial photographs (e.g. clear cut areas, young deciduous stands, lying dead wood), on the scale of 50 ha grid. The habitat model was evaluated by different metrics and showed high performance support (e.g. PCC = proportion of correctly classified cases >0.72, AUC = area under the receiver operating curve >0.84, for details see Teuscher et al. 2011). Based on the habitat suitability maps by Teuscher et al. (2011) we constructed search areas of around 500–1,000 ha for fieldwork (approx. 450 50 ha grid cells) and assigned them among the participants. Thereby, >95 % of grid cells with any expected Capercaillie occurrence in the habitat suitability model of Teuscher et al. (2011) were considered. We finally used those 384 grids for analysis, which were searched two times in summer (May–September) and two times in winter (October–April) period between 2007 and 2011. In this way, we were able to obtain homogenous search cover for species occurrence on the whole landscape. The location of all types of species records, i.e., tracks, feathers, droppings, and direct observation, was determined using handheld GPS devices and assigned to the respective grid cell. Multiple droppings sampled from the tracks of one individual (tracking possible only in winter snow) were recorded as one individual. Family groups were also counted as one record only. Thus, this approach provided both, count data (abundance) and presence/absence data on the basis of grid cells.

Human impact

To assess the potential of human impact on a landscape scale for the Bohemian Forest, we charted maps of recreation and forestry activity—both legal and illegal human activities—based on direct enquiries of local and regional experts. We asked park rangers, foresters, hunters, naturalists, and other area experts to evaluate the level of human activity of each of the three activity categories (tourism in summer, tourism in winter, and year-round average forestry activity) on the grid of 50 ha cells (see above), and scored each separately for the years 2009 and 2010. We created these enquiry maps (grids in topography maps of 1:50,000 scale) according to management units in forestry and National Park administrations, where the responsible persons (3–5 persons per unit) accordingly know their area best and often for decades. For every grid cell, the forms were accordingly completed to the following scale: 0, no activity; 1, slight activity; 2, mid-level activity; and 3, intense activity. Grid cells were simply rated by hand and later returned for numerical entry to GIS (Quantum GIS) shape files. To ensure congruent data sets, the participants were informed during initial seminars about reference areas having the different levels. We averaged the values of feedback from multiple respondents for each grid cell, which resulted in its final intensity score. Summer tourism and winter tourism was surveyed separately and were afterwards summed up as year-round assessment as they were clearly correlated ($r = 0.69$, $p < 0.001$, $df = 382$; now ranging from 0.0 to 6.0).

Statistical analysis

To explain the variation in our count data, we used the predictors (1) habitat quality, (2) forestry intensity, (3) recreation intensity, and (4) distance to the next known lekking site and grid cell (in meters). For global spatial arrangement of our target grid cells (space), arranged along the mountain ridges (see Fig. 1), we derived a simple spatial variable from the first axis of a principal components analysis (PCA) using X and Y values of our grid cells. For none of the predictor variables did the correlation exceed $|r_{spearman}| > 0.58$.

Count data from such a specifically formed landscape (note that Capercaillie are found mostly along the mountain ridge, Fig. 1), as analyzed here, present two different challenges from a statistical point of view. First, owing to many zeros (grids without records), one may expect zero inflation (but see Warton 2005). Second, the spatial arrangement poses the question of spatial independency of the observations. A spatial independency of the residuals of the models is required to obtain reliable results for the predictors. We considered these challenges in our target variable and in the spatial dependency in a four-step analysis. First, we fitted simple generalized linear models with Poisson distribution using the spatial variable. Then we fitted a zero-inflated model using the function *zeroinfl*, implemented in the package pscl (Zeileis et al. 2008) within the framework of R v. 2.15.2 (R Core Team 2012). Zero-inflated count models are two-component mixture models combining a point mass at zero with a proper count distribution. We used as count model a Poisson model and for modeling the unobserved state (zero vs. count), a binary model that captures the probability of zero inflation. We then compared the simple Poisson model and the zero-inflated model using the Vuong test (Vuong 1989). The latter model fully accounts for zero inflation (Zuur et al. 2007; Zuur 2009). From this model, we used the residuals and tested for spatial independency by spline (cross)-correlogram with average autocorrelation coefficient and 95 % confidence bands based on 999 replications (function *spline.correlog* in the package ncf within R; Bjørnstad and Falck 2001, see Fig. 3). Finally, we also fitted a generalized linear mixed model with Poisson distribution using function *glmer* implemented in package lme4 (Bates et al. 2013), controlling fully also for small-scale spatial effects by random effects of X, Y, and X*Y, by creating a trend surface (see Hothorn et al. 2011). This model was inspected also for possible overdispersion, but this was not the case.

Results

With the help of trained volunteers and local experts, we managed to systematically and non-invasively

Table 1 Fixed variable descriptive statistics

Variable	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Habitat quality	0.05	0.30	0.48	0.47	0.62	0.94
Forestry activity	0.00	0.17	1.00	1.05	2.00	3.00
Recreation activity	0.00	1.00	2.00	2.35	3.60	6.00
Lek sites	162.5	1,173.3	1,992.4	2,131.6	2,887.4	7,484.7
Spatial effect	−0.09	−0.03	−0.01	0.00	0.02	0.16

Habitat quality is the quality indicator incorporated from the habitat model of Teuscher et al. (2011) and represents the year-round probability of Capercaillie (*Tetrao urogallus*) occurrence in the study area. Forestry activity and recreation represent the two categories of human impact based on evaluations of activity levels (0, 1, 2, 3). Spatial effect is an incorporated effect found in early model testing and is based on the shape and exposure of the study area (results of principal component analysis; transformed to values ranging from 0.0 to 1.0). Lek sites correspond to the distance between the Capercaillie record and the nearest neighboring known lek site in the study area

Table 2 Summary of the count and zero-inflated models

Model and factor	Estimate	Standard error	z-Value	Pr (>|z|)
Count model coefficients (Poisson with log link)				
(Intercept)	2.46	0.12	20.89	<0.001
Habitat	0.76	0.15	5.13	<0.001
Forestry	−0.04	0.03	−1.17	0.242
Recreation	−0.13	0.02	−7.28	<0.001
Distance lek	−0.0004	0.00001	−28.6	<0.001
Spatial	−3.13	0.58	−5.44	<0.001
Zero-inflated model coefficients (binomial with logit link)				
(Intercept)	−0.84	0.89	−0.944	0.345
Habitat	−2.97	0.65	−4.557	<0.001
Forestry	0.17	0.18	0.981	0.327
Recreation	0.14	0.076	1.806	0.071
Distance lek	0.0005	0.0004	1.420	0.156
Spatial	−2.44	2.96	−0.83	0.410

The zero-inflated model shows the effect of selected factors habitat, forestry, recreation, and spatial on presence or absence of Capercaillie (*Tetrao urogallus*)

acquire valuable data to analyze landscape-wide influence of human activities on Capercaillie in the Bohemian Forest. For descriptive summary of the data see Table 1.

Our final data set comprised 384 grid cells covering approximately 19,200 ha (Fig. 1) in the potential Capercaillie habitat. In these cells over the four samplings, we obtained a total of 1,743 Capercaillie records with a mean of 4.5 records per 50 ha grid cell ($SE = 0.40$, max = 56 records). In 136 grid cells (35 %), no traces of Capercaillie were detected.

The comparison of the Poisson model and the zero-inflated model revealed a clear preference for the latter model (Vuong non-nested hypothesis test statistic: 5.03, $p < 0.001$). The zero-inflated model revealed a highly significant increase of probability of Capercaillie occurrence and count numbers with increasing habitat suitability (Table 2). Recreation negatively affected the count numbers, but not the occurrence. Forestry activity significantly affected neither the counts nor the zeros. The distance to the next known lek site had a strong negative effect only on the count numbers. Also the global spatial component affected the count numbers. The overall explanation power of the model was $r = 0.45$ (Pearson correlation coefficient of count data vs. predicted data, $t = 9.765$, $df = 382$, $p < 0.001$). However, inspection of the spline correlogram still revealed a spatial dependency of the residuals up to ~3 km (Fig. 2). Thus, we additionally fitted a generalized linear mixed model, controlling for space as random factor. Despite the control for space, this model still corroborated the findings of our zero-inflated model, with a significant positive impact of habitat and negative impacts of distance to lek sites and recreation. Therefore, we can assume that our results of a negative influence of recreation and distance to lek site and a positive influence of habitat suitability are robust, even though there is some unexplained variation in space up to 3 km in the zero-inflated model.

Discussion

With non-invasive methods, the help of local experts (questionnaires), and a team of trained volunteers (field work), and with controlling for habitat quality

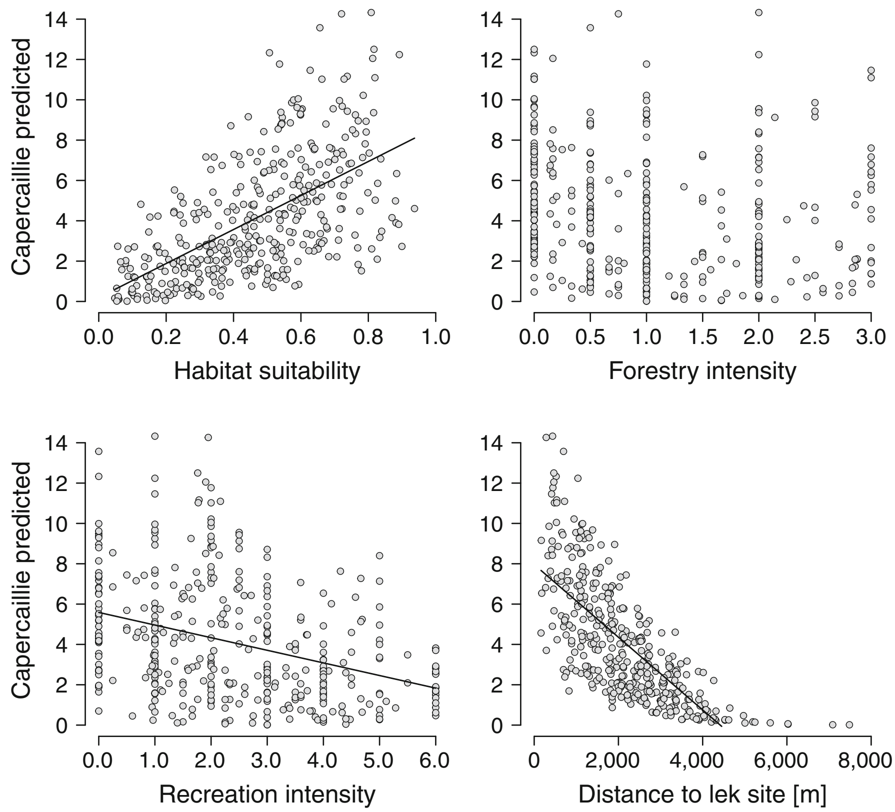

Fig. 2 Results from zero-inflated model using the model prediction (predicted number of Capercaillie per grid cell) as a function of habitat suitability (derived from Teuscher et al. 2011), forestry intensity, recreation intensity, and the spatial distance to the next known lek site, hypothesized to affect Capercaillie occurrence (behavioral response) in the Bohemian Forest (Czech Republic, Germany). For illustrative reasons, the regression lines are only shown for coherent results from both model parts (count and presence-absence data)

and lek sites we found a negative response of patch use by Capercaillie to anthropogenic disturbance caused by recreation on a landscape level. This result provides evidence for human avoidance and therefore reduction of habitat quality for this umbrella species. We therefore suppose an anthropogenic "landscape of fear" for the Capercaillie in the Bohemian Forest area.

Although humans seeking recreation are not predators of the Capercaillie, several studies have shown a behavioral or elevated stress level response in this species (Thiel et al. 2008; Čas 2012). The mere non-consumptive presence of recreationists is considered to have a direct impact on wildlife (van der Zee 1990). Our findings corroborate results from previous studies from near-by areas (e.g., Black Forest, Alps; e.g., Thiel et al. 2008).

Recreation—considering either the number of recreationists or the frequency of land use—plays a deterrent role in the density of patch use. Our study extended previous results and demonstrated a spatial manifestation of behavioral responses at the landscape level. We cannot directly explain why the bird avoids tourists on landscape scales, as opposed to using humans as shields against predators (Berger 2007), particularly as it is not hunted in the study area. However, anthropogenic avoidance has also been demonstrated for the related Black Grouse (*T. tetrix*) at the tree line of the Swiss Alps (Braunisch et al. 2011), and recreational homes negatively affected the breeding success of another grouse, the Willow Ptarmigan (*Lagopus lagopus*) (Stoen et al. 2010).

To quantify forestry and human recreational activities in the Bohemian Forest, we used an indirect approach by distributing map-based questionnaires to local specialists in the Bohemian Forest, such as rangers, foresters, and tourist guides, who know this territory very well. Most of them have decades of on-site experience. Thus, we are convinced of the reliability of our data sets in their accurate portrayal of human activity in the study area for the categories examined (see Table 1). We believe that the acquired forestry activity data are also of high accuracy because rangers and foresters continuously plan timeframes and survey spatial dimensions of forestry activities,

Table 3 Model summaries of the generalized linear mixed Poisson model with space (X, Y, X*Y) as random factor

Fixed effects	Estimate	Standard error	z-Value	Pr (>|z|)
(Intercept)	0.651	0.371	1.755	0.079
Habitat	2.912	0.465	6.26	<0.001
Forestry	−0.012	0.112	−0.107	0.915
Recreation	−0.158	0.052	−3.019	0.003
Distance lek	−0.0006	0.00008	−7.214	<0.001

Calculation based on data set with 384 50 ha-grid cells with function *glmer* in lme4 package (Bates et al. 2013)

such as bark beetle mitigation. Our approach, in contrast to measurements such as net tourist counts alongside trails (e.g., Summers 2000; Summers et al. 2007; Erb et al. 2012), taps into the knowledge of area experts and community members and captures tourism activity outside trails as well as illegal activities, such as off-track skiing or use of closed trails. Other survey methods would consider such areas as areas with no disturbances. These illegal activities are of special importance when dealing with disturbance to wildlife as such unpredictable events are a major source of stress for wildlife that makes adaptation by animals impossible (Knight and Cole 1995; Miller et al. 2001; Braunisch et al. 2011).

Our questionnaires were based on the 50 ha grid cell system previously applied for habitat analysis, which allows for 1:1 comparison to the model's spatial dimensions (Teuscher et al. 2011) and provides a practical basis for possible management decisions. Also forestry and tourism management activities in the Bohemian Forest are based on the 50 ha scale—the typical size of forest stands (see Teuscher et al. 2011; Teuscher et al. 2013). As we aimed to cover the entire landscape, an approach of quantifying activity on individual trails or even measurements of distances to the next Capercaillie records (see Taylor and Knight 2003a; Thiel et al. 2007) would not be helpful for managers working at the landscape scale.

The results of our study demonstrated that not only habitat quality but also disturbance by recreation actively influences the distribution of Capercaillie, identifying these factors as possible drivers of the population health and in turn, drivers of the carrying capacity of the study region (see Summers et al. 2007). The anthropogenic disturbance in the form of recreational activities played a significant role in Capercaillie abundance (see Table 2; Fig. 2, Appendix I in Supplementary Material). However, in contrast to our prediction, it was not a significant factor determining Capercaillie presence or absence—the purely binomial presence or absence in grid cells within the Capercaillie habitat (note that the grid cells were selected based on the habitat suitability model of Teuscher et al. 2011) was not affected by human disturbance. Smaller scales (e.g., 1 ha cells) might have shown strong effects on Capercaillie presence or absence (Table 3).

Decreasing tourism activities lead to an increase in Capercaillie densities, mirrored in the detection of Capercaillie in most of the suitable grid cells, even with high levels of human activity; higher Capercaillie densities were recorded only in grid cells of remote areas with low human activity pressure (see map in Appendix in Supplementary Material). Thiel et al. (2008) similarly found in the Black Forest (Germany) that human presence does not seem to prevent Capercaillie from using the habitat but may trigger how many individuals or how often a grid cell will be used. We also analyzed the spatial distribution and activity ranges of Capercaillie in the study region (Rösner et al., unpublished data). In this ongoing study using microsatellites, single unique haplotypes (individuals) repeatedly frequented grid cells with high human activity, such as mountain peaks. Records of such individuals may have influenced presence or absence data of the model, which could explain the divergence from the expected results.

We assessed habitat quality using an existing habitat model and found it to be an important factor for spatial distribution. We concluded that human disturbance is not related to habitat use in terms of spatial distribution. The model output showed that habitat quality strongly and consistently influenced both Capercaillie presence and frequency. Habitat composition factors, such as elevation, amount of dead wood, and clearings have been tested by Teuscher et al. (2011). The significant correlations found indicate that as areas of these types increase, the frequency of Capercaillie also increases.

The strength of habitat quality as a factor explaining occurrence and abundance identifies this factor as being integral to Capercaillie conservation. However, habitat quality must be coupled with appropriate patch size for successful protection of the species in the Bohemian Forest. This demand is supported by a study

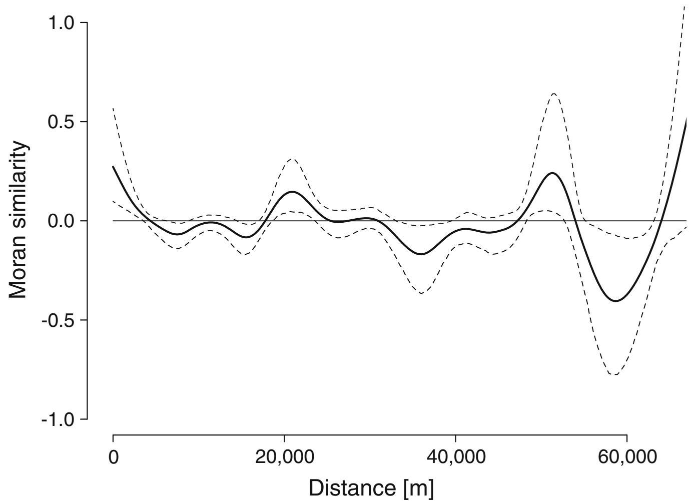

Fig. 3 Spline(cross)-correlogram with average autocorrelation coefficient and 95 % confidence bands (function *spline.correlog* in the package ncf within R; Bjørnstad and Falck 2001) for the residuals of the zero-inflated model (in Fig. 2)

on Capercaillie in Switzerland (Bollmann et al. 2011), where patch size was the most important predictor for patch occupation. The previously developed grid system with a cell size of 50 ha ensures both a scale with a resolution lower than the scale of spatial activities of our focal species (mean activity ranges of about 550 ha, Storch 1995) and a scale unit large enough to derive recommendations for management (Graf et al. 2005; Teuscher et al. 2011). Today, only about 20 % of the entire transboundary national park area is suitable for the Capercaillie (see Teuscher et al. 2011; Teuscher et al. 2013), and the results of our study indicated that these areas are influenced by human disturbance. Only 12 % of this core area (384 grid cells) is reported with no recreation activities. As a consequence, an increase in recreation in time (e.g., night activities) or space (e.g., establishment of new hiking trails) will therefore further reduce available space and habitat quality for the focal species.

In contrast to habitat quality and recreation, forestry activity did not explain the presence or absence of the Capercaillie. However, the zero-inflated model revealed that this factor positively influences the abundance of the species, possibly owing to the open areas created. Such patches are of different sizes and "cleaned" of trees infected by bark beetles to mitigate further calamities and thus might locally increase the habitat heterogeneity for the focal species. Although the habitat structure in these areas is obviously changed, the forestry activities themselves often last only for a few days. This starkly contrasts the timespan of the continuous recreational activities. However, one should consider that deforestation and the accompanying preparation of forest roads might increase the penetration of predator species, such as foxes (*Vulpes vulpes*) and wild boars (*Sus scrofa*), to Capercaillie breeding habitats (Storch 1991; see Kurki et al. 2000). Nevertheless, in a recent artificial grouse-nest predation experiment carried out by our group, no increase of nest predation with increasing recreation could be found (Seibold et al. 2013). However, structural changes at lek sites might also severely change the population structure (Rolstad and Wegge 1989).

Our results also supported the importance of lekking sites in the spatial arrangement of the whole population. We did not explicitly and intensively sample at lekking sites as done in genetic monitoring programs in Switzerland (e.g. Mollet et al. 2003). Nevertheless, we still found a strong influence of existing lekking sites on the spatial arrangement. When we controlled for habitat suitability and known lekking sites, we also found an effect of space up to 3 km. These findings strongly support the view that the social behavior of the Capercaillie itself also influences their landscape distribution. For example, Capercaillie apparently choose habitats not only of suitable structure but also because of the presence of conspecifics. This may help to avoid enemies by warning signals (calls, flushing noise) or by learning of younger individuals from adults for highly suitable microhabitats like bilberries. Another social behavior affecting their landscape distribution is the dissolving of families in autumn, when subadults start to disperse in the larger surroundings of the natal sites (Storch 2001). The spatial dependency of the residuals may also be influenced by unknown lek sites, which were recently established in the rapid changing forest landscape by disturbances (see Müller et al. 2010).

Our study underscores the importance of ecological research at the landscape scale to reveal large-scale species response to human activities. The results strongly support meaningful Capercaillie conservation and management plans that aim at maintaining refuges of adequate size, high habitat quality and lek sites kept free of human disturbance. Maps of anthropogenic fear (see Appendix I in Supplementary Material) may in general be useful to support conservation managers in designating management decisions for both, refuge areas for threatened species and priority areas for recreation activities.

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