# Habitat suitability modulates the response of wildlife to human recreation

Joy Coppes[a], Ursula Nopp-Mayr[b,*], Veronika Grünschachner-Berger[c], Ilse Storch[d], Rudi Suchant[a], Veronika Braunisch[a,e]

[a] Forest Research Inst. of Baden-Wuerttemberg FVA, Freiburg, Germany
[b] Institute of Wildlife Biology and Game Management, Dep. of Integrative Biology and Biodiversity Research, Univ. of Natural Resources and Life Sciences, Vienna, Austria
[c] Office for Wildlife Biology and Management, Gusswerk, Austria
[d] Wildlife Ecology and Wildlife Management, Univ. of Freiburg, Germany
[e] Conservation Biology, Inst. of Ecology and Evolution, Univ. of Bern, Switzerland

ABSTRACT

Outdoor recreation activities are growing in popularity, causing increasing pressure on wildlife. There are various ways in which wildlife reacts to recreation activities, ranging from behavioural to physiological responses, with regional variation in response-intensity within the same species. We tested whether the effects of human recreation are modulated by overall structural habitat suitability, using a model that included vegetation and topography, at both the regional and local habitat use scale. By undertaking a systematic, plot-based survey over 13 years in 13 study regions across central Europe, we studied how recreation infrastructure and habitat suitability interact and affect the variation in regional densities and local habitat use of an endangered model species: the western capercaillie (*Tetrao urogallus*). Both regional densities and local habitat use varied greatly between study years and regions. Capercaillie densities were positively correlated with average habitat suitability, but significantly reduced when over 50% of the area was influenced by recreation activities. Habitat suitability was the main predictor determining local habitat use. Recreation infrastructures were avoided: the effect being stronger in poor habitat conditions, while slightly mediated by high habitat suitability. Our results indicate that effects of recreation activities might be mitigated by improving habitat suitability; however this has limits because it only affects local scale habitat use but not regional densities. We stress the importance of recreation-free areas which must cover extensive (i.e. > 50%) parts of the species range.

## 1. Introduction

With increasing popularity of outdoor recreation, growing numbers of recreationists and continuing diversification of recreation activities, the effects of recreation on wildlife are well recognized as an important conservation issue (IUCN, 2016). A growing body of literature illustrates the various ways in which wildlife can be affected by recreation activities in their habitat (Steven et al., 2011; Larson et al., 2016), ranging from physiological changes (Walker et al., 2006; Thiel et al., 2011; Arlettaz et al., 2015), reduced breeding success (Anderson and Keith, 1980; Ahlund and Götmark, 1989; Mallord et al., 2007), changes in abundance (Patthey et al., 2008; Wolf et al., 2013), community composition (Miller et al., 1998) to changes in territory establishment in birds (Bötsch et al., 2017). Behavioural reactions include direct fleeing or flushing upon encountering humans (Thiel et al., 2007; Stankowich, 2008; Sönnichsen et al., 2013), which may impact energy budgets and possibly affect fitness. More subtle behavioural

reactions are changes in vigilance behaviour in regularly disturbed areas (e.g. close to recreational infrastructures such as hiking trails or skiing pistes) (Jayakody et al., 2008), or a temporal avoidance of disturbed areas (Coppes et al., 2017a). Reduced use of such disturbed areas (Immitzer et al., 2014; Coppes et al., 2017b) might effectively be equated with habitat loss or deterioration. However, individual behavioural reactions do not reflect consequences at a population level (Gill et al., 2001). Thus, effects of recreation activities on demographic parameters and, as a consequence, on population densities have to be classed as key questions in conservation management.

In many documented cases, the reaction of wildlife to human presence is similarly to their reaction to predators (Frid and Dill, 2002; Beale and Monaghan, 2004). However, free-living animals can also habituate to non-lethal encounters with humans as it is the case in most recreation activities (Thompson and Henderson, 1998) and the "deterring effect" of human presence may even shield prey species from

predation under specific circumstances (Leighton et al., 2010; Shannon et al., 2014). Such effects strongly depend on the environmental conditions together with the number and behaviour of recreationists (Pearce-Higgins et al., 2007), and it might even be affected by the history of human exploitation in an area (Storch, 2013). Reactions of animals to human recreation are highly species-specific (Blumstein et al., 2005; Ficetola et al., 2007) and often linked to behavioural and morphological or life-history traits (Blumstein et al., 2005; Kangas et al., 2010): ground nesting birds, for example, have been found to be more sensitive to recreational disturbance compared to species breeding in cavities (Kangas et al., 2010) and species with larger body mass are considered more sensitive to recreational disturbance compared to smaller species (Blumstein et al., 2005; Weston et al., 2012). Wolf et al. (2013) found indications that birds species which forage on ground vegetation and shrubs seem to be more susceptible to human disturbance compared to species foraging in trees. Responses to human presence might even differ among individuals of the same species (Carrete and Tella, 2011; Coppes et al., 2018).

The intensity of individual reactions to human recreation within the same species might vary between different habitat types or habitat characteristics providing food and cover: van der Zande et al. (1984) found a more pronounced negative effect of recreation on two bird species in deciduous forests compared to coniferous forests. Vegetation structures associated with cover (i.e. foliage density, dense shrub or forest layers) have been shown to affect flushing distances (Fernández-Juricic et al., 2002; Fernandez-Juricic et al., 2004), with shorter flushing distances in denser forests providing more cover (Thiel et al., 2007). The degree to which wildlife can survey its surroundings (i.e. visibility) is also affecting vigilance behaviour (Metcalfe, 1984; Whittingham et al., 2004), with increased vigilance in visually obstructed habitats (Whittingham et al., 2004). Boyer et al. (2006) recorded increased foraging rates of birds in areas with high visibility, minimizing the time spent on open areas with higher predation risk. In the case of a ground nesting bird, the distance of spatial avoidance around recreation activities depended on the shrub cover, with less

pronounced avoidance of areas with high shrub cover (Coppes et al., 2017b). This observation was most likely linked to the availability of good hiding structures. Wolf et al. (2013) found impacts of recreation activities on birds to be less distinct along trails with a well-developed, structurally rich vegetation with both favourable foraging and hiding structures. From a conservation perspective, given that disturbance effects might be highly habitat-specific (Murison et al., 2007), understanding the habitat conditions where disturbance effects are strongest (Sutherland, 2007) is crucial to designing adequate mitigation measures.

To assess if and how structural habitat suitability - from this point referred to as *habitat suitability* - may modulate wildlife responses to recreation activities, we studied effects of recreation infrastructures on local densities and habitat selection in a grouse species red-listed at national and European levels: the western capercaillie (*Tetrao urogallus*), from here on referred to as capercaillie. Capercaillie are considered to be habitat specialists (Rolstad and Wegge, 1987; Klaus et al., 1989; Zohmann et al., 2014), and habitat suitability is an important factor explaining local habitat use (Storch, 2002). Data were sampled in multiple years across a large number of study areas, spread over a wide geographical range of Central Europe, covering both a large range of habitat conditions and population status, ranging from stable to decreasing populations. We expected (1) habitat suitability to be the main predictor for explaining overall capercaillie densities as well as local-scale habitat selection; and (2) negative effects of human recreation infrastructure on both aspects. We hypothesized, however, that these negative effects would be stronger under poor habitat conditions, compared to the species' response under highly suitable habitat conditions.

## 2. Methods and materials

### 2.1. Study areas

This study comprises 13 different study areas in different capercaillie populations spread over a large geographical range (Fig. 1). Three study areas were located in the Black Forest (BF 1 to BF 3), south-
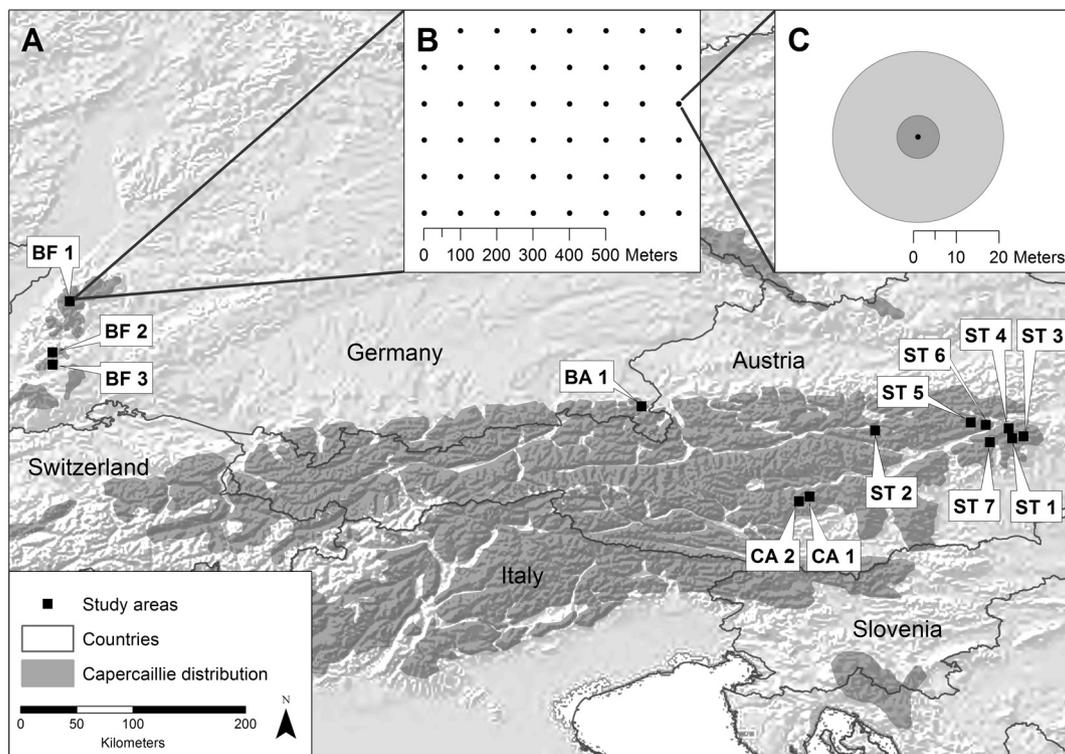


**Fig. 1.** The study areas (black squares) in Germany and Austria (panel A) in relation to the capercaillie distribution (dark grey) (Coppes et al., 2015). In each study area, data were collected using a systematically distributed grid of sample plots (panel B); signs of capercaillie presence were collected within a 5 m radius (panel C, dark grey), and variables for habitat suitability calculation measured within a 20 m radius around the plot centre (panel C, light grey).

**Table 1**

Study areas with their size, average altitude, dominating tree species, number of sampling plots per year (N plots) and the number of sampling years (N years).

| Study area | Country | Size (ha) | Main tree species | Average altitude (m a.s.l) | N plots | N years |
|---|---|---|---|---|---|---|
| BA 1 | DE | 1900 | Spruce, Beech | 1012 | 486 | 10 |
| BF 1 | DE | 200 | Spruce, Pine | 924 | 171 | 4 |
| BF 2 | DE | 350 | Spruce, Beech | 933 | 308 | 4 |
| BF 3 | DE | 220 | Spruce, Beech | 1129 | 202 | 4 |
| CA 1 | AT | 500 | Spruce, Larch | 1532 | 439 | 3 |
| CA 2 | AT | 200 | Spruce, Larch | 1432 | 198 | 3 |
| ST 1 | AT | 220 | Spruce, Larch | 1394 | 200 | 5 |
| ST 2 | AT | 520 | Spruce, Larch | 1381 | 502 | 1 |
| ST 3 | AT | 400 | Spruce, Larch | 1307 | 372 | 4 |
| ST 4 | AT | 250 | Spruce, Larch | 1295 | 197 | 2 |
| ST 5 | AT | 240 | Spruce, Larch | 1219 | 201 | 2 |
| ST 6 | AT | 420 | Spruce, Larch | 1315 | 393 | 3 |
| ST 7 | AT | 350 | Spruce, Larch | 1296 | 200 | 6 |

western Germany. One study area was located in the Bavarian Alps (BA 1), south-eastern Germany. The remaining study areas were located in the provinces of Styria (ST 1-7) and Carinthia (CA 1-2) in Austria.

In all study areas the dominant tree species was Norway spruce (*Picea abies*), with European beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*) as secondary tree species in the German study areas and European larch (*Larix decidua*) as secondary tree species in the Austrian study areas (Table 1). Average altitudes ranged between 924 and 1432 m above sea level. All study areas were located in forests managed for timber production. Study areas were chosen based upon monitoring data and advice from local experts (i.e. ornithologists, hunters and forestry personnel) to ensure capercaillie were present. The study areas represent a large range of habitat conditions, landscape configurations, and population states: In the Black Forest, a lower mountain range, the capercaillie population is highly fragmented (Braunisch et al., 2010) and has been decreasing over the past decades (Coppes et al., 2016). In the Bavarian study area, located on the edge of the larger Alpine distribution of capercaillie, population numbers are also declining (xy unpubl. data). In contrast the study areas in Styria and Carinthia (Austria) are located in the central and eastern-edge of the Alpine capercaillie distribution and populations are assumed to be stable (xy unpubl. data).

### 2.2. Model species

The capercaillie is a large, ground nesting forest grouse species (Johnsgard, 1983). It resides in semi-open to open coniferous or mixed forests with a rich ground vegetation (Storch, 2002; Summers et al., 2004; Bollmann et al., 2008; Graf et al., 2009), occurring over a wide geographical range across Europe (Klaus et al., 1989; Coppes et al., 2015). While the species is widely distributed in Scandinavia and Russia with large populations numbers, the Central and Southern

European populations are smaller, they are mainly restricted to mountain ranges and declining in many areas (Storch, 2007). We chose the capercaillie as a model species because (1) it is considered an umbrella species for structurally complex and species rich boreal forests (Suter et al., 2002; Pakkala et al., 2003), (2) it occurs over a wide geographical range and (3) it has been shown to react sensitively to habitat changes (Suchant and Braunisch, 2004). Several studies found negative effects of recreational activities on capercaillie (Summers et al., 2007; Thiel et al., 2011; Moss et al., 2014; Rösner et al., 2014; Coppes et al., 2017b), e.g. elevated stress levels (Thiel et al., 2008; Thiel et al., 2011; Coppes et al., 2018), avoidance of areas near forest roads (used both by vehicles as well as recreationist) in winter (Summers et al., 2007) or avoidance of trails used for recreational activities in summer (Moss et al., 2014) in Scotland. Similarly, Coppes et al. (2017b) found capercaillie avoided recreational infrastructure in the Black Forest, one of our study regions.

### 2.3. Data collection

Data were collected between 2005 and 2017, in the months July and August. A plot-based sampling design was applied: plots were arranged in a regular grid of 100 ∗ 100 m, which resulted (depending on the size of the study area) in between 171 and 439 plots per site (Table 1). The only exception was in the Bavarian Alps (BA 1), the largest study area, where the distance between plots was 200 ∗ 200 m for logistic reasons. The plots were located in the field using a handheld GPS. At each plot, a variety of habitat parameters (Table 2), which have been shown to be relevant for capercaillie in previous studies (Storch, 2002; Suchant and Braunisch, 2004; Braunisch et al., 2014; Zohmann et al., 2014), were recorded within a 20 m radius around the plot centre (Fig. 1) following the method described in Storch (2002). In addition, to assess the presence or absence of capercaillie, a 5 m radius around the plot centre was

**Table 2**

Habitat parameters for calculating the capercaillie habitat suitability index (HSI, Storch, 2002). The reference radius for all parameters was 20 m around the plot centre (total plot size = 1256.6 m²). Both categorical and continuous parameters were included, with data both collected in the field (Fieldwork) and derived from a digital elevation model (DEM).

| Predictor | Description (unit) | Type | Source |
|---|---|---|---|
| Successional stage | Successional stage<br>1 = Non forest<br>2 = Clearcut with regeneration<br>3 = Thicket<br>4 = Older stages | Categorical | Fieldwork |
| Canopy cover | Canopy cover (%) | Continuous | Fieldwork |
| Ground vegetation height | Height of ground vegetation (cm) | Continuous | Fieldwork |
| Bilberry cover | Cover of bilberry (*Vaccinium myrtillus*) (%) | Continuous | Fieldwork |
| Regeneration cover | Cover of tree regeneration (%) | Continuous | Fieldwork |
| Slope | Slope (degree) | Continuous | DEM |
| Relative elevation | Elevation above the farmland floor (meters) | Continuous | DEM |

searched for indirect signs for 10 min; in the Bavarian study area the search time was 15 min (Fig. 1, panel C) Storch (2002). Signs of capercaillie presence were either collected (feathers, droppings and eggshells) or photographed (e.g. sand-baths) and verified by a team of capercaillie experts. Capercaillie droppings can be found over longer time periods after defecation (Poggenburg et al., 2018) and searching for indirect signs of presence is an established method to study capercaillie occurrence (Coppes et al., 2016) and habitat use (Summers et al., 2007; Moss et al., 2014; Zohmann et al., 2014). Before sampling, all field assistants were trained in habitat assessment, capercaillie ecology, and in the identification of indirect capercaillie signs to ensure consistency and high data quality.

### 2.4. Model predictors

Aiming at an independent and consistent estimate of habitat suitability across all study areas we used a mechanistic, knowledge-based approach (Sachser et al., 2017) to calculate a habitat suitability index (HSI, see U.S. Fish and Wildlife Services (1981)) for our focal species at each sampling plot according to Storch (2002). This mechanistic habitat suitability model was derived from empiric data and expert-knowledge, addressing both summer and winter habitat suitability. It has been widely applied to assess capercaillie habitat suitability across Central Europe. As we sampled and focussed on recreation effects in the summer months, we calculated the HSI for summer (Storch, 2002), which combines seven variables (slope, successional stage, elevation, canopy cover, ground vegetation height, bilberry cover and cover of regeneration, Table 2). The resulting suitability scores for every plot range from 0 (unsuitable) to 1 (highly suitable) (for detailed calculation see Storch, 2002). To assess relative habitat suitability for each study area we averaged the HSI over all plots per area and year (Avg_HSI). As a proxy for human disturbance during summer, we calculated the distance to the nearest summer recreation infrastructure (hiking or mountain-biking trail) for all plots. The majority of the trails designated for recreation are on forest roads and are therefore used for forestry works, by hunters and recreationists, but they represent only a fraction of all forest roads. Part of the forest roads not officially designated for recreation activities are however also regularly used by recreationists (Coppes and Braunisch, 2013). As a proxy of intensity of human recreation per study area, we calculated the percent of sample plots located within a distance of 145 m to recreation infrastructure (Recr_area); this corresponds to the mean distance, at which radio-tagged capercaillie showed avoidance of summer recreation infrastructure in the Black Forest (Coppes et al., 2017b). This variable was converted into a categorical predictor (Recr_pressure), which represented two classes of recreations pressure in the study areas in terms of potentially disturbed areas (Table 3).

### 2.5. Statistical analysis

#### 2.5.1. Relative capercaillie densities per study region
To study the effects of habitat suitability, recreation infrastructure and their interaction on yearly relative capercaillie densities at the scale of the study area, we modelled the percentage of plots with capercaillie signs per area (in the following referred to as "relative capercaillie density") and year as a function of the average habitat suitability index (Avg_HSI), the percentage of plots within 145 m of recreation infrastructure (Recr_area) and the interaction term of these two predictors. We first tested for correlations between predictors using Spearman's Rank correlation. To stabilize the variance in our response variable, we used a logit transformation of the percent of capercaillie signs per area. We used univariate generalized linear mixed models (GLMM, R-package: lme4 (Bates et al., 2015)), including the study area as random effect, to test for a linear effect. For predictors, where no linear effect was found, we plotted the predictor values against relative capercaillie density, to visualize the shape of their influence. In case this plot brought evidence for a step-shaped relationship, the resulting threshold was used to generate a new, categorical predictor variable.

#### 2.5.2. Local habitat use
To study possible interactions between habitat suitability and recreational infrastructure on the probability of capercaillie presence at the plot-scale, we used GLMM's with a binominal error structure (logit link), including the year nested in the study area as random effects. As predictor variables we used the habitat suitability index (HSI) at each plot, its distance to nearest recreation infrastructure (Recr_dist) and the interaction between these two predictors. To achieve convergence in the GLMM's we standardized the predictors by subtracting the mean and dividing by the standard deviation and tested for correlations between predictors using Spearman's Rank correlation. To allow for comparison of the effect sizes we calculated the mean and 95% confidence interval of the odds ratio for all predictors. As Coppes et al. (2017b) showed that summer recreation is unlikely to affect capercaillie beyond a distance of 1092 m, we created two GLMM's: one using the entire dataset (full model), and one including only the data of plots lying within a 1092 m distance to recreation infrastructure (reduced model). We evaluated the performance of our models in terms of discrimination power between presence and absence plots by calculating the area under the receiver operator characteristics curve (AUC) using the R-package (AICcmodavg, Mazerolle, 2014). All statistical analyses were performed using R-statistics version 3.4.3 (R Development Core Team, 2017).

## 3. Results

Between 2005 and 2017, a total of 15,481 plots were sampled, in 2835 plots there were signs of capercaillie presence. Of the 13,557 plots closer than 1092 m to recreation infrastructure, we observed signs of capercaillie presence on 2278 plots.

### 3.1. Relative capercaillie densities per study region

The two predictors (Avg_HSI and Recr_area) were moderately negatively correlated ($r_s = -0.53$). The GLMM's revealed a significant linear relationship between the average habitat suitability index and the capercaillie density, but not for the percentage of sample plots located within a distance of 145 m to recreation infrastructure (Recr_area) (Table A.1). The visual interpretation of the scatterplot suggested a step-shaped response to the percentage of plots within 145 m of recreation infrastructure (Fig. 2): areas with less than 50% Recr_area (i.e.

**Table 3**
Predictors included in the generalized linear mixed models, analysing the effects of habitat suitability (HSI) and recreation infrastructure on the density (a) and on local habitat use (b) of capercaillie.

| Model | Predictor | Description | Unit | Type | Scale |
|---|---|---|---|---|---|
| a) | Avg_HSI | Mean habitat suitability for the study area | 0–1 | Continuous | Study area |
| | Recr_area | Proportion of study area within distances < 145 m of recreation infrastructure | Percent | Continuous | Study area |
| | Recr_pressure | Less than 50% (low) or over 50% (high) of the study area being within 145 m of recreation infrastructure | Low-high | Categorical | Study area |
| b) | HSI | Habitat suitability index per plot | 0–1 | Continuous | Plot |
| | Recr_dist | Distance to nearest recreation infrastructure | Meters | Continuous | Plot |
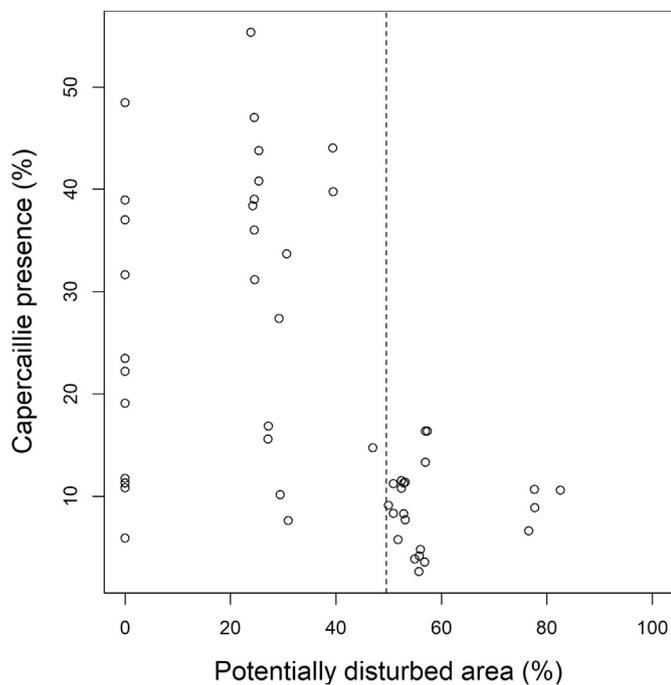
**Fig. 2.** Scatterplot showing the percentage of sampling plots with relative capercaillie densities per site and study year in relation to the percent of plots within 145 m of recreation infrastructure. The dashed line in the right panel marks 50%.

**Table 4**
Generalized linear mixed models describing the relative capercaillie density per study area as a function of average habitat suitability (Avg_HSI) and the binary predictor recreation pressure (Recr_pressure) (panel A), as well as the interaction between the two predictors (panel B). Study areas with over 50% of the sampling plots within 145 m of recreation infrastructure were classified as "high pressure" and as "low pressure" otherwise. "Low pressure" served as the reference category. SD indicates the standard deviation of the random factor (study area).

| A | SD Study area: 0.489 | | |
|---|---|---|---|
| Predictor | Estimate | Std. error | P-value |
| Intercept | −2.422 | 0.558 | 0.001 |
| Recr_pressure (high) | −0.900 | 0.383 | 0.038 |
| Avg_HSI | 3.139 | 1.198 | 0.013 |

| B | SD Study area: 0.503 | | |
|---|---|---|---|
| Predictor | Estimate | Std. error | P-value |
| Intercept | −2.51 | 0.684 | < 0.001 |
| Recr_pressure (high) | −0.606 | 0.926 | 0.526 |
| Avg_HSI | 3.435 | 1.497 | 0.028 |
| Avg_HSI*Recr_pressure (high) | −0.907 | 2.561 | 0.726 |

dashed line in Fig. 2) showed higher capercaillie presence rates compared to the areas with a higher percentage of plots close to recreation infrastructure.

The threshold was applied to create a binary predictor of human recreation pressure (Recr_pressure) assigning "low pressure" to areas with less than 50% disturbed plots and "high pressure" to areas with more than 50%. The combination of this variable with the average HSI in a linear mixed model revealed a positive relationship between capercaillie observation densities and habitat suitability and a negative effect of high recreation pressure (Table 4, panel A). However, we found no significant interaction between the two predictors on the

study region scale (Table 4, panel B). In addition, the large standard deviation of the random effect (study area) indicates a large effect of the study area on the capercaillie density (Table 4).

*3.2. Habitat use analysis*

At the sampling-plot scale, predictors (Recr_dist, HSI) were only weakly correlated (Spearman rank: Full model = 0.22, Reduced model = 0.19). Both in the full model and the one based on the reduced dataset, the probability of capercaillie presence was positively correlated with increasing habitat suitability and with increasing distance to recreation infrastructure (Table 5). In addition, an interaction between the two variables was detected showing that the effect of recreation infrastructure was higher under unfavourable habitat conditions and slightly buffered in case of suitable conditions (Fig. 3, Fig. A.1). In both models, the odds ratio of HSI was higher compared to those of distance to recreation (Recr_dist), indicating habitat suitability being the more important predictor (Table 5). The large standard deviations of the random effects indicate a large effect of study area and study year on the probability of finding a capercaillie sign (Table 5). Both models performed well in discriminating between presence and absence plots (i.e. AUC values above 0.75, Table 5).

**4. Discussion**

We analysed the effects of recreational activities and habitat suitability on relative densities and habitat use of a locally endangered bird species. Our sample included different populations of capercaillie across a large geographical range, covering diverse habitat conditions for the focal species and a range of human recreation activity levels. Our results indicate that recreational infrastructure affects habitat use and might even lead to lower densities of a locally endangered species. Study areas with over 50% of the habitat potentially disturbed by recreation activities (i.e. within 145 m of recreation infrastructure) held significantly lower relative capercaillie densities compared to areas less disturbed by recreation (Table 2). These results correspond to previous studies showing other bird species being resilient to low levels of recreation disturbance, but being negatively affected by high levels of disturbance (Morse et al., 2006, Pearce-Higgins et al., 2007). The average habitat suitability proved to be meaningful in explaining the amount of capercaillie signs found per study area, but - contrary to our hypothesis - we could not find any evidence that habitat suitability mitigated impacts of recreation intensity on relative capercaillie densities. However, we can still not exclude that the absence of a signal is due to limitations in the underlying sample. Even though we investigated 13 different study areas, spread over a large geographical range, the dataset used for analyses at the study area scale is still relatively small. Future studies including more study areas might therefore reveal a signal that was not detected in our sample. Furthermore it would be advisable to include data on recreation intensity, and not just the location of the recreation infrastructure in future studies. Our results indicate that improving habitat suitability over a large scale is likely to benefit local capercaillie populations.

Contrary to the results at the larger spatial scale (i.e. study area), we found a clear interaction between the effects of the distance to recreation infrastructure and habitat suitability on local-scale habitat selection. The probability of habitat use was lower in close vicinity of recreation infrastructure, and this effect was amplified under poor and slightly mitigated under good habitat conditions (Fig. 3). This shows that specific vegetation structures can modulate wildlife responses to human recreation activities (Kangas et al., 2010; Wolf et al., 2013; Coppes et al., 2017b), e.g. by providing visual shelter, and that habitat suitability which includes both good foraging conditions and cover plays a major role. Nevertheless, the compensatory effect of habitat suitability was only small and good habitat conditions led only to a slight increase in probability of presence, with effects most pronounced

**Table 5**

Generalized linear mixed models describing the probability of capercaillie presence per sampling plot as a function of habitat suitability (HSI), the distance to recreation infrastructure (Recr_dist) and the interaction thereof, across the whole study area (a: full model) and including only plots within the area potentially influenced by recreation infrastructure, i.e. within 1092 m distance to recreation infrastructure according to Coppes et al. (2017b) (b: reduced model). The odds ratios ( ± 95% confidence interval) were calculated to compare the effect sizes. Estimates of the random factors are the SD Study area, and SD Year:Area. The performance of models was evaluated using the area under the receiver operator characteristics curve (AUC).

| Predictor | a) Full model | | | | b) Reduced model | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | AUC: 0.777 ± 0.005 | | | | AUC: 0.784 ± 0.005 | | | |
| | SD Study area: 0.605 | | | | SD Study area: 0.623 | | | |
| | SD Year:Area: 0.407 | | | | SD Year:Area: 0.391 | | | |
| | Estimate | Std. error | Odds ratios (95% CI) | P-value | Estimate | Std. error | Odds ratios (95% CI) | P-value |
| Intercept | −1.682 | 0.183 | 0.19 (0.13–0.27) | < 0.001 | −1.798 | 0.195 | 0.17 (0.11–0.24) | < 0.001 |
| Recr_dist | 0.328 | 0.046 | 1.39 (1.27–1.52) | < 0.001 | 0.223 | 0.032 | 1.25 (1.17–1.33) | < 0.001 |
| HSI | 0.546 | 0.027 | 1.73 (1.64–1.82) | < 0.001 | 0.603 | 0.030 | 1.83 (1.72–1.94) | < 0.001 |
| Recr_dist*HSI | −0.144 | 0.023 | 0.87 (0.83–0.91) | < 0.001 | −0.121 | 0.024 | 0.89 (0.85–0.93) | < 0.001 |
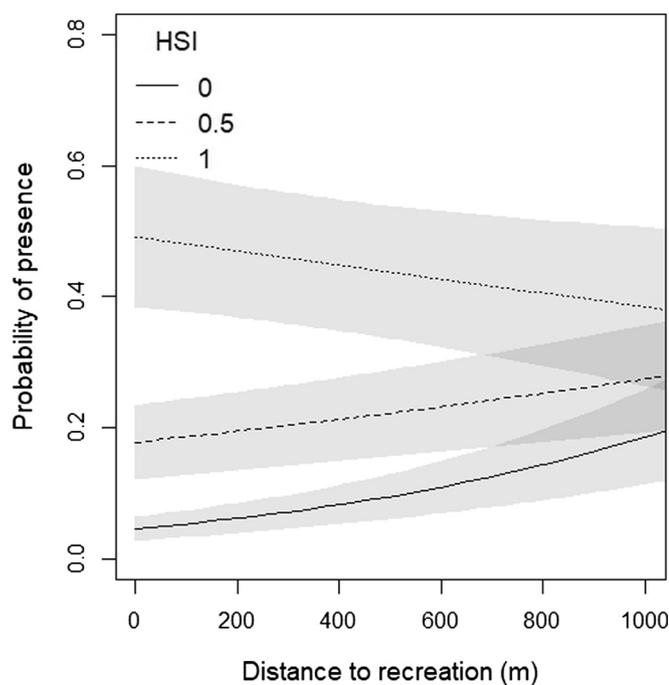


**Fig. 3.** Interaction between habitat suitability (HSI) and distance to recreation infrastructure. The probability of finding a capercaillie sign within different distances to recreation infrastructure is shown for different habitat suitability values (HSI = 0, 0.5, 1) for the "reduced model". The model considers only plots within the potential effect-range of recreation infrastructure in < 1092 m distance (Coppes et al., 2017b).

in close vicinity to recreation infrastructure. Consequently, habitat improvement might be one accompanying management aspect close to human recreation activities, but it might not entirely compensate for disturbing effects of human presence. Habitat suitability was the most important variable in explaining capercaillie presence/absence, however, according to the odds ratios, it's impact only marginally exceeded the one of recreation infrastructure (Table 5). This indicates limitations in reducing impacts of recreation infrastructures by merely improving habitat suitability. Highly suitable habitat per definition both provides good food supply and shelter within short distances (Storch, 2002). In highly suitable habitat, it is therefore easier to hide while being close to good foraging conditions compared to poor habitats. Capercaillie habitats with low HSI-scores are characterised by dense or very sparse canopy cover and little or to high ground vegetation, offering only poor

shelter or escape options against predators, disturbances and unfavourable weather conditions. Concurrently, such habitats provide poor feeding resources (i.e. ground vegetation rich in bilberry and insects). It has been shown, that human disturbance along recreation infrastructure is comparatively predictable in time and space for many wildlife species to adjust to it (Miller et al., 2001; Baines and Richardson, 2007; Coppes et al., 2017a): in fact, capercaillie might be more likely to take the risk of encountering a human for availing of good habitat. The fact that they avoid the infrastructure designated for human recreational activities indicates that the infrastructure forms a landscape of fear (Laundré et al., 2010; Rösner et al., 2014). However, while direct presence of humans might have negative effects, indirect factors linked to human recreation activities might be responsible for avoidance of recreational trails (Watson and Moss, 2004), such as increased predator presence (Storch and Leidenberger, 2003).

Local avoidance of zones adjacent to recreation activities might be considered functionally equivalent to habitat loss, as important resources close to trails are not - or only temporarily - accessible, which can in turn affect large parts of a population (Coppes et al., 2017b). Our findings for capercaillie are in line with observations for other grouse species: For black grouse, Patthey et al. (2012) described spatial avoidance of roads, forest tracks or walking paths by hens during the summer months and Immitzer et al. (2014) reported significantly lower probabilities of black grouse presence within a 50 m buffer zone around hiking trails. Such zones of avoidance mean effective loss of habitats, at least within certain temporal windows of human presence.

As habitat loss and habitat deterioration have been ranked as top priority threats for European grouse species by national experts (Storch, 2007), net habitat losses due to human presence might be a critical drivers of the species´ occurrence. Our results suggest that local mitigation through high habitat suitability can increase the local probability of use of potentially disturbed areas, but may buffer such population effects only up to a certain point: In the case of capercaillie there seems to be a threshold (i.e. 50% of potentially disturbed area) above which population densities drop significantly in relation to recreational activities.

In contrast to previous studies which investigated effects of human disturbance on wildlife using case studies (i.e. few study areas), our study includes multiple study areas, with diverse habitat conditions as well as differences in human recreational use. We found a large variance between study areas and years; at both spatial scales the SD values of the random effects in our models were of similar magnitudes as those of the predictors (Recr_dist, HSI). One potential source of variance might be the intensity of use of the recreation infrastructures (i.e. the number of people using the infrastructure), which is likely to differ between areas, but was out of scope to be quantified in our study. The

differences between areas might also be explained by large-scale landscape effects: whereas the German study areas were located in fragmented forest landscapes (Storch, 2007; Coppes et al., 2016), the Austrian study areas were mostly located in continuous forest landscapes and at higher altitudes with colder and therefore climatic conditions more favourable for capercaillie (Braunisch et al., 2013). Due to our consistent results across this large geographical range as well as time span, we are confident that our results are widely applicable.

## 5. Conclusions and management implications

Our results agree with those of previous studies showing that vegetation structure can moderate wildlife reactions to recreation activities (Kangas et al., 2010; Wolf et al., 2013). Consequently, active habitat management may mitigate detrimental effects of recreation activities on local habitat use to some degree. However, this buffering effect was relatively small and could not compensate for negative effects of high recreation pressure on population densities.

Considering negative impacts of human recreation on capercaillie revealed by other studies, ranging from behavioural adaptations (Summers et al., 2007; Thiel et al., 2007; Moss et al., 2014; Coppes et al., 2017b) to physiological effects (Thiel et al., 2011; Coppes et al., 2018), we therefore advise to apply the precautionary principle, when planning new recreational activities in capercaillie habitat (Braunisch et al., 2015). Especially in areas with low and/or declining population numbers, densities of recreation infrastructure should be minimized (i.e. the area influenced by recreation infrastructure should be reduced to below 50% as a minimum) to avoid detrimental effects on local populations. At a local scale, habitat structures along recreational trails

should be managed to improve habitat suitability (this study) and decrease visibility ranges (Wolf et al., 2013; Coppes et al., 2017b).

A frequently recommended management measure to reduce negative effects of recreation on wildlife is to create wildlife refuges, where recreation activities are prohibited (Braunisch et al., 2011; Moss et al., 2014; Larson et al., 2016; Coppes et al., 2017a; Coppes et al., 2017b). Our study emphasizes the importance that such refuges cover significant parts of a species range (i.e. > 50% for capercaillie) as well as the importance of high quality habitats within the refuges.

## Appendix A

Table A.1
Results of the generalized linear mixed models relating the percentage of plots with capercaillie signs per area and year to the average habitat suitability (Avg_HSI) and the percent of sample plots located within a distance of 145 m to recreation infrastructure (Recr_area). Descriptions of the predictors can be found in Table 3.

| Predictor | SD Study area: 0.536 | | |
| --- | --- | --- | --- |
| | Estimate | Std. error | P-value |
| Intercept | −2.598 | 0.593 | < 0.001 |
| Recr_area | −0.012 | 0.007 | 0.111 |
| Avg_HSI | 3.878 | 1.139 | 0.002 |

Table A.2
Generalized linear mixed models describing the probability of capercaillie presence per sampling plot as a function of habitat suitability (HSI), the distance to recreation infrastructure (Recr_dist) and the interaction thereof, across the whole study area (full model). The odds ratios ( ± 95% confidence interval) were calculated to compare the effect sizes. Estimates of the random factors are the SD Study area, and SD Year:Area. The performance of models was evaluated using the area under the receiver operator characteristics curve (AUC). The results of the reduced model are presented in Table 5.

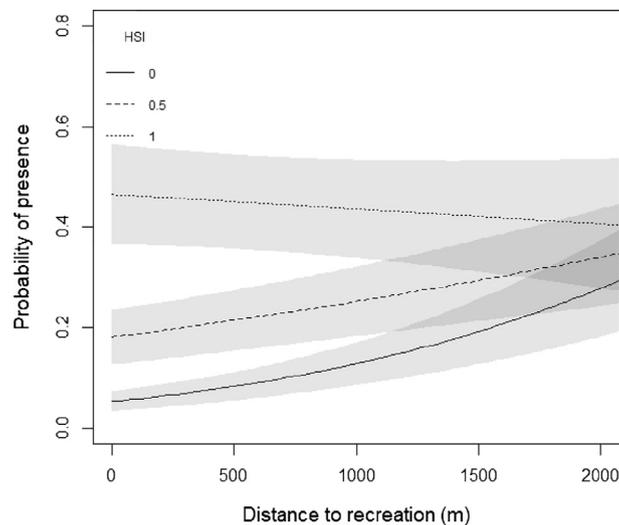| Predictor | Full model | | | |
| --- | --- | --- | --- | --- |
| | AUC: 0.777 ± 0.005 | | | |
| | SD Study area: 0.605 | | | |
| | SD Year Area: 0.407 | | | |
| | Estimate | Std. error | Odds ratios (95% CI) | P-value |
| Intercept | −1.682 | 0.183 | 0.19 (0.13–0.27) | < 0.001 |
| Recr_dist | 0.328 | 0.046 | 1.39 (1.27–1.52) | < 0.001 |
| HSI | 0.546 | 0.027 | 1.73 (1.64–1.82) | < 0.001 |
| Recr_dist*HSI | −0.144 | 0.023 | 0.87 (0.83–0.91) | < 0.001 |

**Fig. A.1.** Interaction between habitat suitability (HSI) and distance to recreation infrastructure. The probability of finding a capercaillie sign within different distances to recreation infrastructure is shown for different habitat suitability values (HSI = 0, 0.5, 1) for the "full model", including all data.

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