



Outdoor recreation causes effective habitat reduction in capercaillie *Tetrao urogallus*: a major threat for geographically restricted populations

Joy Coppes, Judith Ehrlicher, Rudi Suchant and Veronika Braunisch

J. Coppes (joy.coppes@forst.bwl.de), J. Ehrlicher, R. Suchant and V. Braunisch, Forest Research Inst. of Baden-Wuerttemberg FVA, Freiburg, Germany. VB also at: Conservation Biology, Inst. of Ecology and Evolution, Univ. of Bern, Switzerland.

Outdoor recreation inflicts a wide array of impacts on individual animals, many of them reflected in the avoidance of disturbed areas. The scale and spatial extent, however, at which wildlife populations are affected, are mostly unclear. Particularly in geographically isolated populations, where restricted habitat availability may preclude a relocation to undisturbed areas, effective habitat reduction may remain underestimated or even unnoticed, when animals stay in disturbed areas and only show small-scale responses. Based on telemetry data, we investigated the spatial and seasonal effects of outdoor recreation – in relation to landscape and vegetation conditions – on western capercaillie *Tetrao urogallus*, considering two scales, home range and within-home range habitat selection. We determined the distance-thresholds up to which recreation infrastructures were avoided and estimated the extent of affected habitat for the isolated Black Forest (southwestern Germany) study population. While outdoor recreation did not affect home range selection, strong effects on habitat use within the home range were detected: distance to recreation infrastructure (hiking and cross-country skiing trails, ski pistes) was the main determinant of habitat selection in winter; in summer, mountain bike trails and hiker's restaurants were avoided up to an average distance of 145 m (CI: 60–1092 m). Around winter-infrastructure, relative avoidance was recorded up to 320 m (CI: 36–327 m), it was reduced, however, when dense understory provided visual cover. Of the entire population area, between 8–20% (summer) and 8–40% (winter) were affected by outdoor recreation, mainly in the high altitudes. Even without evident large-scale shifts in species distribution, local-scale avoidance of outdoor recreation can substantially contribute to effective habitat reduction. Based on our results we recommend a general reduction in recreation infrastructure density in key habitats, the establishment of undisturbed wildlife refuges with a diameter of at least 800 m, as well as enhancing visual protection by maintaining a strip of dense understory along trails.

With the growing numbers of outdoor recreationists, their impact on the environment is likely to be increasing (Rankin et al. 2015, Tolvanen and Kangas 2016). Wildlife responds to the presence of humans in their habitats (Beale and Monaghan 2004), with reactions varying from physiological responses such as increased heart rate (Weimerskirch et al. 2002) or increased stress hormone levels (Walker et al. 2006, Formenti et al. 2015) to behavioral reactions which include fleeing or flushing (Keller 1995, Miller et al. 2001, Thiel et al. 2007, Sönnichsen et al. 2013) and behavioral adaptations such as changes in vigilance behavior (Fernández-Juricic and Telleria 2000, Beale and Monaghan 2004, Jayakody et al. 2008). Recreation activities have been shown to reduce woodland bird densities (van der Zande et al. 1984), bird community composition and nest predation (Miller et al. 1998) or breeding success (Anderson and Keith 1980, Ahlund and Götmark 1989). Effects of this so called 'anthropogenic disturbance' – in this context defined as any form of human presence that triggers one of the above responses in wildlife – varies widely between species (Ficetola et al. 2007), and can

differ between sexes in the same species (Baydack and Hein 1987, Moss et al. 2014). Furthermore they strongly depend on the exact type of human activity or even the way humans behave during the same type of activity (Fernández-Juricic et al. 2005). A behavioral reaction (i.e. fleeing, flushing) will bear direct energetic costs (Arlettaz et al. 2015, Tablado and Jenni 2015), whereas repeated disturbance might lead to reduced use or abandonment of otherwise suitable habitats (Taylor and Knight 2003, Buckley 2011, Ciuti et al. 2012, Immitzer et al. 2014, Tablado and Jenni 2015) which would effectively result in habitat loss or deterioration. Where these reactions clearly pertain to individuals, the effects on wildlife populations have are only rarely quantified (Gill et al. 2001, Liley and Sutherland 2007) which is mainly linked to the scale at which the disturbance takes place (Gill 2007). Although avoidance of disturbed habitat seems one of the most evident reactions of animals towards human presence, it is difficult to assess the spatial extent of effective habitat reduction at population level, as the scale at which disturbance effects operate is often unknown, and may deviate

from the scale at which population responses are considered. Especially in geographically isolated populations, where restricted habitat availability may hinder a large-scale relocation to undisturbed areas, effective habitat reduction may be underestimated or even remain unnoticed, when animals stay in disturbed areas and only show local-scale responses.

Anthropogenic disturbance has long been recognized as a problem for capercaillie *Tetrao urogallus* conservation in central Europe (Storch 2007), where populations are spatially restricted to mountain habitats (Segelbacher et al. 2003). As these regions are at the same time hotspots for outdoor recreation, potential conflicts between human recreation and capercaillie conservation have become a major focus in several management plans (Hennig and Künzl 2011, Braunisch and Suchant 2013). Various studies showed the sensitivity of capercaillie towards human presence: although Brenot et al. (1996) and Moss et al. (2014) did not find a significant effect of anthropogenic disturbance on capercaillie reproduction, high intensities of winter recreation have been associated with increased flushing distances (Thiel et al. 2007) and elevated stress hormone levels (Thiel et al. 2008, Thiel et al. 2011). Capercaillie have been shown to avoid the vicinity of hiking trails in summer (Moss et al. 2014) and roosting trees close to woodland tracks in winter (Summers et al. 2007), while an overall reduction of local capercaillie densities was recorded in areas highly frequented by recreational activities (Rösner et al. 2013). These studies show that capercaillie are influenced by anthropogenic disturbance, however at which scale this affects individual habitat selection, and how these effects translate into effective habitat reduction at the population level, is still unclear (Storch 2013).

Based on telemetry, we studied the effects of human outdoor recreation and associated infrastructure on capercaillie habitat selection at two spatial scales: 1) home range-selection within the study area and 2) habitat selection within the home range in relation to landscape and vegetation conditions during winter and summer. We hypothesized, that variables representing anthropogenic disturbance would significantly affect habitat use, but might be counteracted by topo-climatic constraints during home range-selection. To estimate the amount of affected habitat at the population level, we determined the distances up to which areas influenced by human presence were avoided and extrapolated the results to the total area occupied by a geographically restricted capercaillie population in southwestern Germany. We illustrate the magnitude at which small-scale individual responses to outdoor recreation can accumulate to large-scale habitat deterioration and present management options to reduce or mitigate these effects.

Material and methods

Study area

The study was conducted in the Black Forest, a lower mountain range, southwestern Germany of 7000 km² in size. The study area was located around the highest mountain 'Feldberg' with altitudes ranging between 700 and 1493 m a.s.l. (Fig. 1) mainly consisting of forest, intermixed with open areas used for cattle grazing in summer and ski pistes

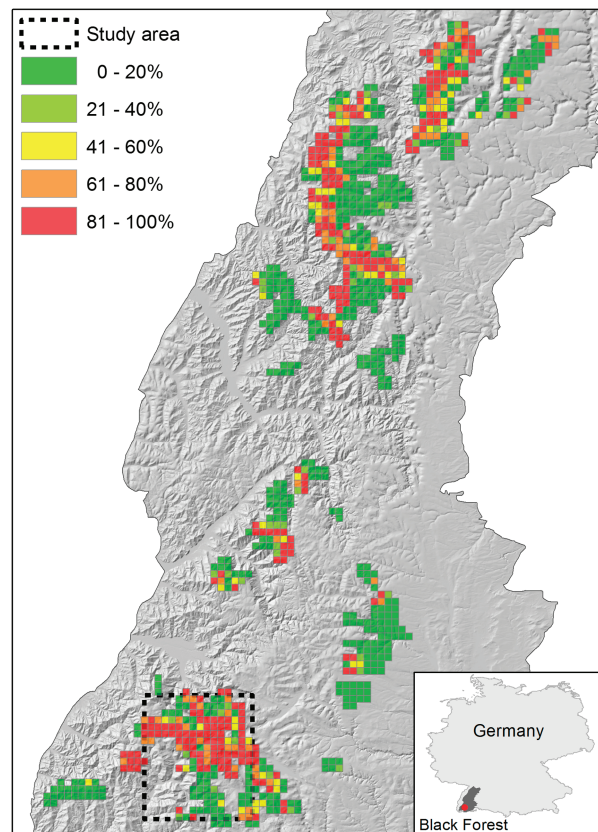


Figure 1. Capercaillie distribution in the Black Forest, southwestern Germany (shown are all 1 km² squares with capercaillie presence). Colors indicate the proportion of habitat within the respective square that is influenced by winter recreation (i.e. within 320 m from winter recreation infrastructure).

during winter. We focused on 8284 ha of managed forests, dominated by Norway spruce *Picea abies* (49%), European silver fir *Abies alba* (19%) and common beech *Fagus sylvatica* (22%; Suchant et al. 2003). The Feldberg and the surrounding mountains attract large numbers of recreationists, both during winter and summer. In winter there are several ski pistes, cross-country skiing trails, snowshoe trails and designated winter hiking trails; in addition, various off-trail activities (i.e. snowshoeing, geo-caching, collecting berries and mushrooms) are performed in the area (Coppes and Braunisch 2013). During summer, the area offers a dense network of hiking and mountain bike trails. Over the past decade, visitor numbers have been steadily increasing with 35% more visitors in 2015 compared to 2004 (Statistisches Landesamt 2016).

Model species

We chose the western capercaillie as a model species as it has been shown to be highly sensitive towards human disturbance, while its spatial distribution shows a high degree of co-occurrence with outdoor recreation (Thiel et al. 2008, Storch 2007). The species occurs over a wide geographical range across Northern Eurasia and is thus not threatened globally (BirdLife-International 2012), but is red-listed in all central European countries (Storch 2007) due to its small,

declining and isolated populations (Segelbacher et al. 2003, Storch 2007, Coppes et al. 2015). The Black Forest capercaillie population is the largest central European population outside the Alps, but is isolated from other populations in Europe (Segelbacher et al. 2003) and highly fragmented (Braunisch et al. 2010, Coppes et al. 2016). Based on annual counts at the leks, the population is estimated at about 400 to 500 individuals (Coppes et al. 2016) which roughly corresponds to the estimated minimum viable population size as calculated by Grimm and Storch (2000). Over the last 30 years capercaillie numbers have rapidly declined by about 65% (Coppes et al. 2016), which resulted in being red listed as 'endangered' in the state of Baden-Württemberg (Hölzinger et al. 2007).

Since 1988, the capercaillie distribution in the Black Forest has been monitored. Every five years, the minimum area of species distribution is delineated, based on a collation of all available direct and indirect evidence of capercaillie presence provided by foresters, hunters, ornithologists, conservation volunteers and research personnel. Forest patches are classified as 'inhabited' when at least three capercaillie records occurring with a maximum distance of 1000 m from another have been collected within the preceding five year period, and are delineated by the minimum polygon encompassing these records (Braunisch and Suchant 2006, Coppes et al. 2016). The Black Forest capercaillie population is currently distributed across 45 666 ha (2013), forming four main subpopulation clusters (Fig. 1). The telemetry study was conducted in the southern Black Forest subpopulation (Coppes et al. 2016).

Capercaillie data

To avoid negative effects on mating and reproduction, catching and tagging of the birds was performed in autumn (September–November) using walk-in nets which were put up in various locations throughout the study area, mainly in forest gaps and clearings. The weight of the transmitters was kept below 3% of the body weight, resulting in males equipped with a 40–69 g backpack radio-transmitter and females with a 25–40 g backpack radio-transmitter (model GPI, Titley Electronics, Ballina, Australia; model A1540, Atstrack Advanced Telemetry Systems, Isanti, MN; and model PTT-100, Microwave Telemetry, Columbia, MD). Using a handheld antenna, birds were located by 'homing in', i.e. determining the direction of the signal from at least three locations (Kenward 2001). Birds were only located during daytime (defined as the time with daylight one hour after sunrise and before sunset) so as to represent the time when most recreation activities are performed. On average, one relocation per bird was taken at each tracking day, and relocation times for each bird were shifted across the daytime so as to avoid a daytime-bias.

We evaluated locations taken during two predefined time periods, summer (June–September) and winter (December–March). The seasons were defined so as to exclude shifts in habitat use related to the mating season (April–May) where individuals accumulate at the leks, and to exclude the peaks of spring and autumn dispersal (Moss et al. 2006). The

winter season encompassed only days with a continuous snow layer, to assure that winter recreation infrastructure was usable. Data of an individual and season were only included in the analysis if at least 20 locations in the respective season were available (Table 2).

Environmental variables

The predictor variables we hypothesized to affect capercaillie habitat use were classified into three categories: landscape and topography, vegetation structure, and human presence (Table 1). Of the first category, topographical variables (altitude, slope, aspect) were calculated from the digital elevation model with a 25 m resolution. Mean temperature (°C) in winter (December to March) and in summer (June to September) were derived from the worldclim-dataset (Hijmans et al. 2005) (<www.worldclim.org>) and downscaled from a resolution of 1 km to 100 m based on the SRTM-V4 digital elevation model as described by Zimmermann and Roberts (2001). Forest cover and distance to forest edges (outer, inner, both) were derived from the official topographic and cartographic information system of Germany (ATKIS, <www.atkis.de>). Outer forest edges were defined as edge between forest and non-forested open areas (i.e. grazing meadows, settlements), inner forest edges as the edges to gaps and clearings inside the forest. Vegetation structure was mapped in summer at forest-stand level, i.e. homogeneously structured forest management units with a mean size of 4.0 ha (min: 0.1, max: 45.7). Variables describing tree species and ground vegetation composition as well as vertical and horizontal stand structure (Table 1) were recorded using the method described in Suchant and Braunisch (2004). Predictors indicating human presence included the locations of roads, settlements, parking sites and restaurants, which were adopted from the official topographic and cartographic information system of Germany (ATKIS). Recreation infrastructure was derived from regional touristic information maps, distinguishing between infrastructure for activities in summer (hiking trails and mountain biking routes) and winter (winter hiking trails, snowshoe trails, cross country skiing trails and back country skiing routes as well as ski pistes). In addition, for both seasons the distance to the next recreational infrastructure – independent of its type – was assessed. All predictors were prepared as raster maps with a 10 × 10 m resolution. To account for possible radio tracking errors, we calculated the mean for continuous and the majority for categorical variables within a circular moving window with 50 m radius, which corresponded to the mean location error (as determined in preceding tests). Variable preparation was processed using ArcGIS 10.3 (ESRI 2014).

To determine the extent of habitat deterioration through outdoor recreation for the entire distribution area of the Black Forest capercaillie population, area-wide data on designated hiking and mountain bike trails and official winter recreation (i.e. ski-lifts and cross-country skiing trails) were adopted from the Tourism and Recreation Information System TFIS Baden-Württemberg, Germany

Table 1. Predictor variables of the categories landscape and topography, vegetation structure and human presence retained in the models (Table 3 and 4).

Predictor type	Variable name	Description (unit)	Type	
Landscape and topography	Altitude	Altitude (m a.s.l.)	continuous	
	Slope	Slope (degree)	continuous	
	Northing	Northness (cosine aspect)	continuous	
	Temperature_W	Average temperature (December to March) (°C)	continuous	
	Outer Forestedge	Distance to nearest outer forest edge (km)	continuous	
	Inner Forestedge	Distance to nearest Inner forest edge (km)	continuous	
	Forestedge	Distance to nearest outer or inner forest edge (km)	continuous	
Vegetation structure	Stand	Stand type 0 = Spruce > 95% (reference category) 1 = Spruce-Mix (> 50% Spruce) 2 = Beech-Mix (> 50% Beech)	categorical	
	Canopy_cover	Canopy cover (%)	continuous	
	Successional stage	Successional stage 0 = Open (reference category) 1 = Regeneration 2 = Thicket 3 = Pole stage 4 = Tree stage 5 = Old forest	categorical	
	Structure	Horizontal layers in canopy 1 = One layer (reference category) 2 = Two layers 3 = > Two layers	categorical	
	Softwoods	% of Softwoods trees (Sorbus sp., Salix sp., Alnus sp.)	continuous	
	Shrub_distr	Distribution of Shrubs (1.3 – 5 m) 0 = No Shrubs (reference category) 1 = Single trees 2 = Small groups (5–20 m diameter) 3 = Large groups (21–40 m radius) 4 = Evenly spread	categorical	
	Canopy_gaps	Number of canopy gaps per ha (n)	continuous	
	Shrub_cover	Cover of shrub layer (1.3–5 m) (%)	continuous	
	Ground_height	Height of ground vegetation (cm)	continuous	
	Ground_cover	Cover of ground vegetation (%)	continuous	
	Bilberry	Bilberry cover (%)	continuous	
	Grass	Grass cover (%)	continuous	
	Moss	Moss cover (%)	continuous	
	Fern	Fern cover (%)	continuous	
	Herbs	Cover of other herbaceous plants (%)	continuous	
	Human presence	Hiking_dist	Distance to marked hiking trails in summer (km)	continuous
		Biking_dist	Distance to marked mountain bike trails in summer (km)	continuous
Recreation_W		Distance to any winter recreation infrastructure (km)	continuous	
Road_dist		Distance to (trafficable) roads (km)	continuous	
Settle_dist		Distance to settlements (km)	continuous	
Restaurant_dist		Distance to guesthouses or restaurants (km)	continuous	
Parking_dist		Distance to car parking places (km)	continuous	

(<www.lgl-bw.de>). Since no official, area-wide source for snowshoe trails, back country skiing tracks or designated winter hiking trails was available, and since many of the summer hiking trails are not officially open or accessible during winter, we complemented our dataset with data provided by specific user groups on the internet. Websites (<www.outdooractive.de, www.gpsies.com>, <www.bergfex.de>) were searched for tracks of snowshoe trails, back-country skiing tours or winter hiking trails. On these websites, both private persons as well as official municipal touristic organizations publish tracks of tours which they advise to use for winter recreation. GPS tracks (.kml files) were downloaded and transferred to shape files using ArcGIS 10.3 (ESRI 2014). This resulted in an area-wide dataset of ascertained outdoor recreation infrastructure for both seasons.

Statistical analysis

Habitat selection

For each bird seasonal ‘home ranges’ were calculated, which we define here as the 100% minimum convex polygon (MCP) encompassing the telemetry locations. To assess habitat selection at two spatial habitat scales a used versus non-used design was applied, comparing the presence data with two sets of pseudo-absence locations, in the following termed as ‘absence’. To model home range selection within the study area (second order habitat selection, Johnson 1980), the presence locations of each individual were contrasted against the same number of random locations generated outside of the home range of each respective individual, excluding a 100 m buffer (twice the average telemetry error

to avoid overlaps between the surroundings of presence and pseudo-absence points), but within a maximum distance of 3.9 km (average maximum distance between locations for tagged capercaillie in this study) to ensure that all locations could potentially be reached by the respective individual. To analyze habitat use within the home range (third order habitat selection, Johnson 1980), we generated a second set of absence locations within the MCP home range, again with a minimum distance of 100 m (twice the average telemetry error) to existing telemetry locations (Supplementary material Appendix 1 Fig. A1).

Habitat selection was analyzed using generalized linear mixed effects models (GLMM, R-package: lme4, Bates et al. 2014) with a binomial error structure (logit link), including the individual as a random factor. First, starting with the initial set of variables (Table 1), we discarded of pairs of strongly correlated variables (Spearman's $R > |0.5|$) the variable that explained less in a univariate model according to Akaike's information criterion AIC (Burnham and Anderson 1998). Multivariate models, testing all possible combinations of the remaining variables, were then fitted using the dredge function (R-package MuMin, Bartón 2013) in order to find the most parsimonious model according to the AIC. If models did not differ significantly ($\Delta AIC < 2$) from the 'best model', model averaging was applied. For each season we fitted a model for 1) home range selection within the study area and 2) habitat selection within the home range. The models' performance to discriminate between all presence and absence locations was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC, R-package AICcmodavg, Mazerolle 2014). To assess the relative importance of the predictors in the final model, a leave-one-out jackknife procedure was applied, omitting each variable at a turn and calculating the difference in AIC (ΔAIC) between the reduced and the final model.

To verify whether the data of both sexes could be pooled, we tested – prior to modelling – for sex-specific differences in habitat use by univariately comparing the presence data of males and females with regard to the environmental variables using univariate generalized linear mixed models (logit link) with the individual as a random factor.

In addition, we tested for a possible bias due to different numbers of relocations per bird and associated MCP sizes on the model results by subsampling all individuals with the minimum number of presence locations for the respective season. To avoid a temporal bias, we took only the first locations of each individual into account and generated the same number of absence locations within and outside the respective (smaller) MCP as previously described.

Distance thresholds

To assess whether there were distance-thresholds up to which the presence of outdoor recreation infrastructure significantly reduced presence probability, conditional inference trees were calculated (CIT, R-package 'party', Hothorn et al. 2011). This method uses recursive partitioning to select significant predictor variables in an hierarchical way and to identify the threshold that best splits the dataset into predicted presence

and absence (Hothorn et al. 2006). To account for multiple testing a Bonferroni correction was applied. The 95% confidence interval (CI) of each threshold value was determined, using bootstrapping (1000 replicates). Conditional inference trees were run using a minimum split criterion (minsplit) of 50. In a first step, univariate CIT's were applied to the recreation infrastructure variables. In a second step, we tested whether the avoidance of recreation infrastructure would be modulated by the vegetation structure along the trails and the associated possibility to hide, which might offer a possibility to mitigate effective habitat reduction by forest management. Therefore, a multivariate CIT was run including the significant outdoor recreation infrastructure variable combined with three variables that could offer visual protection, ground vegetation height, ground vegetation cover and shrub cover. All statistical analyses were performed using the software R (R Core Team).

Habitat deterioration at the population level

To estimate amount of habitat affected by outdoor recreation throughout the Black Forest capercaillie population we calculated the proportion of the area inhabited by capercaillie (as of 2013, Coppes et al. 2016) that was located within the critical distance thresholds. To ensure a conservative estimate (i.e. not to overestimate the influence of recreation activities) the affected area was only calculated using the average threshold value and its lower 95% confidence interval. In addition to the overall proportion of influenced habitat, we calculated the respective proportion for the distribution area mapped within each 1 km² square with capercaillie presence, using ArcGIS 10.3 (ESRI 2014).

Results

Capercaillie data

Using the predefined filtering criteria, data of 12 individuals (6 females, 6 males) with a total of 1024 locations were included in the analysis. Due to the loss of birds over time, more data for the winter (11 birds, 881 locations) compared to the summer season (7 birds, 213 locations) was available (Table 2). On average there were 30 (range: 23–37) locations per bird in summer and 62 (range: 25–99) locations in winter. In summer, the average MCP-home range sizes of males ($n = 3$) was with 581 ha (SD: ± 355 ha) more than twice as large as those of females ($n = 4$) with 207 ha (± 32 ha). During winter the birds' home range size decreased, with males ($n = 6$) using on average an area of 182 ha (± 48 ha) whereas females ($n = 7$) had an average MCP size of 86 ha (± 30 ha). MCP-size was significantly correlated with sex (linear model, $p = 0.0035$) and relocation number in winter ($p = 0.0007$) but not in summer. Only one female (ID 59 in summer 2005, Table 2) was found on a nest, for all other females no reproduction could be confirmed, although nest losses in an early stage of breeding cannot be excluded. No significant differences in habitat use between males and females could be determined (Supplementary material Appendix 1 Table A1), so the data of both sexes were pooled for following analyses.

Table 2. Number of locations per individual and season and resulting sizes of the resulting minimum convex polygon (MCP). Weight of the bird was measured and age was estimated (based on plumage and beak size) at time of catching: 0 = young of the same year, 1 = young of the previous year, 2 = older.

ID	Sex	Season	Year	Locations	MCP (ha)	Weight (kg)	Age
39	Male	Summer	2004	25	639.06	3	2
43	Male	Summer	2004	23	984.53	2,7	0
47	Female	Summer	2004	25	174.29	1,9	2
54	Female	Summer	2005	37	253.88	1,7	2
55	Female	Summer	2005	33	181.26	1,9	2
56	Male	Summer	2005	35	119.8	2,4	0
59	Female	Summer	2005	35	219.04	1,9	0
40	Male	Winter	2003–2004	26	151.07	3,4	2
43	Male	Winter	2003–2004	38	184.51	2,7	0
47	Female	Winter	2003–2004	30	55.55	1,9	2
52	Male	Winter	2004–2005	99	255.35	4,1	1
53	Female	Winter	2004–2005	77	127.65	1,8	2
54	Female	Winter	2004–2005	86	100.35	1,7	2
55	Female	Winter	2004–2005	86	94.07	1,9	2
56	Male	Winter	2004–2005	99	196.65	2,4	0
56	Male	Winter	2005–2006	25	98.72	2,4	0
57	Male	Winter	2004–2005	84	204.08	3,7	2
58	Female	Winter	2004–2005	42	78.21	1,8	0
59	Female	Winter	2004–2005	92	110.02	1,9	0
59	Female	Winter	2005–2006	27	35.80	1,9	0

Habitat selection

Home range selection within study area

Home range selection within the study area was well explained by the models, both for summer ($AUC = 0.807 \pm 0.021$) and winter ($AUC = 0.885 \pm 0.009$) (Table 3a, 4a). In

summer it was mainly determined by landscape and topography variables, with home ranges mainly located in high altitudes (Table 3) in forest core areas, i.e. apart from outer forest edges and roads. Stands with extensive shrub cover and more than two horizontal layers were significantly avoided (Table 3a), while other vegetation variables (stand type,

Table 3. Generalized linear mixed models explaining summer habitat selection of capercaillie at two scales: (a) home range selection within the study area and (b) within-home range habitat selection. The relative importance of each predictor is indicated by the drop in Akaike's information criterion (ΔAIC) when omitting this variable.

Type	Variable	(a) Summer in study area AUC: 0.807 ± 0.021 SD (individual): 0.079				(b) Summer in home range AUC: 0.786 ± 0.022 SD (individual): < 0.001			
		Estimate	SE	Sign.	ΔAIC	Estimate	SE	Sign.	ΔAIC
	Intercept	-12.970	2.125	***		-10.490	1.982	***	
Landscape	Altitude	0.010	0.001	***	47.4	0.005	0.002	**	4.1
	Outer Forestedge	2.420	0.544	***	25.7	1.714	0.590	**	9.7
	Inner Forestedge					-0.701	0.770		0.4
Human	Road_dist	1.518	0.371	***	19.9				
	Settlement_dist					0.605	0.430		1.6
	Bike_dist					1.133	0.433	**	7.3
	Restaurant_dist					1.115	0.313	***	10.2
Vegetation	Hike_dist					-0.680	0.695		0.1
	Stand_spruce-mix	-0.034	0.338		6.7	0.081	0.402		25.6
	Stand_beech-mix	0.583	0.432			2.042	0.533	***	
	Structure_2layers	0.162	0.278		15.0				
	Structure_> 2Layers	-0.992	0.349	**					
	Canopy_cover	-0.014	0.014		4.4				
	Canopy_cover^2	< -0.001	< 0.001		5.5				
	Canopy_gaps	0.082	0.160		5.1				
	Shrub_cover	-0.024	0.009	*	14.3				
	Shrub_distr_Single					-1.102	0.327	***	21.9
	Shrub_distr_Sgroup					-1.833	0.445	***	
	Shrub_distr_Lgroup					-1.364	0.387	***	
Shrub_distr_Spread					-0.416	0.725			
Grasses	0.007	0.010		5.3					
Ground_cover					0.032	0.007	***	18.9	
Herbs					0.012	0.013		2.3	

Table 4. Generalized linear mixed models explaining winter habitat selection of capercaillie at two scales: (a) home range selection within the study area and (b) within-home range habitat selection. The relative importance of each predictor is indicated by the drop in Akaike's information criterion (Δ AIC) when omitting this variable.

Type	Variable	(a) Winter in study area AUC: 0.885 ± 0.009 SD (individual): 0.445				(b) Winter in home range AUC: 0.754 ± 0.012 SD (individual): 0.355			
		Estimate	SE	Sign.	Δ AIC	Estimate	SE	Sign.	Δ AIC
Landscape	Intercept	-6.140	2.580	*		-4.366	1.359	**	
	Slope	-0.090	0.011	***	62.8	-0.069	0.011	***	42.8
	Forestedge	4.437	0.486	***	94.6				
	Temperature_W	-0.102	0.023	***	19.7				
Human	Northing					1.163	0.704		0.1
	Road_dist	-0.335	0.234		1.3	-1.383	0.221	***	41.5
	Recreation_W	-2.629	0.500	***	28.8	5.491	0.571	***	101.2
Vegetation	Parking_dist	2.955	0.236	***	201.6	2.059	0.244	***	82.1
	Shrub_distr_Single	-0.005	0.265		49.5	0.455	0.177	*	26.4
	Shrub_distr_Sgroup	-1.704	0.364	***		-0.332	0.293		
	Shrub_distr_Lgroup	-0.452	0.339			0.641	0.215	**	
	Shrub_distr_Spread	-2.147	0.463	***		-1.326	0.396	***	
	Bilberry	0.005	0.004		0.8	0.009	0.004	*	2.0
	Canopy_cover	0.185	0.069	**	5.8				
	Canopy_cover^2	-0.001	< 0.001	**	7.8				
	Shrub_height	0.010	0.003	***	11.3				
	Fern	0.009	0.008		0.1				
	Herbs	0.011	0.007		2.3				
	Grass					0.031	0.005	***	34.5
	Moss					0.015	0.008		0.6
	Stand_spruce-mix					2.566	1.327		6.4
	Stand_beech-mix					1.984	1.315		
	Stand_beech					1.581	1.326		
	Structure_2Layers					-0.248	0.172		1.1
Structure_>2Layers					0.259	0.188			
Softwoods					0.017	0.008	*	1.4	
Suc_Regeneration					-0.312	1.538		2.4	
Suc_Thicket					-0.285	1.359			
Suc_Pole					-0.129	1.352			
Suc_Tree					0.087	1.337			
Suc_Old					-0.517	1.342			

canopy cover, canopy gaps and cover of grasses) played no role. In winter, home ranges were placed in large distance to parking places, preferably within the forest interior i.e. within a large distance to the outer forest edges (Table 4a). Capercaillie avoided steep slopes and stands with high shrub cover, while preferring areas with cold winter temperatures (i.e. high altitudes) and stands with an intermediate canopy cover. Interestingly, we found a negative correlation with distance to winter recreation, indicating that capercaillie winter home ranges encompassed a higher density of recreation infrastructure than present in the surrounding landscape.

Habitat selection within home range

Habitat selection within the home ranges was explained with a slightly lower accuracy (summer: $AUC = 0.786 \pm 0.022$; winter: 0.754 ± 0.012 , Table 3b, 4b). In summer habitat selection was mainly determined by vegetation structure, as the birds preferred stands with beech intermixed with conifer trees (beech-mix), little understory and a high ground vegetation cover. Also within the home range, higher altitudes were preferred and outer forest edges avoided (Table 3b). Moreover, used locations were recorded in a significantly greater distance to restaurants and mountain bike trails than the non-used locations, whereas no difference was found

for hiking trails. In winter, habitat selection was mainly explained by the distance to winter recreation and distance to parking places, which were strongly avoided (Table 3b). During winter capercaillie, preferably used gentle slopes and stands with intermediate shrub cover, high cover of bilberry and grasses, and a high proportion of softwood trees providing food resources. Projecting the predictions to the study area illustrates the relative avoidance of 'human presence' variables, especially recreation infrastructure, in both seasons (Fig. 2).

Effect of relocation number and MCP size

The winter models recalculated with the reduced, sub-sampled data set, showed similar results compared to the final models based on the complete data set, regarding both, home range selection in the study area and habitat selection within the home range (Supplementary material Appendix 1, Table A2). Due to the reduced sample size, some vegetation variables were no longer significant in the reduced model, but showed a similar trend. However, all variables related to recreation infrastructure and human presence remained significant in both models. Since relocation numbers per bird in summer were generally small, the variation between individuals was low and no correlation with MCP size was

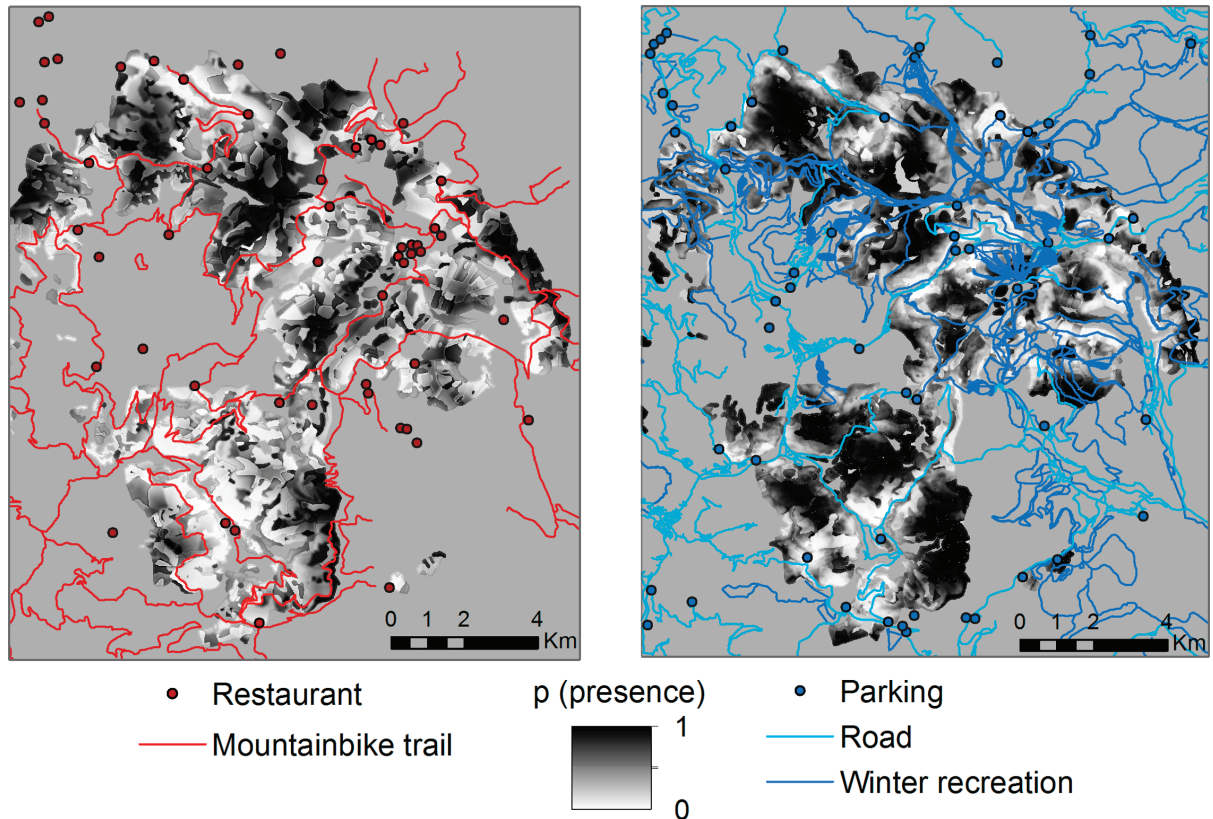


Figure 2. Predicted probability of capercaillie presence in summer (left) and winter (right), in relation to the ‘human presence’-variables (Table 1) significantly affecting habitat selection in the respective season (Table 3b and 4b).

found, no additional test was performed for the summer model.

Distance thresholds to recreation infrastructure

The distance-thresholds up to which outdoor recreation infrastructure significantly lowered capercaillie habitat use differed between the summer and winter recreation infrastructure. Whereas in summer mountain bike trails were avoided up to an average distance of 144.7 m (95% CI: 60.0–1091.5 m), winter infrastructure affected habitat use up to an average distance of 319.5 m (95% CI: 35.8–327.1 m). In summer, the presence of hiding possibilities (i.e. ground vegetation cover, ground vegetation height or shrub cover) did not alter habitat use within the critical distance to the trail. In winter, however, the presence of extensive shrub cover (> 46%; Fig. 3), significantly increased the probability of habitat use in the vicinity to winter recreation infrastructure. For the other variables which could indicate hiding possibilities (i.e. ground cover and ground vegetation height) no such effect was found.

Habitat deterioration at the population level

The area affected by winter recreation (skiing pistes, cross-country skiing, winter hiking trails, snowshoe trails and back-country skiing) ranged between 3764 ha (i.e. 8.2% of total capercaillie distribution area) when applying the lower 95% CI of the threshold (35.8 m), and 18 422 ha (i.e. 40.3% of

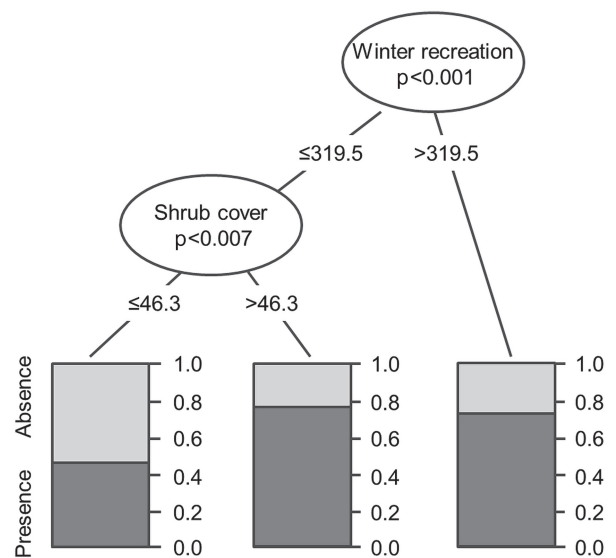


Figure 3. Multivariate conditional inference tree (minsplit = 50) showing how the relative probability of capercaillie presence within and beyond the critical distance to winter recreation infrastructure is modulated by the presence of visual cover (i.e. shrub cover). Habitat variables and the significance levels (p-values) of the thresholds (indicated on the branches of the tree) are provided in the ovals, the bars at the end of the branches show the resulting probability of capercaillie presence with the respective variable combination.

total capercaillie distribution) when using its average (319.5 m). The area located within the critical distances to mountain bike trails (i.e. lower CI: 60 m, mean: 144.7 m) ranged between 3923 ha (8.6%) and 8934 ha (19.7%) of the total capercaillie distribution (Supplementary material Appendix 1 Table A1). The proportion of habitat influenced by recreation infrastructure was not equally distributed over the Black Forest but accumulated in the higher altitudes (Fig. 1, Supplementary material Appendix Fig. A1).

Discussion

Effects of human recreation

Quantifying the effects of human presence on habitat selection of disturbance-sensitive wildlife is crucial for framing adequate management recommendations; yet, the results could strongly depend on the scale at which habitat selection is considered. Our results show that recreation infrastructure, as proxies for anthropogenic disturbance, affected capercaillie habitat selection both in summer and winter. However, while the location of the birds' home ranges was not (summer) or even slightly positively (winter) associated with recreation infrastructure, the birds strongly avoided the vicinity to these features within their home ranges. This effect was particularly pronounced in winter and can be explained by the topographic restrictions which do not only constrain the spatial distribution of central European mountain populations (Graf et al. 2005, Braunisch and Suchant 2007), but also the possibilities for winter sports, resulting in a locally high level of co-occurrence and associated human-wildlife conflict (Braunisch et al. 2011). Because the high elevation areas generally offer the best habitat conditions for capercaillie, with cold, rough climate conditions naturally shaping open forests rich in ground vegetation cover (Braunisch and Suchant 2007), capercaillie might be forced to trade off suitable habitat for disturbance by human recreation. This is partly compensated by the small-scale avoidance of recreation infrastructure, which, however results in an effective decrease of usable habitat within the home range. To date it is unknown if this effect also translates into fitness consequences, however, increased flushing distances (Thiel et al. 2007) as well as higher levels of corticosterone metabolites (Thiel et al. 2008, 2011) in areas with a high level of recreation intensity suggest potential negative consequences on body condition and overall fitness.

Distance thresholds

Previous studies also found significant avoidance of recreational trails by capercaillie with distance-thresholds ranging from 73 m (Summers et al. 2007) up to 125 m (Moss et al. 2014). The threshold values we determined were slightly higher, but in a similar order of magnitude, with mountain bike trails being avoided up to an average distance of 145 m and winter recreation infrastructure up to 320 m. This similarity – despite the studies were performed in different areas using different study methods – indicates that the results might apply to a wide geographical range for capercaillie. However, both recreation intensity (number of people using

a trail) as well as the recreation type (biking, skiing, hiking, snowshoeing) is likely to affect the reaction of wildlife (Fernández-Juricic et al. 2005, Moss et al. 2014). The exact (spatial and temporal) use of all trails or infrastructures was unknown in our study which might explain the large confidence intervals we found, especially in summer. Under some conditions, e.g. in times of low recreation intensity, some trails might even attract birds by providing the possibility for gastrolith intake, dusting baths or to dry out after rain. On the other hand, people or dogs leaving the trails might result in a much larger 'disturbance band' than given by the physical width of the trails (Moss et al. 2014). Moreover, the statistical method for deriving thresholds might explain differences in results. Conditional inference trees do not allow accounting for a clustered data structure, i.e. for variance between individuals, however, they are explicitly designed to find the optimal cut-off value that best separates presence and absence, instead of arbitrarily selecting the threshold at a presence-probability of 0.5.

Importantly, avoidance-thresholds did not coincide with flushing distances, showing that disturbance-effects range far beyond the distance at which behavioral responses are triggered. Thiel et al. (2007) found a flushing distance of capercaillie in the Black Forest of 27 ± 0.6 m, which is far lower than the distances determined in our or other studies (Summers et al. 2007, Moss et al. 2014), indicating that one should be careful when applying flushing distances as a measure for quantifying the amount of habitat affected by human presence (Blumstein et al. 2003).

Anthropogenic disturbance versus habitat quality

The landscape and vegetation features we found to determine habitat selection were in line with other studies from central Europe (Rolstad and Wegge 1987, Bollmann et al. 2005, Braunisch and Suchant 2007). In summer capercaillie preferred forest areas at higher elevations, interspersed with beech, low shrub cover and a high cover of ground vegetation (Table 3). For the winter season tagged birds preferred shallow slopes in the higher altitudes with cold winter conditions, stands with softwood trees and a high cover of ground vegetation such as grass and bilberry, indicating open forest conditions (Table 4). Despite sex-specific differences in home range size, habitat selection patterns of males and females did not differ with regard to landscape, vegetation or human recreation variables, which however might be due to a small sample size. Our study also corroborates findings from the Bavarian Forest that both habitat quality as well as anthropogenic disturbance influences habitat use by capercaillie (Rösner et al. 2013), yet, we could show that capercaillie responds differently to the trade-off between both aspects, depending on the scale of habitat selection. While at the home range level the impact of anthropogenic disturbance is overruled by suitable landscape conditions, at the small scale the avoidance of human presence comes to the fore, particularly in winter. Yet, even at the small scale, the distance up to which recreation infrastructure is avoided, is modulated by vegetation structure. In winter, capercaillie stayed on average closer to the trails if good hiding possibilities were available (i.e. a dense shrub layer exceeding 46%, Fig. 3) although dense understorey is generally avoided by the birds (Table 4).

This indicates that vegetation conditions may locally modify the spatial extent of habitat deterioration.

Although our tagged birds avoided the vicinity of mountain bike trails, an effect which was also not mitigated by vegetation conditions, we could not find a similar effect for hiking trails. A reason might be that, due to their high speed, mountain bikes represent a highly unpredictable source of disturbance, while slowly approaching hikers might be earlier detected and avoided by hiding in the vegetation. Interestingly, our birds also showed a strong avoidance of parking areas where visitors accumulate, this also corresponds to the results of Moss et al (2014) showing an avoidance of 'forest entrances'.

Our sample size was limited, with regards to both, the number of tagged birds and the number of relocations per bird, due to the inherent difficulties of using VHF telemetry with rare species. The fact that the MCP size still increased with the number of relocations suggests that our MCP did not encompass the full seasonal home range of several of our individuals but rather represented a (core) part of it. Nevertheless, even when further reducing the sample size by subsampling a similar, minimum number of presence locations for each individual, and considering only absence locations within the correspondingly smaller MCP, effects of human infrastructure remained significant (Supplementary material Appendix 1 Table A2) while most of the other habitat variables, with only a few exceptions, showed a similar trend. We therefore assume that we might still underestimate the impact of human recreation on capercaillie.

Effective habitat reduction at population level

When extrapolating our results to the whole expanse of the Black Forest population, we found that between 8 and 40% of the current distribution area is influenced by recreation infrastructure in winter and between 8 and 20% in summer. This calculation only represents a rough approximation, as neither modulations by vegetation conditions, nor the actual intensity of use was taken into account. Moreover, we did not consider effects of hiking trails although such effects were found by other studies (Summers et al. 2007, Moss et al. 2014). Finally, since our extrapolation also does not include off-trail activities (e.g. geocaching and other off-trail activities, Coppes and Braunisch 2013), and since the affected area was only calculated using the average and lower CI of the distance threshold, our estimate is likely to underestimate the spatial extent of human recreation effects on the Black Forest capercaillie population. Even though our area-estimates do not reflect total habitat loss but habitat deterioration indicated by a significant reduction in presence probability, and although these effects could not yet be linked to fitness consequences, such as reduced reproduction (Brenot et al. 1996, Moss et al. 2014) or survival which would be necessary to quantify effects on population level (Gill et al. 2001), we show the immense scale at which human recreation effects may operate. We therefore assume that this source of disturbance is substantially contributing to the dramatic decline in capercaillie populations recorded all across the central European mountain populations in the

past decades (Coppes et al. 2016). Our study also reveals that the conflict between wildlife conservation and a socioeconomically important factor, namely nature based recreation, is particularly reinforced when both, wildlife populations and outdoor activities are geographically and topographically restricted and that co-occurrence at the population scale must not necessarily indicate the species' insensitivity. We therefore support the postulation that future studies investigating the effects of anthropogenic disturbance on wildlife should specifically address effects at population level instead of merely focusing on individuals (Storch 2013). Assessing and quantifying fitness consequences (e.g. on reproductive output or survival) will be key aspects in this context, and might even reveal hidden impacts even in situations of apparent habituation. Finally it will be crucial to elucidate the effectiveness of mitigation measures. However, the call for more research should not hinder active management to mitigate effects of anthropogenic disturbance on wildlife.

Management recommendations

Given the spatial extent of impact, appropriate management measures are indispensable to avoid or at least mitigate negative effects of human recreation. Particularly in key habitats with a dense recreation infrastructure network, the construction of new trails or recreational activities should be avoided and activities concentrated on existing trails. Furthermore a network of wildlife refuges, in which recreational activities are banned, should be established (Braunisch et al. 2011), which will likely benefit not only capercaillie but also a wide array of other species (Anderson 1995, Whitfield et al. 2008). To ensure such refuges are accepted by the public, tourist organizations should be integrated in the planning process from an early stage and recreationists should be informed how their activities affect wildlife (Marion and Reid 2007). Given the large distances up to which effects were recognizable, refuges with at least 800 m diameter would be required to fully eliminate negative effects (this study, Moss et al 2014). Yet, our results also indicate that forest structures can reduce these critical distances. In areas with existing recreational infrastructure, we therefore advise forest managers to keep a strip of dense forest with a pronounced shrub layer along the trails, which can reduce both negative effects on capercaillie habitat use in winter, as well as the number of people leaving the trail for off-trail activities (Coppes and Braunisch 2013). In regions highly frequented by outdoor recreation, we strongly recommend that habitat restoration measures, i.e. the creation or maintaining of structurally diverse, open forest habitat with canopy gaps, should generally take place in sufficient distance or with sufficient visual protection from the trails. Finally, with our spatially explicit predictions (Fig. 2) optimal locations for wildlife refuges, i.e. suitable forest patches in low-disturbed areas, can be determined. Given the geographic isolation of the central European mountain populations (Segelbacher et al. 2003) the topo-climatic restriction of potential habitat (Braunisch and Suchant 2007) and the close interplay between vegetation-structure related habitat suitability and the effects of human presence (this study), concerted action at the population level is required, ideally coordinated through

large-scale action plans (Braunisch and Suchant 2013) which – due to the assumed umbrella function of the species (Suter et al 2002) – is likely to benefit the wider mountain forest community.

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Supplementary material (Appendix JAV–01239 at <www.avianbiology.org/appendix/jav-01239>). Appendix 1.