



Between natural and human disturbance: Ecology
and conservation of a remnant population of the
Western Capercaillie (*Tetrao urogallus*)
in the Bohemian Forest

Dissertation
am Fachbereich Biologie
der Philipps-Universität Marburg
Allgemeine Ökologie und Tierökologie

vorgelegt von

Sascha Rösner

Marburg, Dezember 2021

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... für Nico!

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2 Declaration of author's contributions

My PhD thesis entitled '*Between natural and human disturbance: Ecology and conservation of a remnant population of the Western Capercaillie (Tetrao urogallus) in the Bohemian Forest*' was carried out at the Philipps-Universität Marburg, under the supervision of Prof. Dr. Roland Brandl.

In **Chapters I, II and III**, I present independent scientific manuscripts, which I published or submitted as leading author. The contributions of me and my co-authors for each of the papers and manuscript are described below. I further present a list of publications within the project. My contributions to these manuscripts are described in Chapter 12. The contributions of the authors for each manuscript are stated as following:

Chapter I (published)

Rösner S, Brandl R, Segelbacher G, Lorenc T, Müller J (2014). Noninvasive genetic sampling allows estimation of capercaillie numbers and population structure in the Bohemian Forest. *European Journal of Wildlife Research* 60, 789–801. doi:10.1007/s10344-014-0848-6

I organized and conducted field work, managed and conducted sampling storage, lab work and logistics. I prepared data for laboratory work and for the analysis. I analyzed the data and wrote the manuscript. Together with my co-authors we improved the manuscript and revised an earlier version of the manuscript. RB and JM helped with statistical analysis and GS helped with analysis of genetic data. JM is the PI of the project, conducted field work, developed research ideas, and

structured the project. TL conducted and coordinated field work in CZ. All co-authors helped to improve earlier versions of the manuscript and the revision.

Chapter II (published)

Rösner S, Mussard-Forster E, Lorenc T, Müller J (2014). Recreation shapes a landscape of fear for a threatened forest bird species in Central Europe. *Landscape Ecology* 29, 55–66. doi:10.1007/s10980-013-9964-z

I organized and conducted field work, managed and conducted sampling storage, lab work and logistics. I prepared the count data for GIS work and for the analysis. I analyzed the data and wrote the manuscript. JM is the PI of the project, developed research ideas, and structured the project. EM-F managed the questionnaire data and prepared GIS work. TL organized questionnaire data from Šumava. JM helped with statistical model analysis. All co-authors helped to improve earlier versions of the manuscript and to prepare a revision of the manuscript.

Chapter III (Submitted and under review: Wildlife Research)

Rösner S, Schabo DG, Palme R, Lorenc T, Mussard-Forster E, Brandl R, Müller J (2021, submitted to *Wildlife Research*, CSIRO) High quality habitats and refuges from tourism reduce personality-based stress responses in a sensitive forest specialist.

I coordinated the project, managed, and conducted field work and sample collection, coordinated samples and laboratory work, performed analysis, and wrote the manuscript. RP conducted all FCM lab work, helped to structure the project at initial stage, improved the manuscript, EM-F coordinated questionnaires and managed data accordingly, and TL coordinated and conducted field work in the Šumava National Park. RB supported the project at every stage, helped with statistical analysis and improved the manuscript. DGS helped to perform statistical analysis and helped to write and improve the manuscript. JM is PI of the project, conducted field work, developed research ideas, structured the project, and assisted with the improvement of the manuscript.

3 Zusammenfassung

Die Waldökosysteme Europas werden durch menschlichen Einfluss sehr stark überformt. Weniger als 40 % der gesamten Landfläche sind heute noch von Wäldern bedeckt und nur vier Prozent davon unterliegen einem strengen gesetzlichen Schutz. Natürlicherweise werden Waldökosysteme durch Störungen und Prozesse auf unterschiedlichen räumlichen und zeitlichen Skalen dynamisch verändert und in ihren strukturellen Merkmalen geprägt. Diverse natürliche Störgrößen stehen dabei oft in einem positiven Zusammenhang mit der Qualität des Lebensraums und der biologischen Vielfalt. Jedoch verändern menschliche Eingriffe durch z. B. Bewirtschaftung die Dynamiken dieser raum-zeitlichen Muster. Während generalistisch lebende Arten in der Lage sein können, sich an diese neuen Dynamiken anzupassen, reagieren Waldspezialisten – oft prioritär im Naturschutz - meist negativ auf menschliche Eingriffe und gelten daher als Indikatoren. Um herauszufinden, inwieweit natürliche und menschliche Störungen eine störungssensible, auf Wälder spezialisierte Art beeinflussen, habe ich mich bei meiner Forschung mit einer Population des Auerhuhns (*Tetrao urogallus*) in zwei benachbarten Nationalparks, Šumava (Tschechische Republik) und Nationalpark Bayerischer Wald (Deutschland) sowie die umliegenden Wirtschaftswälder (Böhmerwald) befasst. Meine Arbeiten hatten dabei folgende Ziele: (i) die Populationsgröße und die genetische Populationsstruktur des Auerhuhns zu bestimmen, (ii) die räumlichen Verteilungsmuster der Art zu erfassen und zu analysieren, und (iii) die physiologischen Stressreaktion in Relation zu verschiedenen Störungsregimen zu analysieren.

Im Rahmen meiner Studien konnte ich für das gesamte Untersuchungsgebiet eine Populationsgröße von ca. 550 Individuen ermitteln. Die populationsgenetischen Analysen zeigten, dass diese Population bei gleichbleibenden Umweltbedingungen langfristig als überlebensfähig einzustufen ist. Darüber hinaus ergaben meine Autokorrelationsanalysen keine signifikante räumliche genetische Struktur und damit einen ungehinderten Genfluss über den gesamten Böhmerwald. Die Population gilt meinen Ergebnissen zu Folge damit aktuell als größte Reliktpopulationen der mitteleuropäischen Mittelgebirge. Die Ergebnisse meiner Studie deuten zudem darauf hin, dass nach einem starken Rückgang der Populationsgröße in den 1970er Jahren die anschließende Bestandsstützungsmaßnahme das langfristige Überleben der bedrohten Art gefördert hat.

Insgesamt konnte ich in mehr als 60 % der untersuchten 50 ha - Rasterzellen Auerhühner nachweisen. Die reine Präsenz als auch die Abundanzen standen dabei selbst innerhalb geeigneter Lebensraumtypen in einem negativen Zusammenhang mit touristischen Aktivitäten. Dies weist darauf hin, dass Habitats mit menschlichen Aktivitäten von den störungssensiblen Auerhühnern aktiv gemieden werden. Die Daten zu forstwirtschaftlichen Aktivitäten ließen jedoch keinen derartigen Trend erkennen. Zusammenfassend zeigen diese Ergebnisse deutlich, dass ein gezieltes Lenken von Freizeitaktivitäten in den Schutzgebieten zum Artenschutz dringend erforderlich ist. Ausgewählte Zonen sollten dabei explizit als Rückzugsgebiete für diese Flaggschiffart ausgewiesen und frei von jeglicher Störung

gehalten werden. Diese Forderung wird durch einen weiteren Teil meiner Studien eindeutig unterstützt, da die physiologischen Stressreaktionen der 1,096 untersuchten Individuen mit zunehmender Lebensraumqualität deutlich verringert waren. Hingegen konnten Gebiete mit erhöhtem Besucheraufkommen mit erhöhten Stressreaktionswerten in Verbindung gebracht werden; zumindest, wenn man die Individualität der „echten Individuen“ berücksichtigte. Störungen durch forstwirtschaftliche Aktivitäten führten dagegen nicht zu einem signifikanten Anstieg der physiologischen Reaktionen. Dies deutet darauf hin, dass sich Individuen in ihrer physiologischen Reaktion auf Störungen durch touristische Erholungsaktivitäten erheblich unterscheiden.

Zusammenfassend konnte ich damit eindeutig zeigen, dass sowohl die Überwachung der Populationsgröße als auch der physiologischen Stressreaktionen - vorzugsweise auf individueller Ebene - in Kombination mit Analysen der Lebensraumqualität und möglicher Störfaktoren geeignete Instrumente sind, um wertvolle Basisdaten für die Entwicklung von Managementstrategien zum Schutz des Auerhuhns zu liefern. Der allgemeine Erhaltungszustand der Population lässt auf gute Voraussetzungen für ihren künftigen Fortbestand schließen. Da ich jedoch nur zwei Drittel der Individuen innerhalb der Grenzen der Nationalparke nachweisen konnte, ist eine kohärente Managementstrategie, insbesondere im Hinblick auf die Komplexität der Lebensräume, unerlässlich, um das langfristige Überleben der Population in der Region zu gewährleisten. Zudem zeigen die Ergebnisse deutlich, dass sowohl die räumlichen Verteilungsmuster als auch die physiologischen Stressreaktionen auf touristische Erholungsaktivitäten reagieren. Entsprechend sollte ein umfassendes und grenzüberschreitendes Überwachungsprojekt in Verbindung mit Managementplänen eingerichtet werden, welche ein intelligentes Konzept zur Besucherlenkung beinhalten. Die wesentliche Größe stellt hierbei die

Einrichtung ausreichend großer Rückzugsgebiete mit qualitativ hochwertigen Lebensräumen dar. Zudem sollte ein solcher Plan auch weitere Veränderungen in den Waldstrukturen beobachten, da sich das Ökosystem nach den großflächigen Windwurfereignissen und Borkenkäfer-kalamitäten in einem fortlaufenden Sukzessionsprozess befindet. Wie sich solche Veränderungen auf die Habitatnutzung des Auerhuhns auswirken, ist bisher jedoch nicht schlüssig geklärt.

Insgesamt konnte ich zeigen, dass das Auerhuhn als Waldspezialist eine geeignete regionale Indikatorart darstellt, die selbst in Nationalparkflächen sensibel gegenüber Störgrößen reagiert, und zwar entweder durch räumliches Ausweichen oder durch erhöhte Stressbelastung. Die angewandten Methoden sind daher sehr gut geeignet, um die Nationalparkbehörden bei evidenzbasierten und naturnahen Managemententscheidungen zu unterstützen, welche sowohl den Schutz der Wildtiere als auch die nachhaltige Erholung der Menschen als Schutz-Ziel berücksichtigt.

4 Summary

Human activities have strongly modified forest ecosystems across Europe. Today, less than 40 % of the total land surface area are covered by forests and only 4 % of those are strictly protected. Forest ecosystems are naturally shaped by disturbances that modulate their structural characteristics at different spatiotemporal scales. In general, intermediate natural disturbances are positively associated with habitat quality and biodiversity, but human interventions strongly modify the spatiotemporal patterns of these dynamics. While habitat generalist species may be able to adapt to these novel dynamics, forest specialist species - often a priority for conservation - mostly respond negatively to human interference. To assess to what extent natural and human disturbances influence an elusive forest specialist species, I focused my research on a population of the Western Capercaillie (*Tetrao urogallus*) covering two adjacent national parks, Šumava National Park (Czech Republic) and the Bavarian Forest National Park (Germany). In particular, I studied (i) the population size and genetic population structure of the Capercaillie population, (ii) its spatial distribution and (iii) its physiological stress response to various disturbance regimes.

Within the scope of my studies, I determined a population size of approximately 550 individuals and therefore revealed this population as viable and one of the largest relict populations in the low mountain ranges of temperate Europe. Moreover, autocorrelation analysis revealed no significant spatial genetic structure and unrestricted gene flow across the entire Bohemian Forest. These findings indicate that after a strong decline in population size in the 1970ies the subsequent re-

enforcement program promoted the long-term conservation of this endangered species.

Furthermore, I recorded Capercaillie in more than 60 % of the studied grid cells. The intensity of habitat use (presence/absence and number of Capercaillie records) was negatively associated with increasing anthropogenic recreational activities (tourism) even within suitable habitat types pointing to the avoidance of certain areas with human activities. Forestry activities did not reveal any trend in changes of presence, absence or count data of Capercaillie. These results highlight the relevance of restricting recreation activities even in protected areas by setting aside selected zones to preserve the refuge of this flagship species. This is clearly supported by my studies showing that the physiological stress response levels of 1.096 individuals decreased with increasing habitat quality. Further, increasing tourism intensity was associated with elevated physiological stress response levels at least when controlling for true individuals by the use of genetic fingerprinting technology. Management disturbances in terms of forestry activities – on the other hand – did not indicate any increase in physiological response. These findings suggest that individuals differ considerably in their physiological response to disturbances through touristic recreational activities.

To conclude, I was able to clearly demonstrate that both monitoring of population size and physiological responses - preferably at the individual level - in combination with analyses of habitat quality and possible disturbance factors are adequate tools for delivering valuable baseline data for the development of management strategies for the conservation of the Capercaillie, the emblematic

forest specialist of both national parks. The overall conservation status indicates a good prerequisite for the future persistence of the population. However, given that only two thirds of the individuals were detected within the boundaries of the national parks, a coherent management strategy particularly regarding the complexity of habitats is essential to guarantee the long-term viability of the population. As the results clearly show that both the spatial distribution patterns and the physiological stress responses respond to touristic recreation activities, a comprehensive cross-border monitoring project in combination with management plans should be established. Such a management plan should provide an intelligent visitor guidance concept with sufficient refuge zones in high quality habitats to preserve this forest specialist species. Moreover, such a monitoring project should also consider changes in forest structures given that the forest still is – after large scale wind-throw events and bark beetle calamities – under ongoing successional changes which will likely modulate the habitat use of the Capercaillie. The Capercaillie as forest specialist has been shown to serve as a suitable regional indicator species for guiding the national park authorities in evidence-based and close-to-nature management decisions considering both of their aims: wildlife conservation and sustainable human recreation.

5 General Introduction

Naturally, approximately 80 % of the terrestrial surface in Europe are thought to be covered by forests (Zanon et al. 2018). However, human activities have converted half of these forest ecosystems into agricultural and urban areas (Foley et al. 2005; Zanon et al. 2018). Furthermore, the composition and structure of the remaining forests have been altered throughout the last 2,000 years (Zanon et al. 2018). In consequence, today, forests cover only approximately 40 % of the total land surface in Europe (Ceccherini et al. 2020). Recent studies, however, indicate an increase in forest cover in Europe (Palmero-Iniesta et al. 2021). The majority of these forests in Europe (> 95 %) are managed intensively for timber production and non-timber forest products (FAO 2006; Duncker et al. 2012; EUROPE 2015; FAO and UNEP 2020). About 18 % of Europe's forests are located in protected areas (FAO and UNEP 2020) with a minor proportion of four percent being strictly protected (FAO 2006) and are thus essential for biodiversity conservation (Reid et al. 2005; Ceccherini et al. 2020).

Naturally, forests are highly dynamic ecosystems with disturbances being important drivers that permanently modulate their structure and functioning (Franklin et al. 2002a; Turner 2010; Johnstone et al. 2016; Thom and Seidl 2016). These natural disturbances are observed at different spatial scales and classically comprise fires, storms, landslides, or insect calamities whose impact range from the tree individual to the stand to the landscape level (Remmert 1998; Franklin et al. 2002b; Johnstone et al. 2016; Thorn et al. 2017). These spatial dynamics span over long periods, which can cover several hundreds of years according to the

maximum age of long-lived tree species. For central European forests these spatio-temporal dynamics are well depicted in the 'mosaic-cycle concept' (Remmert 1998).

In general, intermediate natural disturbances have positive effects on biodiversity and habitat quality (Wilkinson 1999; Seidl et al. 2011; Thom and Seidl 2016). Through a mosaic of altering (micro)habitats, many species with different autecological habitat and resource requirements are supported with valuable ecological niches throughout their life cycles (Scherzinger 2009). Human interventions of these natural disturbances and dynamics, such as clear-cutting, the establishment of age classed monocultures or the suppression of natural fires, have strongly modified the spatial and temporal mosaic patterns in managed forests (Farrell et al. 2000). Nowadays, even strictly protected areas are not completely left untouched, but are partly controlled or affected by humans, for example through fire suppression, wildlife management and manifold recreation activities (Guz and Kulakowski 2020). Thus, core areas of forest ecosystems are often embedded in a surrounding of managed forests comprising a broad variety of forest practices (Schelhaas et al. 2018) or are at least penetrated by infrastructure like major roads (Selva et al. 2011; Ibisch et al. 2016).

Human interference has been shown to inevitably decrease species richness across taxa (Paillet et al. 2010). Yet, these effects are not consistent for all taxa but differ according to their traits or specialization (Økland et al. 2003; Penone et al. 2019; Tinya et al. 2021). While many studies show that habitat generalists may adapt to novel condition or even benefit from disturbances (Ryall and Fahrig 2006;

Colles et al. 2009; Büchi and Vuilleumier 2016; Schall et al. 2018), forest specialist species respond mostly negatively (maladaptive, see Tuomainen and Candolin 2011) to human interference and are generally declining in managed forest ecosystems (Devictor et al. 2008b, a). This is explained not only by the loss of essential resources such as habitat or food availability, but also by human interference even in strictly protected forests (Paillet et al. 2010). Spatial avoidance through changed behaviors or maladaptive responses through decreased individual fitness or elevated mortality by, e.g., increased stress may ultimately result in decreased population viability (Badyaev 2005; Tuomainen and Candolin 2011). Forest specialists are often priority targets or indicator species for conservation management (Buchanan et al. 2011). It therefore is essential to unveil to what extent natural and/or human disturbance influence the population status of these specialist species even in protected areas.

To assess the overall conservation status of a focal species, **firstly**, knowledge about population size and spatial structure provides valuable baseline information (Mace et al. 2008; Tella et al. 2013). Population size is used to group the threat status of a species (IUCN 2021) and informs in relation to the concept of minimum viable population size (mvp, see Shaffer 1981 and Samson et al. 1985). Further, data on genetic diversity and genetic variation depict vital information about the evolutionary potential and/or the history within a population (Samson et al. 1985; Gilpin and Soule 1986) and provide insight into the persistence of the species in a given area under different management practices.

Secondly, to assess the impact of the manifold disturbances on forest specialists, the spatial distribution pattern of the species is a key parameter to evaluate its local conservation status. This pattern provides insights into the availability of habitat types as well as their overall quality for the focal

species (MacArthur and Levins 1964; Morris 2003; Teuscher et al. 2013). While the availability of habitats in general and their quality provide first essential information regarding the presence of a species, the actual use of habitat is also driven by interactions with other species or resource distributions (Stanko et al. 2006; Johnson 2007; Mosser et al. 2009; Kajtoch et al. 2012; Seibold et al. 2013). Anthropogenic disturbances can also contribute to the avoidance of certain areas also referred to as “landscape of fear” (Landré et al. 2001; Tolon et al. 2009; Ciuti et al. 2012). Thus, the analysis of the spatial distribution of a forest specialist may provide promising insights into the local use of suitable habitat types in a protected area under different management practices or disturbance regimes (Samson et al. 1985).

Thirdly, although forest specialists might still be present in specific areas or habitats, the physiological condition of the individuals might already be impacted, e.g., by frequent disturbances. In consequence, and as a prerequisite for maintaining a stable population, direct measures of the fitness and performance of individuals can give vital insights into the physiological condition of an endangered species (Johnson 2007a). Here, the assessment of the physiological stress response, i.e., by measuring glucocorticoids metabolite concentrations (Möstl and Palme 2002; Palme et al. 2005; Möstl et al. 2009) serves as an easy measure to determine reactions – even at the individual level – to manifold kinds of disturbance (Sheriff et al. 2011; Dickens and Romero 2013; Palme 2019).

Thus, the measure of physiological stress response can provide an early warning indicator for the body conditions of individuals under different disturbance regimes and management practices and will help to take management actions to protect the overall “health” status of the population.

6 Objectives

In this thesis I studied the consequences of natural and human disturbance on an avian forest specialist species in two adjacent national parks, Šumava National Park (Czech Republic) and the Bavarian Forest National Park (Germany). These national parks comprise a suitable study area for this question since they comprise a variety of habitat types and structures, different management regimes and variation of human disturbances. Moreover, a suitable focal species, the Western Capercaillie (*Tetrao urogallus*, Linné 1758, hereafter Capercaillie) inhabits this forest landscape which is threatened and therefore listed in Annex I, II and III of the European Council Directive (Birds Directive) on the protection of wild birds (79/409/EEC). Capercaillie are known as a resident forest specialist inhabiting almost the entire boreal forest of Eurasia (Juana and Kirwan 2020; Coppes et al. 2021). Distributional core areas in Europe are Scandinavian forests and mountain forest with altitudes > 800 m (e.g. Alps, Pyrenees, Carpathian Mountains) (Klaus et al. 1989; Storch 1993, 1995, 2001; Klaus and Bergmann 1994; Juana and Kirwan 2020). It requires highly complex microhabitats and resources over the course the life cycle and across seasons (Pakkala et al. 2003; Scherzinger 2009). Exemplary, secure breeding habitats for ground nests are needed such like warm and insect-rich microhabitats for the fledglings as well as specific requirements for traditional lek sites are needed for mating (Pakkala et al. 2003; Scherzinger 2009). Therefore, the Capercaillie is in general considered as an important flagship and umbrella species in mountainous, boreal, and alpine forest ecosystems especially in the context of open, multilayered

forests and their bird diversity (Suter et al. 2002; Pakkala et al. 2003; Graf et al. 2007; Kortmann et al. 2018). Accordingly, the Capercaillie is also considered as a flagship species for the two national parks where I conducted my research (Kortmann et al. 2018). Yet, the extent to which even in near-natural and strictly protected forest ecosystems such sensitive species are affected on population level by natural and man-made disturbance has not yet been conclusively clarified.

Additionally, knowledge on the population history in the national parks is available showing a severe population decline 35 years ago with only approximately 100 birds remaining in 1985 in the entire area (16 only within borders of Bavarian Forest National Park (Scherzinger 2003) and a subsequent breeding and release program to supplement the local population with a total of 1,376 individuals released between 1985 and 2000 (Scherzinger 2003).

As a result of the above-mentioned developments, the authorities of both national parks now requested updated knowledge about the current conservation status of the Capercaillie population for further developments of targeted management plans. Therefore, essential baseline information about current distribution patterns, habitat suitabilities, and the population size were needed. Further, possible impacts of management regimes or human disturbance on the population and its distribution and “health” were sought.

Accordingly, I therefore focused and structured my main overall objectives. Herewith, I hoped to significantly contribute data and results to the conservation of the species in the area in

general and significantly support management decisions for a sustainable wildlife management in special.

All major chapters have either been published peer reviewed and published (chapter I, II) or submitted to a scientific journal and under review (chapter III). Each chapter can be thus read independently comprising its specific introduction, followed by a broad variety of materials and methods, the specific results, and the subsequent discussion sections, accordingly. In addition, each manuscript provides a short summary alongside the reference lists. I am closing my thesis with a general conclusion including an integration of all chapters, management recommendations and future perspectives.

In **chapter I**, I determined the population size and structure of the Capercaillie across an area of about 120,000 ha. To do so, fresh droppings were collected, and a stratified random sub-set of the samples was genotyped using ten microsatellite markers. With these data at hand, I estimated the current population size and determined the population's spatial and genetic structure. I published this chapter together with colleagues here: **Rösner et al. (2014a) Noninvasive genetic sampling allows estimation of capercaillie numbers and population structure in the Bohemian Forest. Eur J Wildlife Res 60:789–801.**

In the second chapter (**chapter II**) I focused on the effects of human activities on the spatial distribution pattern of the species across the landscape scale of the national parks and surrounding forests. Specifically, I tested whether recreational and forestry activities impact the habitat use of suitable habitat types. **Rösner et al. (2014b) Recreation shapes a landscape of fear for a threatened forest bird species in Central Europe. Landscape Ecol 29:55–66.**

In the third chapter (**chapter III**) I asked how physiological stress response measures of the capercaillie are affected by habitat quality, abiotic factors and anthropogenic disturbance. For that I examined 1,096 droppings and determined the fecal corticosterone metabolites and tested their associations with temperature, habitat quality, sex, and anthropogenic activities. Based on a genotyped sub-set of the data I was able to control for individual differences and thus controlling for personality. **Rösner et al. (Wildlife Research, under review, Dez. 2021): High quality habitats and refuges from tourism reduce personality-based stress responses in a sensitive forest specialist.**

7 Chapter I: Noninvasive sampling allows estimation of Capercaillie numbers and population structure in the Bohemian Forest

I aimed to determine the population size and structure of the Capercaillie across an area of about 120,000 ha. To do so, fresh droppings were non-invasively collected on the landscape level. A stratified random sub-set of the sample were genotyped using ten microsatellite markers (Segelbacher et al. 2000). With these data at hand, I estimated the current population size and determined the population's spatial and genetic structure. In addition, the method provided individual-based information about dispersal and space use.

My contribution: I organized the entire field work with about 70 volunteers, managed and conducted sampling storage, lab work and logistics. I prepared data for laboratory work and for the analysis. I analyzed the data and wrote the manuscript. Together with my co-authors we improved the manuscript and revised an earlier version of the manuscript.

Note: Within the Interreg-Project (ETZ 2014-2020, Freistaat Bayern - Tschechische Republik, Projekt Nr. 99), we conducted a follow-up field survey applying exactly the same standards as

published here (Rösner et al. 2014a). The repeated approach (Rösner 2018, unpublished) with 1,324 dropping samples (from 2016 – 2018) and DNA analysis of 600 randomly selected samples revealed updated information on the population size. By applying the same statistical approach, I revealed a mean population size of 605,2 (+/- 130,6, see appendix 18.3). This result strongly supports the finding that the population is viable (see Grimm and Storch 2000). However, when only considering the samples collected within the border of the national parks, the population size reveals only 409 individuals. This is similar to an estimated size of 365 individuals from data in 2009 – 2011 (Rösner et al. 2014a). Therefore, still, the two national parks are not supporting a sufficient population size to be viable. The conservation of birds outside the strictly protected areas should therefore also be in focus for conservation and management actions approach (Rösner 2018, unpublished), s. Appendix.

Rösner S, Brandl R, Segelbacher G, Lorenc T, Müller J (2014). Noninvasive genetic sampling allows estimation of capercaillie numbers and population structure in the Bohemian Forest. *European Journal of Wildlife Research* 60, 789–801. doi:10.1007/s10344-014-0848-6

Noninvasive genetic sampling allows estimation of capercaillie numbers and population structure in the Bohemian Forest

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Abstract Wildlife conservation and management of endangered species requires reliable information on the size and structure of populations. One of the flagship species in European wildlife conservation is the forest-dwelling capercaillie (*Tetrao urogallus*), where several populations are endangered. In the Bohemian Forest, e.g., the population severely declined 30 years ago with only 100 birds remaining in 1985. Subsequently, breeding and release programs were conducted to supplement the local population. The current distribution and population size, however, remained unknown. With recent habitat changes and increasing recreational activities, a reliable population estimate to inform conservation plans was needed. A team of scientists and volunteers collected fresh capercaillie droppings covering an area of about 120,000 ha. We genotyped ten microsatellite loci to estimate the current population size and to determine the population's spatial and genetic structure.

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Population size and density estimators revealed a population size of approximately 500 individuals, which is thus one of the two largest relict populations in the low mountain ranges of temperate Europe. The population clustering revealed gene flow across the entire study area. Several genotypes were documented with multiple recaptures at spatial distances between 10 and 30 km additionally corroborating gene flow across the entire landscape of the study area. Males were more closely related than females on small spatial scales up to 3 km, indicating lower dispersal rates in males. We conclude that the population currently appears to have a viable size and shows unrestricted gene flow across state borders and management units of the entire Bohemian Forest. However, long-term viability of this population requires a transboundary strategy to sustainably protect and monitor this isolated capercaillie population in Central Europe.

Keywords *Tetrao urogallus* · Citizen science · Capture-recapture · Wildlife management

Introduction

The conservation and management of an endangered species requires reliable estimates on variables describing the population status as well as their temporal and spatial dynamics. The size of a focal population provides important baseline information to assess the species' conservation status, initiate potential conservation activities, and allow the evaluation of the success or failure of previous management activities. However, most conservation efforts are initiated when population sizes are already critically low (Czech et al. 2000; Taylor and Knight 2003). Such rapid and short-term activities are costly, particularly when time-consuming ex situ breeding or expensive translocations are needed. Therefore, conservation

ecology provides noninvasive methods to establish monitoring of endangered species (e.g., Bonin et al. 2007; Wilson and Delahay 2001).

Throughout Europe, many grouse (Tetraoninae) population sizes are declining, and the remaining populations are increasingly fragmented (Storch 2001, 2007) due to habitat destruction and increasing recreational activities (e.g., Moss et al. 2000; Pollo et al. 2003; Thiel et al. 2011). To support local grouse populations, animals are released for subsidy or birds are reintroduced (see Seiler et al. 2000).

Many local capercaillie populations in Central Europe have become extinct during the last century (Klaus et al. 1989), or isolated by hundreds of kilometers. Given the patchy distribution of suitable habitats in combination with its restricted juvenile and adult dispersal that seldom exceeds >10 km (see review in Storch and Segelbacher 2000), natural (re-)colonization of suitable habitats across large distances is unlikely (Rolstad 1989; Suchant and Braunisch 2004). Moreover, only one of the populations in the low mountain ranges of Central Europe, in the Black Forest, exceeds a population size of 500 individuals (Segelbacher et al. 2003a, 2008) that is believed to be the minimum viable population size for this species (Grimm and Storch 2000).

The capercaillie is also found in the Bohemian Forest, which stretches across the border between the Czech Republic and Germany and includes the transboundary national parks Šumava (Czech Republic) and Bavarian Forest (Germany). In the area of the Bavarian Forest National Park, the population size decreased dramatically from 250 birds in 1945 to merely 26 individuals in 1984–1985 (Scherzinger 2003). For the Šumava National Park, Bufka (2011) estimated less than 100 birds before 1990. Thus, a breeding and release program was established, with a total of 1,376 individuals released between 1985 and 2000 (Hlavatá 2002; Scherzinger 2003). However, the success of this program has not yet been evaluated, and the present population size and genetic structure are unknown.

After the breakdown of the Iron Curtain and subsequent political decisions, formerly undisturbed mountain areas are now intensively used especially by increasing recreational activities such as hiking in summer and snowshoeing in winter which propose a major threat to wildlife (Arlettaz et al. 2007; Paudel and Kindlmann 2012). As capercaillie are considered to be very sensitive to disturbance (Thiel et al. 2007) and habitat change (Thiel et al. 2008a, b), conservation managers on both sides of the border initiated a noninvasive survey of the capercaillie's current population status and structure in the entire Bohemian Forest to optimize conservation planning.

Here, we report the results of the genetic analysis of capercaillie droppings sampled across the entire landscape of the Bohemian Forest (German and Czech side). Specifically, our study aimed to determine (i) the current capercaillie population size and (ii) the spatial and genetic structure and diversity of the capercaillie population living in the Bohemian Forest.

Material and methods

Study area

The study was carried out in the Bohemian Forest (Fig. 1), a low mountain range of approximately 119,000 ha in size that includes the Šumava National Park in the Czech Republic (69,039 ha) and the Bavarian Forest National Park in Germany (24,368 ha). Between 6 % (winter) and 10 % (nonwinter seasons) of the national parks areas are considered as suitable capercaillie habitat consisting of forests dominated by Norway spruce (*Picea abies*) above 1,100 m a.s.l. (Teuscher et al. 2011). The study area also included forests of surrounding protected landscape areas in both countries (Fig. 1). Only in peripheral regions, few villages and roads penetrate the forest ecosystem. Despite a small gap in the southeastern part of the forest (lower altitudes and settlements, see distribution of samples in Fig. 1), almost the entire mountain ridge is therefore suitable capercaillie habitat. Therefore, our study covers the entire potential capercaillie habitat in the area. Altitudes of capercaillie occurrence range from 700 to 1,450 m a.s.l. (Teuscher et al. 2011). Winter spans from November to April, with snow cover for approximately 100–200 days per year at altitudes above 900 m a.s.l. (Bässler 2004).

Focal species

The capercaillie (*Tetrao urogallus*, L. 1758) is the largest tetraonid species in Europe and inhabits forests from Scandinavia to eastern Siberia (von Blotzheim et al. 1994; Storch 2001; Thiollay et al. 1994). The boreal forests harbor the largest populations of this grouse (about 760,000 to 1,000,000 breeding pairs; BirdLife International 2012). In temperate Europe, its distribution is mainly linked to natural coniferous forests (Storch 2001; Segelbacher and Piertney 2007, but see Alda et al. 2013) with the largest population in the Alps and smaller populations across low mountain regions with altitudes above 900 m a.s.l. (Mollet et al. 2003; Storch 2001). In the low mountain ranges, besides very few small populations (e.g., Vosges and Fichtel Mountains), only the Black Forest and the Bohemian Forest are known to harbor larger numbers of capercaillie (Storch 2001, 2007).

Data collection

During 14 months from autumn 2009 to spring 2011, and after intensive theoretical and practical trainings, about 70 volunteers, i.e., laypersons, park rangers, foresters, scientists, non-professional ornithologists, hunters, and students collected fresh capercaillie droppings on the entire potential capercaillie habitat in the Bohemian Forest (approximately 22,000 ha; for details, see Teuscher et al. 2011; Rösner et al. 2014). For systematic fieldwork, we used a previously established 50-

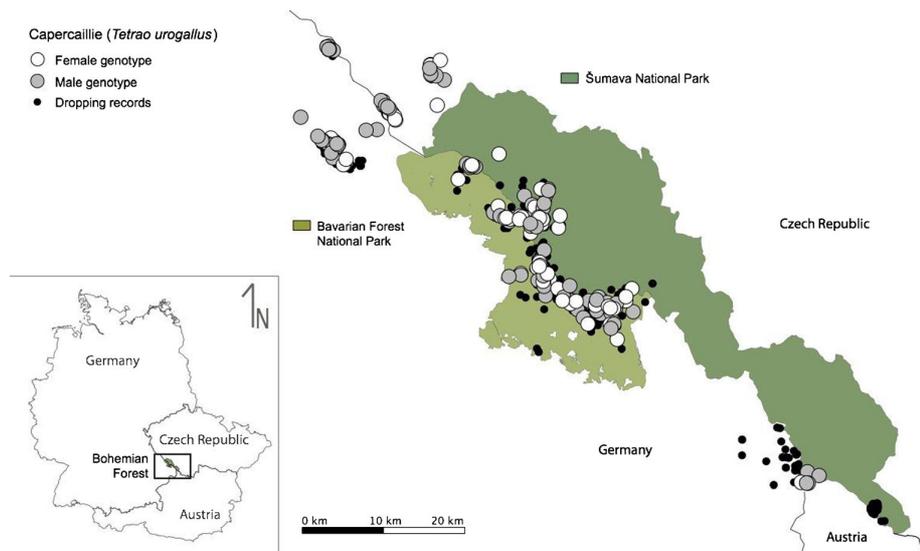


Fig. 1 Distribution map of *Tetrao urogallus* records (1,535 “operational individuals,” 219 genotypes) in the Bohemian Forest (all potential capercaillie habitat has been systematically sampled in Šumava and Bavarian Forest national park and surrounding protected landscape areas) collected between autumn 2009 and spring 2011. Black points indicate the sample

distribution of all dropping records. Large points show identified genotypes (530 samples). Samples with “recaptured genotypes” ($N=184$) are plotted with median locations for better readability (white = female, gray = male). All samples outside the national parks are situated in protected landscape areas

ha grid system (see Teuscher et al. 2011, 2013), where a variable set of grid cells (a search area) with suitable capercaillie habitat (see Teuscher et al. 2011) was assigned to two persons in charge and visited at least twice for dropping collection. In accordance to current habitat situation, search areas were slightly adjusted during fieldwork to best cover all potential capercaillie occurrences. All locations of capercaillie records were determined using handheld GPS devices and assigned to the corresponding grid cell number, respectively. To avoid pseudoreplications (compare Thiel et al. 2008b) and minimize any disturbances, we prevented intensive collection at known lek sites by only exploring them once around noon between March and April. Only very fresh droppings were collected while walking parallel transects of about 10 m distance. Furthermore, spatially clumped and multiple droppings around feeding places, alongside individual tracks in the snow, or under single resting trees were considered to stem from the same individual and were therefore assigned to one “operational individual.” At sites with high capercaillie densities, we assigned collection of samples to different operational individuals if a distance of at least 30 m separated samples of the same sex (compare Thiel et al. 2008b). Each sample consisted of one to approximately seven droppings, for which we noted the geographic coordinates (see above), the weather conditions, and the sex predicted from the relative diameter of the dropping (Thiel et al. 2008b; Rösner et al. unpublished). The exact sex was later confirmed genetically. Only fresh droppings (2–3 days after fresh snowfall in winter and wet droppings in summer) were sampled, stored cool

during fieldwork by the use of thermal packs, and frozen at $-20\text{ }^{\circ}\text{C}$ on the day of collection and kept frozen until further processing.

Subsampling and laboratory work

Overall, the collection comprised about 7,500 droppings resulting in 1,535 operational individuals. For genetic analysis, we used a subset of 550 stratified random samples. To equally cope with both sexes, random sampling was applied for either sex (275 samples, respectively). Here, the sex of the samples is based on estimation during fieldwork (see above). Furthermore, we sampled at least one dropping from each of the 252 grids with records to ensure that samples from across the entire area were included.

DNA was extracted from fresh droppings using the QIAamp Stool Kit (Qiagen) with a modified extraction protocol based on Jacob et al. (2010). Extracted DNA was purified by repeated washing and removing PCR inhibitors (InhibitEX and specific buffers, Qiagen) and genotyped for ten microsatellite loci specific for the capercaillie using the established primer pairs TUD1, TUD3, TUD5, TUD6, TUD7, TUT2, TUT3, and TUT4 (see Segelbacher et al. 2000; Segelbacher 2002) and BG15 and BG18 (Piertney and Höglund 2001). DNA was amplified by polymerase chain reaction (PCR) following the published multiplex protocol by Jacob et al. (2010) and run on an ABI 3730 Sequencer (Applied Biosystems), and allele scorings were conducted using GeneMapper v. 4.0 (Applied Biosystems). Samples

were only considered for analysis when allele scoring was repeatedly consistent over three consecutive runs at a minimum of nine loci. This means that samples where more than one allele repeatedly failed to amplify (allelic dropouts) were excluded from further analysis. We used Micro-Checker software (van Oosterhout et al. 2004) to detect null alleles. We used the program PEDANT ver. 1.0 (Johnson and Haydon 2007) to estimate the rate of genotyping error per allele due to allelic dropout and false alleles.

Sex was determined using the chromosome-specific primers P2 and P8 following published protocols (Griffiths et al. 1998). To assure reliable sex determination, PCR amplification of the sex-specific markers was run twice to verify the results. Nine samples yielded contrasting results in the two runs and were excluded from sex-specific analyses. All laboratory work was conducted by ecogenics GmbH, Switzerland (www.ecogenics.ch).

Population size

To assess the current population size in the study area, we applied 13 statistical estimators to the genotypic data set. Eight of these estimators are species richness estimators: the lower bound estimator (Chao 1984), two coverage estimators by Chao and Lee (1992), coverage duplication-estimator (Chao and Bunge 2002), a Jackknife estimator by Burnham and Overton (1978, 1979), the unconditional nonparametric maximum likelihood (NPML) estimator (Norris and Pollock 1998), the penalized conditional NPML by Wang and Lindsay (2005), and the Poisson-Compound Gamma estimator by Wang (2010). We used the package SPECIES in R v. 3.0.1. Here, all estimators are implemented allowing Monte Carlo simulations for estimator comparisons (Wang 2011, R Core Team 2013). We used the default settings for all estimators as suggested by the authors (Chao 1984; Chao and Lee 1992; Chao and Bunge 2002; Burnham and Overton 1978, 1979; Norris and Pollock 1998; Wang et al. 2005; Wang 2010). We extracted the expected population size (N), standard errors (SE; when available), and 95 % confidence intervals (CI) using bootstrapping with 200 samples as suggested by Wang (2011). Due to errors in bootstrapping algorithm (Wang, personal communication), CIs are not given for the Poisson-Compound Gamma estimator by Wang (2010).

With respect to multiple observations and the spatial distribution of individuals, we further applied five population density estimators that are based on capture-recapture approaches and are explicitly developed for noninvasive genetic data sampling (for reviews, see Beja-Pereira et al. 2009; Lukacs and Burnham 2005). We used the R packages Capwire v. 1.1.4 (Pennell et al. 2013) and secr v. 2.7.0 (Efford 2011). Both approaches allow for multiple capture (recapture) events per sampling occasion. Capwire (Pennell et al. 2013) applies a modified population size estimator originally published by

Miller et al. (2005). Here, we applied two models that differ in the “capture probability” of the detected genotypes: the equal capture model (ECM) and the two innate rates model (TIRM). TIRM model results were fit against ECM using likelihood ratio test (1,000 bootstraps). A parametric bootstrap with 1,000 bootstraps provided confidence intervals of the population size estimates (Pennell et al. 2013). The secr package (Efford 2011) was used to apply likelihood-based spatially explicit capture-recapture approaches for population size estimations (see Efford 2011, Efford and Fewster 2013). As secr models incorporate spatial information of the capture-recapture events, we defined each of the searched 50-ha plots as a “trap” as required for input data set. Here, trap locations were provided as center points (geographic XY coordinates) of the respective grid cell. We applied detector type *count* for calculation as it allows the repeated capture of individuals (genotypes) at the same occasion (trap) (see Efford 2011). We calculated three different models in accordance with the three different detection functions (HN = half normal, HR = hazard rate, EX = exponential). All models assume that animals hold home ranges and the capture probability declines with increasing distance from its center. Models differ in the parameters λ (capture probability at the home range center) and σ (capture probability with increasing distance to home range center). A spatial buffer (in meters) around the detector array (traps) was determined on the basis of the given capture events using the integrated function *suggest.buffer()*. We accordingly used the three suggested buffers: 4,956 m (model HN), 4,889 m (HR), and 4,970 m (EX). Finally, the best model fit was selected by the use of Akaike’s information criterion (AIC).

Genetic population structure

To estimate the “probability of identity” (PI), we calculated the average probability of two individuals sharing the same multilocus genotype (Lacy and Sherman 1983) using GenAIEx v. 6.4 (Peakall and Smouse 2006). We used chi-square tests using Arlequin v. 3.5.1.3 to test for possible deviations from Hardy-Weinberg equilibrium (Excoffier and Lischer 2010).

To examine whether capercaillie genotypes are randomly distributed in the study area or show a genetic structure, we performed spatial autocorrelation analysis using the relatedness coefficients r (Smouse et al. 2008) as implemented in GenAIEx v. 6.4 (Peakall and Smouse 2006). We performed two-tailed tests to detect differences between the relatedness coefficients r of a null model (9,999 random permutations of all genotypes in space) and the observed genotypes within given distance classes. To assign unique genotypes with multiple recoveries to the pairwise distance classes, we calculated median coordinates of multiple geographic positions.

We applied Bayesian clustering algorithms using Markov Chain Monte Carlo (MCMC) with the software Structure v.

2.3.4 (Evanno et al. 2005; Pritchard et al. 2000) and Geneland v. 4.03. (R package version) (Guillot et al. 2005, 2012) to explore genetic population structuring and possible spatial genetic discontinuities. Both programs analyze multilocus genetic data to assign genotypes to groups of individuals (Pritchard et al. 2000; Guillot et al. 2005). Computations in Structure were applied with a set of 20 iterations for each number of expected subpopulations (K) from $K=1$ to $K=12$, and 5×10^4 MCMC repeats after an initial burnin of 5×10^4 runs. To estimate the posterior probability of the number of subpopulations, we used the log-likelihood $L(K)$ as provided in the Structure output (Pritchard et al. 2000) and calculated ΔK in accordance to Evanno et al. (2005). In Geneland, we performed 1×10^5 iterations with a thinning of 100 (1,000 iterations saved) for a maximum of $K=12$ subpopulations. The entire MCMC inference was repeated with 20 independent runs to provide the results with the highest a posteriori probabilities (Guillot et al. 2005). Computations were applied including the geographic positions of 215 multilocus genotypes (four genotypes are lacking exact geographic positions). To cope with the mobility of our focus species, we used the “location uncertainty” option (Guillot et al. 2005, 2012) and set it to 1.5 km based on the mean activity ranges of genotypes detected in our study area (see “Results”). We calculated F-statistics and analysis of molecular variance (AMOVA) by assigning all genotypes to the population cluster according to the highest posterior probability as given from Geneland output (Evanno et al. 2005).

Spatial activities

We determined activity ranges of genotypes with multiple recapture events using the minimum convex polygon approach (MCP; Quantum GIS Development Team 2012). We calculated ranging distances as pairwise distances between capture and recapture points and tested for differences between sexes using Wilcoxon signed rank test as implemented in R (R Core Team 2013). We handled cartographic information and produced maps using QGIS (Quantum GIS Development Team 2012, v. 1.8.0 Lisboa) in combination with R v. 3.0.1 (R Core Team 2013).

Results

Within a 14-month period, our team of volunteers and non-professional scientists managed to noninvasively and systematically collect thousands of droppings from the reclusive capercaillie. Approximately 7,500 droppings were assigned to 1,535 operational individuals. We found droppings in 252 out of approx. 400 searched 50-ha cells of our grid system (approximately 12,600 ha, 63 % of the searched study area).

Dropping locations ranged from protected landscape areas at the edge of the study area in the northwest alongside almost the entire mountain ridge to the southeasternmost forests close to Austria (see Fig. 1). Samples were mainly found at higher altitudes, with an almost area-wide occurrence of this species above 1,000 m a.s.l. along the mountain ridge of the two national parks and protected landscape areas (Fig. 1).

Overall, 546 of the 550 randomly selected DNA samples provided reliable genotyping results. None of the genotyped samples and loci showed signals of null alleles (Micro-Checker analysis, van Oosterhout et al. 2004). Two loci (TuD7, TuD5) showed one private allele (ESM Appendix I). Genotype distribution of all ten loci and over all loci did not deviate from Hardy-Weinberg equilibrium after Bonferroni correction of the P values (all $P > 0.05$, see ESM Appendix I). The analysis of locus-specific polymorphism and heterozygosity revealed between 3 and 12 alleles (mean=6.1, SE=1.0) for the ten different loci (ESM Appendix I) with locus TuD6 showing a maximum of 12 different alleles. The mean observed heterozygosity (H_o) was 0.641 (SE=0.022) and the expected heterozygosity $H_e=0.623$ (SE=0.017; ESM Appendix I). Average rate of genotyping error per allele due to allelic dropout and false alleles was 0.059 and 0.0011, respectively.

Overall, 218 (40 %) of the genotyped samples came from the Šumava National Park in the Czech Republic, 144 (26 %) from the Bavarian Forest National Park, and 184 (34 %) from the adjacent protected landscape areas (both countries, see Fig. 1). Genotyping analysis of all 546 DNA samples (see above) revealed 219 unique genotypes with 113 males and 97 females (nine were not sexed successfully) leading to a sex ratio (males/females) of 1:0.85 across the entire study area. The probability of two individuals sharing the same genotype (probability of identity, PI) was $P=5.5 \times 10^{-9}$. Hence, each genotype represented one individual bird.

The majority (184, 86 %) of all individual genotypes were observed at least twice (mean=2.4 observations/genotype, max=16 observations of a single genotype). The number of recaptures was much higher for males (811 pairwise recaptures) than for females (157 recaptures). Overall mean distance of all recaptured genotypes (968 pairwise recaptures) was 1.2 km (SE=0.1). The maximum distance between two recaptures of a genotype, a male, was 34 km. Note that this bird showed disturbed behavior, being tame and fearless, and even attacking the volunteer while displaying. However, eight long-distance movements >20 km were recorded from different males. All documented recapture distances >5 km (37 pairwise records) also belonged to males (81 %). Most recaptures in the distance class >5 km of both sexes were documented between two consecutive mating seasons (February–May 2010 and March–April 2011). In contrast, droppings of a male were found 27.8 km afar from the place where droppings were detected the day before (2nd and 3rd March 2011). It is important to note that we only know the date of collection and

not the exact age of the droppings. We also found examples for extreme stationary behavior. For example, in the late mating season of the previous year (May 8th 2010), the bird was recorded a few meters besides the place of recovery from the 3rd of March 2011.

The mean distance between recaptured females (1.0 km, SE=0.3) was significantly lower (Wilcoxon test, $W=1,939$, $P<0.01$.) than that of males (1.2 km, SE=0.1). A similar pattern was found when we compared the activity ranges of individuals with more than two recapture events (64 individuals). The mean activity ranges across all genotypes was 1.6 km² (164 ha), with a corresponding mean perimeter length of 5.5 km. Males (42 individuals) used significantly larger areas (mean=289 ha, SE=79.6) than females (22 individuals, 15 ha, SE=4.0; Wilcoxon test, $W=15,589$, $P<0.001$).

In average, the 13 different species richness and population size estimators (see Wang 2011; Pennell et al. 2013; Efford 2011) resulted in a population size of $N=488.2$ (SE=29.01), ranging from $N=246$ (ECM) to $N=606$ (Wang et al. 2005, Fig. 4, ESM Appendix III). Boundaries of 95 % confidence intervals ranged between 233 and 616 (Table 1, Fig. 4, ESM Appendices II and III).

The two models implemented in Capwire calculated estimates of 246.0 (ECM) and 333.0 (TIRM, ESM Appendix III). The likelihood ratio estimate (LRE) selected TIRM above ECM (157.91, $P<0.0001$). The three spatially explicit mark-recapture models HZ, EX, and HN in *secr* provided values between 453.6 (HZ) and 418.9 (HN). Here, AIC selected the hazard rate model as the best fit (AIC=6,713.6) above EX (AIC=7,205.2) and HN (AIC=7,945.5) (ESM Appendix III). For the three management units, we applied species richness estimates and found mean population sizes: Šumava National Park=234 (SE=6.9), Bavarian Forest National Park=155 (SE=5.7), and protected landscape areas=188 (SE=4.0, Table 1, ESM Appendix II).

Autocorrelation analysis revealed no significant spatial structure for the entire set of 210 genotypes. However, sex-specific analysis showed a significantly closer genetic

relatedness (two-tailed tests; both P values=0.01) of male capercaillie than expected by chance within the smallest distances classes of 1.0 and 3.0 km. Hence, males showed a fine-scale genetic structure. At larger distances up to 85 km (max distance between two different genotypes records), we found no significant spatial structure in males. Females did not show significant spatial genetic structure in either of the distance classes (all P values>0.05, Fig. 2).

Both Bayesian clustering analyses with Structure and Geneland software suggested a substructure of $K=3$ subpopulations. Structure software outputs showed the highest probability values at $K=3$ indicating three clusters in the population (Fig. 3). The 20 independent runs in Geneland also revealed a clear picture of substructure with three clusters. Here, values rapidly converged at $K=3$ after a burnin of 200 iterations (ESM Appendix IV). Almost 70 % of the independent MCMC iteration runs were supportive for the tripartite substructure ($K=3$, ESM Appendix IV). When plotting posterior probabilities of all genotypes, cluster 2 comprised most of the samples (75 %, 162 genotypes). According to that, cluster 2 formed a core area comprising the two national parks (ESM Appendix IV; compare Fig. 1). While cluster 1 included the genotypes recorded in the easternmost area of the Bohemian Forest (15 genotypes, 7.0 %), cluster 3 consisted of 38 genotypes (17.7 %) in the northern protected landscape areas (ESM Appendix IV).

The estimate of the overall genetic differentiation F_{ST} was very low and not significant ($F_{ST}=0.002$, $P=0.324$) with all genetic variation (100 %) within individuals ($F_{IT}=0.004$, $P=0.40$). The overall F_{IS} was very low ($F_{IS}=0.002$, $P=0.447$). For females, the overall F_{ST} was calculated as $F_{ST}<0.001$ ($P=0.464$) and for males $F_{ST}=0.015$ ($P=0.001$). F_{IS} for the three clusters were $F_{IS}=0.263$ (cluster 1), $F_{IS}=-0.255$ (cluster 2), and $F_{IS}=-0.302$ (cluster 3) (ESM Appendix V). The AMOVA revealed low and nonsignificant F_{ST} values ranging from $F_{ST}=0.011$ to $F_{ST}<0.00$. Sex-specific AMOVA analysis revealed no significant differences in females ($F_{ST}>0.005$, all $P>0.21$) but showed significant pairwise differences between

Table 1 The capercaillie (*Tetrao urogallus*) population sizes averaged (±SE) from eight species richness estimators (R package SPECIES, Wang 2011) with the lowest and highest boundaries of 95 % confidence

	Mean N (±SE)	Lowest boundary (95 % CI)	Highest boundary (95 % CI)	Number of samples analyzed	Number of genotypes (male/female)
Entire Bohemian Forest	556 (7.1)	544	616	546	219 (113/97)
Šumava National Park	234 (6.9)	216	323	218	104
Bavarian Forest National Park	154 (5.7)	141	218	144	59
National parks combined	365 (0.7)	360	387	362	153
Protected landscape areas	188 (4.0)	182	223	184	79

intervals (CI). Note that nine genotypes were not sex-determined. For detailed information on the estimators used and the results obtained with each estimator, see ESM Appendix II

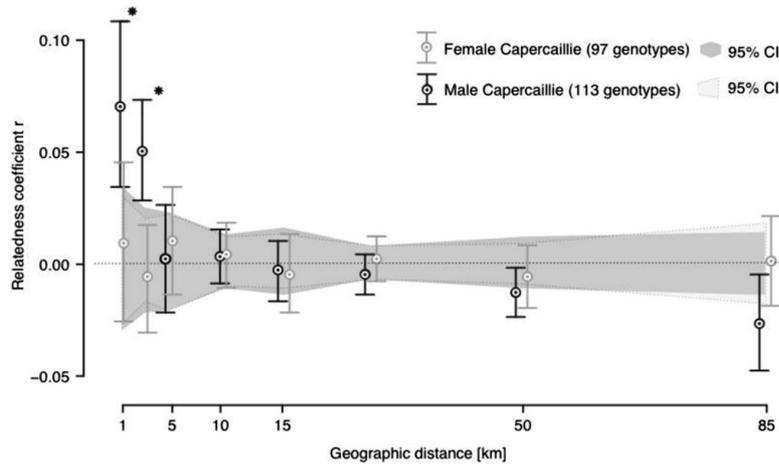


Fig. 2 Correlogram of spatial autocorrelation analysis for male and female individuals ($N=210$) of capercaillie (*Tetrao urogallus*) in the Bohemian Forest (Czech Republic, Germany). Relatedness coefficients r between genotypes in given distance classes as a function of pairwise genetic distance (Smouse et al. 2008). Calculations based on 9,999

permutations and 9,999 bootstraps; 95 % confidence intervals are given. Distance classes indicate the end point of pairwise geographic distances between genotypes. Asterisks indicate significant differences within distance classes (two-tailed test, $P < 0.05$)

male genotypes of the southern cluster (cluster 1) and the core cluster (cluster 2, $F_{ST}=0.063$, $P=0.004$) and the northern cluster (cluster 3, $F_{ST}=0.064$, $P=0.003$), respectively.

Discussion

In this study, we demonstrate that population size in the elusive capercaillie can be assessed with noninvasive genetic methods across a large spatial scale in a short time with the help of many volunteers.

Methodological approach

After intensive seminars and field trainings, our team of laypersons and nonprofessional scientists (citizen science approach, e.g., Dickinson et al. 2010; Lepczyk et al. 2009) managed within a time frame of mere 14 months to pick up thousands of capercaillie droppings across the entire transboundary landscape of the Bohemian Forest (20,000 ha of the forest ecosystem). In fact, net time of main fieldwork even spanned only over a few weeks during late winter (March–beginning of April) when weather conditions were best (cold temperatures, fresh snow falls). These

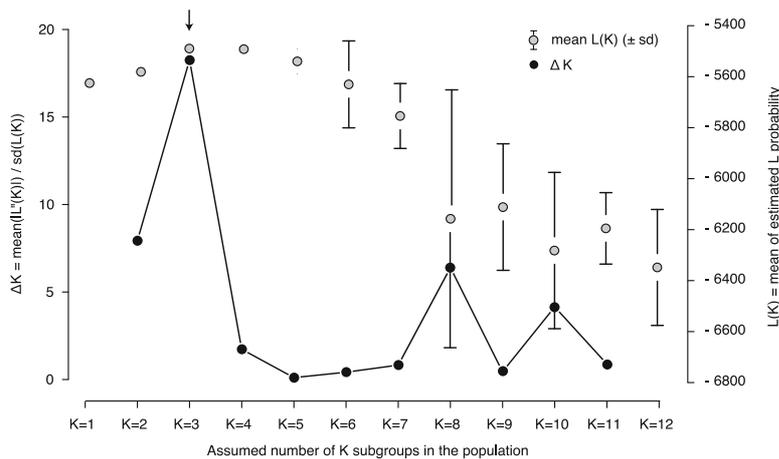


Fig. 3 Inference of the number of genetic clusters (K) within the capercaillie (*Tetrao urogallus*) population in the Bohemian Forest. Results of 20 independent runs for $K=1$ to $K=12$ with 10,000 MCMC iterations as calculated from the Structure results (Evanno et al. 2005). Black points show delta K (ΔK) calculated according to Evanno et al. (2005). $\Delta K =$

$\text{mean}(L''(K)) / \text{sd}(L(K))$. Highest value at $K=3$ (see arrow) indicates the most likely number of subpopulations. Mean log-likelihood scores ($L(K)$, gray points) as a function of the number of genetic groups ($K=1$ to $K=12$), calculated over 20 independent runs for each K . Error bars show standard deviations ($\pm SD$)

noninvasively and systematically compiled samples composed the database for this study. We obtained 99 % successfully amplified genotypes from droppings. This is similarly high as the maximum value in the literature of 98 % obtained by Regnaut et al. (2006). However, most other studies yielded considerably lower values of, e.g., 48 % when genotyping capercaillie feces (e.g., Jacob et al. 2010). We attribute our effective genotyping to the rigorous sampling protocol and the intensive preparation of volunteers before the fieldwork. Our study underscores the value of citizen science as research tool in general (Dickinson et al. 2010, see FeederWatch example by Bonter and Cooper 2012) and even verifies its application in single-species projects of rare and endangered species. Thus, we are convinced that our “rapid assessment” with enthusiasts was appropriate to compile reliable baseline data to evaluate the preceding breeding and release program and to manage upcoming new threats, e.g., increasing recreation activities (see below).

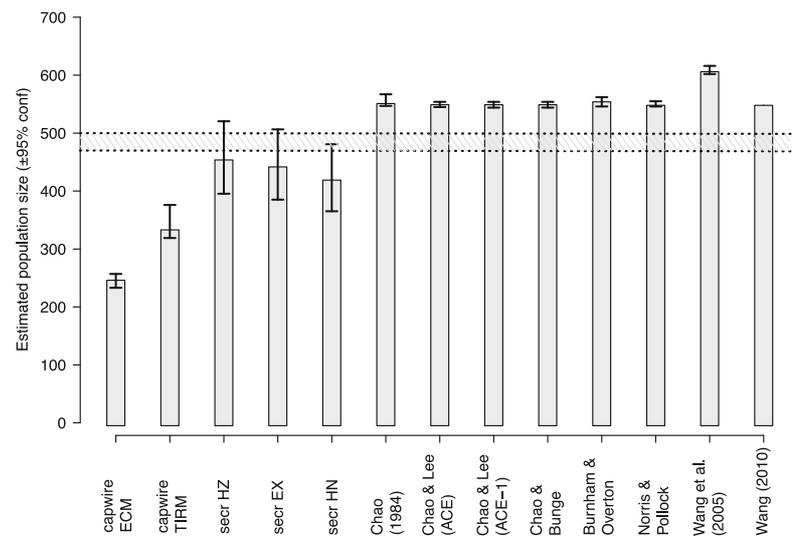
Population size

Conservation management of both national parks now calls for precise information about the current population status of the species. To receive information about the current population size, we applied a range of population size estimators to the multiple recaptures of genotypes. Thirteen models revealed a mean population size of about 490 birds ($N_{\text{mean}} = 488.2$, $SE = 29.01$). Highest values between 500 and 600 animals resulted from the eight different rarefaction estimators (see Wang 2011), whereas the three spatially explicit capture-recapture models (Efford 2011) resulted in intermediate values of about 400 to 500 animals. The two “capture with replacement” models (see Pennell et al. 2013) resulted in lowest

values of 200 to 400 animals. In general, the applied estimator approaches were most reasonable for our data set. However, the two latter estimates should be taken with caution as the Capwire package is known to perform best for population sizes below 100 individuals (Luikart et al. 2010).

The results indicate the Bohemian Forest to harbor the second largest capercaillie population within the Central European low mountain ranges, with the Black Forest having the largest population ($N \approx 600$; Suchant and Braunisch 2008). The population size is therefore within the assumed range of the minimum viable population (MVP, Fig. 4) size of 470 to 500 birds which is needed for long-term survival (extinction risk $< 1\%$ for the next 100 years as reported by stochastic models; Grimm and Storch 2000; Storch 1995), as well as the estimate of 100 birds suggested by Marshall and Edwards-Jones (1998). However, the mere number of birds is not the only driver of survival or extinction of local populations (Grimm and Storch 2000; Boyce 1992). Other factors such as the demographic structure, the status of population fluctuation (typical in tetraonids, see Ranta et al. 1995; Storch 2001), the breeding success (Baines et al. 2004), and offspring mortality (Saniga 2002) are known to affect the probability of species survival (see Boyce 1992). Therefore, future studies should implement these factors for a population viability analysis (PVA). Because one third (34 %) of the entire population inhabits forests outside the management areas of national parks, future conservation efforts have to ensure the connectivity and persistence of habitats of sufficient quality. The conservation priorities for the peripheral clusters become even more apparent by the fact that the number of individuals inside the national park areas ($N = 366$, see [ESM Appendix](#)) is smaller than the MVP (470 to 500 animals, see Grimm and Storch 2000).

Fig. 4 Comparison of 13 capercaillie (*Tetrao urogallus*) population size estimations. Mean number of population size and upper and lower confidence intervals (95 %) are shown. Minimum viable population size of 470–500 individuals (Grimm and Storch 2000) is given as dashed line. Confidence intervals for estimator from Wang (2010) are not available. ECM equal capture model, TIRM two innate rates model (Pennell et al. 2013), HZ hazard rate, EX exponential, HN half normal (Efford 2011)



Spatial activity and relatedness

The spatial distribution of the 7,500 droppings confirmed findings from previous habitat models for the Bohemian Forest by Teuscher et al. (2011, 2013), showing that capercaillie mainly occupy the coniferous high mountain forests above 1,000 m a.s.l. While we detected few long-distance movements (up to 34 km), most birds moved only short distances of about 1 to 2 km with mean activity ranges of 1.6 km². This is in line with the highly restricted geographical movement of capercaillie reported from elsewhere (Storch 1997). Although our recapture data are coarse (about two recaptures per genotype) compared to data from intensive field studies, the mean activity range of genotypes matched earlier estimates obtained from telemetry (dozens of bearings per individuals, e.g., Thiel et al. 2008b). Storch (1997) and Thiel et al. (2008) reported mean areas of home ranges in the Alps and the Black Forest of 1.1–1.9 km². Similar to our findings, male birds used significantly larger areas than female birds (Thiel et al. 2008a, b). Gjerde and Wegge (1989) reported smaller home ranges in southeast Sweden during winter (0.3–0.6 km²), with males also using significantly larger areas. The surprisingly good match between home range sizes obtained through genetic and other field methods underlines the potential of noninvasive sampling of droppings to retrieve important information for rare species or species that are difficult to investigate (e.g., Smith et al. 2006; but see Fedy et al. 2008).

Our spatial autocorrelation analysis revealed sex-specific differences in the genetic structure of the studied population. Relatedness among females did not show fine-scale genetic structure at any of the distance classes (Fig. 2). In addition, AMOVA results among females of the three clusters (see below) did not reveal significant differentiations. This indicates random genetic relatedness of females across the study area, which is supported by findings from other studies that detected female-biased dispersal that might lead to unrestricted gene flow on local scales (e.g., Storch 1997; Segelbacher and Storch 2002; but see Mäki-Petäys et al. 2007). In our study, we found some males to be highly mobile, and all long-distance recoveries >20 km (eight records, max=34 km) were recorded from males. Similarly long-distance movements were recorded by recoveries of ringed males in Russia and Austria (von Blotzheim et al. 1994). However, the majority of our records were detected within the species' mating season. Yearling cocks, for example, are known to visit different lek sites during the mating season (Storch 2001). Therefore, these findings rather reflect short-term movements than dispersal patterns in general.

Males were more closely related at small spatial scales as expected by chance (Fig. 2). The spatial scales of 1 to 3 km fit the size of activity ranges around lek sites (Wegge and Rolstad 1986; Gjerde and Wegge 1989) and might therefore be explained by their philopatric behavior, the breeding sites being

often situated near the leks (see Hjorth 1970), and their lek mating characteristics. As we restricted sampling at known lek sites to a minimum, we expect an even more pronounced small-scale genetic structure with increasing sample numbers from leks. Furthermore, only very few active leks are known for the entire area (approx. 10, Rösner et al. unpublished), which might lead to higher relatedness among males as relatives establish at leks in the vicinity of their natal areas (see Regnaut et al. 2006; Alda et al. 2013). Moreover, adult males show high lek site fidelity (Wegge and Larsen 1987) and mating success is highly skewed, with only one or very few successfully mating males (Mäki-Petäys et al. 2007; Storch 1997). As a consequence, reproducing males are often relatives, which may lead to kinship at lek sites (Segelbacher et al. 2007; Regnaut et al. 2006). This is also supported by spatial autocorrelation analysis, where males in the Black Forest revealed closer relationship at closer distances up to 6 km and decreased with larger distances (Segelbacher et al. 2008). This behavior might lead to high levels of inbreeding. Close relatedness among males and subsequent inbreeding effects have been observed for other grouse species with similar lek breeding systems, i.e., black grouse (Höglund et al. 1999) and lesser prairie chicken (*Tympanuchus pallidicinctus*) (Bouzat and Johnson 2004). However, we did not detect any signal of inbreeding within males (relatedness coefficient between 0.05 and 0.10). As numerous long-distance movements >10 km are recorded within the species-specific mating season of the capercaillie (March–April), we expect males to travel between the few lek sites which therefore maintain gene flow between the widely scattered lek sites in the area (between 3 and 30 km, unpublished data). Similar findings of females, in contrast, are known to intensively and regularly travel between leks (Storch 1997), which would lead to a greater contribution of gene flow compared to males.

Spatial and genetic population structure

The posterior probability analysis of Geneland structured the Bohemian Forest capercaillie into one large core population covering the transboundary national parks and two smaller clusters in the peripheral protected landscape areas (ESM Appendix IV). Although we did not detect any long-distance movements between the small cluster in the southeast (and the fact we did not record any capercaillie occurrence in a broad area of about 15 km between them; Fig. 1), the overall genetic differentiation of $F_{ST} < 0.001$ indicates still high levels of gene flow. In contrast, differentiation between the core area and adjacent cluster 3 in the northwest was marginally significant ($P=0.08$). Here, we repeatedly detected dispersal between the locally clustered records. These groups are separated by small valleys with roads and settlements which might inhibit the gene flow to some extent.

Hence, low genetic differentiation among the capercaillie subpopulations suggests sufficient gene flow across the entire forest area. Movement patterns along the mountain ridge of over 30 km underline the possibility that individual birds may move between all subpopulations and, hence, maintain gene flow across the entire landscape (up to 85 km). In contrast, populations in the Black Forest (Braunisch et al. 2010) and Bavarian Alps (Segelbacher et al. 2003a, b) revealed signatures for spatial structure at scales of only 10 km (Sachot et al. 2006; Storch 1993, 1995; Storch and Segelbacher 2000; but see Fronhofer et al. 2012; Segelbacher et al. 2008). In the Bavarian Alps, the highly fragmented landscape with unsuitable farmland and pastures between subpopulations is regarded as the main reason for the genetic isolation (Segelbacher et al. 2003a, b; 2008). This suggests that individuals do not move from one subpopulation to another through unsuitable habitats and subpopulations are even regarded as sinks (Segelbacher et al. 2003a, b). In contrast, Regnaut (2004) state that capercaillie's flight ability is sufficient to maintain gene flow across valleys and urban areas in the Jura population. Hence, continuous forests suitable for capercaillie above 1,000 m a.s.l. in the Bohemian Forest (see Teuscher et al. 2011, 2013) guarantee the gene flow throughout the entire population, which underlines the conservation value of the investigated area.

Besides sex-specific small-scale genetic structuring, we detected a coherent genetic population structure. However, it seems to be unclear how much autochthonous birds contributed to the current population genetically. We suggest that gene flow intermixed all alleles descendant from introduced individuals throughout the entire population. This is supported by the high mobility detected in the area and that multiple aviaries for bird release were scattered throughout the study area. Furthermore, the release of birds spanning over several decades (Scherzinger 2003) allowed for broad intermixture of genes. However, as neither genetic material from the formerly released birds nor from the previous autochthon population is available, we could not analyze whether the presently living birds are descendants of either group. Therefore, we recommend further investigations of historic DNA to evaluate the potential influence of the nonautochthon genetic material introduced to the area.

Conservation perspectives

Although the capercaillie conservation program in the Bohemian Forest was initiated almost 30 years ago (Scherzinger 2003), our study is the first to report the capercaillie population size and genetic structure across borders. We found that the population is relatively large, only slightly fragmented in space but show gene flow across the entire study area. However, and in contrast to the assumption that all efforts of reinforcements in Central Europe were unsuccessful (Storch

2001), we are convinced that the population subsidies strongly supported the survival of the Bohemian Forest population.

Given their poor dispersal abilities across landscapes (Storch 2001), we expect almost no connection and, hence, no gene flow to or from neighboring populations (e.g., the Austrian Alps are >160 km away). To our knowledge, the Bohemian Forest population was not yet genetically compared to other European populations. Yet, almost all other geographically isolated Central European remnant populations are known to show pronounced genetic differentiation (Segelbacher et al. 2003a).

Our results demonstrate that only about two thirds of the birds are detected in the national parks. Therefore, changes in forestry management or practices might seriously affect the two peripheral subpopulations (but see Wegge and Rolstad 2011). Even in the national parks, the sensitive grouse is exposed to harassment through, e.g., strongly increasing recreation activities (van der Zee 1990). Further, due to substantial natural disturbances of windstorms and bark beetle calamities (Seidl et al. 2011), the population is exposed to mitigation activities through intensified logging.

We therefore suggest the establishment of a monitoring program to regularly assess the trend of population size and structure of the population using the methods we have described here. We suggest monitoring efforts every 5 years for the following reasons: Firstly, the interval would be within the lifespan of capercaillie in the wild (max 10 years documented by ring recoveries, Cramp and Simmons 1980; and reproduction in the wild usually at minimum age of >3 years, von Blotzheim et al. 1994) and, therefore, guarantee possible genotype recoveries. Secondly, the interval would allow to monitor the expected rapid habitat changes in the core areas of the national parks. And thirdly, we intend to not overstress the volunteer's engagement. The regular monitoring will further guarantee the evaluation of the species' status in all Special Protection Areas (SPA, according to Article 4 of the EC Birds Directive, <http://jncc.defra.gov.uk/page-1373>) in the study region, which is required once per decade within the EU Natura 2000 network. In addition, we aim to analyze stress hormone metabolites from the area-wide collected droppings. This would allow us to infer the stress load of the population and its spatial variation in relation to the above-mentioned threats (e.g., Thiel et al. 2005, 2008b).

Although other survey methods, such as telemetry, produce reliable data on spatial activities, genetic structure, or stress load of birds (e.g., Alda et al. 2011; Rutkowski et al. 2005; Segelbacher et al. 2008), invasive methods are often based on professional ornithologists, are often expensive, require longer time frames (Segelbacher et al. 2008), and yield relatively small sample sizes (e.g., Thiel et al. 2008a, b). We believe that our approach allows for an efficient and rapid assessment of populations even across larger spatial scales.

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8 Chapter II: Recreation shapes a “landscape of fear” for a threatened forest bird species in Central Europe

Within the second chapter I focused on the effects of human activities on the spatial distribution of the focal species across the landscape scale of the national parks and surrounding forests. Specifically, I tested whether the intensities of recreational and forestry activities impact the habitat use and distribution.

My contribution: I organized the entire field work with about 70 volunteers for Capercaillie records and dropping collections. I managed data of

sampling records, data from “questionnaires” and prepared count data and geolocations for the analysis. I analyzed the data and wrote the manuscript. Together with my co-authors we improved the manuscript and revised an earlier version of the manuscript.

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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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Tomáš Lorenc · Jörg Müller

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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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Keywords *Tetrao urogallus* · Human disturbance · Tetraonidae · Citizen science · Non-invasive data collection

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

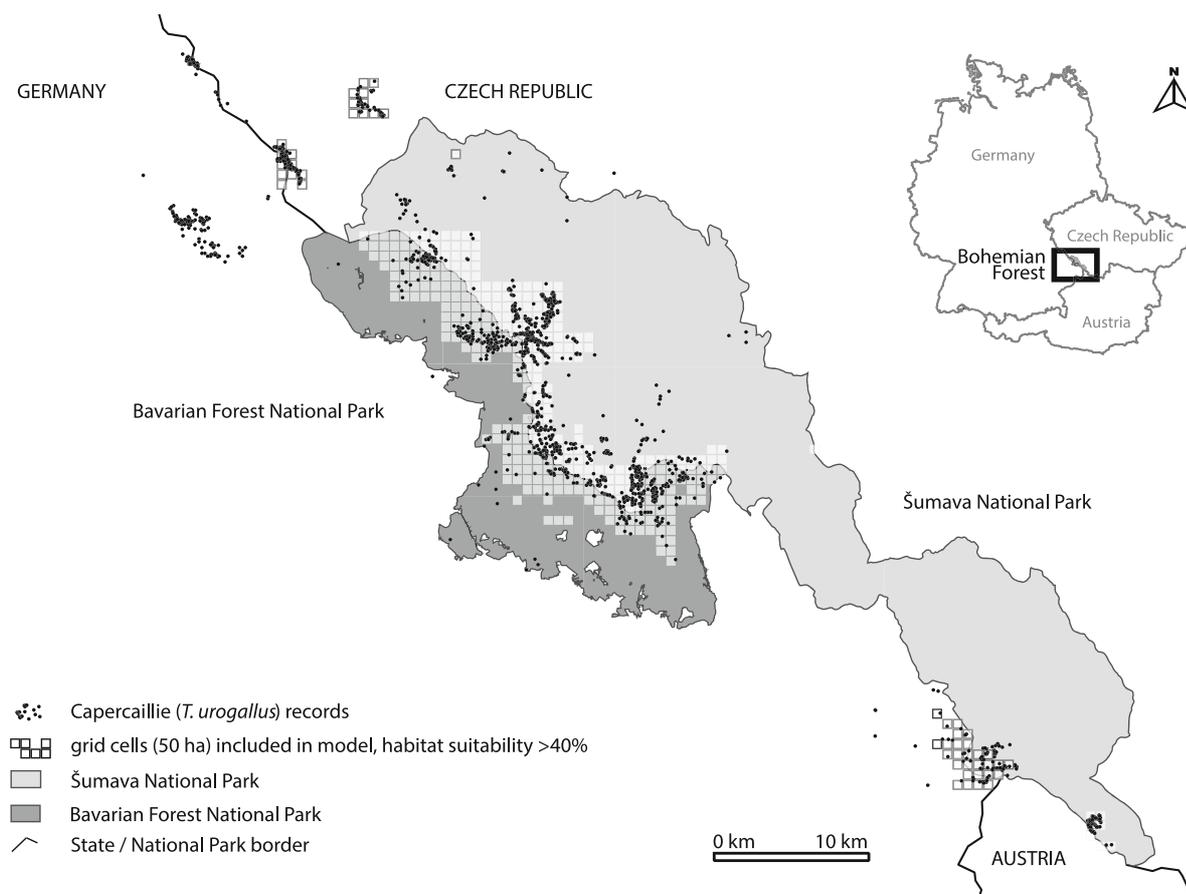


Fig. 1 Map of the study area in the Bohemian Forest. The Šumava National Park (Czech Republic) and Bavarian Forest National Park (Germany) are highlighted in gray. Points indicate the sample distribution of all Capercaillie (*Tetrao*

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 $|r_{\text{spearman}}| > 0.58$.

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.

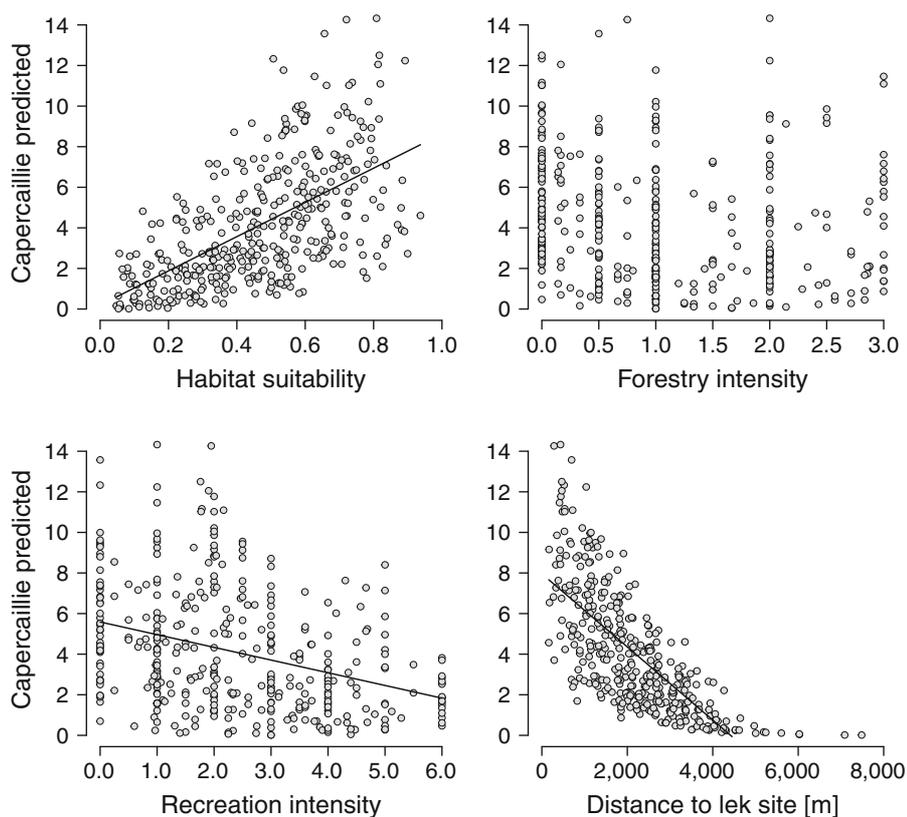
Our final data set comprised 384 grid cells covering approximately 19,200 ha (Fig. 1) in the potential Capercaillie habitat. In these cells over the four samplings, we obtained a total of 1,743 Capercaillie records with a mean of 4.5 records per 50 ha grid cell ($SE = 0.40$, max = 56 records). In 136 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

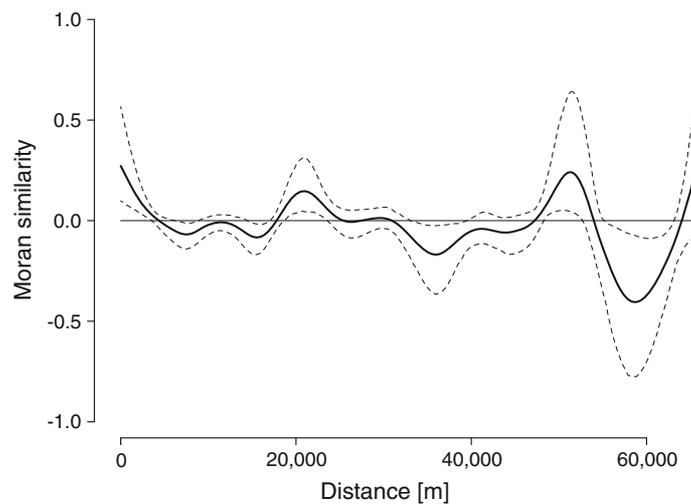
Capercaillie abundance (see Table 2; Fig. 2, Appendix I in Supplementary Material). However, in contrast to our prediction, it was not a significant factor determining Capercaillie presence or absence—the purely binomial presence or absence in grid cells within the Capercaillie habitat (note that the 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 microsattelites, 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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9 Chapter III: High quality habitats and refuges from tourism reduce personality-based stress responses in a sensitive forest specialist

In this chapter, I asked how physiological stress response measures of Capercaillie are affected by habitat quality, abiotic factors and anthropogenic disturbance. For that I examined 1,096 droppings in the laboratory. Fecal corticosterone metabolites (FCM) were measured and afterwards tested for their possible associations with temperature, habitat quality, sex, and anthropogenic activities. Based on a sub-set of genotypes, I was able to control for individual differences and thus controlling for personality.

My contribution: I organized the entire field work for Capercaillie records, dropping collection and "questionnaires" on disturbance regimes. I handled data of sampling records, disturbances, samples and laboratory work. I organized data from lab and field work and analyzed the data. I wrote the first draft of the manuscript and together with my co-authors improved the model analysis and improved an earlier version of the manuscript.

Rösner S, Schabo DG, Palme R, Lorenc T, Mussard-Forster E, Brandl R, Müller J (submitted to Wildlife Research) High quality habitats and refuges from tourism reduce personality-based stress responses in a sensitive forest specialist.

High quality habitats and refuges from tourism reduce personality-based stress responses in a sensitive forest specialist

Short summary

Conservation of elusive target species relies on reliable data on the population health. We collected droppings of an entire population of the shy capercaillie to analyse its stress load in relation to habitat characteristics and human disturbances. Capercaillie individuals' stress levels decreased in habitats of higher quality and offside from tourism activities calling for the establishment of disturbance free refuge areas.

Abstract

The assessment of suitable habitats is often evaluated based on mere abundance data of the focal species. Yet, a variety of environmental factors such as temperature, resources and human disturbances might force animals to avoid otherwise high-quality habitats. Additionally, 'personalities' or individual capacities to cope with such factors, manifest in the physiological stress response, may also contribute to avoidance. Combining measures of stress response of individual animals with habitat suitability models may contribute essential insights to the development of species conservation plans. Here, we used a landscape-level approach to assess whether habitat quality, abiotic factors and human disturbance affect the physiological stress response of a forest specialist, the capercaillie (*Tetrao urogallus*), and to what extent these relationships are determined by the personality of the individual i.e. accounting for genotypes. We applied a non-invasive approach by collecting 1,096 droppings across the entire range of study which consisted of two adjacent national parks spanning the border between the Czech Republic and Germany. We used measures of faecal corticosterone metabolites

(FCMs) to evaluate the physiological stress response. To test the influences of temperature, habitat quality, season, sex, as well as forest management and tourism intensity on the FCM levels, we used generalised additive mixed effect models (GAMMs). The same model was applied for a reduced subset of randomly selected and genotyped samples. This approach allowed us to control for possible individual differences (such as repeated measures within individual genotypes). Both models revealed decreasing FCM levels with increasing habitat quality and showed no relationship between increasing forestry intensity and FCMs. When accounting for genotypes, we found a significant positive effect from increasing tourism intensity, while this relationship was not significant in the full dataset. Our results highlight three conclusions for the conservation of capercaillie: i) high quality habitats reduce stress levels; ii) tourism-free refuge areas are important for conservation, and iii) individual personality appears to be a strong determinant of response to environmental factors. Therefore, generalizing management recommendations from mere observations in single individuals onto entire populations may be inappropriate.

Introduction

Reproduction, survival and ultimately the distribution of species are mainly driven by the availability and distribution of suitable habitats (e.g. Morris 2003; Griffen and Norelli 2015; Boyce et al. 2016). Consequently, ecologists, conservationists and wildlife managers often assess the availability and quality of habitats as a surrogate for evaluating the status of threatened species and communities (van Horne 1983; Johnson 2007; Mosser et

al. 2009; Grünkorn et al. 2014; Immitzer et al. 2014; Plummer et al. 2020). Potentially suitable habitats are often evaluated and predicted by habitat models (Storch 2002; Buchanan et al. 2011; Teuscher et al. 2011) or habitat suitability indices (Burgman et al. 2001; Jacquin et al. 2005a). Conversely, mere counts of the abundance of focal species in a given set of habitat characteristics are also often used as a simple indicator for habitat quality (Johnson 2007; Homyack 2010; Morris 2003; Bock 2004; Kajtoch et al. 2012; but see Adamik 2005), assuming that under an 'ideal free distribution' (see Fretwell and Lucas 1970), free ranging animals actively select habitats of high quality and avoid habitats of low quality (Morris 2003; Johnson 2007).

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

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

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

The endocrinal response of a species to different stressors shows a high inter-individual variability, owing to phenotypic plasticity, sex, life history or habituation of individuals to stressors (Blas 2015; Dickens and Romero 2013). Individual differences in coping with stress have been associated with distinct behavioral traits known as animal personalities (Carere et al. 2010; Wolf and Weising 2012; Merrick and Koprowski 2017). Such behavioral traits comprise for instance explorative behavior, i.e. resource use (Fidler 2011; Serrano-Davies et al. 2017), activity/space use (Hawkes 2009) or habitat selection (Merrick and Koprowski 2017) and have been linked with individual fitness (Sih et al. 2004) and demographic parameters (Anthony and Blumstein 2000). It is important to note that by using non-invasive, anonymous faecal samples, unknown levels of pseudo-replication within the population may bias conclusions (Biro and Dingemans 2008; Biro 2013). Consequently, potential differences in personality need to be considered when assessing the population status of a species (Anthony and Blumstein 2000; Smith and Blumstein 2013).

In this study, we combined a landscape-level field endocrinological approach in two adjacent national parks, Šumava National Park (Czech Republic) and the Bavarian Forest National Park (Germany), to evaluate the impact of habitat quality, abiotic factors, human disturbance, and animal personality on the physiological stress response of the endangered Western capercaillie (*Tetrao urogallus*). The capercaillie is highly sensitive to human disturbances. It is a forest specialist

umbrella species for highly structured forest ecosystems (Storch 2002). Previous work developed habitat suitability models for different regions across the species' distributional range (see Braunisch and Suchant 2007; including our study area; Teuscher et al. 2011), as well as baseline information and techniques to determine the physiological stress response in terms of FCM levels (see Thiel et al. 2005). Consequently, the capercaillie is an ideal model species for applying field endocrinology to advance models of habitat suitability. Here, we related a) habitat quality derived from a habitat suitability model developed in the study area (Teuscher et al. 2011; Teuscher et al. 2013), b) different abiotic and individual factors affecting the species performance (e.g. minimum daily temperature, season, sex) as well as c) the intensity of forestry and tourism activities to measures of the physiological stress response (FCMs) obtained from droppings non-invasively collected in the field. We repeated the analyses for a subset of genotyped individuals to account for effects of personality on these relationships.

Specifically, we tested the following hypotheses: *i*) Capercaillie exhibit decreased FCM levels with increasing habitat suitability; *ii*) Capercaillie exhibit higher FCM levels at low temperatures, i.e. during harsh conditions, and males show higher levels than females, *iii*) Capercaillie respond with increased FCM levels to both increasing forestry and tourism activity and *iv*) the above patterns should be more pronounced when accounting for personality.

Material and Methods

Study Area

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

(93,407 ha) and includes the Bavarian Forest National Park (24,368 ha, Germany, 49°00'N 12°40'E), Šumava National Park (69,039 ha, Czech Republic, 49°06'45"N 13°08'09"E) and the adjacent protected landscape areas of Austria, Czech Republic, and Germany (Fig. 1). Elevations range from 650 m to 1,420 m a.s.l. (Bässler et al. 2009). The local climate is characterised by mean annual temperatures ranging from 3.8°C to 8.4°C and average annual rainfall between 1,295 mm and 1,771 mm (Bässler 2004). At low elevations, snow cover is present about 100 days per year and at high elevations for up to 200 days per year (Heurich 2005).

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

Both, private and state foresters on both sides of the border carry out forestry activities in the region. Forestry practices – including bark beetle mitigation activities - differ on either side of the

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

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

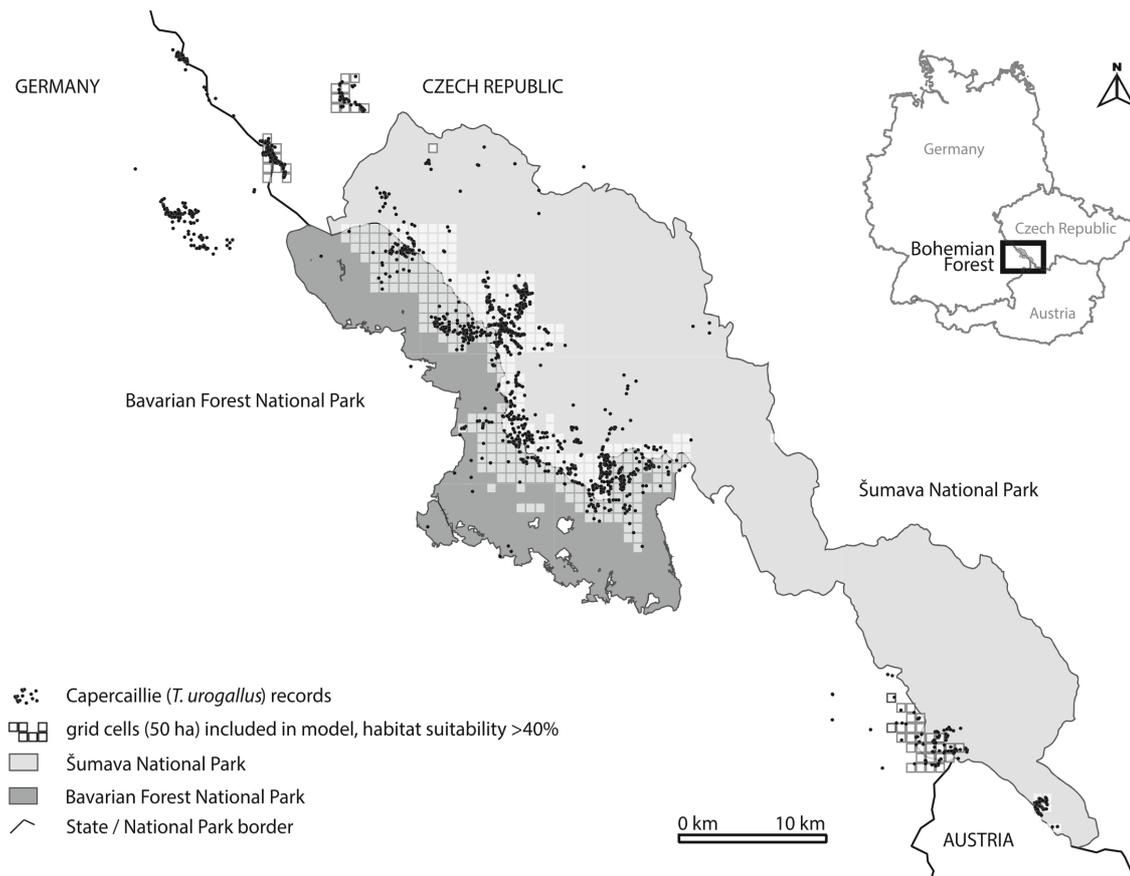


Figure 1: Map of the study area covering Šumava National Park (Czech Republic, light grey) and Bavarian Forest National Park (Germany, dark grey) and adjacent landscape protection areas. Points indicate the distribution of all capercaillie (*Tetrao urogallus*) samples between 2006 and 2017. Grid cells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

Focal species and local population

The western capercaillie (*T. urogallus*, L. 1758) is a forest-dwelling grouse species inhabiting coniferous and mixed coniferous-deciduous forests from Scandinavia to eastern Siberia (von Blotzheim et al. 1994; Thiollay et al. 1994; Storch 2001; Mikoláš et al. 2017). It is the world's largest grouse species and exhibits a strong sexual dimorphism, with males weighing circa double the amount of females (between 3,300 g and 4,300 g in males vs 1,440 g and 1,500 g in females; de Juana and Kirwan 2019). Capercaillie exhibit strong territoriality, with males defending their lek sites during the mating season. Strong individual differences in mating behaviour are well-known in the species

(Wegge and Larsen 1987; Storch 1997; Wegge et al. 2003). Mating starts at the end of March. While individuals are solitary during spring and summer, they form flocks of 2-10 individuals from late autumn throughout winter (Bauer et al. 2005).

In central Europe, the core area of its distribution is restricted to the Alps (Storch 2001; Storch 2007). Only a few small populations persist in low mountain ranges with elevations above 900 m a.s.l. (e.g., Vosges and Fichtel Mountains; Mollet et al. 2003; Storch 2001), with only the Black Forest (Storch 2001; Storch 2007) and the Bohemian Forest (Rösner et al. 2014) populations known to exceed the minimum viable population size. Thirty years ago, the Bohemian Forest population had

severely declined to about only 100 birds as recorded in 1985 (Scherzinger 2003; Rösner et al. 2014). Authorities then established breeding and release programs to supplement the local population (Scherzinger 2003; Rösner et al. 2014). In previous studies, we used non-invasive population genetics methods and multiple density estimators for the calculation of population sizes and estimated the current population at approximately 500 to 600 birds in the study area (Rösner et al. 2014; Bečka and Rösner 2019).

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

Data collection and field work

In a citizen science approach, a team of about 70 volunteers (hunters, wildlife enthusiasts, ornithologists, rangers, students, laypersons etc.) collected capercaillie droppings on a landscape level. After volunteer recruitment, we trained all participants in seminars, workshops, and field trainings to guarantee reliable data collection. For systematic fieldwork, we adopted a previously established grid system with 50 ha cells used for forest inventories, the development of habitat models, and other fieldwork in the national parks (Teuscher et al. 2011; Teuscher et al. 2013). The 50-ha grid system matched both, the scale of

average activity ranges of the focal species (550 ha, see Storch, 1995) and the spatial resolution needed for management implementation on the landscape level in both national parks (see Teuscher et al. 2011).

Collection of droppings

FCM levels in droppings are strongly affected by storage temperature and age (Thiel et al. 2005). Thus, we mainly collected droppings during the cold season when samples were preserved on snow. Samples collected during snow-free periods were only used if they were very fresh and wet with a high probability of having originated that same day. Samples were collected in two field campaigns: campaign 1 from October 2009 to May 2010 (with late snow at high elevations in May of that year) as well as campaign 2 from October 2010 to April 2011. Dropping collection took place in the known distribution of the capercaillie in the study area, roughly above 800 m a.s.l. (Teuscher et al. 2011). The search area covered 358 grid cells and approximately 22,000 ha (Rösner et al. 2014a). Each grid cell was searched at least twice. Parallel transects of about 10 m distance were walked with a team of volunteers recording all fresh droppings (2 to 3 days after fresh snowfall in winter and wet droppings in summer). Fresh dropping samples were kept cool during fieldwork until further processing in the lab following best practice guidelines established previously (Thiel et al. 2005). Samples were frozen at -20 °C at the end of each day's fieldwork. Known lek sites were only visited once between March and April to avoid pseudo-replications and minimize disturbances (compare Thiel et al. 2008). Spatially clumped droppings (around feeding places, alongside individual tracks or under roosting sites) were assigned to one 'operational individual' (see Thiel et al. 2008; Rösner et al. 2014b). Hence, most samples consisted of one to approximately seven droppings from one operational individual, for which we noted an individual identifier number, GPS

information, date and time. According to the species breeding ecology, samples were categorized into two seasons, winter (15. Oct – 15. April, after breeding and before mating) or summer (16. April – 14. October, mating and breeding season), for further analyses.

In total, within a period of 14 months, our team of volunteers collected about 7,500 droppings across 252 different 50 ha cells covering elevations from 747 m to 1,423 m a.s.l. The records were distributed across almost the entire study area and were assigned to 1,439 operational individuals (Fig. 2) when they were not only spatially but also temporarily grouped together during field work. Some droppings missed e.g. location data and were therefore excluded from the data set, resulting in $n = 1,096$ samples of operational individuals for further analyses.

FCM analysis

For laboratory work and the analysis of FCM levels, we used at least one fresh dropping per operational individual ($n=1,096$). Further processing followed Thiel et al. (2005). In short, we used 0.5 g of fresh dropping material, which was extracted with 5 ml of 60% methanol (Thiel et al. 2005; Thiel et al. 2011) before an aliquot was analyzed in a cortisone enzyme immunoassay (Rettenbacher et al. 2004; see Thiel et al. 2005 for details). Extraction and analysis of FCM were performed at the University of Veterinary Medicine, Vienna, Austria. Concentration measures were provided in nanograms FCMs per gram of fresh dropping weight [$\text{ng} \times \text{g}^{-1}$].

Genotyping

To track down repeated measures of true individuals, we genotyped a subset of 550 samples on ten microsatellite loci (Segelbacher et al. 2000). We extracted DNA from fresh droppings using the QIAamp Stool Kit (Qiagen) with a modified extraction protocol based on Jacob et al. (2010).

Extracted DNA was purified by repeated washing and removing polymerase chain reaction (PCR) inhibitors (InhibitEX and specific buffers, Qiagen). Samples were genotyped on ten microsatellite loci specific for the capercaillie using the established primer pairs TUD1, TUD3, TUD5, TUD6, TUD7, TUT2, TUT3, and TUT4 (Segelbacher et al. 2000) and BG15 and BG18 (Piertney and Hoeglund 2001). DNA was amplified by polymerase chain reaction (PCR) following the published multiplex protocol by Jacob et al. (2010) and run on an ABI 3730 Sequencer (Applied Biosystems). Allele scorings were done using GeneMapper v. 4.0 (Applied Biosystems).

Samples were only considered for analysis if allele scoring was repeatedly consistent over three consecutive runs at a minimum of nine loci. This means that samples where more than one allele repeatedly failed to amplify (allelic dropouts) were excluded from further analysis. This resulted in 476 successfully genotyped samples, revealing 195 different individuals. We used Micro-Checker software (van Oosterhout et al. 2004) to detect null alleles. We used the program PEDANT ver. 1.0 (Johnson and Haydon 2007) to estimate the rate of genotyping error per allele due to allelic dropout and false alleles. For further details on genotyping see Rösner et al. (2014b).

Sex determination

For each operational individual, sex was estimated from the relative diameter of the dropping (Thiel et al. 2008). For the subset of 195 individuals revealed by genotyping (s. above), sex was determined using chromosome-specific markers (P2 and P8) following published protocols (Griffiths et al. 1998). To verify the result, PCR amplification was run twice for each sample (for laboratory details see Rösner et al. 2014). Genetic sex determination revealed $n=163$ female and $n=32$ male individuals. Accuracy of estimating sex in the field was assessed for the dataset of $n=476$ genotyped samples using accuracy tests (R package

rUtilities, version 2.1.5). Overall accuracy of correctly estimating sex in the field was 87% (n = 476).

Human disturbance: Forestry and tourism intensity

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

Habitat suitability

In a previous study, we established a habitat suitability model for the capercaillie for the entire region, based on abundance data. In short, elevation a.s.l., lying deadwood, clear cut areas and a certain amount of young coniferous stands were identified to be key factors determining habitat suitability (for details, see Teuscher et al. 2011, 2014). Habitat suitability values (0-100%) were extracted from Teuscher et al. (2011) for each grid cell of the established 50 ha grid in this study.

Climatic conditions

It is known that temperature is a decisive factor for the distribution of capercaillie (Teuscher et al. 2011, 2014). To obtain temperature values, we assigned each grid cell to the nearest of three climate stations maintained by the National Park administration of the Bavarian Forest and assigned the daily minimum temperature in °C of the date of sampling to the grid. Values were corrected for elevation a.s.l. of the according grid cell with 0.6 °C difference per 100 m difference in elevation.

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

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

Data analysis

The response of FCM levels to habitat, abiotic, sex and human disturbance was analyzed using generalised additive mixed models (GAMM) with thin plate regression splines. We included habitat quality, daily minimum temperature, intensity of forestry, intensity of tourism, sex, season (winter vs. summer) as well as sampling campaign (campaign 2, campaign 1) as model predictors (Table 1). We did two separate analyses, one for the entire dataset of all samples (operational individuals, n=1,096) and one for the subset dataset of samples with known genotypes (n=476). In both models, habitat quality, forestry intensity, tourism intensity and daily minimum temperature at time of sampling were added as smooth terms (see Table 1), and sex, season, and sampling campaign as parametric predictors. In the model for the dataset of all samples, grid cell was included as random effect. In the model for the dataset of 476 genotyped samples, grid cell and genotype were included as random effect. Continuous predictors were scaled to zero mean and unit variance. Variance components were calculated for the predictors (smoothed terms). Model calculations and

extraction of variance components of the smoothed terms (function `gam.vcomp`) were performed with GAMM4 ver. 0.2-5 (Wood and Scheipl 2017) and R ver. 3.6.0 (R core team, 2019).

Results

Physiological Stress Response

Across all samples (n = 1,096), mean FCM levels were $149 \pm 125 \text{ ng} \times \text{g}^{-1}$ dropping (range: min 3.0 – max. 1639.8). FCM levels decreased with increasing habitat quality for both the model with all samples as well as the model with genotyped individuals only (Table 2, Fig. 2). The estimated proportion of the total variability attributed to habitat quality was relatively low (<1%) in both models (Fig. 2). We further found a phase pattern with highest physiological stress response at low temperatures as well as at high minimum daily temperatures in both models (Table 2, Fig. 2). The estimated variance component for temperature explained most of the total variability (>84%) in both models (Fig. 2). FCM levels were significantly lower during winter ($144 \pm 112 \text{ ng} \times \text{g}^{-1}$ mean \pm SD, hereafter) than during summer (234 ± 257) and lower during the second field campaign ($142 \pm$

101) than during the first (155 ± 140) in both models (table 2). Male operational individuals showed a significantly higher FCM level (157 ± 131) than female operational individuals (130 ± 106).

FCM levels showed neither a clear relationship with forestry intensity in the model with all samples (estimated variance component 9.9%) nor in the model with genotyped individuals (estimated variance component <1%, Table 2, Fig. 2). In the full model, also tourism intensity was not

associated with FCM levels (estimated variance component 5.8%, Table 2, Fig. 2). However, when controlling for individual identity in the model with genotyped individuals, we found a significant increase in FCM levels with increasing tourism intensity (Fig. 2). Here the estimated variance component explained 14.5% of the total variability (Fig. 2).

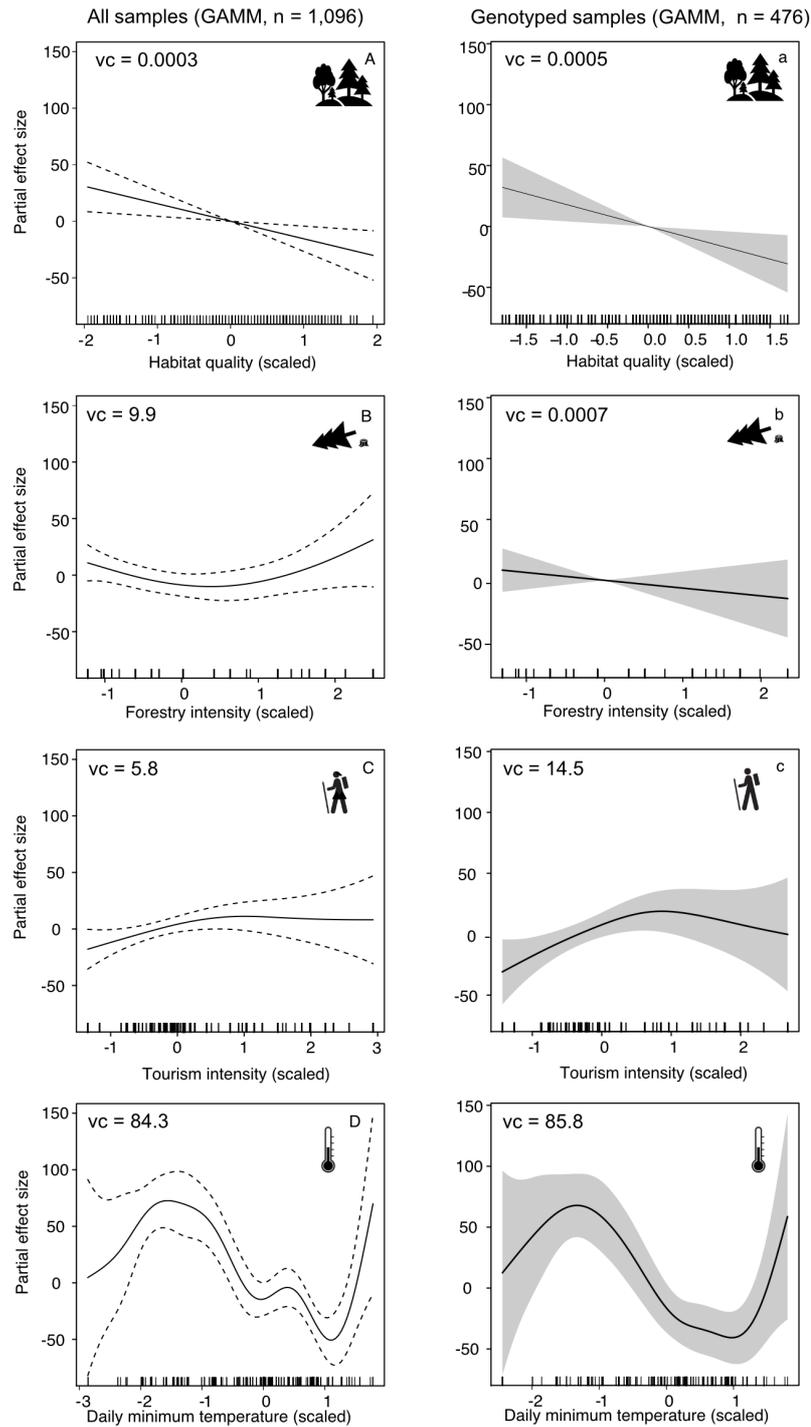


Figure 2. Partial effect plots showing results from GAMM models relating faecal corticosterone metabolite (FCM) levels (ng/g dropping) as a function of the environmental predictor variables with smoothed terms for habitat quality, forestry intensity, tourism activity and daily minimum temperature. Variance components associated with each smoothed term are shown in the upper left corner of the boxes. The left column shows the GAMM model for $n = 1,096$ samples and grid cell as random effect; the right column shows results of the model with a subset of $n = 476$ samples of genotyped individuals with grid cell and genotype as random effects. Dashed lines (left) and grey areas (right) indicate the 95% confidence intervals conditional on the estimated smoothed parameters of the model. Estimated variance components (vc) are depicted for each smoothed term.

Table 2: Generalized additive mixed model results explaining faecal corticosterone metabolite (FCM) levels. Left: Model covering all n = 1,096 samples and grid cell as random effect. Right: Model with n = 476 genotyped individuals and grid cell and genotype as random effects. Predictors and their explanations are given in table 1.

Model with operational individuals Sample size n = 1,096					Model with genotyped individuals n = 476				
	Estimate	se	T value	Pr (> t)		Estimate	se	T value	Pr(> t)
intercept	320.1	18.34	12.54	< .0001***	intercept	237.56	24.11	9.85	< .0001***
season (winter)	-96.7	18.5	-5.2	< .0001***	season (winter)	-97.42	23.21	-4.197	< .0001***
sex (estimated, male)	29.1	7.9	3.7	< .001 ***	sex (estimated, male)	24.80	12.97	1.912	.0565
sampling campaign (year)	-24.8	9.7	-2.6	< .05 *	sampling campaign (year)	-21.11	13.90	-1.519	.1295
Approx. sign. of smooth terms:	Edf	Ref.df	F	p value		Edf	Ref.df	F	p value
s(scale(Habitat quality))	1.00	1.00	7.68	.006 **	s(scale(Habitat quality))	1.00	1.000	6.802	.0094**
s(scale(Forestry intensity))	2.23	2.23	1.82	.131	s(scale(Forestry intensity))	1.00	1.000	0.877	.3496
s(scale(Tourism intensity))	1.92	1.92	1.87	.111	s(scale(Tourism intensity))	2.206	2.206	2.802	.0477*
s(scale(daily minimum temperature))	6.68	6.68	11.0	< .0001***	s(scale(daily minimum temperature))	4.779	4.779	7.856	< .0001***
R-sq.(adj) = 0.14					R-sq.(adj) = 0.18				
lmer.REML = 13,487					lmer.REML = 5,838				
Scale est. = 12,473					Scale est. = 12,176				
n = 1,096					n = 476				

Discussion

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

Sex

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

vigorously defend their territories at lek sites and display intensively to attract females (Klaus et al. 1989).

Temperature and season

The highest stress response in our study was found in cold temperatures as well as at lowest minimum daily temperatures (late winter, early spring). This is consistent with previous work showing that during periods of low temperatures, capercaillie feed on conifer needles, which represent a low-caloric energy source (Lindén 1984; Andreev 1988; Klaus et al. 1989; Lindsay et al. 2020). With limited daylight hours during this period of the year, it is difficult to acquire enough energy to maintain a good bodily condition. Consequently, overall activity is usually reduced (Storch 1993). During such harsh periods of the year the metabolic rate needs to increase to initiate foraging and to mobilise energy stores – processes which include elevated corticosterone levels, resulting in the high FCM levels also found here (Astheimer et al. 1992; Harvey et al. 1984; but see Wingfield et al. 1995). High FCM levels at high minimum daily temperatures in late April again correspond to the beginning of the mating season during which capercaillie are generally more stressed, particularly males (Klaus et al. 1989).

Habitat quality

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

Human disturbance

We found higher tourism intensity to have a negative impact on the physiological stress response of capercaillie. This adds to previous work showing that tourism activities reduce the frequency of occurrence (Rösner et al. 2014), have an impact on habitat use (Coppes et al. 2017) and particularly in winter evoke a physiological stress response in capercaillie (Thiel et al. 2008, 2011). Given that tourism activities reduce the local occurrence of capercaillie (Rösner et al. 2014) and effectively reduce their habitat (Coppes et al. 2017), a general habituation in capercaillie seems not plausible (Powell 2013). Nevertheless, it has been shown that individuals differ considerably in their physiological response to disturbances through touristic recreational activities (Coppes et al. 2018). Individual tolerance of human presence or even individual habituation to human activities occurred in several bird species (Arlettaz et al. 2007, Gaudet and Somers 2013; Kitchen et al. 2011).

Such differences in coping with stress have been linked to distinct behavioral traits, i.e. breeding performance (Bókony et al. 2009) or individual personalities (Carere et al. 2010; Wolf and Weising 2012; Merrick and Koprowski 2017). Our study also indicates similar difference in individual susceptibility of birds to tourism: the negative effect of tourism intensity on the stress response was detectable only when controlling for individual personalities (see Fig. 2). Repeated measures of single, well-habituated individuals potentially blurred this negative effect of tourism in the model for all non-genotyped samples. Therefore, measuring the stress response of the same individuals and thus distinct animal personalities at different points in time can provide important information to assess the response of wildlife to environmental and human disturbances. Thereby, assessing the reproductive status of potentially habituated individuals within the population would be a pivotal future step to assess the potential long-term consequences of tourism for the status of the species.

Besides direct negative effects of human presence and activities, such as disturbance through noise (Francis and Barber 2013), also indirect effects might contribute to higher physiological stress responses of capercaillie. The presence of trails and changes in vegetation structure through tourism activity may alter the detectability of approaching predators and thus predation pressure (Borkowski et al. 2006; Dowd 2010), which is among the key factors determining FCM levels (Thiel et al. 2011). Predation pressure may be higher close to trails (Dowd 2010), and thus, tourism activities may alter the 'landscape of fear' (see Laundré et al. 2010). Potential fitness and reproductive consequences are unknown. Yet, elevated physiological stress response to tourism may lead to reduced fitness as even stress-tolerant birds show lower reproductive rates (Strasser and Heath 2013). Ultimately, this may also lead to an

avoidance of high-quality habitat (Coppes et al. 2007; Rösner et al. 2014). Thus, tourism activities appear to be an important factor when assessing species distribution and population health on a landscape scale.

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

Conclusions

Taken together, our findings add to previous work that environmental conditions such as habitat quality, temperature, season as well as the sex of animals are determining factors in the physiological stress response in capercaillie. Moreover, accounting for individual differences in the stress response on the landscape level revealed that human impact in terms of tourism intensity elevated FCMs of this highly sensitive forest specialist. These findings highlight that beyond solely focusing on undisturbed and high-quality refuge areas, species conservation management should

consider individual personalities across the population, e.g. through genotyping, when making management recommendations. This is particularly important as generalizations from observations of single animals onto entire populations may be inappropriate as is often done in conservation practice.

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10 Discussion and synthesis

Naturally, forests are highly dynamic ecosystems often shaped via multiple natural disturbances (Spînu et al. 2020; Kuuluvainen et al. 2021). Human interventions, however, strongly alter these natural dynamics (Kuuluvainen et al. 2021) and therefore act as disturbance factor in natural ecosystems. Habitat specialists are more prone to any changes in habitat availability and habitat quality than habitat generalists (Pandit et al. 2009). Therefore, any modifications in the distribution, size and structure in the population of specialists serve as a good indicator for changes in the forest ecosystem (Julliard et al. 2004; Devictor et al. 2008b). In my thesis I therefore used a forest specialist, the Capercaillie, to study how different disturbances modify its distribution, habitat use, population size, genetic population structure and physiological response.

10.1 Population size and genetic structure

Knowledge about the population size of threatened species is essential for conservation management (Mace et al. 2008). Here, monitoring of animal numbers and their spatial genetic structure is a crucial approach to provide valuable baseline information within and across populations (Mace et al. 2008; Tella et al. 2013; IUCN 2021). Based on a genetic mark-recapture approach (Chapter I), I used fresh droppings to estimate population size and population genetic structure in the two adjacent national parks, Šumava National Park (Czech Republic) and the Bavarian Forest National Park (Germany) and the surrounding area (Rösner et al. 2014a). The

estimators delivered a mean population size of approximately 550 individuals and identified thus one of the largest relict populations in the low mountain ranges of temperate Europe (see also Rösner 2018, unpubl.; Kratzer et al. 2021). These findings are in line with a minimum viable population size of ca. 470 individuals (Grimm and Storch 2000). Following the strong population decline until the mid 80ies and the consecutive breeding and release program with an annual release of approx. 60 individuals (Scherzinger 2003), the population has recovered to a viable size in 2011 that even increased to approx. 650 individuals in 2018 (Rösner 2018, unpubl.). This assessment was supported by the extensive gene flow and the absence of distinctive spatial genetic structure within the population across the entire study area (Rösner et al. 2014b). Given that two thirds of the individuals were detected within the two national parks, a coherent management strategy particularly regarding the complexity of habitats is essential to guarantee the long-term viability of the population.

Whether the present population size and structure are solely a result of the breeding and release program (Scherzinger 2003) or whether natural disturbances such as storms and bark beetles (Müller and Job 2009; Lausch et al. 2012; Lehnert et al. 2013; Thorn et al. 2016, 2017) have supported the population growth can unfortunately not be resolved as baseline genetic data prior to the release program is missing. Across Europe, a variety of other release programs have attempted to augment small or re-establish locally extinct populations of Tetraonids (Seiler et al. 2000; Klaus et al. 2009; Siano and Klaus 2011). As most other re-establishment or re-enforcement

programs either failed or are still ongoing (Siano and Klaus 2011), a final evaluation is not possible especially since the methodological approaches are not documented (Bump 1963; Seiler et al. 2000). Due to the high level of uncertainty regarding success or failure of single re-establishment programs (Bernardo 2012) reintroduction biologists clearly call for thorough planning, detailed documentations and evaluation processes (Seddon et al. 2007).

10.2 Spatial distribution patterns and human disturbance

The assessment of the spatial distribution of species can reveal valuable information about habitat selection and – in turn – habitat suitability (Johnson 2007b). Yet, the habitat use of species is not only driven by habitat quality but also by spatial avoidance of natural and human disturbances (Laundré et al. 2001, 2010; Tolon et al. 2009; Ciuti et al. 2012). In chapter II, I therefore combined occurrence measures of Capercaillie with assessments of human recreational and forestry disturbance on 50 ha grid cells in the study area (Rösner et al. 2014c). I recorded capercaillie in more than 65 % of all investigated grid cells (19.200 ha) (Rösner et al. 2014c). My model analyses showed a negative impact of recreational activities on the intensity of habitat use of Capercaillie even within suitable habitat types which suggest the avoidance of certain areas with human activities also referred to as “landscape of fear” (Laundré et al. 2010; Rösner et al. 2014c). In contrast, forestry activity did not show a clear impact on the habitat use of Capercaillie. These results corroborate previous findings on avoidance of human activities of Capercaillie, other grouse species and other vertebrates (Thiel et al. 2008a; Braunisch et al. 2011; Allan et al. 2019; Tost et al. 2020; Doherty et al. 2021). Moreover, the findings highlight the need of restricting recreation activities even in protected areas by setting aside

selected zones to preserve the refuge of forest specialist flagship species (IUCN, Birds Directive 79/409/EEC). Furthermore, my findings confirm the suitability of the Capercaillie as an indicator species of forest disturbance, as it is sensitive enough to indicate disturbance even in national parks, the highest protection category of conservation areas in Germany and the Czech Republic. Refuge zones in protected areas should cover all resources, should be of adequate size, and habitat quality and should contain sufficient numbers of lek sites as these turned out to be important for maintaining mating dynamics even across large spatial scales. More precisely it is known that both, male and female birds move to or between leks sites up to a distance of 4.0 km (Wegge and Larsen 1987; Wegge et al. 2003). Thus, my study highlights that future management concepts should consider the entire landscape for designing refuge zones to preserve the presence of the emblematic flagship species also for touristic activities and their revenue in the region. In addition to these distributional approaches, physiology measures could guide and evaluate conservation activities more precisely (Sheriff et al. 2011; Dickens and Romero 2013).

10.3 Physiological response

In recent decades, several studies have indicated that inferring habitat quality by the sheer number of individuals can lead to erroneous conclusions (Horne 1983; Johnson 2007b; Mosser et al. 2009). This is because, despite good habitat conditions, individual factors such as the presence of predators or human disturbance can cause species to avoid certain areas and thus cluster in areas of lower quality (Johnson 2007b; Laundré et al. 2010; Rösner et al. 2014c). To disentangle the positive abundance-habitat quality relationship (van Horne 1983) from a variety of so far unidentified environmental factors, conservation physiology approaches repeatedly call for the assessment of

physiological aspects within populations across study areas (Sheriff et al. 2011; Dickens and Romero 2013). I applied this approach in chapter III of my thesis, where I used non-invasively collected samples with concentration measures of faecal corticosterone metabolites (FCMs) to determine the physiological stress response of Capercaillie. I found decreasing FCM levels with increasing habitat quality supporting previous knowledge that such undisturbed refuge habitats provide optimal conditions such food, shelter etc. for this highly sensitive forest specialist (Thiel et al. 2005, 2008b). The results further show that FCM levels were highest at low temperatures and that males have higher FCM levels than females. This shows that during harsh abiotic conditions the low caloric energy source and the limited time with daylight challenge the Capercaillie to maintain a good body condition with males even being more stressed due to territory defense and display behavior during mating season. While FCM levels were not related to forestry intensity, increasing tourism intensity was associated with increasing FCM levels when controlling for true individuals by genotyping. This suggests that individuals considerably differ in their physiological response to human disturbance (Coppes et al. 2018) which adds a level of complexity to species conservation management. Similar findings have been shown for other bird species (Arlettaz et al. 2007) with individual tolerance in coping with stress being associated with behavioral traits (Bókony et al. 2009) and/or personalities (Carere et al. 2010). Whether or not the different physiological responses detected across the study area affect fitness, susceptibility to disease, and ultimately reproductive success is not clear. Therefore, future studies should include reproductive success to predict the long-term development of the population.

10.4 Synthesis

All presented results have important implications for the conservation management of the Capercaillie, the emblematic forest specialist of both national parks, Bavarian Forest and Šumava Forest. My research discloses that re-enforcement programs can be successful as after the strong decline of records in the 1970s and 1980s, the re-enforcement activities (Scherzinger 2003; Siano and Klaus 2011) together with natural disturbances such as storms and bark beetles (Müller and Job 2009; Lausch et al. 2012) led to a viable population size with unrestricted geneflow (Rösner et al. 2014b; Rösner 2018). The overall conservation status therefore indicates a good prerequisite for the future persistence of the population. It is, however, important to note that the area of the two national parks alone is too small to sustain a long-term viable population (Grimm and Storch 2000) which highlights the value of the surrounding area for the protection of the species. Moreover, my findings underscore, that analyses of the distribution and stress response – even within protected areas – are valuable for conservation management, especially as they relate to the sensitivity of species to human disturbance (Thiel et al. 2008b, 2011; Coppes et al. 2018; Döpfer et al. 2019). As tourism and mitigation measures (salvage logging) to bark beetle calamities are increasing outside the national parks (Kortmann and Thorn 2018; Kortmann et al. 2021; Gandhi et al. 2022), management and monitoring concepts should include peripheral areas as well (Rösner 2018). However, such concepts should aim to restrict recreation activities particularly in protected areas by setting aside selected priority zones (special protection areas, Annex I Birds Directive) to preserve refuges for this flagship species which has currently an unfavorable conservation status in Europe (Burfield et al. 2004; Storch 2007; International 2012). To this end, my findings emphasize that monitoring stress responses of species can serve as early warning indicator to deduce whether the required

implementations achieve their goals. Especially in the winter season strict visitor guidance is of particular importance, as my results showed that physiological stress response was highest during harsh abiotic conditions, i.e., at low (winter) temperatures, low caloric energy sources and limited daylight, challenging the Capercaillie to maintain a good body condition (Thiel et al. 2008b, 2011). Given that my data are in majority based on observations and measures from the winter season more information about the breeding season should be acquired in future field work activities. Such year-round physiological data of Capercaillie would then also allow to better manage recreation activities across the entire season.

To conclude, my studies on a forest flagship species in the Bohemian Forest revealed important baseline information about its current population status (population size, genetic pattern and distribution). More specifically, I provided evidence that re-enforcement programs are good options for long-term conservation of endangered species. Here, non-invasive methods can be used to monitor the distribution of focal species across entire areas. In combination with information on habitat quality and disturbance regimes, individual-based physiological analyses can provide further insights into the status of the focal species. This data can be used to target habitat enhancement and simultaneously identify stress regions for conservation managing of the endangered species. By targeting flagship species in such monitoring programs, conservationists are empowered for target-oriented management to protect entire communities.

11 Perspectives

During the course of my study, my findings have raised additional issues whose investigation could optimize the conservation management of the flagship species and its associated communities.

In the study area the success of the re-enforcement program could not be separated from the massive habitat changes caused by natural disturbances such as bark beetle outbreaks or windstorms (Rösner et al. 2014b; Thorn et al. 2016). Such uncertainties about the success or failure of re-enforcement approaches are rather the rule than the exception (Bernardo 2012) which argues for better documentation and monitoring of such programs (Seddon et al. 2007). More explicitly, the success of re-introduction and re-enforcement programs can be considerably enhanced by experimental and modelling approaches in the planned areas, for example by considering habitat suitability modelling with incorporation of disturbance factors (Seddon et al. 2007). Here, a close collaboration between scientists and practitioners will contribute to the success on the ground by e.g., genotyping individuals prior to their release and thus being able to track their performance. Performance measures such as physiological aspects of released animals, e.g., physiological stress levels, could substantially improve re-introduction and re-enforcement programs (Tarszisz et al. 2014; Coppes et al. 2018) which could be even extended to the monitoring of reproductive success, for example by parental analysis.

The re-enforcement program of the Capercaillie has very likely benefitted from the natural disturbances. These natural disturbances have not only increased the structural heterogeneity of the

forest ecosystem but even improved the habitat quality for entire communities (Lehnert et al. 2013; Beudert et al. 2015; Kortmann and Thorn 2018). However, our knowledge is very limited on how post-disturbance processes such as increasing canopy closure during succession (Palmero-Iñesta et al. 2021) affect the habitat quality of an indicator species like the Capercaillie in the long-term (Kortmann and Thorn 2018; Kortmann et al. 2018). Since we conducted the habitat model analysis in the early stages of the project based on aerial images (Teuscher et al. 2011, 2013), today's improved spatial and temporal resolution and accessibility of remote sensing data (Jacquin et al. 2005b) offer a promising approach to associate population development of the Capercaillie to habitat changes with regard to canopy closure or microclimatic conditions. Such changes might modulate the distribution, population size and in consequence the carrying capacity of the forest and finally the overall conservation status of the flagship species.

Modern sensor technologies might further help to develop multi-scale habitat suitability models also specifically for lek sites and breeding grounds. The identification of such sites will strongly support the establishment of core protection areas covering the complex habitat requirements within the annual cycle of the Capercaillie on the landscape level (Graf et al. 2004; Braunisch and Suchant 2007; Scherzinger 2009; Apa et al. 2021). More specifically, the protection of known lek sites is an important prerequisite to guarantee gene flow as these are used by the neighboring Capercaillie within a radius of 4,0 km and at the same time promote other bird species with their very specific structural

characteristics (Pakkala et al. 2003). Regular monitoring of lek sites with optical sensors (Kratzer et al. 2021), sound recorders and artificial intelligence (Abrahams 2019; Mühlhng et al. 2020) can deliver real-time changes in usage or occupancy, e.g., incidences, sex ratios, or phenology of mating activities.

Capercaillie mainly inhabit the study area at about 700 m to 1,450 m a.s.l. (Teuscher et al. 2011, 2013). Two other disturbance sensitive flagship species of the study area, Hazel Grouse (*Tetrastes bonasia*) and Black Grouse (*Lyrurus tetrix*) are habitat specialists of bogs and deciduous, multi-layer structured mixed stands at lower altitudes (Kortmann et al. 2018; Tost et al. 2020). To retrieve information on management and disturbance-related habitat changes across the complete altitudinal gradient of the national parks and their surroundings it would thus be advisable to monitor these flagship species with a similar non-invasive approach as for the Capercaillie. This would allow to find out whether the species react in the same way to disturbances and would thus be suitable for cross-species monitoring also with regard to individual variability in responses to disturbance. In fact, we already collected droppings of these species in the study area (see Rösner 2018, unpubl., and Appendix 18.2) which are currently being analysed to estimate the population size by colleagues from Šumava (M. Starý, pers. comm. 2021). Results will provide important baseline data for conservation management across habitats in the study area and can be implemented in a joint grouse monitoring (see below).

To further enhance monitoring programs of grouse species, monitoring of parasite infestations should be implemented as many tetraonids are known to suffer from parasitic infections, i.e., gastrointestinal nematodes can reduce their fecundity (Jankovska et al. 2012; Tomczuk et al. 2017; Fanelli et al. 2020a; Sokó and Pluta 2021). Moreover, chronic stress weakens animals and might even trigger outbreaks of endoparasites

which ultimately influence their population development (Cattadori and Hudson 2000; Cattadori et al. 2005; Sokó and Pluta 2021). As infestation rates in Galliformes might differ among habitats (Fanelli et al. 2020a) it might be promising to combine habitat models with stress and parasite monitoring to identify areas where stressed animals are exposed to higher infestation rates. Such models would also allow to integrate exposed infestation threats at higher altitudes due to climatic change (Fanelli et al. 2020a) as well as the occurrence of new (endo-)parasites or pathogens in the population (Fanelli et al. 2020b, a). Thus, implementing a parasitological approach, i.e. recording parasites and their prevalence, into a grouse monitoring program would provide insights into the “population health” of the different species at the landscape level and could be easily incorporated into the sampling protocol of further processing of droppings. In a small spotlight investigation of samples from 2010, I documented two genera of parasites, i.e. nematodes, but with very low prevalence (see Appendix 18.1).

The European and national conservation law postulates the designation of “Special Areas for Conservation” for the Capercaillie (Appendix I, Birds Directive, 79/409/EEC). Therefore, I finally call for action for further research and cross-border monitoring of Capercaillie in the Bohemian Forest for strengthening and improving the conservation status of the species:

- ⇒ Establishment of a trans-boundary monitoring program for field work, laboratory, analysis and evaluation
- ⇒ Dropping samplings on landscape level in a 5-year interval using a “rapid assessment approach”
- ⇒ Based on these droppings, applying DNA genotyping to estimate populations size on a regular basis

- ⇒ Based on these droppings, monitoring of FCM levels and parasite prevalence should be monitored on a regular basis
- ⇒ Spot-light analysis of gastro-intestinal parasites across the range of FCMs to possibly detect issues of “population health”
- ⇒ Re-visit habitat analysis approaches of Teuscher et al. (2011) using high resolution remote sensing (LiDAR, Radar) to identify core areas for special year-round protection zones covering a triptych of lek sites, winter habitats and breeding habitats
- ⇒ Initiate sensor-based monitoring (e.g. optical and audio sensors) to better understand the known lek sites, and retrieve information about e.g. sex ratios or changes in numbers of birds attending
- ⇒ Continue to include Hazel Grouse and Black Grouse as flagship species with a similar approach for deciduous forests at lower altitudes and bog habitats, respectively

Finally, I hope that the studies presented by my co-authors and me will provide broad support to further use evidence-based approaches to guide conservation activities and decisions. Specifically, monitoring of valuable indicator species with established methods, will provide reliable and comparable data for conservation science and practice. Here, joined approaches on baseline knowledge from protected areas and cultural landscapes are important to better distinguish pitfalls and sustainable potentials to successfully protect biodiversity.

12 List of publications within the project

In the context of my thesis about the conservation and management of Capercaillie in the Bavarian Forest National Park - together with many co-authors - we published a list of other papers in various journals. These papers either were published as a result of a master thesis which I co-supervised or as joined analysis of related topics in conjunction with the data acquired during my project.

Please find the references, the list of co-authors, a brief information about the context of this paper as part of my thesis and our activities within the Capercaillie research project.

12.1 Modelling habitat suitability for the Capercaillie *Tetrao urogallus* in the national parks Bavarian Forest and Šumava

Reference: Teuscher M, Brandl R, Rösner S, Bufka L, Lorenc T, Förster B, Hothorn T, Müller J (2011). Modelling habitat suitability for the Capercaillie *Tetrao urogallus* in the national parks Bavarian Forest and Šumava. *Ornithologischer Anzeiger* 50, 97–113.

My contribution: Together with Roland Brandl and Jörg Müller, I co-supervised the master thesis, coordinated the fieldwork for the sampling records 2009-2011, prepared data for analysis, helped to improve earlier versions of the manuscript.

As a baseline study for the Capercaillie project, we decided to develop a habitat suitability model for the study area, covering both national parks. In the framework of Miriam Tauscher's master

thesis at the Philipps-University Marburg, we used Capercaillie records for presence data and environmental data derived from aerial photographs in the same time period. The resulting raster data and grid cells with the habitat suitability indices were then used for the analysis of e.g. disturbance data in relation to Capercaillie abundance and stress load in the main chapters of this thesis.

Abstract: The Capercaillie *Tetrao urogallus* relies on structurally rich forests and therefore functions as an umbrella species for plants and animals associated with old-growth conifer forests. Populations in Central Europe are declining due to changes in forest structure, habitat loss and increased stress due to human outdoor activities. The aim of this study was to analyse habitat suitability for the Capercaillie in the Bohemian Forest (comprising the Bavarian Forest and the Šumava National Park). Using a new method to build generalized additive models, we identified altitude, lying dead wood, clear cut areas and small amounts of young coniferous forest as important factors for the Capercaillie occurrence throughout the year. In winter, only altitude and lying dead wood with mixed regeneration were important. Calibration plots indicated that the calculated occurrence probabilities are a good representation of actual occurrences. Furthermore, our models showed a good performance when evaluated by the AUC-metric. These models provide for the first time detailed cross-boundary maps for management decisions (e.g. for new hiking trails), which are not in conflict with the conservation of the Capercaillie.

The original paper is available here: www.og-bayern.de/wp-content/uploads/2013/08/Inhalt_OA_50_2_3_2011.pdf

12.2 Forest inventories are a valuable data source for habitat modelling of forest species: an alternative to remote-sensing data

Reference: Teuscher M, Brandl R, Förster B, Hothorn T, Rösner S, Müller J (2013) Forest inventories are a valuable source for habitat modelling of forest species: an alternative to remote sensing data. *Forestry* 86: 241-253. DOI:10.1093/forestry/cps081

My contribution: Together with R. Brandl and J Müller, I co-supervise the master thesis. I further helped to improve the manuscript prior to submission and during a revision.

The first approach of our research project on the population status of Capercaillie included the development of a habitat suitability model (see Teuscher et al. 2011, see above) based on aerial imagery. For this model, we adopted a grid system previously developed by the Bavarian Forest national park with each cell covering 50 ha in size. In a next step, forestry inventory data with higher resolution (200 m x 200 m) were examined as suitable habitat variables in habitat modelling of the Capercaillie. All models performed very good (AUC > 0.85) and the predicted occurrence maps similarly matched those of the observed distributions. Hence, forest inventories should be considered as suitable tools for habitat distribution models for forest species.

Abstract: Habitat and species-distribution models are important tools in ecology, conservation, and wildlife management. For the modelling of the species' habitat on small spatial scales, the availability of suitable habitat variables is crucial. Collecting data in the field often incurs considerable costs. Forest agencies, however, collect data on forest structure and composition on a large

extent and with a fine grain (200 m × 200 m) during their forest inventories. Despite this the potential use of these data for habitat modelling and therefore conservation and wildlife management is still broadly neglected. Here, we evaluated and compared the performance of models based on environmental data derived purely from forest inventories, inventory data plus additional ecological information gained during the inventory, and aerial photographs to model the habitat of a forest species, the capercaillie (*Tetrao urogallus* L.). The best models developed from each of the three data sources showed a similar performance over the area (28 450 ha) and the considered grain (50 ha grids); all models had an area under the receiver operating characteristic curve (AUC) value. 0.85, and various other metrics used for evaluating the models showed little differences. In all calibration plots, the predicted probabilities of presence were very similar to that of the observed probabilities, which indicated that our maps of the habitat suitability are a good representation of the real occurrences. This modelling of the capercaillie's habitat using existing forest inventory data was successful because the variables collected in standard inventories also have some meaning for the ecology of the species. To model the habitat of forest species that need special resources outside the scope of forestry, possible additional variables could be sampled at low extra costs during such large inventories. There is therefore the potential for forest inventories, currently undertaken to support commercial forestry, to be applied in conservation, thereby supporting a multifunctional forestry.

12.3 Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities

In this paper, we aimed to disentangle whether natural parameters (vegetation structure or egg characteristics) or human disturbance drives predation risk of predation on ground breeding birds. Artificial nests with quail eggs were exposed experimentally and daily predation rates recorded accordingly. Forest characteristics like small scale vegetation cover decreased and canopy cover on the other hand increased the predation rates.

Reference: Seibold S, Hempel A, Piehl S, Bässler C, Brandl R, Rösner S, Müller J (2013) Forest vegetation structure has more influence on predation risk of artificial ground nests than human activities. *Basic and Applied Ecology* 14: 687–693. <https://doi.org/10.1016/j.baae.2013.09.003>

My contribution: Sebastian Seibold, Jörg Müller and Claus Bässler initiated the experiment and supervised the candidates. I provided background data and information for design planning and field work of A. Hempel and S. Piehl. I read the manuscript prior to submission and helped to improve it.

Abstract: As a major process affecting the reproductive success of birds, nest predation influences population density and dynamics and forces species to adapt to ecological and evolutionary time scales. The disentangling of potential natural and anthropogenic drivers of nest predation is crucial for the conservation of species. Thus, we investigated the effects of elevation, egg characteristics, vegetation structure and human activities on daily nest predation rates of artificial ground nests by baiting 700 artificial nests with quail eggs along an elevational gradient of about 1100 m. After 25 days, we found an overall daily nest predation rate of 0.045. Our generalized linear mixed model revealed increasing daily predation rates with increasing forest management, no impact of recreational activities, and lower daily predation rates in the vicinity of buildings. Furthermore, daily predation rates declined with

increasing density of near-ground vegetation and increased with increasing tree cover. Finally, we found no influence of elevation, matching of egg and ground colouration, and dead wood on daily nest predation rates. Our results revealed that the risk of nest predation depends more on vegetation structure than on current levels of recreational activities. Moreover, the negative relation of nest predation risk and near-ground vegetation indicates that the changing forest structure after natural disturbances (e.g. wind throw or bark beetle infestation), which is tolerated within the benign neglect strategy applied by the authorities of protected areas, decreases the predation risk, whereas salvage logging increases this risk.

12.4 Forest structure following natural disturbances and early succession provides habitat for two avian flagship species, capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*)

In the context of natural disturbances, the Bavarian Forest is an ideal study area as it was hit by a few natural disturbance events in consecutive years: Storms and draughts followed by large scale bark beetle calamities. On a large scale, the forest ecosystem was heavily re-structured, and questions arose whether the sensitive habitat specialists may be affected or may cope with this new situation. Mareike K. and her team considered this question by analysing both Capercaillie und Hazel Grouse count data from our citizen science approach and analysed changes in relation to high-resolution of air-borne LIDAR data.

My contribution: I prepared and provided the temporal and spatial information of presence data of both Capercaillie and Hazel grouse. Data on Hazel Grouse was acquired by the team I supervised and managed for the dropping collection

project. I helped to improve the manuscript including an earlier revision.

Reference: Kortmann M, Heurich M, Latifi H, et al (2018) Forest structure following natural disturbances and early succession provides habitat for two avian flagship species, capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*). *Biological Conservation* 226:81–91. <https://doi.org/10.1016/j.biocon.2018.07.014>

Abstract: Boreal and mountainous forests are a primary focus of conservation efforts and are naturally prone to large-scale disturbances, such as outbreaks of bark beetles. Affected stands are characterised by biological legacies which persist through the disturbance and subsequent succession. The lack of long-term monitoring data on postdisturbance forest structure precludes understanding of the complex pathways by which natural disturbances affect forest structure and subsequently species presence. We analysed the response of capercaillie (*Tetrao urogallus*) and hazel grouse (*Tetrastes bonasia*) to bark beetle infestations. We combined high-resolution airborne light detection and ranging (LiDAR) with a 23-year time series of aerial photography to quantify present-day forest structure and stand disturbance history. Species presence was assessed by collecting droppings of hazel grouse and capercaillie in a citizen science project. Structural equation models showed that the probability of hazel grouse presence increased with increasing disturbance, and the probability of both hazel grouse and capercaillie presence increased with succession. Indirect effects of bark beetle infestations, such as a reduced abundance of deciduous trees and an enhanced herb layer cover, were positively associated with capercaillie presence. Decreasing canopy cover increased the probability of hazel grouse presence. The high temporal and spatial heterogeneity of bark beetle infestations created forest structures that meet the contrasting habitat requirements of both, capercaillie and hazel grouse. This heterogeneity resulted from

biological legacies such as decomposing snags, and the simultaneous regrowth of natural regeneration. A benign-neglect strategy towards bark beetle infestations could hence foster capercaillie and hazel grouse in mountainous forests.

13 List of publications: Other scientific work

In this chapter, I shortly introduce my published studies which I conducted before and alongside my studies on the Capercaillie.

Prior to my project on Capercaillie conservation in the Bohemian Forest, I focused my research on other target species in the context of wildlife biology and population genetics. Starting from my Diploma thesis about the ecology of the **Northern Raven** (*Corvus c. corax*) in a lowland forest ecosystem in eastern Poland, I continued my research on this generalist passerine and published the core results.

Alongside my studies on the Capercaillie and the Raven, I initiated or joined other projects mainly in the focus on bird (community) ecology and conservation often in close context to forest ecosystems. Currently, I am extending my movement ecology work on a songbird community, birds of prey from **Cape Vultures** (*Gyps coprotheres*), via **Red Kites** (*Milvus milvus*) to **Common Buzzards** (*Buteo buteo*) and started to study a mammalian mesopredator; the **Raccoon** (*Procyon lotor*).

Please find a chronological list of articles and book chapters published by me and my co-authors in the context of the above-mentioned projects.

Rösner S, Selva N (2005) Use of the bait-marking method to estimate the territory size of scavenging birds: a case study on ravens *Corvus corax*. *Wildlife Biology* 20, 183–191.

Rösner S, Selva N, Müller T, Pugacewicz E, Laudet F (2005) Raven *Corvus corax* ecology in a primeval temperate forest. In: Jerzak L, Kavanagh BP, Tryjanowski P (eds.): *Ptaki krukowate Polski*

[*Corvids of Poland*]. pp 385-405 pp, Bogucki Wyd. Nauk., Poznań.

Rösner S, Bogatz K, Trapp H, Grünkorn T, Brandl R (2010) No evidence of skewed secondary sex ratios in nestlings of the Common Raven (*Corvus corax*). *Journal for Ornithology* 150: 293-297. <https://doi.org/10.1007/s10336-008-0350-6>

Rösner S, Gießelmann UC, Meyer J, Schwager M, Wiegand T, Lück-Vogel M, Brandl R (2010) Coloniality of birds in the Kalahari – spatial distribution of trees and nests of the Sociable Weaver (*Philetairus socius*). In: Schmiedel U, Jürgens N [Eds.] *Biodiversity in Southern Africa, Vol 2: Patterns and Processes at Regional Scale*. pp. 179-183, Klaus Hess Publishers, Göttingen & Windhoek.

Krug CB, Brandl R, Boonzaier C, Cabral J, Esler KJ, Grant PBC, Heelemann S, Horn A, Keil M, Kongor RY, Meyer J, Nottebrock H, Poschlod P, Reisch C, **Rösner S**, Samways SJ, Schurr FM, Vrdoljak S, Vrdoljak S (2010) Keeping the Cape Lowland archipelago afloat. – In: Hoffman, M. T., Schmiedel, U., Jürgens, N. [Eds.]: *Biodiversity in southern Africa. Vol 3: Implications for land use and management*: pp. 151-179, Klaus Hess Publishers, Göttingen & Windhoek.

Bacht M, **Rösner S**, Müller J, Pfeifer R, Stadler J, Brandl R, Opgenoorth L (2012) Are Ring Ouzel (*Turdus torquatus*) populations of the low mountain ranges remnants of a broader distribution in the past? *Journal of Ornithology* 154, 231–237. doi:10.1007/s10336-012-0889-0

Rösner S, Cimiotti DV, Brandl R (2013) Two sympatric lineages of the Raven *Corvus corax jordanii* coexist on the Eastern Canary Islands. *Journal of Ornithology* 155, 243–251.

Schabo DG, Heuner S, Neethling MV, **Rösner S**, Uys R, Farwig N (2016) Long-term data indicates that supplementary food enhances the number of breeding pairs in a Cape Vultures colony. *Bird Conservation International* DOI: 10.1017/S0959270915000350

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17 Erklärung / Declaration

Ich versichere, dass ich meine Dissertation mit dem Titel:

„Between natural and human disturbance: Ecology and conservation of a remnant population of the Western Capercaillie (*Tetrao urogallus*) in the Bohemian Forest,“

selbstständig und ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfsmittel bedient habe.

Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg, den 21.12.2021



Sascha Rösner

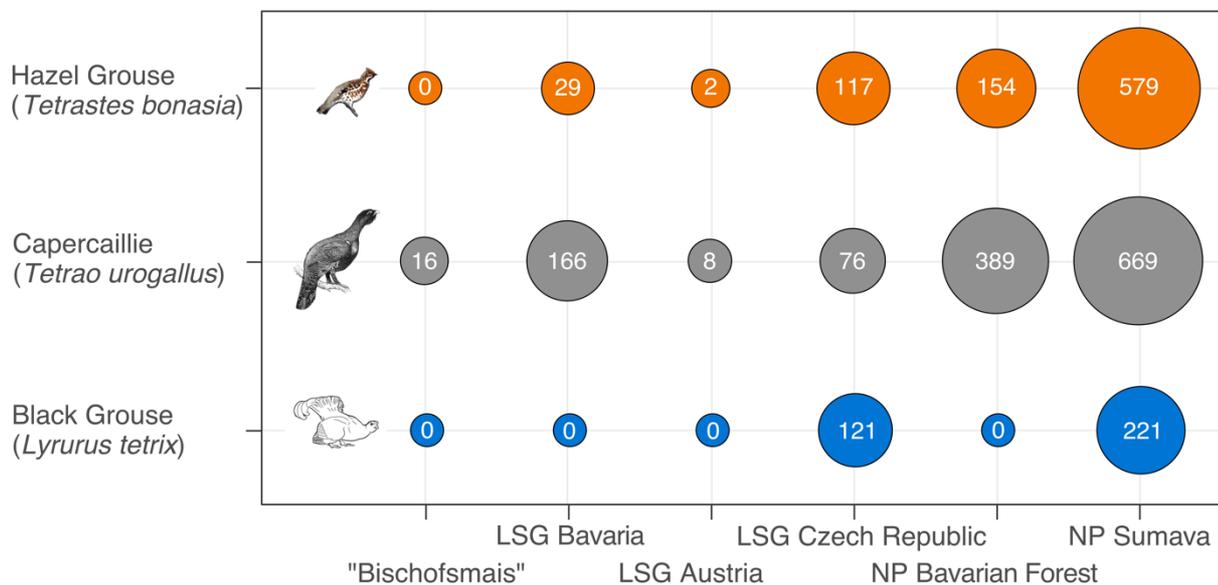
18 Appendix

18.1 Parasite screening

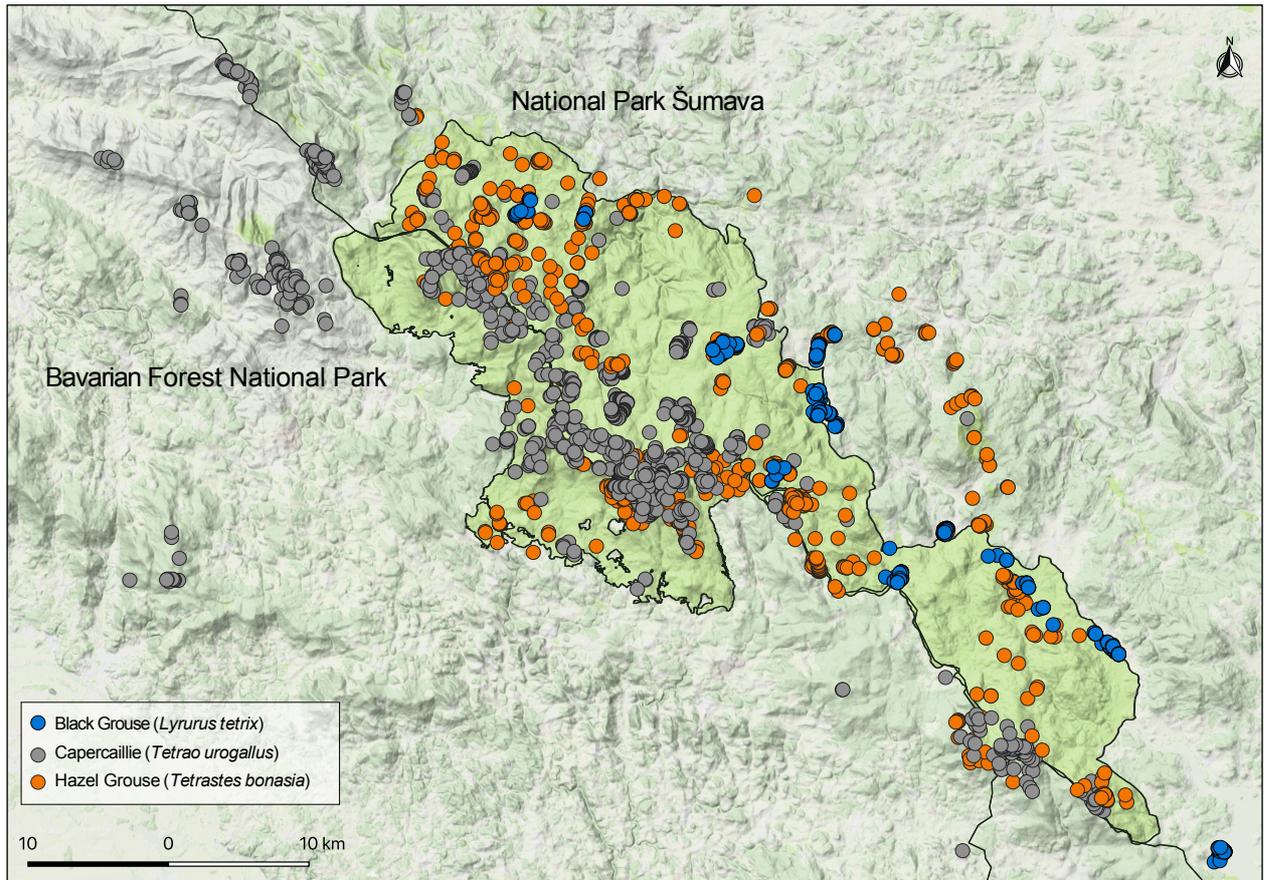
Table of recorded gastro-intestinal parasites (Nematodes, Genus) from dropping samples collected in the Bavarian Forest and Šumava National Parks in 2010.

	Infestation	<i>Ascaridia</i> spp.	<i>Capillaria</i> spp.	No record
-	none	-	-	176
+	low	10	16	-
++	medium	1	4	-
+++	high	-	-	-
# samples	$\Sigma = 207$	11 (5.3 %)	20 (9.6 %)	176 (85 %)

18.2 Sampling of droppings 2016 - 2018

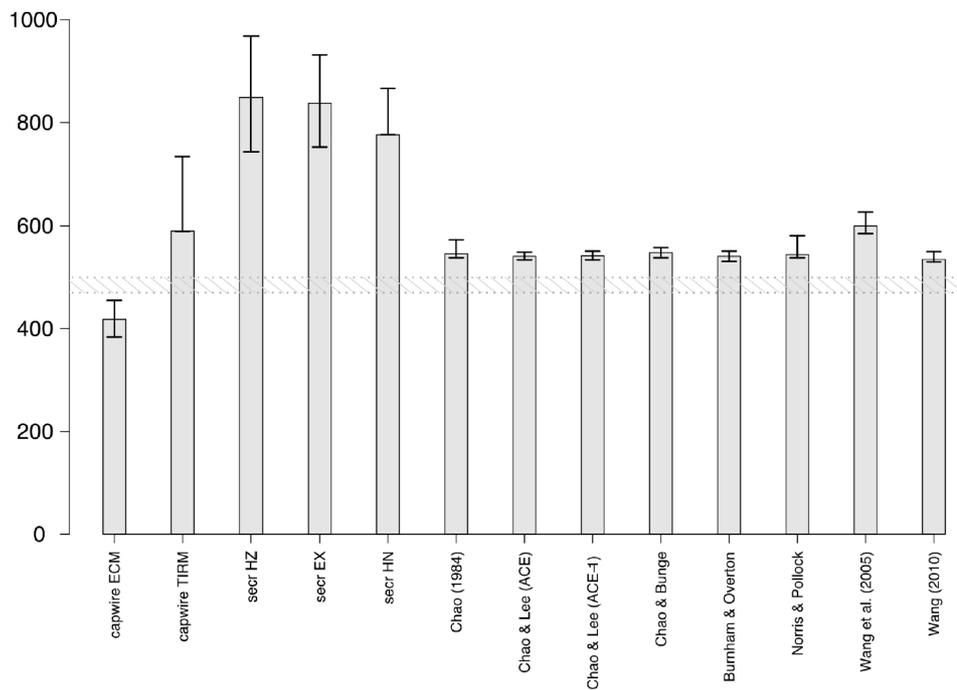


Number and distribution of detections (fecal samples, feather finds, visual observations, etc.) of Black Grouse (*Lyrurus tetrix*), Capercaillie (*Tetrao urogallus*), and Hazel Grouse (*Tetrastes bonasia*) from November 2016 to April 2018 throughout the study area. LSG = landscape conservation area, NP = national park (Rösner 2018).



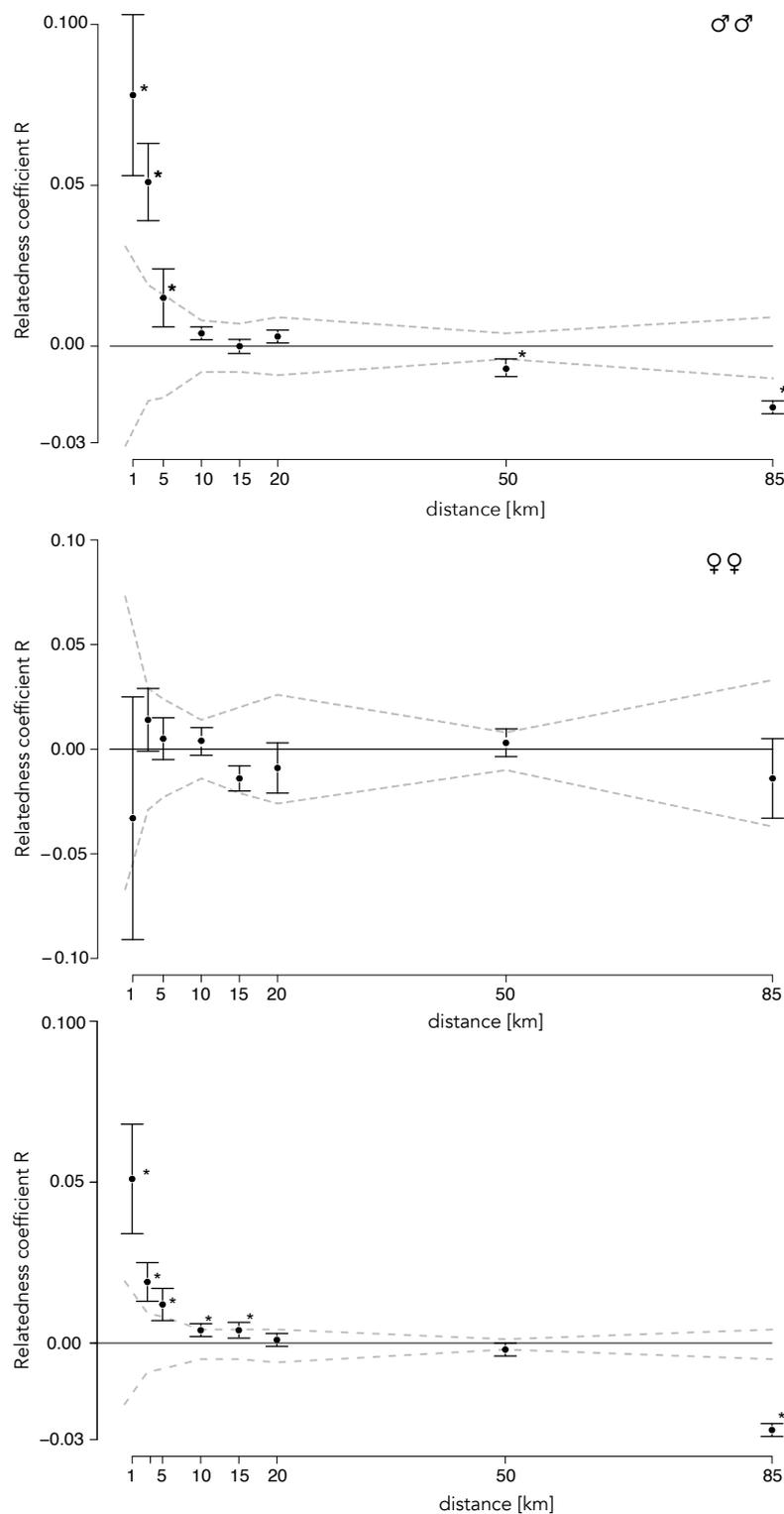
Distribution of fecal samples of Black Grouse (*Lyrurus tetrix*), Capercaillie (*Tetrao urogallus*), and Hazel Grouse (*Tetrastes bonasia*) collected between November 2016 to April 2018 throughout the study area (Rösner 2018, unpubl.).

18.3 Population size estimation 2016 – 2018



Comparative population size estimates of Capercaillie (*Tetrao urogallus*) from the study area. "Bavarian Forest and Bohemian Forest" in 2016 and 2017, indicating the upper and lower estimate ranges. The gray shaded area shows the minimum and long-term viable population size according to Grimm & Storch (2000). Source: Rösner (2018, unpublished report).

18.4 Genetic relatedness in relation to spatial distance



Relatedness coefficient R in relation to spatial distance [km] of the entire population (bottom) and separated by sex (females, males). Dashed line: upper and lower 95 % confidence intervals (CI) above the null hypothesis for no spatial structure of randomized data (9,999 iterations and 9,999 bootstraps). Black dots: Data genotypes under consideration for pairwise comparisons within each distance class \pm 95% confidence intervals. Asteriskus: Significant differences ($p \leq 0.034$).

