Variation in impacts of recreational outdoor activities on wildlife

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Introduction

Outdoor recreation activities are linked to positive effects on health conditions (Connolly et al. 2002, Godbey 2009), reduction in stress (Godbey & Blazey 1983, Orsega-Smith et al. 2004) and increase in well-being for human recreationists (Buchecker & Degenhardt 2015). These benefits have contributed to the increasing popularity and number of people performing outdoor recreation activities (Gartner & Lime 2000, Kuenzi & McNeely 2008, Bell et al. 2009), a trend which is expected to continue into the future (Maida 2018). Recreation or recreation activities, hereby defined as non-motorized human outdoor sports or leisure activities and for the purposes of this study does not include hunting. Recreation activities vary widely in their type and duration and can be performed close to the home as well as further away during holidays (Paracchini et al. 2014). The most popular activities include hiking and biking in summer, and back-country and cross-country skiing and snowshoeing in winter, and are associated with specific recreational infrastructure (e.g. hiking trails, skiing runs, cross-country skiing trails). The importance of outdoor recreation activities to today's society is reflected in the fact that the potential for outdoor recreation of a natural area is considered a major cultural ecosystem service (De Groot et al. 2010, Paracchini et al. 2014). The economic value of outdoor recreation in protected areas worldwide is estimated at $US250 billion annually (Balmford et al. 2015), can significantly contribute to the income of local communities and is often used as a major argument to fund nature conservation activities (Zaradic et al. 2009, Eagles 2014).

The increasing number of people participating in outdoor recreation, however, exerts pressure on the natural areas in which the recreation activities occur, with impacts on ecosystem function, as well as individual species (Pickering & Hill 2007, Steven et al. 2011). Conversely, the naturalness, biodiversity or occurrence of specific emblematic species can play an important role in the attractiveness of this area for recreation activities (Knight 2009, Hammitt et al. 2015, Aasetre et al. 2016). Recreation activities might therefore conflict with another function of natural areas: the preservation of natural habitats and biodiversity (Green & Giese 2004, Niemelä et al. 2005, Pröbstl et al. 2010), with recreation now recognized as a threat for a wide range of species (Ballantyne & Pickering 2013, BirdLife International 2015). It is therefore relevant to study the effects of outdoor recreation activities on natural areas and on species of conservation concern. The impacts of recreation activities on nature can be manifold: Vascular plants can be affected by trampling, altering soil conditions as well as directly destroying vegetation cover (Cole 2004, Pickering et al. 2011), or by the human-induced spread of invasive weeds or pathogens (Kelly et al. 2003). Although there are some examples of wildlife species habituating to human recreation (Thompson & Henderson 1998), there are mounting case studies indicating negative effects of nature-based activities on wildlife (Steven et al. 2011, Larson et al. 2016). Recreation activities are even affecting the effectiveness of protected areas (Reed & Merenlender 2008). The study of the environmental consequences of outdoor recreation activities and their effective management (i.e. recreation ecology) is considered a research field of global importance (Monz et al. 2013).

Ecological hypotheses relevant for wildlife – human recreation interactions

There are several theories which are often applied to explain human-wildlife interactions. Here I briefly discuss the most important dealing with the response of wildlife to human presence and human recreational activities.

Risk-disturbance hypothesis

For wildlife, the mere presence of humans in their habitats can have an effect: generally most species respond to the presence of recreationists similarly as to the presence of a natural predator (Frid & Dill 2002, Beale & Monaghan 2004b). The response of wildlife to human presence is therefore often similar to anti-predator behaviour (Frid & Dill 2002). These responses are considered to bear costs for the individual (Lima & Dill 1990), ranging from direct energetic costs by fleeing or flushing to indirect costs of reduced energy intake or reduced habitat availability due to avoiding areas with frequent human presence (Beale 2007). Therefore, wildlife have to trade-off between the perceived threat of human presence and the costs of a reaction (Lima & Dill 1990, Lima 1998). Increasing numbers of recreationists in natural areas leads to a corresponding increase in the rate of wildlife encounters with humans, resulting in increased antipredator behavioural costs for the wildlife inhabiting these areas. This increase in antipredator costs might bear direct energetic costs, affect energy intake and therefore negatively affect the body condition (Frid & Dill 2002), a status which is called allostatic overload (Möstl & Palme 2002, McEwen & Wingfield 2003, Arlettaz et al. 2015). Allostatic overload can negatively influence the reproductive success and increase the predation rate, both affecting the local population size (Figure 1, (Frid & Dill 2002)).

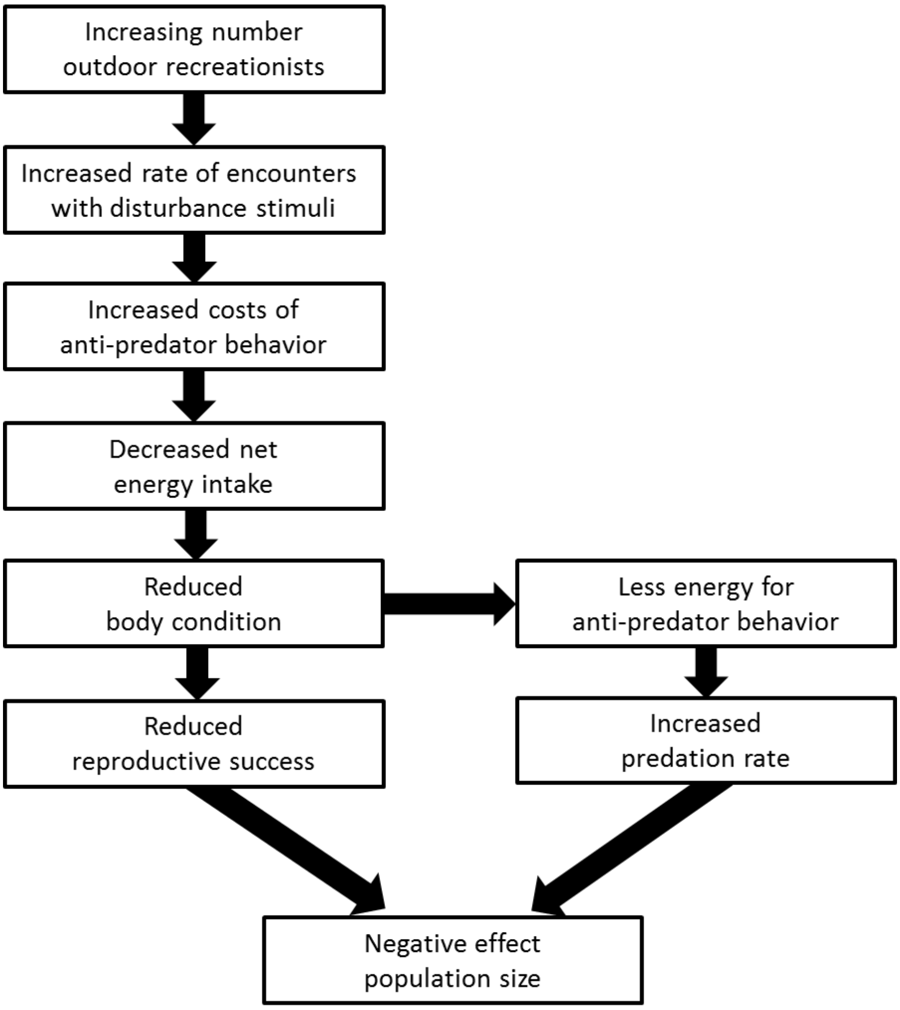

Figure 1: Conceptual model outlining how increasing numbers of recreationists can affect wildlife populations (adapted from Frid & Dill (2002)).

Landscape of fear

The landscape of fear concept implies that animals have the ability to learn and differentiate between areas with high and low perceived predation risk (Laundré et al. 2010). Since predators hunting efficiency is generally below 26 % (Longland & Price 1991, Mech et al. 2001, Laundré et al. 2010), prey species are considered to learn in which habitats the chances of encountering predators are higher and avoid these habitats or areas (Laundré et al. 2010). Since recreation activities area non-lethal (i.e. according to above definition excluding recreational hunting), animals survive encounters with recreationists and can learn in which areas the chances are higher of encountering humans (i.e. along or close to recreational infrastructures). Therefore, recreation activities and associated infrastructure are also hypothesized to create a landscape of fear for wildlife (Rösner et al. 2014).

Habituation

Habituation is the reduction in response to a specific stimuli which is not considered aversive for the animal (Bejder et al. 2009). If wildlife are regularly exposed to non-lethal disturbance stimulus such as recreation activities, and they can recognize that the presence of humans does not pose a threat, they can habituate and show a reduced reaction over time (Thompson & Henderson 1998). For example, birds returned to their nest quicker after repeatedly being disturbed, compared to the first times (Baudains & Lloyd 2007), and ungulates showed reduced flight responses (i.e. lower flight initiation distances) in areas with high rates of human recreation (Stankowich 2008). Whether an animal habituates to recreational disturbance might however depend on the type of recreational activities, and is more likely with recurring, predictably sources of disturbance (Naylor et al. 2009).

Although habituated animals might seem undisturbed by human presence (Thompson & Henderson 1998), it is important to note that this is only a reduction in response, and not the absence of a response (Bejder et al. 2009) and therefore does not completely neutralize negative effects of recreation activities. Since the behavioural reaction does not completely reflect the effects of recreation activities on wildlife (Gill et al. 2001), a behaviourally habituated animal might still be affected physiologically (Walker et al. 2005b).

Attraction

There are however also species which seem to benefit from side-effects of recreational activities. Within forests, bird species preferring forest edges have been found to prefer ecotone areas along recreational trails (Hickman 1990). Similarly generalist bird species seemed to be more abundant closer to recreation trails than further away in grasslands (Miller et al. 1998). In the Bavarian Alps, Storch & Leidenberger (2003) found increased numbers of corvids close to mountain huts, used for recreational activities. It is hypothesized that the presence of food scraps is affecting the habitat use of individuals, as well as the local population numbers of corvids, with possible negative consequences for other species in the area (Storch & Leidenberger 2003). A similar observation has been made around skiing areas: mostly generalist and scavenging birds were found in increasing numbers after the construction of skiing areas in Scotland (Watson 1979). In some areas, wildlife is actively lured to areas close to humans by supplying food or other resources, often with the intention to facilitate wildlife observations or enable wildlife tourism (Orams 2002, Knight 2009). The attraction of specific, often generalist species toward human recreation infrastructures is mostly associated in changes in the species composition and increased predator pressure for prey species (Orams 2002, Storch & Leidenberger 2003).

Human shield hypothesis

The human shield hypothesis states that prey species can learn that predators avoid humans, and therefore actively seek human presence (Berger 2007). Many predators have faced a long history of intensive persecution, which resulted in a strong avoidance of humans (Zimmermann et al. 2001, Lagendijk & Gusset 2008). Support for this hypothesis has been found in predator-prey interactions in relation to human settlements (Berger 2007, Hebblewhite & Merrill 2009). Rogala et al. (2011) found wolves (*Canis lupus*) avoiding trails designated for recreational use over a distance of 400 m, elk (*Cervus elaphus canadensis*) avoided them only up to 50 meters and preferred areas within 400 m of the trails. The preference of areas within 400 m of the trails was attributed to the reduced presence of wolves (Rogala et al. 2011). Whether, and to what extent, animals use humans as shield from natural predation can differ widely between individuals of the same species (Atickem et al. 2014), making it difficult to estimate potential benefits of recreational activities for prey species populations.

Methods to study the effects of recreation on wildlife

There are many different methods and approaches to study whether an animal is affected by the presence of humans and recreational use of areas (Gill 2007). Following is a brief introduction to the most widely applied study methods.

The sensitivity of a species to human presence if often quantified by measuring the distance in which an animal shows a behavioural reaction of moving away from the human, for example, the flight initiation distance (also called flushing distance in birds) (Livezey et al. 2016). The flight initiation distance can vary widely between species (Møller 2008), between individual animals of the same species (Blumstein et al. 2005) as well as between different populations of the same species inhabiting different regions (Thiel et al. 2007). Another method of assessing the sensitivity to disturbance is to measure the distance at which a species starts to observe a human: the alert distance (also called vigilance behaviour) (Fernández-Juricic et al. 2001). Although vigilance does not bear direct energetic costs, the behaviour is changed and might affect energy intake (Fernández-Juricic et al. 2001).

The analysis of spatial data of animals tagged with transmitters can also reveal how a species is affected by the recreation activities in its habitat (Rogala et al. 2011, Marchand et al. 2014). Animals can also be experimentally disturbed to study their reaction (Beale & Monaghan 2004a, Baines & Richardson 2007, Arlettaz et al. 2015). The presence and habitat use of wildlife in relation to different distances to recreational infrastructure can also be studied using camera traps (George & Crooks 2006, Reilly et al. 2017) or indirectly by using signs such as droppings or feathers (Summers et al. 2007, Immitzer et al. 2014). By using behavioural observation and comparing the behaviour of animals in regularly disturbed areas with the behaviour of the same species in undisturbed area, the indirect effects of human recreation activities can be studied (Jayakody et al. 2008).

Since behavioural reactions might not reflect physiological effects or effects on population dynamics (Gill et al. 2001) other effects of recreational activities have also been studied. Bird surveys assessing breeding success (Ellenberg et al. 2006, Ellenberg et al. 2007), breeding pair densities (van der Zande et al. 1984) or species composition (Miller et al. 1998) have been used compare areas close to recreation activities or in regularly disturbed areas, with areas with little or no recreation activities. The often less obvious physiological reactions of wildlife to human presence have been studied by assessing stress hormones, by directly measuring the concentrations in the blood (Fowler 1999) as well as non-invasively by measuring steroid concentrations in faecal samples (Thiel et al. 2011, Arlettaz et al. 2015) or by measuring heartrates (Ackerman et al. 2004, Ellenberg et al. 2006).

Effects of human recreation on wildlife

Depending on the hypothesized effects, study areas, study species and methods, different studies revealed a wide range of reactions of wildlife to human presence for many different taxa, ranging from reptiles, to birds and mammals (Larson et al. 2016). Disturbance is hereby defined as a response in an animal's behaviour or physiological state as a reaction to direct human presence, or human recreational use of the area.

Behavioural responses

The most obvious reaction of an animal to the presence of a recreationist is fleeing or flushing (Stankowich 2008, Livezey et al. 2016). This behavioural reaction causes the animal to interrupt its natural behaviour, possibly affecting energy intake and increasing the energy budget due to additional movement (Stankowich 2008). These additional energy costs have been hypothesized to affect fitness (Frid & Dill 2002). A different behavioural reaction to recreation activities is the change in antipredator behaviour (Jayakody et al. 2008). Jayakody et al. (2008) found red deer (*Cervus elaphus*) to show more vigilance behaviour (i.e. antipredator scanning behaviour) in areas which were within 500 m of designated hiking trails, compared to areas further away from the trails. This was attributed to a behavioural adaptation, with a trade-off between feeding and vigilance behaviour in more regularly disturbed areas resulting in less time for feeding (Jayakody et al. 2008). Manor & Saltz (2003) found that human presence caused increased vigilance behaviour and affected the group size of a social ungulate, with smaller group sizes in areas which were regularly disturbed. Lovari et al. (2007) found red deer (*Cervus elaphus corsicanus*) to have larger homeranges in times of high recreation pressure, with associated negative effects due to increased energy requirements. A different behavioural reaction to human recreation is an increase in aggressive behaviour close to nesting sites, which was found in burrowing owls (*Athene cunicularia*) (Carrete & Tella 2010).

By experimentally disturbing radio tagged black grouse (*Tetrao tetrix*) Baines & Richardson (2007) showed that birds which were regularly flushed (twice weekly) flushed at greater distances compared to birds which were not regularly disturbed. Similarly, capercaillie (*Tetrao urogallus*) flushed at greater distance in areas with high recreational use, compared to areas with low recreational use (Thiel et al. 2007). Wildlife can also temporally avoid human presence by being more active during the night, when there is less human presence in the areas (George & Crooks 2006, Marchand et al. 2014). A spatial avoidance of recreation infrastructure has also been recorded for a variety of species (Miller et al. 1998, Leivits et al. 2009, Immitzer et al. 2014). This reduced use of areas close to recreation infrastructure or activities effectively causes habitat deterioration. This can affect the local abundance of species (Patthey et al. 2008, Alwis et al. 2016) and result in reduced species diversity in such areas (Newsome et al. 2012, Monz et al. 2013). Using bird surveys, Miller et al. (1998) found bird species composition and abundance were different close to recreation trails compared to reference areas without recreation activities. These effects might result from birds not establishing territories in areas which are regularly disturbed (Bötsch et al. 2017). Human recreation activities can also affect breeding success in birds (Watson et al. 2014). Mallord et al. (2007) found a reduced productivity of woodlarks (*Lullula arborea*) in areas which were regularly frequented by human recreationists. A decrease in breeding success due to human recreation activities can be caused by reduced chick survival (Müllner et al. 2004), impaired nestling growth (Remacha et al. 2016) or by increased nest losses (Langston et al. 2007).

Physiological responses

An increasing number of studies are not focussing on behavioural reactions of wildlife to human presence, but rather on the physiological effects (Bélanger & Bédard 1990, Busch & Hayward 2009, Larson et al. 2016). Although some species or animals show little or no behavioural reaction to human presence, physiological responses have been documented (Walker et al. 2005a). Physiological effects to human presence and recreation activities can be studied by monitoring heartrates (Ackerman et al. 2004, Ellenberg et al. 2006) or stress hormone concentrations (Palme et al. 2005, Sheriff et al. 2011, Arlettaz et al. 2015). By experimentally approaching white-fronted geese (*Anser albifrons elgasi*), Ackerman et al. (2004) showed that the birds' heartrate increased 5 seconds before flushing. In nesting Humboldt penguins (*Spheniscus humboldti*) increased heart rates were found when humans approached the nest within 150 m, whereas no apparent behavioural reaction was observed (Ellenberg et al. 2007). Recreational activities have also been linked to increased stress hormone concentrations in a variety of species, with higher concentrations of stress hormones in areas of intensive recreational use (Baltic et al. 2005, Walker et al. 2005b, Monclús et al. 2009, Thiel et al. 2011, Rehnus et al. 2014, Arlettaz et al. 2015, Formenti et al. 2015).

Variation in reactions of wildlife

How wildlife reacts to the presence of human presence can be modulated by a wide range of factors (Tablado & Jenni 2017): For example, responses can differ between areas (Martínez-Abraín et al. 2008). Thiel et al. (2007) found different average flushing distances between different study areas for capercaillie. How wildlife responds to human presence can also vary between seasons (Stillman & Goss-Custard 2002, Stankowich 2008): Oystercatchers (*Haematopus ostralegus*) were found to show less response to human presence in late winter compared to early winter, which was hypothesized to be caused by a reduced energy budget in late winter (Stillman & Goss-Custard 2002). Furthermore the reproductive state can affect the response of wildlife to recreation activities, with a more pronounced reaction (i.e. longer flight initiation distances) of females with young, compared to male ungulates (Stankowich 2008). Behavioral traits of individual animals can vary widely between individuals of the same species (Réale et al. 2007, Carrete & Tella 2010) and consequently, the responses to human presence can also differ between individuals (Carrete & Tella 2011). Differences might be related to the experience of the individual (Knight & Knight 1986), or on its body condition (Beale & Monaghan 2004a). By supplementary feeding turnstones (*Arenaria interpres*) and subsequently approaching them, Beale & Monaghan (2004a) found that birds which were supplementary fed (i.e. in better body condition) showed greater responsiveness and greater flushing distances to human presence compared to birds which were not supplementary fed. Finally, the effects of human disturbance can also differ between sexes of the same species (Baydack & Hein 1987, Thiel et al. 2007, Stankowich 2008, Moss et al. 2014).

Species

Reactions of animals to human recreation are highly species-specific (Blumstein et al. 2005, Ficetola et al. 2007), for example the flight initiation distance, which is often used as a measure of sensitivity to human recreation, varies greatly between species (Blumstein et al. 2003). Miller et al. (1998) found generalist bird species were less affected by the presence of recreational trails compared to more specialist bird species. How a species reacts if often linked to behavioural, morphological or life-history traits (Blumstein et al. 2005, Kangas et al. 2010). Ground nesting birds, for example, have been found to be more sensitive to recreational disturbance compared to species breeding in cavities (Kangas et al. 2010). Furthermore species with larger body mass are considered more sensitive to recreational disturbance compared to smaller species (Blumstein et al. 2005, Weston et al. 2012).

Habitats

How wildlife reacts to recreation activities can also be habitat specific (Murison et al. 2007) and might vary between different habitat types or habitat characteristics that provide food or cover: van der Zande et al. (1984) found a more pronounced negative effect of recreation on two bird species in deciduous forests compared to coniferous forests. Vegetation structures associated with cover (i.e. foliage density, dense shrub or forest layers) have been shown to affect flushing distances (Fernández-Juricic et al. 2002, Fernandez-Juricic et al. 2004), with shorter flushing distances in denser forest providing greater cover (Thiel et al. 2007). The degree to which wildlife can survey their surroundings (i.e. visibility) can also affect vigilance behaviour (Metcalfe 1984, Whittingham et al. 2004), with increased vigilance in visually obstructed habitats (Whittingham et al. 2004). Wolf et al. (2013) found impacts of recreation activities on birds to be less distinct along trails with a well-developed, structurally rich vegetation with favourable foraging and hiding structures.

Type of human recreation

The type of recreation and how the human recreationists behave, can also play major role in how wildlife reacts (Pearce-Higgins et al. 2007, Stankowich 2008). Recreationists staying on designated trails cause a less severe reaction compared to recreationists moving off-trail (Miller et al. 2001). This is generally explained by the fact that recreationists on a designated trail are more predictable for wildlife compared to those that do not stay on trails (Miller et al. 2001, Taylor & Knight 2003, Tablado & Jenni 2017). Furthermore when recreationists are accompanied by a dog, reactions of wildlife are generally more severe compared to recreationists without a dog (Mainini et al. 1993, Lord et al. 2001, Miller et al. 2001). The direct reaction of wildlife to human recreationists can also depend on the group size of the recreationists (Burger & Gochfeld 1991, Geist et al. 2007) and their movement speed (Cooper 1997, Bateman & Fleming 2014).

There is great variation in how wildlife can react to human recreation activities, (Monz et al. 2013) and these reactions can also be modulated by a wide range of factors (Tablado & Jenni 2017), which makes it difficult to generalize the effects of recreation activities on wildlife and derive adequate conservation measures. It is therefore important that new studies examine sources of variation in effects of recreation on wildlife, so as to generate results which can be used to reduce conflict between the dual purposes of outdoor recreation and wildlife conservation (Pouwels et al. 2017). In my doctoral thesis in the field of recreation ecology, I am therefore focusing on different sources of variation in the reactions of wildlife to recreation activities in order to generate results with relevance for future scientists and practitioners alike.

Thesis structure

The main part of my thesis consists out of three peer-reviewed publications and one manuscript which has been submitted to a journal for publication. Every chapter studies a different factor that may modulate wildlife reaction or adaptation to recreation activities in their habitat. Chapter one focuses on temporal (i.e. seasonal and diurnal) variation and reveals how red deer (*Cervus elaphus*) adapt their habitat use to temporally avoid human recreation activities. The second chapter looks at spatial variation and scale-dependency of wildlife responses, showing how capercaillie (*Tetrao urogallus*) respond differently to recreation activities on a landscape compared to a local scale. In chapter three I demonstrate the importance of taking into account inter-individual variation when studying the effects of human recreation on stress responses in wildlife. The fourth chapter studies habitat-dependent variation of responses to recreation, by investigating interactions between habitat suitability and effects of recreation activities on both small-scale habitat use and relative population densities. In the synthesis chapter I summarize the results and conclusions of my work and merge them into a conceptual framework for mitigating recreation effect on wildlife through landscape planning and habitat management.

Chapters and author contributions

Chapter one has been published in the Journal PLoS ONE: Coppes, J., Burghardt, F., Hagen, R., Suchant, R., Braunisch, V. (2017) Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). PLoS ONE 12 (5): e0175134. https://doi.org/10.1371/journal.pone.0175134.

J. Coppes, F. Burghardt, R. Suchant and V. Braunisch designed the study. F. Burghardt collected the data. J. Coppes, V. Braunisch and R. Hagen performed the statistical analysis. J. Coppes wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Chapter two is published in the Journal of Avian Biology: Coppes, J., Ehrlacher, J., Thiel, D., Suchant, R., Braunisch, V. (2017) Outdoor recreation causes effective habitat reduction in capercaillie *Tetrao urogallus*: a major threat for geographically restricted populations. Journal of Avian Biology 48: 1583–1594. https://doi.org/10.1111/jav.01239

J. Coppes, R. Suchant and V. Braunisch designed the study. J. Ehrlacher, D. Thiel and V. Braunisch collected the data. J. Coppes and V. Braunisch performed the statistical analysis. J. Coppes wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Chapter three has been accepted for publication in the Journal of Applied Ecology: Coppes, J., Kämmerle, J-L., Willert, M., Kohnen, A., Palme, R., Braunisch, V. (2018) The importance of individual heterogeneity for interpreting faecal glucocorticoid metabolite levels in wildlife studies. Journal of Applied Ecology. 00:1–12. https://doi.org/10.1111/1365-2664.13140

J. Coppes, J-L. Kämmerle and Veronika Braunisch designed the study. J. Coppes and M. Willert collected and prepared the data. A. Kohnen performed the genetical analysis and R. Palme performed the stress physiological analysis. J-L. Kämmerle performed the statistical analysis. J. Coppes wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Chapter four has been submitted for acceptance in the journal Biological Conservation: Coppes, J., Nopp-Mayr, U., Grünschachner-Berger, V., Storch, I., Suchant, R., Braunisch, V. (submitted) Habitat suitability modulates the response of wildlife to human recreation.

J. Coppes, U. Nopp-Mayr, V. Grünschachner-Berger, R. Suchant and V. Braunisch designed the study. J. Coppes, U. Nopp-Mayr, V. Grünschachner-Berger and I. Storch collected the data. J. Coppes and V. Braunisch performed the statistical analysis. J. Coppes wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Chapter I: Temporal variation

Human recreation affects spatio-temporal habitat use patterns in red deer (Cervus elaphus)

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Abstract

The rapid spread and diversification of outdoor recreation can impact on wildlife in various ways, often leading to the avoidance of disturbed habitats. To mitigate human-wildlife conflicts, spatial zonation schemes can be implemented to separate human activities from key wildlife habitats, e.g. by designating undisturbed wildlife refuges or areas with some level of restriction to human recreation and land use. However, mitigation practice rarely considers temporal differences in human-wildlife interactions. We used GPS telemetry data from 15 red deer to study the seasonal (winter vs. summer) and diurnal (day vs. night) variation in recreation effects on habitat use in a study region in south-western Germany where a spatial zonation scheme has been established. Our study aimed to determine if recreation infrastructure and spatial zonation affected red deer habitat use and whether these effects varied daily or seasonally. Recreation infrastructure did not affect home range selection in the study area, but strongly determined habitat use within the home range. The spatial zonation scheme was reflected in both of these two levels of habitat selection, with refuges and core areas being more frequently used than the border zones. Habitat use differed significantly between day and night in both seasons. Both summer and winter recreation trails, and nearby foraging habitats, were avoided during day, whereas a positive association was found during night. We conclude that human recreation has an effect on red deer habitat use, and when designing mitigation measures daily and seasonal variation in human-wildlife interactions should be taken into account. We advocate using spatial zonation in conjunction with temporal restrictions (i.e. banning nocturnal recreation activities) and the creation of suitable foraging habitats away from recreation trails.

Introduction

An increasing number of people are practicing nature-based tourism, with outdoor recreation activities generating pressure on the ecosystems in which they take place (Flather & Cordell 1995, Stankowich 2008). An important factor of how outdoor recreation affects ecosystems is the disturbance of wildlife by human recreation (Jiang et al. 2009, Reimoser 2012), defined here as any effect on wildlife which is incurred by the presence of recreationists or infrastructure related to recreational activities, irrespective of possible - but mostly unknown - fitness consequences (Yasué 2005, Leblond et al. 2013). Free-living animals often react to human presence in a similar way than to the presence of natural predators (Frid & Dill 2002, Beale & Monaghan 2004). This reaction can have a variety of facets (Knight & Cole 1995, Knight & Temple 1995), ranging from physiological stress responses (Arlettaz et al. 2007, Thiel et al. 2008, Sheriff et al. 2009, Formenti et al. 2015) to behavioural changes (Fernández-Juricic & Telleria 2000, Beale & Monaghan 2004) or a reduction in reproductive success (Beale & Monaghan 2004). Human disturbance might trigger short-term behavioural reactions (i.e. flushing or fleeing) (Miller et al. 2001, Stankowich 2008, Sönnichsen et al. 2013) as well as long-term responses such as avoiding frequently disturbed areas (Taylor & Knight 2003, Immitzer et al. 2014), e.g. recreational infrastructures such as hiking or skiing trails that are regularly used by humans (Sibbald et al. 2011). Both types of reaction can involve direct energetic costs for the animal (e.g. due to fleeing or reduced food intake) which can affect fitness (Phillips & Alldredge 2000, Arnold et al. 2004, Sheriff et al. 2009), and may even outweigh the effects of habitat conditions and natural predators (Ciuti et al. 2012).

In addition, the reactions of wildlife triggered by human recreational activities can cause conflicts with other forms of human land use, such as transportation, agriculture or forestry. For example, fleeing animals can trigger vehicle collisions (Lima et al. 2015), and foraging animals relocating to less disturbed areas might cause damage to crop or tree regeneration (Jeppesen 1987, Reimoser 1988).

To mitigate both the negative effects of human recreation on wildlife and the resulting conflicts with land use, spatial zonation schemes have become an important tool in wildlife management (Dudley 2008). These schemes separate human activities from key wildlife habitats by designating undisturbed wildlife refuges and areas with different levels of restriction to human recreation, sometimes combined with habitat management or hunting regulations. The design of zonation schemes often takes spatial patterns of human-wildlife interactions into account but rarely considers temporal interactions, e.g. variation in diurnal and seasonal overlaps between habitat requirements and recreation activities. Using the red deer (*Cervus elaphus*) as an example organism, we investigated the temporal variation of its habitat use in relation to human recreation infrastructure and zones with different intensities of human disturbance, as established by a zonation scheme.

As one of the largest free ranging herbivores, and widely distributed across the globe (Koubek & Zima 1999, Milner et al. 2006), the red deer is one of the focal species of wildlife management in Central Europe (Bützler 2001, Putman et al. 2011). Red deer are attractive to observe and are therefore highly valued for nature-based tourism (Bützler 2001) and also as a game species (Koubek & Zima 1999, Milner et al. 2006). They are considered an important vector species for seeds (von Oheimb et al. 2005, Iravani et al. 2011) and invertebrates (Ruiz-Fons & Gilbert 2010) and an essential prey for carnivores (e.g. wolf) (Jędrzejewski et al. 2000). With its browsing behaviour it can affect the vegetation structure (Gill & Beardall 2001, Côté et al. 2004, Melis et al. 2005) and there is some evidence for impacts on plant species richness (Hegland et al. 2013). At the same time however, deer browsing and bark stripping causes conflicts with forestry management (Gill 1992, Kiffner et al. 2008, Putman et al. 2011). In addition, thousands of individuals are injured or die in vehicle collisions every year, causing considerable property damage and fatal human injuries (Groot Bruinderink & Hazebroek 1996, Gunson et al. 2011). The major objective of the red deer management in Europe is therefore to minimize the economic damage related to forestry and animal vehicle collisions while maximizing the economic benefits related to ecosystem services and hunting (Seiler 2004, Mysterud et al. 2006, Morellet et al. 2007).

Outdoor recreation has been widely neglected within the management of free ranging ungulates (Stankowich 2008), although red deer have been shown to be influenced by human recreationists (Jeppesen 1987, Jayakody et al. 2008b, Jayakody et al. 2011, Sibbald et al. 2011). Direct reactions to disturbance include instant flight, relocation to areas with dense vegetation cover (Jeppesen 1987, Burghardt et al. 2012) as well as a temporal abandonment of the disturbed area (i.e. for several hours or days) (Jeppesen 1987). Sibbald et al. (Sibbald et al. 2011) found red deer avoided hiking trails, with larger distance to the trail kept during times of high human use compared to times of little use. In areas with high recreation pressure, red deer have been shown to increase their vigilance behaviour which might lead to a decrease in food uptake (Jayakody et al. 2008b). Animals can also adjust their habitat use between hunting season and non-hunting season (Lone et al. 2015), which indicates their behavioural plasticity. However, even though there are several examples where north American elk (*Cervus elaphus canadensis*) have become habituated to human presence (Thompson & Henderson 1998) and even use settlements as habitat (Lubow et al. 2002), this phenomenon is not known from free-ranging European red deer (Staines & Welch 1989, Kloppers et al. 2005). Human disturbance may therefore cause red deer to temporally or permanently abandon optimal habitat and forage in sub-optimal habitats (Jayakody et al. 2011). Increased energy requirements caused by fleeing, in conjunction with seeking cover (Jeppesen 1987) could result in damage to forestry e.g. through bark-stripping in young, dense stands offering visual protection.

The most widely applied method of red deer management involves hunting, to regulate the population and to gain trophies (antlers) and meat (Koubek & Zima 1999, Milner et al. 2006). Furthermore in many areas red deer are provided with supplementary food during winter to reduce bark-stripping or because of animal welfare reasons (Putman & Staines 2004). In the last decades, wildlife refuges have increasingly been designated, with the primary aim to reduce disturbance of deer by recreationists, land use management and hunters (Reimoser 1988, Suchant et al. 2008, Miller et al. 2016). However, it has also been suggested that well-placed refuges may help reduce human-wildlife conflicts (Krishna et al. 2016) and contribute to decreasing damage to forestry by reducing the browsing pressure on the surrounding forest stands (Reimoser 1988). To serve this purpose, refuge systems have been extended to spatial zonation schemes that regulate recreational activities but also hunting and forest management (Dudley 2008). However, management schemes aiming at furthering the coexistence of humans and wildlife must also consider temporal dimensions of human-wildlife interactions (Taylor & Knight 2003, Fernandez-Juricic et al. 2004). Given the seasonal and diurnal differences in recreation activities and the behavioural plasticity of red deer, we expect that the spatial pattern of habitat use in relation to human recreation infrastructure varies considerably between seasons and between day and nighttime, which might also modify the relative importance (i.e. intensity of use) of the zones of a static spatial zonation. To test this, we studied the habitat use of free roaming red deer comparing daytime and nighttime activity in two different seasons using GPS-telemetry. The study was conducted in a red deer management area in south-western Germany in which a spatial zonation scheme had been established, defining red deer refuges (without human recreation), a core zone with limited recreational use and a border zone with unrestricted recreation. The goals of our study were to determine if linear recreation infrastructure (i.e. hiking, biking and skiing trails) and the zonation scheme affected red deer habitat use and whether these effects varied daily or seasonally. From the results we derive recommendations for mitigating impacts of human recreation on ungulates in human-dominated landscapes.

Methods

Ethics statement

Red deer capturing and tagging was carried out under the permit (No. 787.524) issued by the ethical committee of the Regional Council of Freiburg, Baden-Württemberg (Regierungspräsidium Freiburg, Baden-Württemberg). The ethical committee specifically approved this study. GPS collars were attached under anesthesia (125 mg Xylazine + 100 mg Ketamine /ml).

Study area

The study was conducted in the Southern Black Forest, Baden-Württemberg, south-western Germany (Fig 1). In the state of Baden-Württemberg it is official policy to try to keep red deer in five specially designated areas, which are mainly state owned, to avoid conflicts with private forest owners and farmers. Red deer leaving the management areas are shot at sight. The Southern Black Forest red deer management area has a total surface of 17500 ha; our study was performed in the central part of 5984 ha, located at elevations between 800 and 1300m above sea level (a.s.l.). Most of the study area (77%) consists of intensively managed forest (for timber production) dominated by Norway spruce (*Picea abies*), European silver fir (*Abies alba*) and common beech (*Fagus sylvatica*) (Suchant et al. 2003). Extensively managed meadows prevail in the non-forested areas.

The study area is located between two major tourist attractions Lake Schluchsee and the Feldberg Mountain and is intensively and increasingly used for recreation all year round. This is reflected in a 24% increase of tourist visits to the region between 2004 and 2014 (Statistisches Landesamt 2016). In the study area, a dense network of recreation trails has been established: in summer, a total of 162 km (2.71 km/km^2) of paths are accessible, mainly for hiking and biking. During winter, trails for hiking (48 km; 0.8km/km^2) and cross-country skiing (39 km; 0.65km/km^2) are prepared, but there are also off-trail recreational activities (i.e. snowshoeing and back-country skiing) (Coppes & Braunisch 2013). To assess the temporal patterns of human recreationists in the areas, automatic visitor counts were performed on hiking and skiing trails one year after the data collection for the telemetry study. Infrared trail counters (TRAFx), were placed along three designated hiking trails and three cross country skiing trails within the study area from 17.2.2010 to 14.4.2010, showing a peak of recreation activities at noon, with an average number of six persons per hour recorded on hiking trails and two per hour on skiing trails (S2 Fig).

During the duration of our study (2007-2009), 600-700 free-roaming red deer were estimated to be present in winter within the total red deer management area (Forest Research Institute of Baden-Württemberg FVA, unpublished), which corresponded to a density of 3.43-4.00 individuals per km^2. Other ungulates present are roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and sika deer (*Cervus nippon*) (FVA, unpublished). Predators include red fox (*Vulpes vulpes*) and pine marten (*Martes martes*), but with lynx (*Lynx lynx*) and grey wolf (*Canis lupus*) absent, adult red deer have no natural predators in the area (FVA, unpublished).

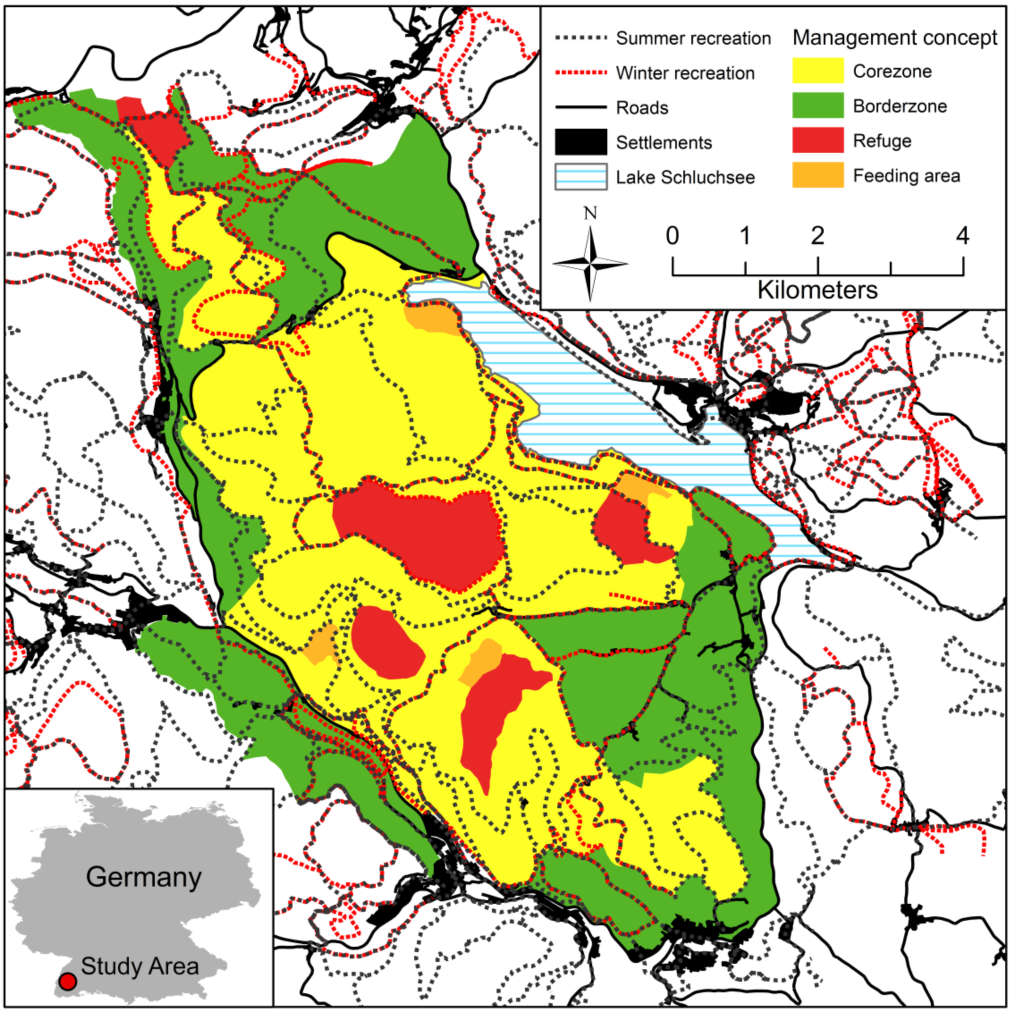

Figure 1: The study area in south-western Germany, with recreation infrastructure (summer/winter) and spatial zonation defining border, core and refuge zones, with different implications for red deer management.

Zoning Scheme

Beginning in 2003, a spatial zonation scheme was developed and implemented using a joint participative process, which included wildlife biologists, foresters, hunters and landowners. It was officially approved in 2008 by the local communities. The scheme includes different zones with regulations concerning not only recreational use, but also hunting, forestry and red deer habitat management (Fig 1, Table 1) (Suchant et al. 2008): A border zone - where no restrictions for recreation apply - surrounds a core zone where recreation is restricted to designated trails. Embedded within the core zone, refuge areas for red deer have been designated, where recreational use is totally banned. During winter the deer are fed at four feeding stations to minimize seasonal migration and thus reduce deer-vehicle collisions, but the animals are not fenced during any time of the year (Suchant et al. 2008).

In the study area the hunting times are more restricted compared to the official state hunting regulations. In the border zone, hunting is only allowed from the 1st of August until 31st of December (i.e. banned in the summer hunting season between May and July). In the core zone hunting activities are additionally banned in December and restricted to interval hunting (i.e. short hunting intervals followed by several days without hunting with the goal to reduce disturbance). In the refuge areas hunting is restricted to driven hunts in three consecutive weeks in October. The aim of the hunting regime in the area is to limit the red deer population size (winter) to an overall number of 400 individuals (2.29 individuals per km^2).

In all zones, forestry is directed towards creating small openings during timber harvesting, to increase natural food resources for the deer. In the border zone, moderate protection measures, such as small scale fencing, can be implemented to avoid damage to forestry caused by deer. In the core zone, damage caused by deer to forestry is accepted. In the refuges and feeding stations no forestry measures (i.e. timber harvesting) are performed during the fawning season (i.e. May and June) and feeding times (i.e. snow conditions). The main goals of this zonation scheme are decreasing damage to forestry across the whole area by allowing the deer to retreat to undisturbed areas with sufficient food in summer and additional feeding in winter, while at the same time creating possibilities for human recreation which includes the possibility to observe and experience red deer (Suchant et al. 2008).

Table 1: Spatial zonation of the study area with management conditions

Zone	**Recreation**	**Hunting**	**Forestry**	**Habitat improvement**
Border zone	No restrictions	No hunting between 31st December and 1st of August	Local adaptations to prevent damage where necessary	Locally: measures to increase natural food supply
Core zone	Access only on marked trails	Only August-November, only interval hunting	Browsing damage and additional effort for damage prevention accepted	Increase of natural food supply
Refuges	Access prohibited	Only three consecutive weeks per year (outside reproduction season)	As in core zone; and no forestry during the reproductive season	Increase of natural food supply and cover
Feeding stations	Access prohibited during winter	No hunting	As in core zone; and no forestry during feeding times	Promotion of cover and reduction of visibility from marked trails

Red deer data

Our analysis was based on telemetry locations of 15 red deer (5 males and 10 females, all age classes, S1 Table) captured and surveyed between 2007 and 2009. Individuals were equipped with a GPS-collar (Vectronic Aerospace, Berlin, Germany; serial number 2000er, 3000er and 6000er) and located every 2 hours. The tracking period of individual animals ranged between 5 and 34 months (S1 Table), depending on the functional duration of the GPS collars and due to individual fatality events. We retained only locations if a minimum of 4 satellites were available and the DOP (dilution of precision) value was smaller than 10 (corresponding to an estimated maximum location error of about 40m (Stache et al. 2012)), resulting in 80% of the locations for further analysis. To model temporal differences in habitat use, each sample was allocated to a season (summer, winter) and a time of day (day, night). Since seasonal differences in habitat use patterns were assumed to be related to prevailing weather conditions rather than being determined by a predefined time period, seasons were defined using standard indicators of weather conditions: The "summer" season started with the flowering of dandelion (*Taraxacum officinale*) (18, 22 and 30 April in 2007, 2008 and 2009, respectively), as measured at the phenology reference station Bernau, 920 m.a.s.l., and ended with the start of the rutting season (15 September, all years). The "winter"-sample contained all locations taken between first of November and the beginning of the summer season in the following year, including only days where a continuous snow-layer was recorded at the nearby weather station (St. Blasien-Menzenschwand, 885 m.a.s.l.). Locations taken outside the defined seasons were discarded.

Among the retained locations, we distinguished between day and night. Day was defined as the time between sunrise and sunset, and night covered the time between the end and the start of the nautical twilight. Due to failing fixes or fixes with too high DOP (i.e. low precision), the number of locations per day and time period varied greatly within and between individuals. To avoid an unbalanced sample, (i.e. some time periods being overrepresented by data showing high spatial and temporal autocorrelation) we adopted a conservative approach, randomly selecting only one location per time period and day for every individual. Of the resulting 24259 locations which were retained for further analysis (S1 Table), 7384 locations pertained to summer, and 16875 to the winter season. The number of locations per individual varied between 244 and 3136 (S1 Table).

Environmental Variables

We distinguished three groups of environmental predictors, pertaining to land cover and topography, vegetation structure and human presence (Table 2). Topographic variables (altitude, slope and exposition) were calculated from the digital elevation model (DEM). Land cover characteristics (waterbodies, meadows, forest) were adopted from the Official Topographic and Cartographic Information System of Germany (ATKIS, www.atkis.de). Vegetation was mapped in the field: forest stand type, canopy cover, tree-species mixture, successional stage, understory composition, cover of herbs and grass as well as bilberry cover (*Vaccinium myrtillus*) was recorded for forest stand units, which represent homogenously structured patches with a mean size of 3.40 ha (min: 0.20, max: 48.20). The variable "visual protection" in summer and winter was recorded in a location where understory conditions were considered representative for the respective forest stand. Using a "chessboard" (100x100cm) with a black and white grid (i.e. 100 10 x10cm squares), placed upright at a distance of 30 m in all four cardinal directions from the observer, the amount of visual protection was then derived from the number of squares that were hidden by the vegetation. Covering an area of 10% of the average stand size, this measurement provides a rough estimation of the possibility for red deer to hide. As vegetation mapping was done in summer, protection in winter was estimated based on the understory type and density, i.e. subtracting the cover provided by broadleaved trees and bushes.

Human infrastructure (roads, settlements) was accessed from the Official Topographic and Cartographic Information System of Germany (ATKIS, www.atkis.de). In addition, we mapped tourism infrastructure in summer (hiking trails, mountain bike routes) and winter (cross country skiing and snowshoe trails, winter hiking paths), the location of the red-deer feeding stations in winter and the different zones of the zoning scheme. For all predictors we prepared raster maps with a 10 x 10 m resolution. To account for potential radio tracking errors, we performed a circular moving window analysis with a radius of 40m (corresponding to the maximum location error), assigning to the focal cell the mean value or, in case of categorical variables, the category that was most frequently present within the window. Variable maps were processed in ArcGIS 9.3 (ESRI 2009).

Table 2: Predictor variables included in the models

Predictor type	**Variable Name**	**Description (unit)**	**Min-Max**	**Type**
Landscape and topography	DHM	Altitude (m a.s.l.)	762 - 1314	continuous
	SLOPE	Slope (degree)	0 - 44	continuous
	NORTHING	Northness (cosine aspect)	-1 - 1	continuous
	EASTING	Eastness (sine aspect)	-1 - 1	continuous
	WATER	Proximity to lakes, rivers and creeks (km)	0.005 - 0.704	continuous
	GREENL	Proximity to greenland (i.e. meadows/ grassland) (km)	0 - 1.343	continuous
	FOREST_250	Forest cover within a 250m radius (%)	0 - 100	continuous
Vegetation	CANOPY_TYPE	Type of canopy trees CAN_NO = No forest (reference category) CAN_CON = Coniferous >95% CAN_CONMIX = Conifer dominated mixed (conifers >50%) CAN_DEC_MIX = Deciduous dominated mixed (deciduous >50%) CAN_DEC = Deciduous >95%		categorical
	CANOPY_COV	Canopy cover (%)	0 - 100	continuous
	SUCCESSION	Successional stage SUC_OPEN = Open (reference category) SUC_REGTHICK= Regeneration & Thicket SUC_POLE = Pole stage SUC_TREE = Tree stage SUC_OLD = Old forest		categorical
	UNDER_TYPE	Type of understory trees UNDER_NON = No understorey (reference category) UNDER_CON = Coniferous >95% UNDER_DEC = Deciduous >95% UNDER_DECMIX = Deciduous dominated mixed (deciduous >50%) UNDER_CONMIX = Conifer dominated mixed (conifers >50%)		categorical
	UNDER_COV	Cover of understory (%)	0 - 90	continuous
	BILBERRY	Bilberry cover (%)	0 - 90	continuous
	HERB_GRAS	Cover of herbs and grass (%)	0 - 100	continuous
	PROTECTION_S/W	Protection from visibility in summer/winter (%)	0 - 75	continuous
Human presence	TOURI_S/W	Proximity to summer tourism infrastructure in summer/winter (km)	S: 0 - 0.752 W: 0 - 1.824	continuous
	TOURI_DENS_S/W	Density of summer/winter tourism infrastructure within 250m (m/ha)	S: 0 - 129 W: 0 - 108	continuous
	ROAD	Proximity to roads (km)	0.006 - 2.321	continuous
	SETTLE	Proximity to settlements (km)	0 - 3.105	continuous
	FEED	Proximity to feeding stations (km)	0 - 6.300	continuous
	HUNT	Proximity to hunter hides (km)	0 - 3.918	continuous
	MGT	Different area-types of the red-deer management scheme (Table 1) MGT_BORDER = Border zone (reference category) MGT_CORE = Core area MGT_REFUGE = Refuge area		categorical

Statistical Approach

To analyze habitat use we adopted a 'used versus available' design at two spatial habitat scales, comparing the presence data with two sets of random locations: First, to determine the factors influencing home range selection within the study area (second order habitat selection (Johnson 1980)), the presence locations of each individual were contrasted against the same number of random locations generated throughout the study area. Second, to analyze habitat selection within the home range (third order habitat selection (Johnson 1980)), we generated a second random sample selected from the individuals' seasonal home ranges. Home ranges were calculated for each year and season separately, using the full data set (i.e. all available locations of the individual for the season) and the 100% minimum convex polygon (MCP) method. Habitat use was analyzed using Generalized Linear Mixed Effects Models (GLMM, R-package: lme4 (Bates et al. 2014)) with a logit link and binomial error structure, including the individual as a random factor. First, starting with the initial set of variables (Table 2), we identified pairs of strongly correlated variables (Spearmans' $R_S > |0.5|$), discarding the variable that explained less within a univariate model. Multivariate models with all possible combinations of the remaining variables were then fitted using the dredge function (R-package MuMin, (Bartoń 2013)) in order to find the most parsimonious model according to Akaikes Information Criterion (AIC) (Burnham & Anderson 1998). Model averaging was applied if several "best models" did not differ significantly (Δ AIC <2). For each season we fitted three models describing (1) home range selection within the study area (day and night pooled), as well as habitat use within the home range during (2) day and (3) night. In addition, we tested for differences in habitat use between day and night, identifying the environmental predictors that significantly discriminated the individual's locations taken at the two different time periods. To assess multicollinearity in the final models (i. e. whether linear combinations of the fixed effects were correlated), we calculated the variance inflation factor (VIF) for all models, using the corvif function in the R-package AED (Zuur et al. 2009). For continuous variables we accepted an VIF of less than 10 (Marquaridt 1970), for factor variables the VIF was corrected for the number of degrees of freedom (VIF^(1/2df)) (Zuur et al. 2009). The importance of individual variables was evaluated by fitting the final models while leaving out the respective variable. The change in AIC (ΔAIC) compared to the final model was then used as an indicator of the variable's relative contribution to the final model. In addition, for every independent variable we calculated the odds-ratio and its 95% confidence interval using the Wald chi-square test (Fox 1997) to approximate its effect on the dependent variable (Fox 1997). Model performance was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC, R-package: AICcmodavg (Mazerolle 2014)). All statistical analyses were performed using the software R (R Version 2.15.1, www.rproject.org).

Results

Home range location

According to the classification of Hosmer and Lemeshow (Hosmer & Lemeshow 2000) our models performed well in explaining home range selection within the study area during both summer (AUC: 0.766 ± 0.003) and winter (0.919 ± 0.002). Home range selection was explained by variables describing landscape, vegetation structure and human presence (Table 3). According to the ΔAIC (Table 3), the zonation scheme was the strongest predictor for home range selection in both seasons: in summer the refuge areas were selected over the core area and the border zone, which served as a reference category (Table 3a), whereas winter home range selection was mainly located close to the feeding stations. The effect of human infrastructure differed between seasons: whereas in summer human settlements were avoided, winter home ranges were selected in closer vicinity to settlements and roads than expected from a random selection. The proximity and density of recreation infrastructure had no significant effect on home range selection. During the summer months deer home ranges were located in forest areas with a high proportion of openings and thickets rich in herbs and grasses whereas in winter older stands (pole and tree stage, and old forest) and south-eastern facing slopes were selected (cf. Table 3 for home range selection in the study area and S3 to S7 Tables for further information regarding the model selection, VIF and odds ratios).

Table 3: Variables determining the home range selection of red deer within the study area in (a) summer and (b) winter. For all variables positive estimates indicate preference, negative estimates indicate avoidance. For predictor names see Table 2. Significance levels are indicated with: * p ≤ 0.05, ** p ≤ 0.01, and *** p ≤ 0.001. Relative variable importance is indicated by ΔAIC, which is the difference in AIC of a model discarding the respective variable compared to the full model.

		(a) Summer (AUC 0.766 +- 0.003)				(b) Winter (AUC 0.919 +- 0.002)			
		SD (Individual): 0.041		AIC: 24334		SD (Individual): 0.059		AIC: 8488	
Type	ıriable	Estimate	SE	Sign.	ΔAIC	Estimate	SE	Sign	ΔAIC
	INTERCEPT	-1.844	0.103	***		2.977	0.185	***	
Vegetation	SUC_REGTHICK	0.449	0.277		71	2.209	0.245	***	227
	SUC_POLE	-0.083	0.270			1.026	0.210	***	
	SUC_TREE	0.031	0.268			1.771	0.190	***	
	SUC_OLD	-0.200	0.272			1.898	0.198	***	
	PROTECT_S/W	<0.001	0.001		2	-0.010	0.002	***	31
	BILBERRY	-0.008	0.002	***	23				
	CAN_CON	-0.981	0.268	***	45				
	CAN_DEC	0.404	0.413						
	CAN_CONMIX	-0.874	0.269	**					
	CAN_DECMIX	-0.761	0.276	*					
	HERB_GRAS	0.018	0.001	***	498				
	CANOPY_COVER					-0.011	0.003	***	16
Landscape	WATER	1.146	0.171	***	48	-0.856	0.286	***	9
	FOREST250	0.536	0.106	***	32				
	SLOPE	-0.004	0.003		4				
	NORTHING					-0.270	0.046	***	36
	EASTING					-1.054	0.054	***	376
Human	MGT_CORE	1.930	0.064	***	1538	-0.498	0.090	***	133
	MGT_REFUGE	2.723	0.077	***		0.529	0.125	*	
	FEED					2.055	0.057	***	2098
	HUNT	1.762	0.051	***	1527	1.896	0.092	***	544
	SETTLE	-0.347	0.028	***	137	0.368	0.068	***	67
	TOURI_S/W	0.147	0.132		2				
	ROAD					0.684	0.102	***	31

Habitat use within the home range

Habitat use within the home range during summer and winter was explained by vegetation, land use and human presence (Table 4). The zoning scheme also ranked among the most important predictors, with refuges and core areas being selected over the border zones in summer (Table 4, S2 Table, available online in Supporting Information). In winter red deer aggregated at the feeding sites during the day, whereas the refuges were predominantly selected during the night (Table 4). However, habitat use differed significantly between the day and nighttime, particularly with regard to the variables related to human presence (Fig 2, Tables 4 and 5). Both in summer and winter recreation trails were avoided during day, whereas a positive association could be found during night (Table 4). In addition, red deer selected areas with shallower slopes and in greater vicinity to water during night. In the summer season, red deer visited bilberry patches during night that were avoided during daytime, whereas in the winter season, they stayed more frequently in the vicinity of roads during nights compared to daytime (Table 5).

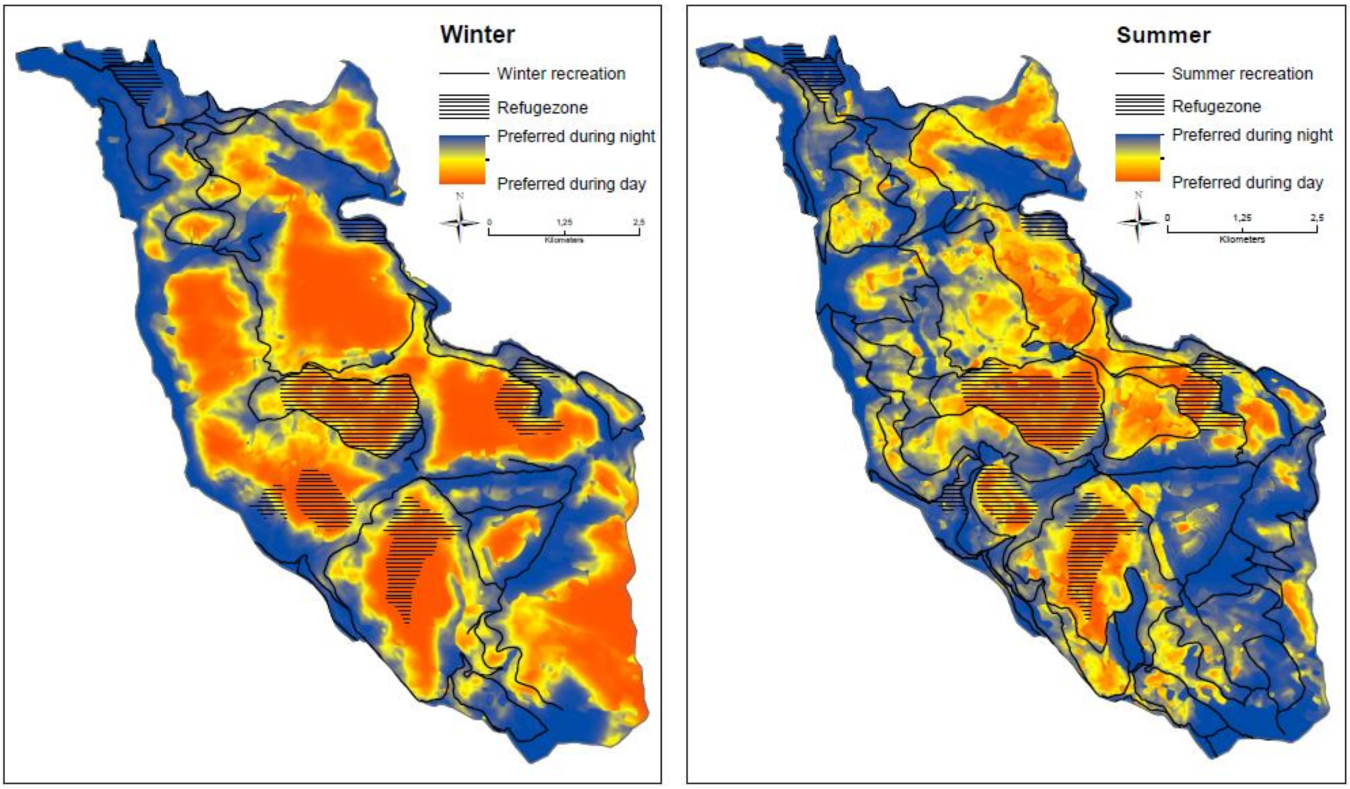

Figure 2: Differences in red deer habitat use between day and night during the winter (left) and summer (right). Red areas indicate zones that are more often used during daytime, while blue areas are more frequented during nighttime. Yellow areas are similarly used during day or night. The hatched areas indicate the location of the refuge zones. The probability of red deer presence for both seasons and times of the day are shown in S1 Fig.

Table 4: Habitat use within the home range in summer and winter, day and night. Models explaining habitat use within the home range in summer (upper panel) and winter (lower panel) during daytime (left) and nighttime (right). For all variables positive estimates indicate preference, negative estimates indicate relative avoidance. For the predictors marked with bold letters the differences between daytime and nighttime habitat use were significant (see Table 5). For predictor names see Table 2. Significance levels are indicated with: * p ≤ 0.05, ** p ≤ 0.01, and *** p ≤ 0.001.

Summer	Day (AUC: 0.684 +- 0.005) SD (Individual): 0.329			AIC: 12040		Night (AUC: 0.810 +- 0.005) SD (Individual): 0.450		AIC: 7317	
Type	Variable	Estimate	SE	Sign.	ΔAIC	Estimate	SE	Sign.	ΔAIC
	INTERCEPT	-4.675	0.226	***		2.190	0.188	***	
Vegetation	CANOPY_COVER	-0.013	0.002	***	37	-0.036	0.002	***	243
	SUC_REGTHICK	**2.412**	**0.224**	***	**352**	**0.498**	**0.466**		**19**
	SUC_POLE	**1.351**	**0.204**	***		**0.743**	**0.437**	*	
	SUC_TREE	**0.653**	**0.199**	**		**0.732**	**0.433**	.	
	SUC_OLD	**0.982**	**0.202**	***		**0.203**	**0.436**		
	BILBERRY	**-0.025**	**0.003**	***	**59**	**0.022**	**0.003**	***	**48**
	PROTECT_S	-0.004	0.001	**	6				
	UNDER_CON	0.731	0.100	***	143				
	UNDER_DEC	1.850	0.245	***					
	UNDER_CONMIX	0.674	0.079	***					
	UNDER_DECMIX	0.148	0.088	.					
	CAN_CON					**-0.760**	**0.433**	.	**26**
	CAN_DEC					**0.405**	**0.617**		
	CAN_CONMIX					**-0.678**	**0.434**		
	CAN_DECMIX					**-1.330**	**0.468**	**	
Landscape	**WATER**	**-2.487**	**0.257**	***	**160**	**1.175**	**0.361**	***	**11**
	EASTING	**0.083**	**0.042**	*	**2**	**-0.409**	**0.055**	***	**68**
	SLOPE	**0.064**	**0.004**	***	**213**	**-0.042**	**0.006**	***	**51**
	NORTHING	-0.279	0.035	***	60				
	FOREST250	**1.583**	**0.224**	***	**51**				
Human	MGT_CORE	1.282	0.158	***	73	1.371	0.136	***	116
	MGT_REFUGE	1.249	0.165	***		1.739	0.163	***	
	TOURI_S	**-1.616**	**0.189**	***	**157**	**0.865**	**0.242**	*	**5**
	HUNT	**1.159**	**0.118**	***	**172**				
	SETTLE					0.254	0.064	***	33
	ROAD					0.503	0.079	***	27

Winter	Day (AUC: 0.849 +- 0.006) SD (Individual): 0.378			AIC: 4067		Night (AUC: 0.880 +- 0.005) SD (Individual): 0.300		AIC: 3405	
Type	Variable	Estimate	SE	Sign.	ΔAIC	Estimate	SE	Sign.	ΔAIC
	INTERCEPT	0.492	0.350			1.992	0.250	***	
Vegetation	CANOPY_COV	-0.012	0.004	**	8				
	CAN_CON	**3.761**	**0.379**	***	126				
	CAN_DEC	**2.887**	**1.377**	*					
	CAN_CONMIX	**3.410**	**0.387**	***					
	CAN_DECMIX	**3.720**	**0.454**	***					
	SUC_REGTHICK					-1.130	0.357	***	281
	SUC_POLE					-1.173	0.215		
	SUC_TREE					0.950	0.158	***	
	SUC_OLD					1.311	0.219	***	
	PROTECT_W					-0.001	0.004	***	11
Landscape	**NORTHING**	**0.241**	**0.074**	**	**9**	**-0.305**	**0.080**	***	**9**
	EASTING	**-0.231**	**0.081**	**	32	**-0.053**	**0.100**	***	**108**
	SLOPE_MEAN					-0.111	0.010	***	127
	WATER					2.776	0.519	***	14
Human	MGT_CORE	-2.434	0.184	***	287	-0.405	0.163		192
	MGT_REFUGE	-1.478	0.227	***		1.717	0.192	***	
	FEED	1.971	0.118	***	**366**				
	HUNT	1.048	0.247	***	**44**	-0.706	0.213	**	8
	TOURI_W	**-0.634**	**0.222**	**	**6**	**2.879**	**0.291**	***	**81**
	ROAD					**1.993**	**0.178**	***	**131**

Table 5: Differences between diurnal and nocturnal habitat selection within the home range with regard to the relevant environmental predictors selected in the final models (Table 4). For predictor names see Table 2. Significance levels are indicated with: * p ≤ 0.05, ** p ≤ 0.01, and *** p ≤ 0.001.

		Summer (AUC = 0.895 +- 0.007) STD (Individual): 0.967			Winter (AUC: 0.866 +- 0.011) STD (Individual): 0.990		
Type	Variable	Estimate	SE	Sign.	Estimate	SE	Sign.
	INTERCEPT	6.661	0.322	***	6.431	0.448	***
Vegetation	CAN_CON	-1.194	0.448		-1.373	0.310	***
	CAN_DEC	-0.557	0.739		-4.467	2.293	*
	CAN_CONMIX	-1.074	0.447		-1.312	0.322	***
	CAN_DECMIX	-1.826	0.459	*	-3.483	0.615	***
	SUC_REGTHICK	-2.172	0.461	***			
	SUC_POLE	-1.234	0.454	***			
	SUC_TREE	-0.323	0.453	*			
	SUC_OLD	-0.341	0.464	*			
	BILBERRY	0.037	0.003	***			
	FOREST250	-2.207	0.250	***			
	UNDERCOV	-0.011	0.002	***			
Landscape	SLOPE	-0.065	0.005	***	-0.112	0.011	***
	WATER	4.110	0.314	***	10.742	0.651	***
	NORTHING	0.258	0.044	***			
	EASTING	-0.203	0.047	***			
Human	ROAD	0.740	0.068	***	2.015	0.230	***
	TOURI_S/W	1.733	0.222	***	8.290	0.478	***
	HUNT	-1.087	0.139	***	-2.689	0.310	***
	MGT_CORE	-0.269	0.208				
	MGT_REFUGE	0.187	0.220	.			

Discussion

Effects of human presence and outdoor recreation

Our study shows how adjustments of behaviour can result in oppositional patterns of wildlife habitat use at day and nighttime, when areas frequented by recreationists are avoided during the day and preferred during the night. Although it is suggested that animals become habituated to human presence (Picton 1999) and might reduce flight-distances in areas with frequent human-wildlife contact (Stankowich & Blumstein 2005), the deer avoided the areas close to the trails during daytime. Whereas in North America it is a widely known phenomenon that deer habituate to humans and even occur in settlements where they are not hunted (Thompson & Henderson 1998), the deer in our study seem to actively avoid human recreationists. This might indicate that red deer are unable to distinguish recreational users and hunters, and therefore temporally avoid areas with high human use. The diurnal pattern was blurred when pooling day and night locations (S2 Table), which highlights the importance of accounting for temporal differences when analyzing human-wildlife interactions.

Linking spatiotemporal patterns of wildlife habitat use to human presence is an important prerequisite for designing efficient wildlife management concepts, even if reducing disturbance is not the primary management goal as it might be the case in hunted species like the red deer. Previous studies showed that red deer respond to the presence of recreationists by fleeing (Sibbald et al. 2011), moving to denser vegetation areas (Jeppesen 1987), increasing vigilance (Jayakody et al. 2008a) and adjusting their foraging behaviour (Jayakody et al. 2011). Sibbald et al. [41] found an avoidance of hiking trails by red deer, which was stronger during the day with higher visitor numbers.

Since the infra-red counter data (S2 Fig), collected shortly after our study on red deer show a strong diurnal variation of use (i.e. many visitors during day, little or none during night) and no other factor in the area which is spatially linked to recreational trails shows a diurnal pattern, we assume that the avoidance of recreational trails by day is caused by a the presence of recreationists. Sibbald et al. (2011), also showed that red deer flexibly adjust their habitat use to the diurnal variation in human presence. Even though we could not directly link deer behaviour to the intensity of recreation activities on the trails, as visitor counts obtained with photo sensors (S2 Fig) were collected one year after the telemetry data, we assume that the diurnal pattern of recreation activities was similar during the time of our study. However, detailed information on the number of visitors per specific trail and time of the day would be favorable for quantifying the number of visitors that triggers an avoidance reaction in red deer.

Apart from human recreational infrastructure, habitat selection was based on a variety of factors related to forage quality (e.g. bilberry, deciduous trees) and essential resources (e.g. water). The predominant use of these habitat features during night but not during the day indicates that resources attractive to the deer are temporally not accessible due to human disturbance. In our study area this applied to the area along the lake, which is highly frequented by recreationists, as well as to clearings with abundant ground vegetation and bilberry patches which are mainly located in open forest with high visibility. During the day, particularly in summer, the deer was more frequently found in dense forest stands providing cover, i.e. thickets and pole stands (Table 4, 5). This finding supports the suggestions by previous studies (Seiler 2004, Morellet et al. 2007) that human disturbance may contribute to reinforce possible conflicts with forestry: if clearings and open forest near trails are not usable for foraging during the day due to disturbance, the deer may be forced to relocate to dense forest stands with cover where they may cause forest damage by tree browsing and bark stripping as no alternative food is available in these stands.

Zoning scheme

To reduce human-wildlife conflicts, zoning schemes might play an important role for wildlife managers confronted with combining varying interests in human dominated landscapes within central Europe. In our study, both seasonal home range selection within the study area, as well as habitat use within the home range, were closely linked to the zoning scheme: red deer selected the refuge areas over the core and border zone of the management scheme and - as expected - stayed close to the feeding stations in winter. We cannot prove a causal effect of zoning on red deer habitat selection though, as no systematically collected data before the establishment of management zones were available and we cannot exclude that the delineation of zones might have been influenced by pre-existing expert knowledge. It is therefore possible that the deer had already preferred these areas prior to the establishment of the zonation scheme, due to other factors such as traditions or the distribution of forage.

Management implications

The diurnal avoidance of human recreation infrastructure by red deer, both in summer and winter, associated with an increased nocturnal use of temporarily inaccessible resources has several implications for the management of natural areas. As the avoidance of trails during the daytime renders some areas and resources inaccessible to the deer, it is important that the animals are not additionally disturbed during the night. Nocturnal sport events (i.e. torch-lit walks, nocturnal orienteering) should thus be strictly regulated in areas with disturbance-sensitive wildlife. In addition, patches of open forest, clearings and meadows, providing alternative food sources should be created within sufficient distance and with visual protection from hiking trails. Wildlife refuges, from which recreation is banned provide undisturbed areas during both, day and night, and are likely to benefit also other disturbance-sensitive wildlife.

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Chapter II: Seasonal variation

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

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Abstract

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

Introduction

With the growing numbers of outdoor recreationists, their impact on the environment is likely to be increasing (Rankin et al. 2015, Tolvanen and Kangas 2016). Wildlife responds to the presence of humans in their habitats (Beale and Monaghan 2004), with reactions varying from physiological responses such as increased heart rate (Weimerskirch et al. 2002) or increased stress hormone levels (Walker et al. 2006, Formenti et al. 2015) to behavioral reactions which include fleeing or flushing (Keller 1995, Miller et al. 2001, Thiel et al. 2007, Sönnichsen et al. 2013) and behavioral adaptations such as changes in vigilance behavior (Fernández-Juricic and Telleria 2000, Beale and Monaghan 2004, Jayakody et al. 2008). Recreation activities have been shown to reduce woodland bird densities (van der Zande et al. 1984), bird community composition and nest predation (Miller et al. 1998) or breeding success (Anderson and Keith 1980, Ahlund and Götmark 1989). Effects of this so called “anthropogenic disturbance” - in this context defined as any form of human presence that triggers one of the above responses in wildlife - varies widely between species (Ficetola et al. 2007), and can differ between sexes in the same species (Baydack and Hein 1987, Moss et al. 2014). Furthermore they strongly depend on the exact type of human activity or even the way humans behave during the same type of activity (Fernández-Juricic et al. 2005). A behavioral reaction (i.e. fleeing, flushing) will bear direct energetic costs (Tablado and Jenni 2015), whereas repeated disturbance might lead to reduced use or abandonment of otherwise suitable habitats (Taylor and Knight 2003, Buckley 2011, Ciuti et al. 2012, Immitzer et al. 2014, Tablado and Jenni 2015) which would effectively result in habitat loss or deterioration. Where these reactions clearly pertain to individuals, the effects on wildlife populations have are only rarely quantified (Gill et al. 2001, Liley and Sutherland 2007) which is mainly linked to the scale at which the disturbance takes place (Gill 2007). Although avoidance of disturbed habitat seems one of the most evident reactions of animals towards human presence, it is difficult to assess the spatial extent of effective habitat reduction at population level, as the scale at which disturbance effects operate is often unknown, and may deviate from the scale at which population responses are considered. Especially in geographically isolated populations, where restricted habitat availability may hinder a large-scale relocation to undisturbed areas, effective habitat reduction may be underestimated or even remain unnoticed, when animals stay in disturbed areas and only show local-scale responses.

Anthropogenic disturbance has long been recognized as a problem for capercaillie (*Tetrao urogallus*) conservation in Central Europe (Storch 2007), where populations are spatially restricted to mountain habitats (Segelbacher et al. 2003). As these regions are at the same time hotspots for outdoor recreation, potential conflicts between human recreation and capercaillie conservation have become a major focus in several management plans (Hennig and Künzl 2011, Braunisch and Suchant 2013). Various studies showed the sensitivity of capercaillie towards human presence: Although Brennot (1996) and Moss et al. (2014) did not find a significant effect of anthropogenic disturbance on capercaillie reproduction, high intensities of winter recreation have been associated with increased flushing distances (Thiel et al. 2007) and elevated stress hormone levels (Thiel et al. 2008, Thiel et al. 2011).

Capercaillie have been shown to avoid the vicinity of hiking trails in summer (Moss et al. 2014) and roosting trees close to woodland tracks in winter (Summers et al. 2007), while an overall reduction of local capercaillie densities was recorded in areas highly frequented by recreational activities (Rösner et al. 2013). These studies show that capercaillie are influenced by anthropogenic disturbance, however at which scale this affects individual habitat selection, and how these effects translate into effective habitat reduction at the population level, is still unclear (Storch 2013).

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

Methods & Materials

Study area

The study was conducted in the Black Forest, a lower mountain range, south western Germany of 7000km2 in size. The study area was located around the highest mountain “Feldberg” with altitudes ranging between 700 and 1493 m.a.s.l. (Fig. 1) mainly consisting of forest, intermixed with open areas used for cattle grazing in summer and ski pistes during winter. We focused on 8284 hectares of managed forests, dominated by Norway spruce *Picea abies* (49%), European silver fir *Abies alba* (19%) and common beech *Fagus sylvatica* (22%; Suchant et al. 2003). The Feldberg and the surrounding mountains attract large numbers of recreationists, both during winter and summer. In winter there are several ski pistes, cross-country skiing trails, snowshoe trails and designated winter hiking trails; in addition, various off-trail activities (i.e. snowshoeing, geo-caching, collecting berries and mushrooms) are performed in the area (Coppes and Braunisch 2013). During summer, the area offers a dense network of hiking and mountain bike trails. Over the past decade, visitor numbers have been steadily increasing with over 35% more visitors in 2015 compared to 2004 (Statistisches Landesamt 2016).

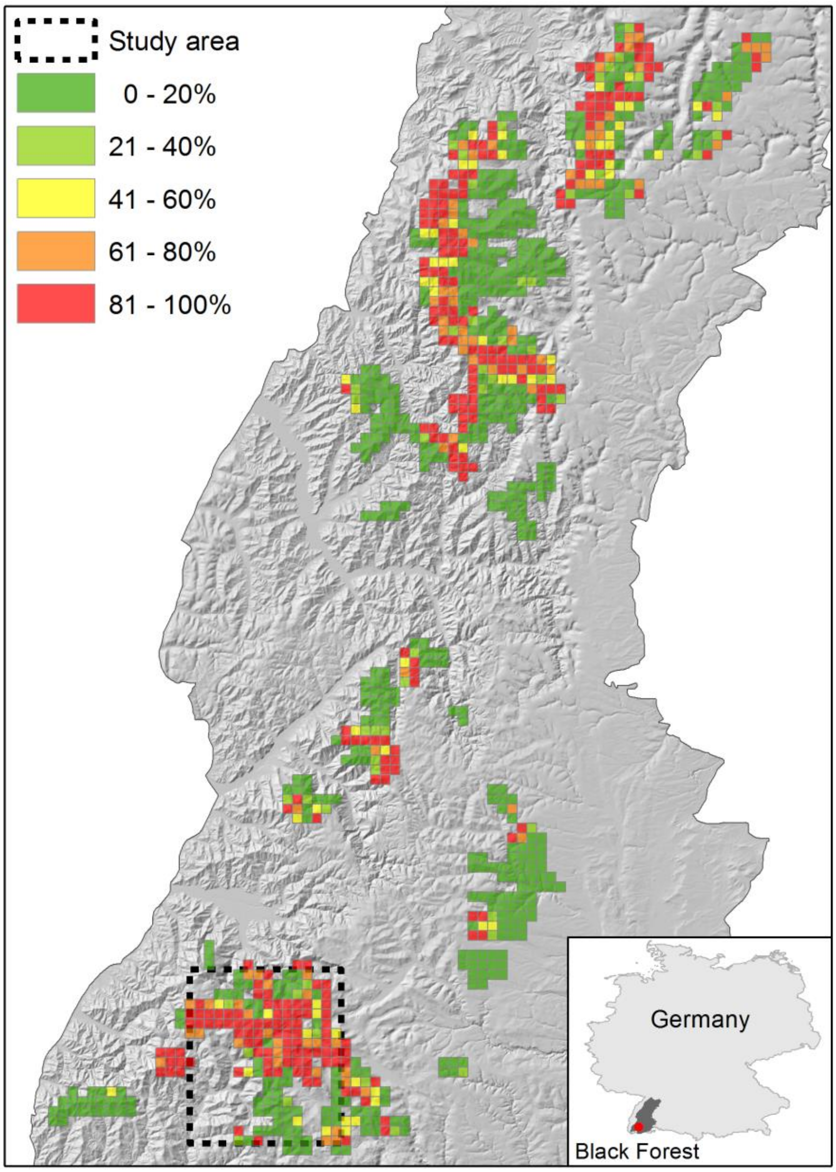

Figure 1: Capercaillie distribution in the Black Forest, southwestern Germany (shown are all 1 km^2 squares with capercaillie presence). Colors indicate the proportion of habitat within the respective square that is influenced by winter recreation (i.e. within 320 m from winter recreation infrastructure).

Model species

We chose the western capercaillie as a model species as it has been shown to be highly sensitive towards human disturbance, while its spatial distribution shows a high degree of co-occurrence with outdoor recreation (Thiel et al. 2008, Storch 2007). The species occurs over a wide geographical range across Northern Eurasia and is thus not threatened globally (BirdLife-International 2012), but is red-listed in all Central European countries (Storch et al. 2007) due to its small, declining and isolated populations (Segelbacher et al. 2003, Storch 2007, Coppes et al. 2015). The Black Forest capercaillie population is the largest Central European population outside the Alps, but is isolated from other populations in Europe (Segelbacher et al. 2003) and highly fragmented (Braunisch et al. 2010, Coppes et al. 2016).

Based on annual counts at the leks, the population is estimated at about 400 to 500 individuals (Coppes et al. 2016) which roughly corresponds to the estimated minimum viable population size as calculated by Grimm & Storch (2000). Over the last 30 years capercaillie numbers have rapidly declined by about 65% (Coppes et al. 2016), which resulted in being red listed as "endangered" in the state of Baden-Württemberg (Hölzinger et al. 2007).

Since 1988, the capercaillie distribution in the Black Forest has been monitored. Every five years, the minimum area of species distribution is delineated, based on a collation of all available direct and indirect evidence of capercaillie presence provided by foresters, hunters, ornithologists, conservation volunteers and research personnel. Forest patches are classified as ''inhabited'' when at least three capercaillie records occurring with a maximum distance of 1000 m from another have been collected within the preceding five year period, and are delineated by the minimum polygon encompassing these records (for details see: Braunisch and Suchant 2006, Coppes et al. 2016) . The Black Forest capercaillie population is currently distributed across 45666 ha (2013), forming four main subpopulation clusters (Fig. 1). The telemetry study was conducted in the southern Black Forest subpopulation (Coppes et al. 2016).

Capercaillie data

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

We evaluated locations taken during two predefined time periods, summer (June to September) and winter (December to March). The seasons were defined so as to exclude shifts in habitat use related to the mating season (April-May) where individuals accumulate at the leks, and to exclude the peaks of spring and autumn dispersal (Moss et al. 2006). The winter season encompassed only days with a continuous snow layer, to assure that winter recreation infrastructure was usable. Data of an individual and season were only included in the analysis if at least 20 locations in the respective season were available (Table 2).

Environmental variables

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

Table1: Predictor variables of the categories landscape and topography, vegetation structure and human presence retained in the models (Table 3 and 4).

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

To determine the extent of habitat deterioration through outdoor recreation for the entire distribution area of the Black Forest capercaillie population, area-wide data on designated hiking and mountain bike trails and official winter recreation (i.e. ski-lifts and cross-country skiing trails) were adopted from the Tourism and Recreation Information System TFIS Baden-Württemberg, Germany (www.lgl-bw.de). Since no official, area-wide source for snowshoe trails, back country skiing tracks or designated winter hiking trails was available, and since many of the summer hiking trails are not officially open or accessible during winter, we complemented our dataset with data provided by specific user groups on the internet. Websites (www.outdooractive.de, www.gpsies.com, www.bergfex.de) were searched for tracks of snowshoe trails, back-country skiing tours or winter hiking trails. On these websites, both private persons as well as official municipal touristic organizations publish tracks of tours which they advise to use for winter recreation. GPS tracks (.kml files) were downloaded and transferred to shape files using ArcGIS 10.3 (ESRI 2014). This resulted in an area-wide dataset of ascertained outdoor recreation infrastructure for both seasons.

Statistical analysis

Habitat selection

For each bird seasonal “homeranges” were calculated, which we define here as the 100% minimum convex polygon (MCP) encompassing the telemetry locations. To assess habitat selection at two spatial habitat scales a used versus non-used design was applied, comparing the presence data with two sets of pseudo-absence locations, in the following termed as “absence”. To model home range selection within the study area (second order habitat selection, Johnson 1980) , the presence locations of each individual were contrasted against the same number of random locations generated outside of the home range of each respective individual, excluding a 100 meter buffer (twice the average telemetry error to avoid overlaps between the surroundings of presence and pseudo-absence points), but within a maximum distance of 3.9 km (average maximum distance between locations for tagged capercaillie in this study) to ensure that all locations could potentially be reached by the respective individual. To analyze habitat use within the home range (third order habitat selection, Johnson 1980), we generated a second set of absence locations within the MCP home range, again with a minimum distance of 100 meters (twice the average telemetry error) to existing telemetry locations (Figure S1).

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

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

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

Distance thresholds

To assess whether there were distance-thresholds up to which the presence of outdoor recreation infrastructure significantly reduced presence probability, conditional inference trees were calculated (CIT, R-package “party” (Hothorn et al. 2011)). This method uses recursive partitioning to select significant predictor variables in an hierarchical way and to identify the threshold that best splits the dataset into predicted presence and absence (Hothorn et al. 2006). To account for multiple testing a Bonferroni correction was applied. The 95% confidence interval (CI) of each threshold value was determined, using bootstrapping (1000 replicates). Conditional inference trees were run using a minimum split criterion (minsplit) of 50. In a first step, univariate CIT’s were applied to the recreation infrastructure variables. In a second step, we tested whether the avoidance of recreation infrastructure would be modulated by the vegetation structure along the trails and the associated possibility to hide, which might offer a possibility to mitigate effective habitat reduction by forest management. Therefore, a multivariate CIT was run including the significant outdoor recreation infrastructure variable combined with three variables that could offer visual protection, ground vegetation height, ground vegetation cover and shrub cover. All statistical analyses were performed using the software R (3.2.3 R development core team 2015).

Habitat deterioration at the population level

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

Results

Capercaillie data

Using the predefined filtering criteria, data of 12 individuals (6 females, 6 males) with a total of 1024 locations were included in the analysis. Due to the loss of birds over time, more data for the winter (11 birds, 881 locations) compared to the summer season (7 birds, 213 locations) was available (Table 2). On average there were 30 (range: 23-37) locations per bird in summer and 62 (range: 25-99) locations in winter. In summer, the average MCP-homerange sizes of males (N=3) was with 581 hectares (SD: ±355) more than twice as large as those of females (N=4) with 207 hectares (±32 ha). During winter the birds' homerange size decreased, with males (N=6) using on average an area of 182 hectares (+-48 ha) whereas females (N=7) had an average MCP size of 86 ha (± 30). MCP-size was significantly correlated with sex (linear model, p=0.0035) and relocation number in winter (p=0.0007) but not in summer. Only one female (ID 59 in summer 2005, Table 2) was found on a nest, for all other females no reproduction could be confirmed, although nest losses in an early stage of breeding cannot be excluded. No significant differences in habitat use between male and female could be determined (Table S1), so the data of both sexes were pooled for following analyses.

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

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

Habitat selection

Homerange selection within study area

Homerange selection within the study area was well explained by the models, both for summer (AUC=0.807 ±0.021) and winter (AUC=0.885 ±0.009) (Table 3a and 4a). In summer it was mainly determined by landscape and topography variables, with homeranges mainly located in high altitudes (Table 3) in forest core areas, i.e. apart from outer forest edges and roads. Stands with extensive shrub cover and more than 2 horizontal layers were significantly avoided (Table 3a), while other vegetation variables (stand type, canopy cover, canopy gaps and cover of grasses) played no role. In winter, homeranges were placed in large distance to parking places, preferably within the forest interior i.e. within a large distance to the outer forest edges (Table 4a). Capercaillie avoided steep slopes and stands with high shrub cover, while preferring areas with cold winter temperatures (i.e. high altitudes) and stands with an intermediate canopy cover. Interestingly, we found a negative correlation with distance to winter recreation, indicating that capercaillie winter homeranges encompassed a higher density of recreation infrastructure than present in the surrounding landscape.

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

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

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

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

Habitat selection within homerange

Habitat selection within the homeranges was explained with a slightly lower accuracy (summer: AUC=0.786 ±0.022; winter: 0.754 ±0.012, Table 3b and 4b). In summer habitat selection was mainly determined by vegetation structure, as the birds preferred stands with beech intermixed with conifer trees (beech-mix), little understory and a high ground vegetation cover. Also within the homerange, higher altitudes were preferred and outer forest edges avoided (Table 3b). Moreover, used locations were recorded in a significantly greater distance to restaurants and mountain bike trails than the non-used locations, whereas no difference was found for hiking trails. In winter, habitat selection was mainly explained by the distance to winter recreation and distance to parking places, which were strongly avoided (Table 3b). During winter capercaillie, preferably used gentle slopes and stands with intermediate shrub cover, high cover of bilberry and grasses, and a high proportion of softwood trees providing food resources. Projecting the predictions to the study area illustrates the relative avoidance of “human presence” variables, especially recreation infrastructure, in both seasons (Fig.2).

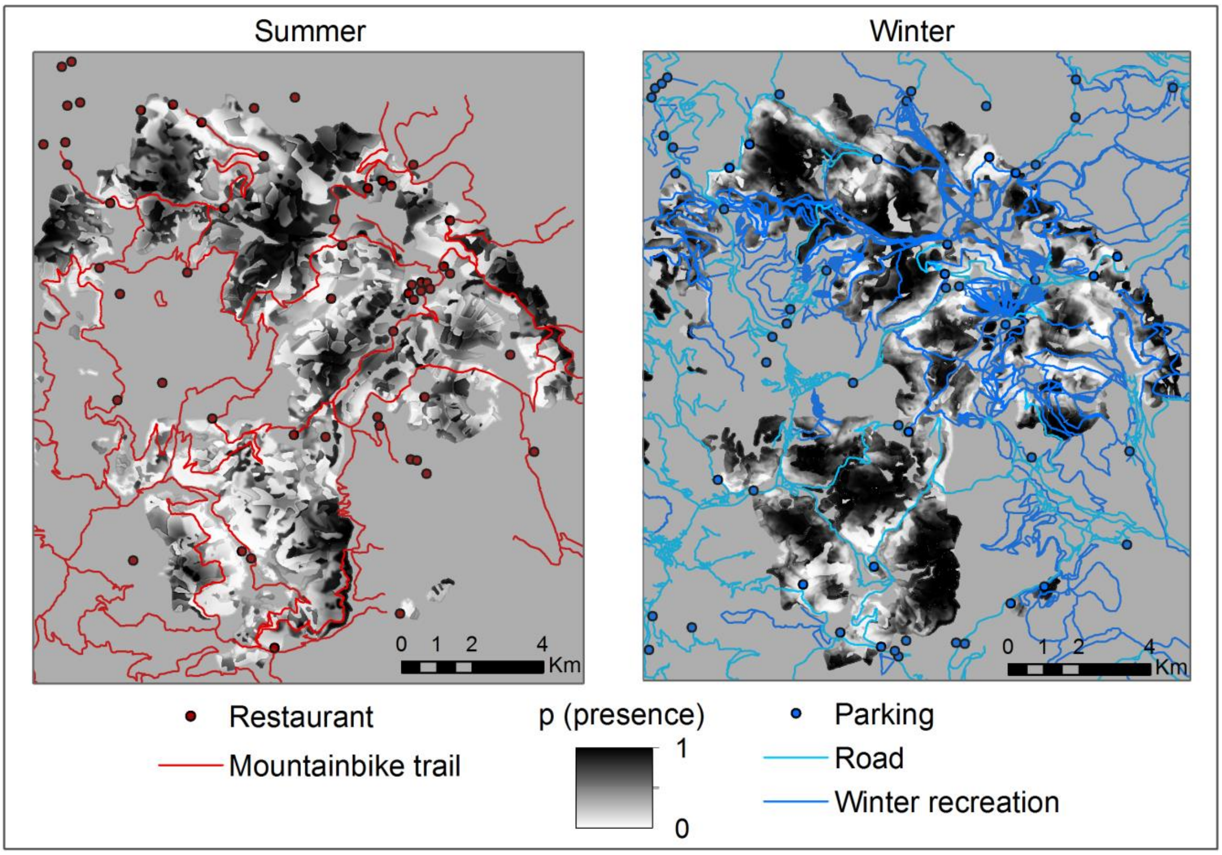

Figure 2: Predicted probability of capercaillie presence in summer (left) and winter (right), in relation to the 'human presence'-variables (Table 1) significantly affecting habitat selection in the respective season (Table 3b and 4b).

Effect of relocation number and MCP size

The winter models recalculated with the reduced, subsampled data set, showed similar results compared to the final models based on the complete data set, regarding both, homerange selection in the study area and habitat selection within the homerange (Table S2). Due to the reduced sample size, some vegetation variables were no longer significant in the reduced model, but showed a similar trend. However, all variables related to recreation infrastructure and human presence remained significant in both models. Since relocation numbers per bird in summer were generally small, the variation between individuals was low and no correlation with MCP size was found, no additional test was performed for the summer model.

Distance thresholds to recreation infrastructure

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

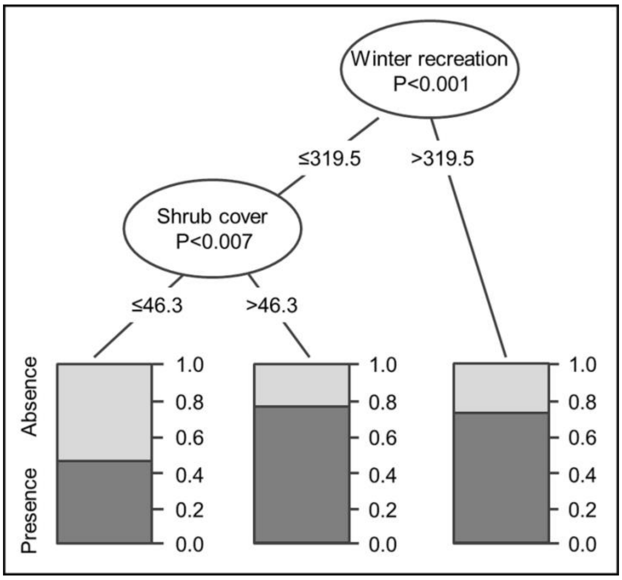

Figure 3: Multivariate conditional inference tree (minsplit = 50) showing how the relative probability of capercaillie presence within and beyond the critical distance to winter recreation infrastructure is modulated by the presence of visual cover (i.e. shrub cover). Habitat variables and the significance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

Habitat deterioration at the population level

The area affected by winter recreation (skiing pistes, cross-country skiing, winter hiking trails, snowshoe trails and back-country skiing) ranged between 3764 ha (i.e. 8.2% of total capercaillie distribution area) when applying the lower 95% CI of the threshold (35.8 m), and 18422 ha (i.e. 40.3% of total capercaillie distribution) when using its average (319.5 m). The area located within the critical distances to mountain bike trails (i.e. lower CI: 60m, mean: 144.7m) ranged between 3923 ha (8.6%) and 8934 ha (19.7%) of the total capercaillie distribution (Supplementary material Table S1). The proportion of habitat influenced by recreation infrastructure was not equally distributed over the Black Forest but accumulated in the higher altitudes (Fig. 1, S1).

Discussion

Effects of human recreation

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

Distance thresholds

Previous studies also found significant avoidance of recreational trails by capercaillie with distance-thresholds ranging from 73 meter (Summers et al. 2007) up to 125 meters (Moss et al. 2014). The threshold values we determined were slightly higher, but in a similar order of magnitude, with mountain bike trails being avoided up to an average distance of 145 m and winter recreation infrastructure up to 320 m. This similarity – despite the studies were performed in different areas using different study methods - indicates that the results might apply to a wide geographical range for capercaillie. However, both recreation intensity (number of people using a trail) as well as the recreation type (biking, skiing, hiking, snowshoeing) is likely to affect the reaction of wildlife (Fernández-Juricic et al. 2005, Moss et al. 2014). The exact (spatial and temporal) use of all trails or infrastructures was unknown in our study which might explain the large confidence intervals we found, especially in summer. Under some conditions, e.g. in times of low recreation intensity, some trails might even attract birds by providing the possibility for gastrolith intake, dusting baths or to dry out after rain. On the other hand, people or dogs leaving the trails might result in a much larger "disturbance band" than given by the physical width of the trails (Moss et al 2014). Moreover, the statistical method for deriving thresholds might explain differences in results. Conditional inference trees do not allow accounting for a clustered data structure, i.e. for variance between individuals, however, they are explicitly designed to find the optimal cut-off value that best separates presence and absence, instead of arbitrarily selecting the threshold at a presence-probability of 0.5.

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

Anthropogenic disturbance versus habitat quality

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

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

Our sample size was limited, with regards to both, the number of tagged birds and the number of relocations per bird, due to the inherent difficulties of using VHF telemetry with rare species. The fact that the MCP size still increased with the number of relocations suggests that our MCP did not encompass the full seasonal homerange of several of our individuals but rather represented a (core) part of it. Nevertheless, even when further reducing the sample size by subsampling a similar, minimum number of presence locations for each individual, and considering only absence location within the correspondingly smaller MCP, effects of human infrastructure remained significant (Table S2) while most of the other habitat variables, with only a few exceptions, showed a similar trend. We therefore assume that we might still underestimate the impact of human recreation on capercaillie.

Effective habitat reduction at population level

When extrapolating our results to the whole expanse of the Black Forest population, we found that between 8% and 40% of the current distribution area is influenced by recreation infrastructure in winter and between 8% and 20% in summer. This calculation only represents a rough approximation, as neither modulations by vegetation conditions, nor the actual intensity of use was taken into account. Moreover, we did not consider effects of hiking trails although such effects were found by other studies (Summers et al. 2007, Moss et al. 2014). Finally, since our extrapolation also does not include off-trail activities (e.g. geocaching and other off-trail activities, see Coppes and Braunisch 2013), and since the affected area was only calculated using the average and lower CI of the distance threshold, our estimate is likely to underestimate the spatial extent of human recreation effects on the Black Forest capercaillie population. Even though our area-estimates do not reflect total habitat loss but habitat deterioration indicated by a significant reduction in presence probability, and although these effects could not yet be linked to fitness consequences, such as reduced reproduction (Brenot et al. 1996, Moss et al. 2014) or survival which would be necessary to quantify effects on population level (Gill et al. 2001), we show the immense scale at which human recreation effects may operate. We therefore assume that this source of disturbance is substantially contributing to the dramatic decline in capercaillie populations recorded all across the Central European mountain populations in the past decades (Coppes et al. 2016). Our study also reveals that the conflict between wildlife conservation and a socioeconomically important factor, namely nature based recreation, is particularly reinforced when both, wildlife populations and outdoor activities are geographically and topographically restricted and co-occurrence at the population scale must not necessarily indicate the species' insensitivity. We therefore support the postulation that future studies investigating the effects of anthropogenic disturbance on wildlife should specifically address effects at population level instead of merely focusing on individuals (Storch 2013). Assessing and quantifying fitness consequences (e.g. on reproductive output or survival) will be key aspects in this context, and might even reveal hidden impacts even in situations of apparent habituation. Finally it will be crucial to elucidate the effectiveness of mitigation measures. However, the call for more research should not hinder active management to mitigate effects of anthropogenic disturbance on wildlife.

Management recommendations

Given the spatial extent of impact, appropriate management measures are indispensable to avoid or at least mitigate negative effects of human recreation. Particularly in key habitats with a dense recreation infrastructure network, the construction of new trails or recreational activities should be avoided and activities concentrated on existing trails. Furthermore a network of wildlife refuges, in which recreational activities are banned, should be established (Braunisch et al. 2011), which will likely benefit not only capercaillie but also a wide array of other species (Anderson 1995, Whitfield et al. 2008). To ensure such refuges are accepted by the public, tourist organizations should be integrated in the planning process from an early stage and recreationists should be informed how their activities affect wildlife (Marion and Reid 2007). Given the large distances up to which effects were recognizable, refuges with at least 800m diameter would be required to fully eliminate negative effects (this study, Moss et al 2014). Yet, our results also indicate that forest structures can reduce these critical distances. In areas with existing recreational infrastructure, we therefore advise forest managers to keep a strip of dense forest with a pronounced shrub layer along the trails, which can reduce both negative effects on capercaillie habitat use in winter, as well as the number of people leaving the trail for off-trail activities (Coppes and Braunisch 2013). In regions highly frequented by outdoor recreation, we strongly recommend that habitat restoration measures, i.e. the creation or maintaining of structurally diverse, open forest habitat with canopy gaps, should generally take place in sufficient distance or with sufficient visual protection from the trails. Finally, with spatially explicit predictions (Fig. 2) optimal locations for wildlife refuges, i.e. suitable forest patches in low-disturbed areas, can be determined. Given the geographic isolation of the Central European mountain populations (Segelbacher et al. 2003) the topo-climatic restriction of potential habitat (Braunisch & Suchant 2007) and the close interplay between vegetation-structure related habitat suitability and the effects of human presence (this study), concerted action at the population level is required, ideally coordinated through large-scale action plans (e.g. Braunisch and Suchant 2013) which – due to the assumed umbrella function of the species (Suter et al. 2002) – is likely to benefit the wider mountain forest community.

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Chapter III: Individual variation

The importance of individual heterogeneity for interpreting faecal glucocorticoid metabolite levels in wildlife studies

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Abstract

1. As a non-invasive and inexpensive method, the use of faecal glucocorticoid metabolites (FGM) analysis in wildlife research is increasing. Various environmental factors have been shown to influence FGM levels, or faecal corticosteroid metabolites (FCM) levels in birds, but most studies do not account for inter-individual variance, which we hypothesized may substantially affect results.

2. We combined FCM analysis with genetic analysis to identify the sex and individual's identity in samples collected in three consecutive winters; with repeated samples per individual, across the entire range of an endangered population of capercaillie Tetrao urogallus in south-western Germany. Using generalized additive mixed models, we modelled FCM levels as a function of sex, season and environmental covariates at two spatial scales: location and home range. We compared two models: one including information on the individual animal and the other excluding this information (i.e. naïve model) to assess the influence of individual heterogeneity on the results obtained.

3. Models accounting for inter-individual differences explained 44.0% and 45.1% (at the location and home-range scale respectively), while only very little (4.0% and 5.1%, respectively) was explained by the environmental predictors. When ignoring individual effects, the model results changed considerably with other, previously non-informative predictors, becoming significant.

4. In the full models, accounting for inter-individual variance, weather conditions had no effect at either scale. FCM levels were negatively correlated with habitat quality at the sampling location, while human recreation at the home-range scale led to elevated FCM levels. In the naïve models, two additional predictors appeared significant: one weather variable at the local scales and two at the home-range scale. In all models, seasonal FCM patterns differed significantly between males and females.

5. Synthesis and applications. By combining faecal corticosteroid metabolites (FCM) analysis with genetic individual assessment, we demonstrate that individual heterogeneity can explain most of the variance in faecal corticosteroid metabolites levels and that ignoring this information can lead to erroneous conclusions when testing for environmental stressors. We therefore stress the importance of identifying individuals when studying faecal corticosteroid metabolites in wildlife and recommend combining faecal corticosteroid metabolites analyses with genetic analyses to adequately address this issue.

Introduction

If confronted with actual or perceived threats, animals elicit stress responses which help them adjust to changes in their environment (Cockrem 2007). One frequently studied stress response in vertebrate ecology is the change in glucocorticoid (cortisol or corticosterone) levels (Möstl & Palme 2002, Sheriff et al. 2011). Those stress hormones with their pleiotropic role within the organisms are recognized as mediators of allostasis that help maintain homeostasis of bodily functions (Sapolsky et al. 2000, McEwen & Wingfield 2003). Although it is natural that corticosteroid levels fluctuate (e.g. due to time of day, season, food availability, social status, reproductive status, age or sex) (Broom & Johnson 1993, Moberg & Mench 2000), prolonged exposure to high levels can reduce growth (Sapolsky 2002), suppress the immune system (Cyr et al. 2007, Stier et al. 2009) or inhibit the reproductive system (Sapolsky 2002), a condition known as allostatic overload (McEwen & Wingfield 2003). This in turn may affect fitness (Boonstra et al. 1998, Rangel-Negrın et al. 2009, Sheriff et al. 2009, Thierry et al. 2013), making it a relevant conservation issue for threatened species. Glucocorticoids are frequently measured to evaluate the response of organisms to various stressors (Touma & Palme 2005, Goymann 2012). In wildlife research, they are often assessed indirectly and non-invasively by analysing their metabolites in faecal samples (Möstl et al. 2002, Thiel et al. 2005), so as to avoid additional stress by capturing or handling the animal, biasing the results (Buehler et al. 2008, Sheriff et al. 2011, Goymann 2012). It is also important to recognize that the faecal metabolites represent an integrated measure of adrenocortical activity at a certain time before the faecal excretion (Palme 2005, Touma & Palme 2005).

Previous studies showed that many endogenous and exogenous factors can affect the concentration of faecal corticosteroid metabolites (hereafter referred to as FCM levels) (Hadinger et al. 2015). In free-living animals, FCM levels can be affected by food availability (Schoech et al. 2007, Jenni-Eiermann et al. 2008), with increased food availability being associated with lower FCM levels (Jenni-Eiermann et al. 2008). Habitat conditions, related to cover or foraging conditions are also suggested to affect FCM levels (Rangel-Negrın et al. 2009). For several species an effect of the ambient temperature has been found, with higher FCM levels during the cold season (Frigerio et al. 2004, Corlatti et al. 2011). Predators have been found to increase corticosterone levels in birds (Cockrem & Silverin 2002), and indirect predator effects, such as mere predator presence or elevated densities (Monclús et al. 2009, Sheriff et al. 2009), can be as important as direct ones (Schmitz et al. 1997, Preisser et al.

2005). Similarly, human recreational activities have been linked to elevated FCM levels in a variety of bird species (Arlettaz et al. 2007, Thiel et al. 2011). Sex-specific (Weingrill et al. 2004, Rangel-Negrın et al. 2009) and inter-individual differences in stress responses and associated FCM levels (Rehnus & Palme 2017) have also been shown in several species.

Despite this variety of drivers and associated sources of variance, most studies focus only on a small number of factors to assess their hypothesized effect on FCM levels. Inter- and intra-individual differences are often neglected (Goymann 2012, Hadinger et al. 2015, Rehnus & Palme 2017). Especially when non-invasive sampling methods are used it is often unknown how many individual animals of a population have been sampled and possible pseudo-replication cannot be excluded (Rehnus & Palme 2017). If and to which extent this may affect the results with regard to the effects of environmental stressors on FCM-levels has not yet been tested.

Declining and endangered in many Central European countries, grouse (Tetraoninae) have become a common model for conservation-related endocrinological studies. As these species are highly susceptible to human disturbance (Summers et al. 2007, Thiel et al. 2011, Storch 2013, Coppes et al. 2017), their stress response has been elucidated particularly in relation to human recreation activities: Elevated FCM-levels were found after repeated flushing in black grouse (*Tetrao tetrix*) (Arlettaz et al. 2015), with decreasing distance to recreational infrastructure in capercaillie (*Tetrao urogallus,* Thiel et al. 2011) and in areas severely disturbed by winter sports in both species (Thiel et al. 2008, Formenti et al. 2015). Furthermore, tree species composition and ambient temperature were found to affect FCM levels in capercaillie (Thiel et al. 2011). All studies were based on FCM extracted from faecal samples collected in winter, when they are well-preserved in the cold environmental conditions. However, whereas most studies distinguished between males and females, which are easily identified based on the size of their droppings, both inter- and intra-individual differences in FCM-levels have not been considered so far.

In our study we collected faecal samples across the entire geographical range of an endangered Central-European capercaillie population. We chose capercaillie as an ideal study model because FCM are calibrated (Thiel et al. 2005), they occur in various landscapes (Klaus et al. 1989), and they respond to various stressors such as predation (Kämmerle et al. 2017), climate change (Braunisch et al. 2013), habitat degradation (Suchant & Braunisch 2004) and human disturbance (Coppes et al. 2017) while being threatened throughout their Central European range (Storch 2007). By combining FCM measurements in three consecutive winters with genetic (i.e. to identify individual animals and determine their sex) and environmental analyses, we tested for individual variation in FCM levels and studied the effect of including or neglecting this information when investigating the effects of several potential environmental stressors on FCM levels: 1) habitat quality, 2) weather conditions and 3) human recreational use. We expected a major effect of sex and individual animal on the FCM levels, which could considerably alter the results if not accounted for within the models. Furthermore we hypothesized that FCM would be higher in areas with low habitat quality (i.e. in dense forests) in cold weather conditions and close to recreational infrastructure.

Materials and methods

Study area and model species

The study was performed in the Black Forest, a lower mountain range in south-western Germany (Fig. 1). The forest, dominated by Spruce (*Picea abies*), Silver fir (*Abies alba*) and Beech (*Fagus sylvatica*) (Kändler & Cullmann 2014), is interspersed with pastures and small settlements, the latter predominantly located in the valleys. The Black Forest holds one of the largest capercaillie populations in central Europe, outside the Alps (Segelbacher et al. 2003, Storch 2007), a species inhabiting well-structured, open mountain and boreal forests (Klaus et al. 1989, Storch 2002, Graf et al. 2009). The Black Forest capercaillie population is isolated from other populations in Central Europe (Segelbacher et al. 2003) and highly fragmented (Braunisch et al. 2010, Coppes et al. 2016). Population size and distribution have been continuously decreasing over the last 30 years (Coppes et al. 2016), with the cause considered to be multifactorial, including habitat deterioration (Suchant & Braunisch 2004), habitat fragmentation (Braunisch et al. 2010), predator abundance (Kämmerle et al. 2017), disturbance through human recreation (Coppes et al. 2017) as well as climate change (Huntley et al. 2007, Braunisch et al. 2013).

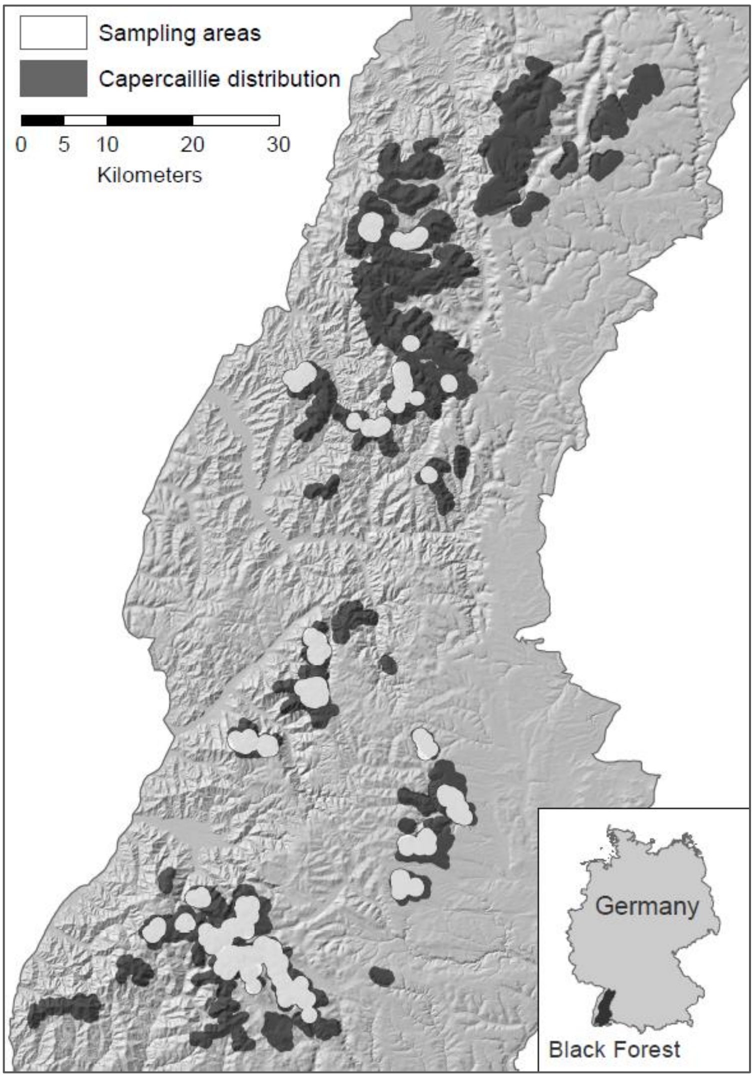

Figure 1: Capercaillie distribution in the Black Forest and the areas where samples were collected for faecal corticosteroid metabolites analysis. The inlay map shows the location of the Black Forest within Germany

Sampling method

Capercaillie faecal samples were collected in winter between November 2012 and May 2016, during periods with snow cover. Sampling areas were distributed over large parts of the capercaillie range in the Black Forest (Fig. 1), and systematically searched between one and three times per winter. However, due to differences in weather, snow and topographical conditions, the surface searched within a single day varied greatly. Samples were collected 3 to 7 days after new snowfall. We only collected samples lying on snow, as Thiel et al. (2005) had shown in an experimental set-up that FCM levels in capercaillie droppings are stable for 7 days if samples were kept at temperatures below 9°C. When several samples were located within a radius of 25 meters, only the freshest one (determined by visual assessment) was collected and its location taken using a handheld GPS (Garmin Etrex30). Samples were cooled during transport and stored at -32°C in the lab. Therefore we assume our FCM measurements are not influenced by storage conditions after defecation.

Model Predictors

To study the importance of including information on individual heterogeneity when assessing the effect of environmental stressors, we tested several environmental predictors. These included spatial information on habitat quality and human recreation, temporal information on weather and season as well as information on sex and identity of the individual (Table 1). To account for the mobility of the species and the time lag between blood corticosteroid levels and the excretion of their metabolites in the droppings (Thiel et al. 2005), we extracted the spatial environmental covariates using circular buffers at two spatial scales; at the "local scale" the predictors were considered within a 20 meter radius (to account for GPS inaccuracies) around the faecal sample location. In addition, we considered the environmental conditions within a 400 meter radius, which is equivalent to an area of 50 hectares (i.e. the size of a small winter home range of capercaillie in the Black Forest (Coppes et al. 2017)). The predictors were prepared using ArcGIS 10.4 (ESRI 2014).

Table 1: Predictor variables tested for their effect on FCM levels in capercaillie. Predictors retained in the models are indicated, otherwise the reason for discarding them is provided ("Decision"). Spatial predictors (i.e. Recr_dist and PropOpen) were calculated at two scales: local scale (average values in a 20 m radius), and home range scale (average values in a 400 m radius).

Group	Name	Description (unit)	Type	Decision
Human recreation	Recr_dist	Average distance to recreational infrastructure within a 20 and 400 m radius (m)	continuous	retained
	Recr_dens	Density (sum of line feature lengths) within a 20 and 400m radius (1257 m^2 and 502655 m^2)	continuous	corr. with Recr_dist
	Prop_recr	Proportion of 20 m or 400 m buffer covered by a 50 m buffer around recreational infrastructure	continuous	corr. with recr_dist
Habitat	PropOpen	Proportion of open forest (<70% canopy cover) within a 20 and 400 m radius. (%)	continuous	retained
	Altitude	Elevation of sample above sea level (m)	continuous	corr. with Tmin3d
Weather conditions	Tmin3d	Minimum temperature in the 3 days before sample was collected (°C)	continuous	retained
	Tmean3d	Mean temperature over 3 day window before sample was collected (°C)	continuous	corr. with Tmin3d
	Tmin7d	Minimum temperature in the 7 days before sample was collected (°C)	continuous	corr. with Tmin3d
	Tmean7d	Mean temperature over 7 day window before sample was collected (°C)	continuous	corr. with Tmin3d
	PrecDays	Number of days without precipitation before the day of sampling (range 3 - 7 days)	continuous	retained
Season	Day	Day of the winter season with 1 as start of winter and 212 as the end of winter.	continuous	retained
Individual	Sex	The sex of the animal (male/female)	categorical	retained
	Indiv	The ID of the individual animal	categorical	retained

Habitat quality

We calculated the proportion of open forest (<70% canopy cover) as a proxy for habitat quality, as it has been identified as a key structural habitat characteristic in various European capercaillie populations (Storch 2002, Suchant & Braunisch 2004, Graf et al. 2009). We used a digital vegetation surface model (1x1 m resolution), which was derived from stereo aerial images of the years 2015 and 2016 as described in Zielewska-Büttner et al. (2016). In a first step, canopy cover was calculated as the proportion of pixels with vegetation of at least 2 m height within a 25 m radius around every raster cell (Zielewska-Büttner et al. 2016). We then calculated the proportion of pixels classified as “open forest” (canopy cover <70%) in a 20 m and 400 m radius around our samples.

Human recreation

To test for an influence of human recreational activities on FCM levels we calculated the mean distance of each sample to the nearest winter recreation infrastructure (i.e. winter hiking paths, cross-country skiing trails, skiing pistes, snowshoe trails) as well as the density (as length per aerial unit) of infrastructure within a 20 m and 400 m radius, respectively. In addition, we applied a 50 m buffer around all recreational infrastructure and estimated the proportion of buffer-area within the two radii. The data on recreational infrastructure were adopted from the official Tourism and Recreation Information System of Baden-Württemberg (TFIS) and complemented with data of snowshoe trails, back-country skiing tours or winter hiking trails provided by specific user groups on the internet (www.outdooractive.de, www.gpsies.com, www.bergfex.de). Since capercaillie are most likely not affected by recreation activities at distances over 400 meters, (Thiel et al. 2011, Coppes et al. 2017), we truncated the distance to recreation at 400 m based on the frequency distribution of the data, i.e. excluding extreme outliers (Supporting Information Fig. S1).

Weather

To test for weather effects on FCM levels, weather data were obtained from the German meteorological service (Deutscher Wetterdienst, www.dwd.de). Precipitation and temperature data of the nearest meteorological station were used for each sample. We corrected for differences in elevation between sample and station by adjusting temperature with -0.6 °C per 100 meter of elevation increase (Liston & Elder 2006). We prepared a number of weather predictors: the number of days without precipitation before the date of sampling (PrecDays) and the minimum temperature as well as the mean temperature over three as well as seven days before the date of sampling (Tmin3d, Tmean3d, Tmin7d, Tmean7d).

Season

Since photoperiod and season can affect FCM levels (Corlatti et al. 2011), all samples were numbered based on the collection date, starting with 1 for the start of winter (1st of November) and ending with 212 at the end of Winter (31st of May) for every year. This resulted in a continuous variable depicting the time of the year.

Endogenous predictors – Genetic analysis

Genomic DNA was extracted from capercaillie droppings using spin columns (QIAamp DNA Stool Mini Kit, Qiagen, Hilden, Germany) according to the manufacturer's protocols. To minimize contamination risks amplification and post-PCR procedures were conducted separately from DNA extraction. All samples were genotyped using 12 microsatellite loci (Jacob et al. 2010) and one sex marker (Kahn et al. 1998) arranged in four multiplex-PCR reactions based on the protocol by Jacob et al. (2010). To avoid genotyping errors, a multiple tube approach with three replicates was implemented. Additionally, negative controls were included in the PCR amplification procedure to exclude contaminations. PCR products were sized on an ABI 3130 DNA Analyzer (Applied Biosystems, Darmstadt, Germany). Fragment length was scored using the program GeneMapper v.4.0 (Applied Biosystems, Darmstadt, Germany). Individuals were identified using GenAlEx 6.503 (Peakall & Smouse 2006) by searching for multilocus genotype matches. Samples that shared all alleles at all loci, excluding loci with missing values, were considered as identical.

FCM analysis

To avoid effects of the sample humidity on the FCM measurements, all samples were dried at 80°C. After careful homogenisation, glucocorticoid metabolites were extracted with 60% methanol (0.5 g droppings plus 5 ml) as described by Palme et al. (2013). FCM metabolites were measured using a cortisone enzyme immunoassay (EIA; Rettenbacher et al. 2004), which has been successfully validated for capercaillie (Thiel et al. 2005). To exclude any bias due to storage, analysis or other conditions, all faecal samples were stored and analysed under the same conditions in the same laboratory.

Statistical analysis

Individual variation in FCM levels

In order to evaluate and visualize inter-individual differences in mean FCM levels, we calculated individual means and associated standard errors (SE) and confidence intervals (CI = 1.96*SE) for each animal with ≥3 samples. Prior to that, we tested whether the mean was correlated with the sample size (i.e. resampling rate) of each individual using Pearson's product-moment correlations. We conducted a repeatability analysis to assess the consistency of FCM among individuals (i.e. the intra-class correlation coefficient, ICC), calculating a) ANOVA-based and Linear Mixed-effect Model (LMM)-based agreement repeatability with confidence intervals and b) adjusted repeatability after accounting for environmental covariates (i.e. human recreation, habitat and weather conditions, Table 1) (Nakagawa & Schielzeth 2010, Wolak et al. 2012). Using the capercaillie individual as grouping factor, we calculated agreement repeatability as implemented in the R-packages ICC (ANOVA-based; (Wolak et al. 2012) and rptR (LMM-based; (Stoffel et al. 2017). Adjusted repeatability in package rptR was estimated based on the final LMM structure specified below (see next section). All ICCs were estimated assuming Gaussian error distributions.

Model generation

In a first step, the initial set of predictors (Table 1) was tested for collinearity by calculating pairwise Pearson correlations (Zuur et al. 2009, Dormann et al. 2012). Of variables with a pair-wise correlation coefficient of $|r| > 0.5$ we retained the one we considered to be of higher ecological relevance. Pre-selection of variables resulted in seven predictors that we hypothesized to be related to the FCM levels: the proportion of open forest, the distance to winter tourism infrastructure, the number of days since the last precipitation event and the minimum temperature within a three-day window. Furthermore the day of season, the sex of the animal and an interaction term was included, as we expected FCM patterns to differ between sexes as a function of the advancement of the mating season. All data were standardized by subtracting the mean and dividing by the standard deviation to aid model convergence and to allow for a comparison of effect sizes.

We modelled FCM levels using generalized additive mixed models (GAMM, e.g. Wood 2006) from the r-package gamm4 (Wood & Scheipl 2017) with a Gaussian error distribution and a log-transformed response variable to meet parametric assumptions and to achieve model convergence. We accounted for variation in the mean FCM levels between individuals and study years by including a random intercept for individual and the year of study. One full GAMM containing all pre-selected predictors was calibrated for each scale (i.e. 20 m and 400 m radius) using cubic regression splines with shrinkage (Wood 2006) to penalize non-relevant predictors to zero.

In a first validation step, we compared the results of the GAMMs to linear mixed-effect models (package lme4, Bates et al. 2015) of equal structure as our GAMMs, including higher order terms for each predictor as indicated by the degrees of freedom estimated for each predictor in our GAMMs (LMM model results are provided in Supporting material Table S1).

We then evaluated the performance of GAMMs as compared to LMMs using 5-fold cross validation (CV) (with the five random partitions containing equal proportions of our data to detect overfitting) by comparing the root mean square error (RMSE) of our final models to the mean RMSE of the CV iterations. Finally, we obtained effect plots with 95 % confidence intervals conditional on the estimated smoothing parameters of the model, while holding all other covariates at the mean (package mgcv, (Wood 2004, 2011). All statistical analyses were performed using the programme R 2.15.0 (R Development Core Team, 2017).

Assessing the importance of individual effects

In order to quantify the effect of inter-individual variation in FCM levels, we partitioned the reduction in model deviance that could be ascribed to the fixed effect (i.e. environmental predictors) and random effect part (i.e. inter-individual differences) of our GAMMs, respectively. Fitting both models using maximum likelihood estimation allowed for comparison across different fixed effect structures.

The model deviance was quantified as the squared sum of residuals (RSS) and we related this to the deviance of a null model to obtain a measure of variance explained (i.e. a pseudo-R²). We constructed the null model as a GAMM containing a single intercept only, but adding the random effect structure of our models as:

$$Nullmod = GAMM\left(y \sim 1 + r_{j,i} + \varepsilon\right)$$

with random intercepts $r_{j,i}$ of equal structure to our full models. To obtain Null deviance, the RSS was calculated based on population level predictions of the null model (i.e. discarding the random effects for predicting).

The variance explained by the models was quantified as the reduction in model deviance attributed to fixed effects, random effects or both combined. We calculated the variance explained by *A)* our full model (using RSS of predicting with the full model on the data), *B)* the fixed effects for unknown random effects (using RSS of population level predictions, i.e. disregarding the random term) and *C)* the fixed effects given our known random effects (as the difference between the RSS of *A* and the RSS of the full model prediction of our null model, i.e. including the random term for predicting). Finally, we dropped the random intercept for the year of the study from the model to estimate the amount of variance explained by individuals alone. For this comparison of the two random effect terms we used models fitted using restricted maximum likelihood (REML). Finally, we validated our calculations by estimating the variance explained by individual differences in the LMMs using the marginal and conditional R² (Nakagawa & Schielzeth 2013).

To test how the results of our analysis were influenced by including the information on inter-individual differences, we refitted our GAMMs keeping all settings the same except that individual was not included as a random effect. We compared these “naïve” models with the corresponding full models (i.e. including individual as a random effect) in terms of significance of predictors and the shape of the effect plots.

Results

Individual variation in FCM levels

A total of 894 samples were collected and genetically analysed in the three winter seasons. Across all seasons 232 individual capercaillies could be genetically identified, 139 of which were male and 93 female (Supporting material: Table S2). The probability of two unrelated individuals sharing the same genotype (PI) was 1.7 x 10^{-10} while the probability of siblings sharing the same genotype (PISib) was 1.0 x 10^{-4}. Individual birds were resampled between 1 and 32 times (mean = 3.8, median = 2 times). There was large inter-individual variation in FCM levels (Fig. 2), which did not correlate with sample size (r=-0.05, t=-0.56, p=0.57). ICCs were accordingly low with confidence intervals excluding zero (ANOVA-based R = 0.21 (0.14 – 0.28); LMM-based R = 0.235 (0.151 – 0.314)). Adjusted repeatability was slightly lower than agreement repeatability (LMM-based 20 m: R = 0.21 (0.14 – 0.29) and 400 m: R = 0.21 (0.14 – 0.29).

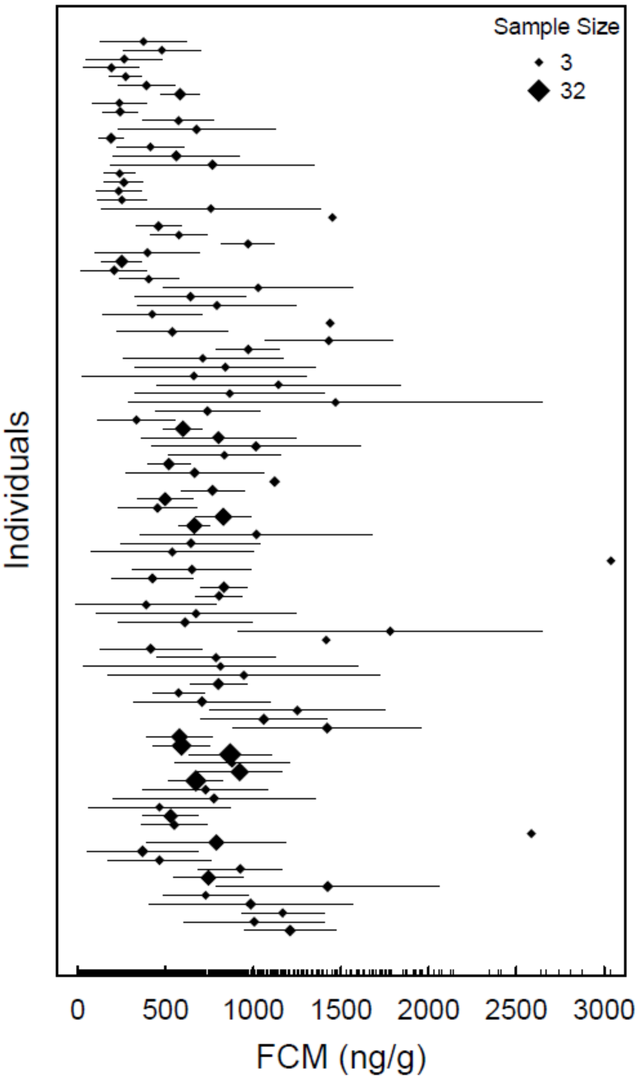

Figure 2: Mean (±95%CI) faecal corticosteroid metabolites levels of individual capercaillie which were sampled at least three times. Samples size is illustrated by the size of the diamonds, with larger diamonds indicating larger sample sizes. For individuals for which no error bars are shown, error bars exceed beyond the extent of the box

Relative importance of individual effects

Our full models (i.e. fixed and random effects combined) explained approximately 44.0 % (20 m) and 45.1 % (400 m) of the variance in the data. The random term of our model explained the majority of variance, while fixed effects only accounted for 4.0 % (20 m) and 5.1 % (400 m) of the explained variance for known random effects (i.e. if individuals and years were known) and only 0.5 % (20 m) and 0.8 % (400 m) of the variance in population level predictions (i.e. for unknown individuals and years). Removing the year of study caused a drop in overall variance explained to 3.0 % (20 m) and 3.2 % (400 m) respectively, thus attributing the bulk of variance explained to the inter-individual differences (20 m: 37.0 %; 400 m: 36.8 %). The same pattern was found for the LMMs, with a marginal R^2 of 0.081 (20 m) and 0.082 (400 m) and conditional R^2 of 0.428 (20 m) and 0.438 (400 m), respectively.

Effect of including individual variation on model outcomes

The GAMMs performed well in CV, with only a slight increase in RMSE in CV as compared to the full model at the 20 m scale (full model RMSE = 0.90; mean CV RMSE = 0.92; Δ = 0.02) and 400 m scale (full model RMSE = 0.89 mean CV RMSE = 0.91; Δ = 0.02). In addition GAMMs performed better in CV than the respective LMMs of similar structure (20 m: Δ = 0.22; 400 m: Δ = 0.12). FCM levels were not related to weather conditions (PrecDay or Tmin3D) at the home range scale (i.e. 400 m radius), but affected by the minimum temperature 3 days before sampling (Tmin3D) at the local scale (Table 2). We found a significant, albeit small decrease of FCM levels with increasing proportions of open forest (ProbOpen) at the local, but not at the home range scale (Table 2, Supporting information: Fig. S2). Distance to human winter recreation infrastructure was significantly related to an increase in FCM levels at the home-range scale, but not at the local scale (Table 2). FCM levels were, however, only elevated if the average distance to recreation infrastructure within the home range was less than approximately 180 meters (Supporting information: Fig. S2). In both models we found a significant interaction between the sex and day of season. Female capercaillie had higher FCM levels than males in November, which continuously decreased during the course of winter (Supporting information: Fig. S3). Male capercaillie, in contrast, showed a more complex, bimodal pattern: Low FCM levels in early winter were followed by a first peak in mid-winter (January). Thereafter FCM levels decreased, before peaking again in April-May (Supporting information: Fig. S3).

Table 2: Generalized additive mixed models explaining the FCM levels on both scales for both the full model (including individual as a random effect, panel a and c) as well as the naïve model (without individuals as random effect, panel b and d). Codes and descriptions of the predictors are given in Table 1. Predictors highlighted in bold become significant when not including the individual as a random effect.

	(a) Full model local scale (20 m radius)				(b) Naïve model local scale (20 m radius)			
	Estimate	Std.error	T value	Pr(>|t|)	Estimate	Std.error	T value	Pr(>|t|)
	6.176	0.266	23.22	<0.001	6.141	0.296	20.74	<0.001
Predictors	Edf			P	Edf			P
Recr_dist	1.017			0.071	0.861			0.087
PrecDay	**1.887**			**0.108**	**8.468**			**0.004**
Tmin3D	2.022			0.044	5.540			0.035
ProbOpen	1.084			0.007	5.540			0.020
Day:SexF	2.375			<0.001	6.046			<0.001
Day:SexM	4.485			<0.001	2.926			<0.001

	(c) Full model home range scale (400 m radius)				(c) Naïve model home range scale (400 m radius)			
	Estimate	Std.error	T value	Pr(>|t|)	Estimate	Std.error	T value	Pr(>|t|)
	6.195	0.258	24.01	<0.001	6.148	0.275	22.37	<0.001
Predictors	Edf			P	Edf			P
Recr_dist	2.917			0.001	6.007			0.006
PrecDay	**1.947**			**0.077**	**8.407**			**0.003**
Tmin3D	**1.947**			**0.061**	**5.831**			**0.019**
ProbOpen	0.678			0.193	8.415			0.124
Day:SexF	2.398			0.001	6.641			<0.001
Day:SexM	4.403			<0.001	2.911			<0.001

The naïve models, not including individual as a random effect, differed considerably from the full models (Table 2, and Figs 3 and 4). In the local scale model one predictor (PrecDay) additionally appeared significant which were not significant in the full model. Similarly, at the home range scale two additional predictors were found significant in the naïve model (PrecDay, Tmin3D) (Table 2, and Figs 3 and 4). The extreme increase in Edf (Table 2) indicates an overfitting of the naïve models, and effect plots revealed ecologically meaningless patterns, regardless of significance in the model (Figs 3 and 4).

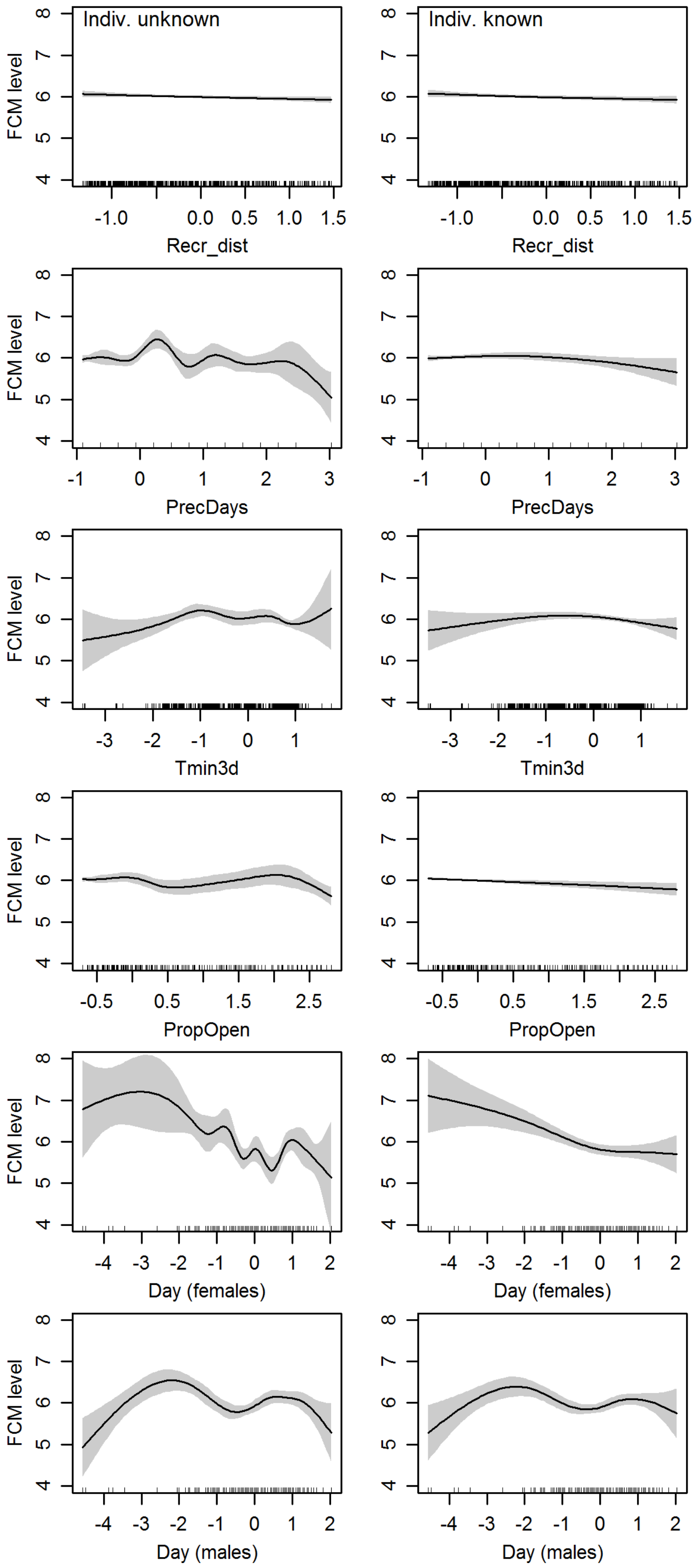

Figure 3: Effect plots showing faecal corticosteroid metabolites levels as a function of the environmental predictor variables, measured at the local scale (i.e. within a 20 m radius) for the models excluding (left) and including (right) information on individual heterogeneity. Grey areas indicate the 95% confidence intervals conditional on the estimated smoothing parameters of the model, while holding all other covariates at the mean. Variable codes and descriptions are provided in Table 1.

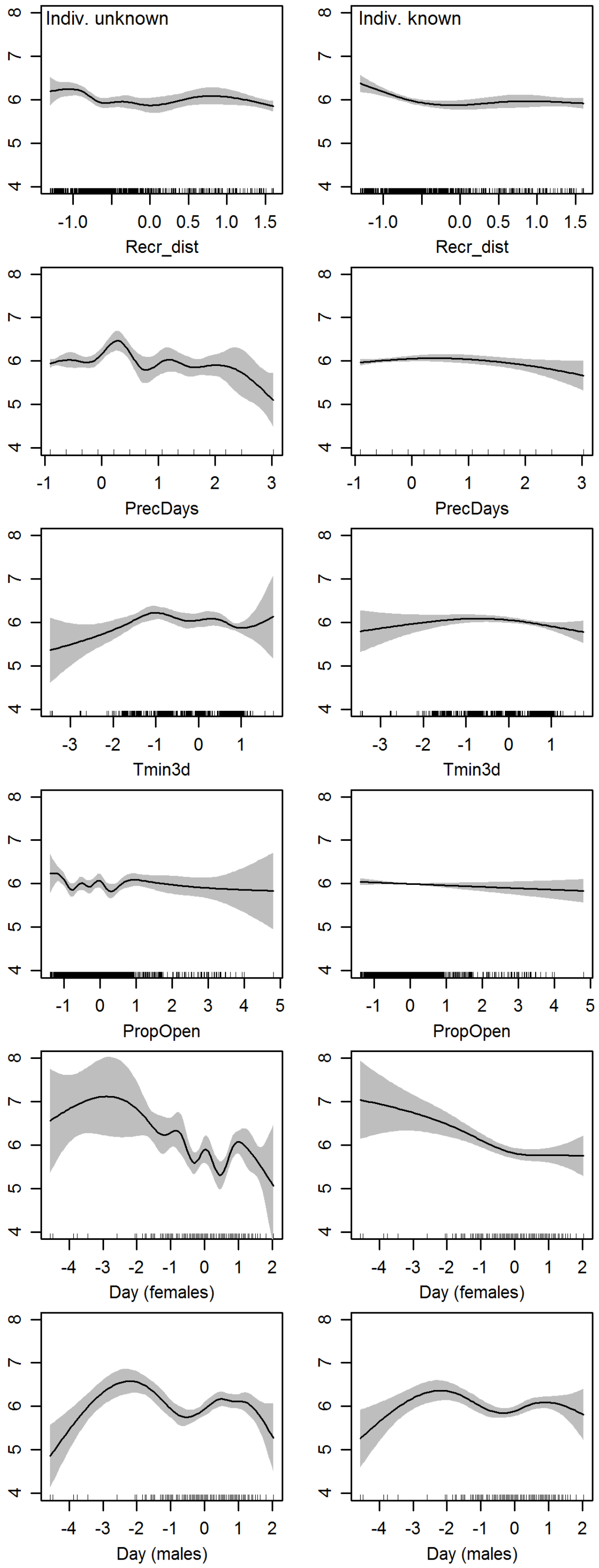

Figure 4: Effect plots showing faecal corticosteroid metabolites levels as a function of the environmental predictor variables, measured at the home-range scale (i.e. within a 400 m radius) for models excluding (left) and including (right) information on individual heterogeneity. Grey areas indicate the 95% confidence intervals conditional on the estimated smoothing parameters of the model, while holding all other covariates at the mean. Variable codes and descriptions are provided in Table 1.

Discussion

Our study is one of the first to investigate FCM levels combined with genetic analysis to identify the individuals in the sample within a free-ranging population over several years. Our results highlight the importance of considering individual heterogeneity when analysing FCM. While our models explained approximately 44.0 – 45.1 % of the variance in capercaillie FCM levels, only 4.0 and 5.1 % thereof could be ascribed to environmental conditions, 36.8 and 37.0 % being associated with inter-individual variation (Fig. 2). This pattern was independent of the scale at which environmental conditions were measured and was supported by the low repeatability values and the fact that the adjusted repeatability was not larger than the agreement repeatability.

Differences in FCM levels between individual animals could be explained by differences in how individuals metabolize corticosterone (Goymann 2012). However individual animals can also respond differently to environmental stressors (Ganswindt et al. 2012, Dickens & Romero 2013). Our results suggest that neglecting these differences may lead to erroneous results, notably an overestimation of environmental effects on FCM levels: Several predictors which had no significant effect in the full models (accounting for inter-individual variance) were found to be significant in the naïve models (Table 2). Moreover, the latter models showed strange, ecologically meaningless effect patterns, partly due to the fact that they were more prone to overfitting (Figs 3 and 4). These findings indicate that one should be cautious when interpreting results without information on the number of individuals sampled (Rehnus & Palme 2017) and their respective resampling rates. If a genetic assignment is not possible, due to financial or other constraints, the sampling design should be adapted so as to maximize the number of sampled individuals while simultaneously minimizing repeated sampling of the same individual. While extending the sampling area will increase the chance of sampling many individuals, the latter bias may be reduced by applying an adequate minimum distance between samples (e.g. corresponding to the territory size in territorial species). Another method would be to attribute samples found within close distance to the same individual (Thiel et al. 2008, Thiel et al. 2011). This could however further blur the results if the samples of two or more individuals are erroneously pooled. Using genetic analysis to obtain information on sex and individual is therefore a major advantage, especially for non-territorial, elusive and disturbance-sensitive species, where samples have to be collected non-invasively and without observing the individual (Rehnus & Palme 2017).

Despite the large proportion of variance explained by the individual animal, we could still confirm significant environmental effects on FCM levels in capercaillie. The strongest effect was found for human recreation at the home range-scale (Table 2), even though we did not account for the number and distribution of recreationists within the area and between years, but only focused on recreation infrastructure. Birds exposed to high densities of recreation infrastructure within their winter-home range showed elevated FCM levels, this effect levelled off, however, when the average distance of recreation infrastructure within the 400 m radius exceeded 180 meters. A similar pattern, with an effect up to 500 meters was found by Thiel et al. (2011). The difference between their and our threshold can most likely be attributed to averaging within 400 m in our study, the fact, however, that effects of recreational infrastructure on capercaillie FCM levels are only measurable up to a certain distance, is also supported by behavioural studies (e.g. Coppes et al. 2017).

Habitat quality is likely to affect FCM levels (Suorsa et al. 2003, Rangel-Negrın et al. 2009, Davies et al. 2013), therefore we expected to find lower FCM levels in samples from areas with a high proportion of open forest representing the habitat favoured by capercaillie, (Rolstad & Wegge 1987, Storch 1995, 2002) compared to dense forests, which represent less suitable habitats. This hypothesis was supported at the local scale, where FCM levels were significantly lower at locations with a high proportion of open forest in the immediate vicinity (Table 2, Supporting information Fig. S2). We did not find this effect at the home range scale, though (i.e. within 400 m radius), possibly due to the fact that there are only few, scattered and small areas with open forest in the Black Forest, which only marginally affect values when averaging the canopy cover within a 400 m radius (home range scale).

Interestingly, we found strong seasonal patterns in FCM levels, which differed markedly between the sexes (Supporting information: Fig. S3). For females, the highest FCM levels were detected during early winter when the first snow appeared, their level dropped later in winter. This pattern may be linked to food constraints: During winter, capercaillie feed almost exclusively on conifer needles, a low-caloric food which is hard to digest (Klaus et al. 1989). Towards the end of winter additional new food sources, especially buds of trees and dwarf shrubs are available. This may explain a decrease in FCM levels in females, which strongly depend on sufficient energy supplies to be in good conditions for reproduction (Schoech et al. 2007). For males we found two distinctive FCM-peaks. Whereas the first peak during mid-winter (January) might be due to the start of winter conditions, and associated change to a low-caloric diet, the second peak at the end of winter (April) is very likely linked to the start of the mating season. Capercaillie are polygynous birds, at the end of winter males display and defend territories at a lekking site to attract females (Klaus et al. 1989). This competitive mating behaviour is likely to contribute elevated stress levels in male capercaillie (Figs 3 and 4) (Thiel et al. 2011).

In addition, we expected that weather conditions affect animal physiology and Thiel et al. (2011) found increased FCM levels in capercaillie in cold conditions. Our model confirmed these results for the local scale: With colder temperatures in the three days before the collection of the samples, significantly higher FCM levels were recorded (Table 2 and Fig 3).

Finally, due to a lack of reliable data across the large extent of the study area, we were not able to test for potential predator effects. The presence of predators can be an important driver for increased glucocorticoid levels in prey species (Sheriff et al. 2009) and high predator densities were the main factor affecting FCM levels in rabbits (*Oryctolagus cuniculus*) (Monclús et al. 2009). Collecting sound data and including this potential stressor in the models would therefore be an important subject to be addressed in further studies.

Conclusions

We demonstrate the importance of including inter-individual differences when studying FCM-levels in wildlife. Individual effects may account for the vast majority of variance in FCM levels and may lead to erroneous results, in our case an overestimation of environmental effects, when disregarded. Adding to the benefits of using FCM instead of invasive blood samples, we see it as a major advantage to combine genetic analysis with FCM measurements to gain more knowledge on the endogenous and exogenous factors influencing FCM levels in wildlife. If genetic individual assessment is not possible, we recommend avoiding pseudo-replication by adopting a sampling strategy that reduces multiple sampling of the same individual. Furthermore, as we found strong sex-specific and seasonal FCM patterns, distinguishing between sexes and ensuring that samples are collected at the same time of season when comparing different areas are of crucial importance for correctly appraising the effects of environmental and human-induced "stressors" affecting FCM-levels in wildlife.

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Chapter IV: Habitat-dependent variation

Habitat suitability modulates the response of wildlife to human recreation

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Coppes, J., Nopp-Mayr, U., Grünschachner-Berger, V., Storch, I., Suchant, R., Braunisch, V. (submitted) Habitat suitability modulates the response of wildlife to human recreation.

Abstract

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

Introduction

With increasing popularity of outdoor recreation, growing numbers of recreationists and continuing diversification of recreation activities, the effects of recreation on wildlife are well recognized as an important conservation issue (IUCN 2016). A growing body of literature illustrates the various ways in which wildlife can be affected by recreation activities in their habitat (Steven et al. 2011, Larson et al. 2016), ranging from physiological changes (Walker et al. 2006, Thiel et al. 2011, Arlettaz et al. 2015), reduced breeding success (Anderson & Keith 1980, Ahlund & Götmark 1989, Mallord et al. 2007), changes in abundance (Patthey et al. 2008, Wolf et al. 2013), community composition (Miller et al. 1998) to changes in territory establishment in birds (Bötsch et al. 2017). Behavioural reactions include direct fleeing or flushing upon encountering humans (Thiel et al. 2007, Stankowich 2008, Sönnichsen et al. 2013), which may impact energy budgets and possibly affect fitness. More subtle behavioural reactions are changes in vigilance behaviour in regularly disturbed areas (e.g. close to recreational infrastructures such as hiking trails or skiing pistes) (Jayakody et al. 2008), or a temporal avoidance of disturbed areas (Coppes et al. 2017a). Reduced use of such disturbed areas (Immitzer et al. 2014, Coppes et al. 2017b) might effectively be equated with habitat loss or deterioration. However, individual behavioural reactions do not reflect consequences at a population level (Gill et al. 2001). Thus, effects of recreation activities on demographic parameters and, as a consequence, on population densities have to be classed as key questions in conservation management.

In many documented cases, the reaction of wildlife to human presence is similarly to their reaction to predators (Frid & Dill 2002, Beale & Monaghan 2004). However, free-living animals can also habituate to non-lethal encounters with humans as it is the case in most recreation activities (Thompson & Henderson 1998) and the "deterring effect" of human presence may even shield prey species from predation under specific circumstances (Leighton et al. 2010, Shannon et al. 2014). Such effects strongly depend on the environmental conditions together with the number and behaviour of recreationists (Pearce-Higgins et al. 2007), and it might even be affected by the history of human exploitation in an area (Storch 2013). Reactions of animals to human recreation are highly species-specific (Blumstein et al. 2005, Ficetola et al. 2007) and often linked to behavioural and morphological or life-history traits (Blumstein et al. 2005, Kangas et al. 2010): ground nesting birds, for example, have been found to be more sensitive to recreational disturbance compared to species breeding in cavities (Kangas et al. 2010) and species with larger body mass are considered more sensitive to recreational disturbance compared to smaller species (Blumstein et al. 2005, Weston et al. 2012). Wolf et al. (2013) found indications that birds species which forage on ground vegetation and shrubs seem to be more susceptible to human disturbance compared to species foraging in trees. Responses to human presence might even differ among individuals of the same species (Carrete & Tella 2011, Coppes et al. 2018).

The intensity of individual reactions to human recreation within the same species might vary between different habitat types or habitat characteristics providing food and cover: van der Zande et al. (1984) found a more pronounced negative effect of recreation on two bird species in deciduous forests compared to coniferous forests. Vegetation structures associated with cover (i.e. foliage density, dense shrub or forest layers) have been shown to affect flushing distances (Fernández-Juricic et al. 2002, Fernandez-Juricic et al. 2004), with shorter flushing distances in denser forests providing more cover (Thiel et al. 2007). The degree to which wildlife can survey its surroundings (i.e. visibility) is also affecting vigilance behaviour (Metcalfe 1984, Whittingham et al. 2004), with increased vigilance in visually obstructed habitats (Whittingham et al. 2004). Boyer et al. (2006) recorded increased foraging rates of birds in areas with high visibility, minimizing the time spent on open areas with higher predation risk. In the case of a ground nesting bird, the distance of spatial avoidance around recreation activities depended on the shrub cover, with less pronounced avoidance of areas with high shrub cover (Coppes et al. 2017b). This observation was most likely linked to the availability of good hiding structures. Wolf et al. (2013) found impacts of recreation activities on birds to be less distinct along trails with a well-developed, structurally rich vegetation with both favourable foraging and hiding structures. From a conservation perspective, given that disturbance effects might be highly habitat-specific (Murison et al. 2007), understanding the habitat conditions where disturbance effects are strongest (Sutherland 2007) is crucial to designing adequate mitigation measures.

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

Methods and Materials

Study areas

This study comprises 13 different study areas in different capercaillie populations spread over a large geographical range (Figure 1). Three study areas were located in the Black Forest (BF 1 to BF 3), south-western Germany. One study area was located in the Bavarian Alps (BA 1), south-eastern Germany. The remaining study areas were located in the provinces of Styria (ST 1-7) and Carinthia (CA 1-2) in Austria.

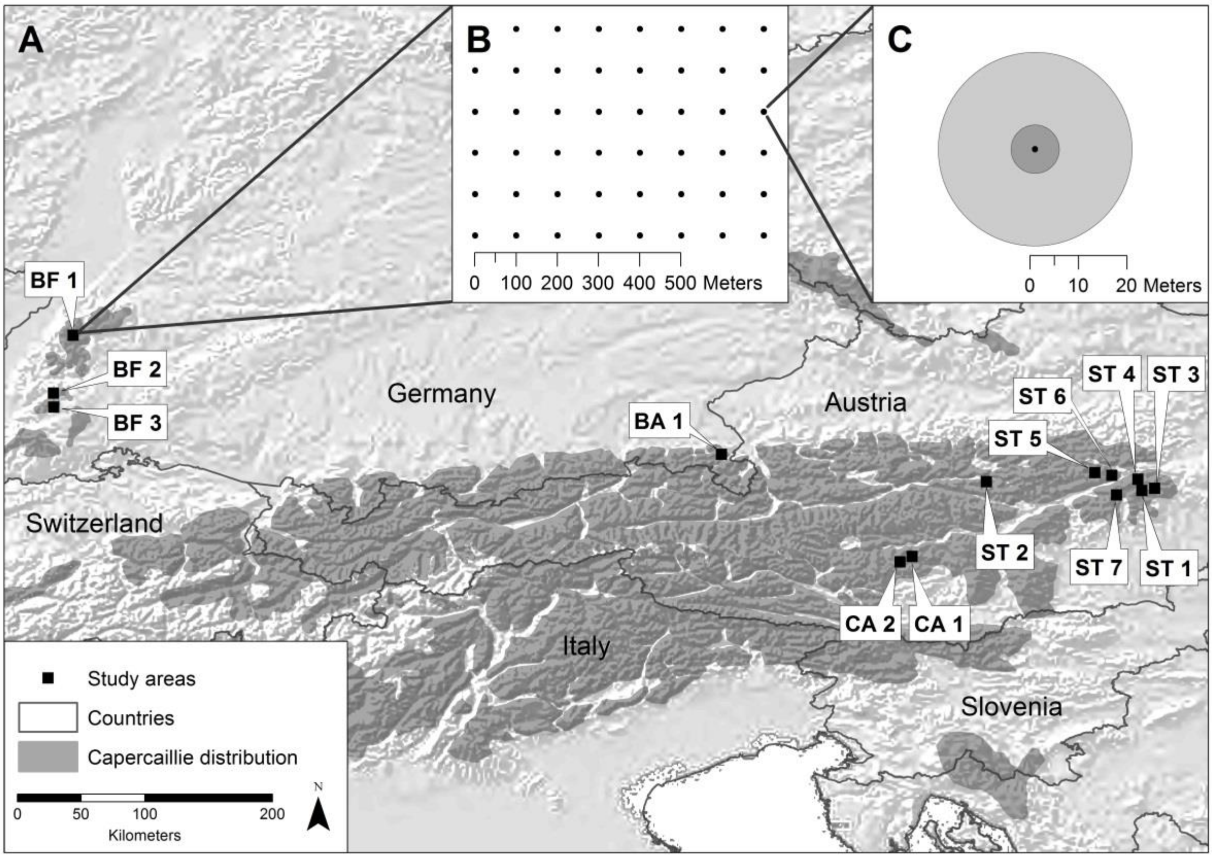

Figure 1: The study areas (black squares) in Germany and Austria (panel A) in relation to the capercaillie distribution (dark grey) (Coppes et al. 2015). In each study area, data were collected using a systematically distributed grid of sample plots (panel B); signs of capercaillie presence were collected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

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

Table 1: Study areas with their size, average altitude, dominating tree species, number of sampling plots per year (N plots) and the number of sampling years (N years).

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

Model species

The capercaillie is a large, ground nesting forest grouse species (Johnsgard 1983). It resides in semi-open to open coniferous or mixed forests with a rich ground vegetation (Storch 2002, Summers et al. 2004, Bollmann et al. 2008, Graf et al. 2009), occurring over a wide geographical range across Europe (Klaus et al. 1989, Coppes et al. 2015). While the species is widely distributed in Scandinavia and Russia with large populations numbers, the Central and Southern European populations are smaller, they are mainly restricted to mountain ranges and declining in many areas (Storch 2007). We chose the capercaillie as a model species because (1) it is considered an umbrella species for structurally complex and species rich boreal forests (Suter et al. 2002, Pakkala et al. 2003), (2) it occurs over a wide geographical range and (3) it has been shown to react sensitively to habitat changes (Suchant & Braunisch 2004). Several studies found negative effects of recreational activities on capercaillie (Summers et al. 2007, Thiel et al. 2011, Moss et al. 2014, Rösner et al. 2014, Coppes et al. 2017b), e.g. elevated stress levels (Thiel et al. 2008, Thiel et al. 2011, Coppes et al. 2018), avoidance of areas near forest roads (used both by vehicles as well as recreationist) in winter (Summers et al. 2007) or avoidance of trails used for recreational activities in summer (Moss et al. 2014) in Scotland. Similarly, Coppes et al. (2017b) found capercaillie avoided recreational infrastructure in the Black Forest, one of our study regions.

Data collection

Data were collected between 2005 and 2017, in the months July and August. A plot-based sampling design was applied: plots were arranged in a regular grid of 100*100 meters, which resulted (depending on the size of the study area) in between 171 and 439 plots per site (Table 1). The only exception was in the Bavarian Alps (BA 1), the largest study area, where the distance between plots was 200*200 meters for logistic reasons. The plots were located in the field using a handheld GPS. At each plot, a variety of habitat parameters (Table 2), which have been shown to be relevant for capercaillie in previous studies (Storch 2002, Suchant & Braunisch 2004, Braunisch et al. 2014, Zohmann et al. 2014), were recorded within a 20 m radius around the plot centre (Figure 1) following the method described in Storch (2002). In addition, to assess the presence or absence of capercaillie, a 5 m radius around the plot centre was searched for indirect signs for 10 minutes; in the Bavarian study area the search time was 15 minutes (Figure 1, panel C) Storch (2002). Signs of capercaillie presence were either collected (feathers, droppings and eggshells) or photographed (e.g. sand-baths) and verified by a team of capercaillie experts. Capercaillie droppings can be found over longer time periods after defecation (Poggenburg et al. 2018) and searching for indirect signs of presence is an established method to study capercaillie occurrence (Coppes et al. 2016) and habitat use (Summers et al. 2007, Moss et al. 2014, Zohmann et al. 2014). Before sampling, all field assistants were trained in habitat assessment, capercaillie ecology, and in the identification of indirect capercaillie signs to ensure consistency and high data quality.

Table 2: Habitat parameters for calculating the capercaillie habitat suitability index (HSI, Storch 2002). The reference radius for all parameters was 20 meter around the plot centre (total plot size =1256.6 m^2). Both categorical and continuous parameters were included, with data both collected in the field (Fieldwork) and derived from a digital elevation model (DEM).

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

Model predictors

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

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

Model	Predictor	Description	Unit	Type	Scale
a)	Avg_HSI	Mean habitat suitability for the study area	0-1	Continuous	Study area
	Recr_area	Proportion of study area within distances <145 m of recreation infrastructure	Percent	Continuous	Study area
	Recr_pressure	Less than 50% (low) or over 50% (high) of the study area being within 145 m of recreation infrastructure	Low-high	Categorical	Study area
b)	HSI	Habitat suitability index per plot	0-1	Continuous	Plot
	Recr_dist	Distance to nearest recreation infrastructure	Meters	Continuous	Plot

Statistical analysis

Relative capercaillie densities per study region

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

Local habitat use

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

Results

Between 2005 and 2017, a total of 15481 plots were sampled, in 2835 plots there were signs of capercaillie presence. Of the 13557 plots closer than 1092 m to recreation infrastructure, we observed signs of capercaillie presence on 2278 plots.

Relative capercaillie densities per study region

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

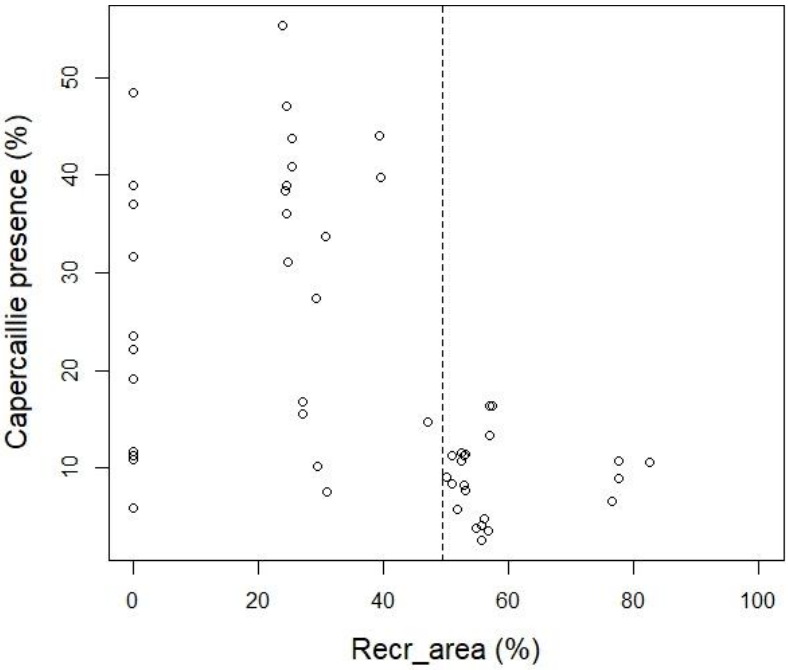

Figure 2: Scatterplot showing the percentage of sampling plots with relative capercaillie densities per site and study year in relation to the percent of plots within 145 meters of recreation infrastructure. The dashed line in the right panel marks 50%.

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

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

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

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

Habitat use analysis

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

Table 5: Generalized linear mixed models describing the probability of capercaillie presence per sampling plot as a function of habitat suitability (HSI), the distance to recreation infrastructure (Recr_dist) and the interaction thereof, across the whole study area (a: full model) and including only plots within the area potentially influenced by recreation infrastructure, i.e. within 1092m distance to recreation infrastructure according to Coppes et al. (2017b) (b: reduced model). The odds ratios (+-95% confidence interval) were calculated to compare the effect sizes. Estimates of the random factors are the SD Study area, and SD Year:Area. The performance of models was evaluated using the area under the receiver operator characteristics curve (AUC).

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

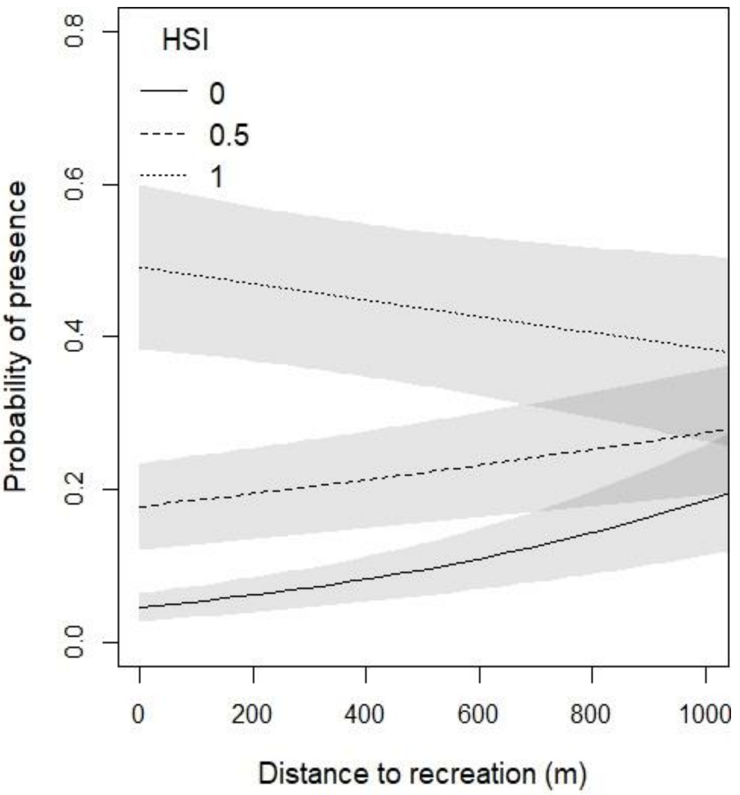

Figure 3: Interaction between habitat suitability (HSI) and distance to recreation infrastructure. The probability of finding a capercaillie sign within different distances to recreation infrastructure is shown for different habitat suitability values (HSI = 0, 0.5, 1) for the "reduced model". The model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

Discussion

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

Contrary to the results at the larger spatial scale (i.e. study area), we found a clear interaction between the effects of the distance to recreation infrastructure and habitat suitability on local-scale habitat selection. The probability of habitat use was lower in close vicinity of recreation infrastructure, and this effect was amplified under poor and slightly mitigated under good habitat conditions (Figure 3). This shows that specific vegetation structures can modulate wildlife responses to human recreation activities (Kangas et al. 2010, Wolf et al. 2013, Coppes et al. 2017b), e.g. by providing visual shelter, and that habitat suitability which includes both good foraging conditions and cover plays a major role. Nevertheless, the compensatory effect of habitat suitability was only small and good habitat conditions led only to a slight increase in probability of presence, with effects most pronounced in close vicinity to recreation infrastructure. Consequently, habitat improvement might be one accompanying management aspect close to human recreation activities, but it might not entirely compensate for disturbing effects of human presence. Habitat suitability was the most important variable in explaining capercaillie presence/absence, however, according to the odds ratios, it´s impact only marginally exceeded the one of recreation infrastructure (Table 5). This indicates limitations in reducing impacts of recreation infrastructures by merely improving habitat suitability. Highly suitable habitat per definition both provides good food supply and shelter within short distances (Storch 2002). In highly suitable habitat, it is therefore easier to hide while being close to good foraging conditions compared to poor habitats. Capercaillie habitats with low HSI-scores are characterised by dense or very sparse canopy cover and little or to high ground vegetation, offering only poor shelter or escape options against predators, disturbances and unfavourable weather conditions. Concurrently, such habitats provide poor feeding resources (i.e. ground vegetation rich in bilberry and insects). It has been shown, that human disturbance along recreation infrastructure is comparatively predictable in time and space for many wildlife species to adjust to it (Miller et al. 2001, Baines & Richardson 2007, Coppes et al. 2017a): in fact, capercaillie might be more likely to take the risk of encountering a human for availing of good habitat. The fact that they avoid the infrastructure designated for human recreational activities indicates that the infrastructure forms a landscape of fear (Laundré et al. 2010, Rösner et al. 2014). However, whilst direct presence of humans might have negative effects, indirect factors linked to human recreation activities might be responsible for avoidance of recreational trails (Watson & Moss 2004), such as increased predator presence (Storch & Leidenberger 2003).

Local avoidance of zones adjacent to recreation activities might be considered functionally equivalent to habitat loss, as important resources close to trails are not - or only temporarily - accessible, which can in turn affect large parts of a population (Coppes et al. 2017b). Our findings for capercaillie are in line with observations for other grouse species: For black grouse, Patthey et al. (2012) described spatial avoidance of roads, forest tracks or walking paths by hens during the summer months and Immitzer et al. (2014) reported significantly lower probabilities of black grouse presence within a 50 m buffer zone around hiking trails. Such zones of avoidance mean effective loss of habitats, at least within certain temporal windows of human presence. As habitat loss and habitat deterioration have been ranked as top priority threats for European grouse species by national experts (Storch 2007), net habitat losses due to human presence might be a critical drivers of the species´ occurrence. Our results suggest that local mitigation through creating high habitat suitability can increase the local probability of use of potentially disturbed areas, but may buffer such population effects only up to a certain point: In the case of capercaillie there seems to be a threshold (i.e. 50% of potentially disturbed area) above which population densities drop significantly in relation to recreational activities.

In contrast to previous studies which investigated effects of human disturbance on wildlife using case studies (i.e. few study areas), our study includes multiple study areas, with diverse habitat conditions as well as differences in human recreational use. We found a large variance between study areas and years; at both spatial scales the SD values of the random effects in our models were of similar magnitudes as those of the predictors (Recr_dist, HSI). One potential source of variance might be the intensity of use of the recreation infrastructures (i.e. the number of people using the infrastructure), which is likely to differ between areas, but was out of scope to be quantified in our study. The differences between areas might also be explained by large-scale landscape effects: whereas the German study areas were located in fragmented forest landscapes (Storch 2007, Coppes et al. 2016), the Austrian study areas were mostly located in continuous forest landscapes and at higher altitudes with colder and therefore climatic conditions more favourable for capercaillie (Braunisch et al. 2013). Due to our consistent results across this large geographical range as well as time span, we are confident that our results are widely applicable.

Conclusions and management implications

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

Considering negative impacts of human recreation on capercaillie revealed by other studies, ranging from behavioural adaptations (Summers et al. 2007, Thiel et al. 2007, Moss et al. 2014, Coppes et al. 2017b) to physiological effects (Thiel et al. 2011, Coppes et al. 2018), we therefore advise to apply the precautionary principle, when planning new recreational activities in capercaillie habitat (Braunisch et al. 2015). Especially in areas with low and/or declining population numbers, densities of recreation infrastructure should be minimized (i.e. the area influenced by recreation infrastructure should be reduced to below 50% as a minimum) to avoid detrimental effects on local populations. At a local scale, habitat structures along recreational trails should be managed to improve habitat suitability (this study) and decrease visibility ranges (Wolf et al. 2013, Coppes et al. 2017b).

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

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Synthesis

The goal of my doctoral thesis, in the field of recreation ecology, was to study how the response of wildlife to recreation activities varies over time and space, between individuals and populations. The interpretation of the wildlife response to recreational activities has allowed the formulation of management options. I applied several methods to study different aspects of this variation on two different species, red deer (*Cervus elaphus*) and capercaillie (*Tetrao urogallus*), revealing variation in responses of the species on both local habitat use as well as on the population level.

Variation of spatial avoidance at individual and population level

As the effects on the population level are considered of higher importance compared to effects on individuals (Buckley 2013, Storch 2013). I applied two methods to study the effects of recreation activities on populations: using the locally threatened capercaillie as a model species, I have shown that the birds' avoidance of recreational infrastructure leads to an effective habitat reduction, concerning large parts (up to 40 %) of its current distribution range in my study area, the Black Forest (chapter 2) which is highly likely to affect population densities. By combining data from several study areas spread over a large geographical range I confirmed the hypothesis that not only local habitat use but also population densities can be affected by recreational activities, if over 50 % of the birds' distribution area is potentially disturbed by recreation activities (chapter 4). This confirms the hypothesis that wildlife can tolerate low levels of recreation activities, but under high levels of recreation negative effects become evident (Morse et al. 2006, Pearce-Higgins et al. 2007).The fourth chapter also reveals the value and importance of including multiple study areas with different habitat and population conditions to study the effects of recreation activities on wildlife.

Temporal variation

In addition to spatial avoidance, I also revealed temporal (i.e. seasonal and diurnal) variation in recreation effects: The second chapter shows strong seasonal differences in the habitat use of capercaillie in relation to winter and summer recreation activities. Moreover, red deer were found to avoid recreation infrastructure (i.e. hiking trails, skiing slopes and trails) during the daytime with human presence (i.e. day), but use these areas more frequently than random when humans are absent (i.e. night) (chapter 2). The deer seem to have adapted their temporal behaviour to ensure they can access all necessary resources in the area despite the presence of human recreationists. This complies with previous studies showing a stronger avoidance of red deer hiking trails during day, compared to night (Sibbald et al. 2011) and that wildlife temporal activity patterns can be influences by recreation activities (Reilly et al. 2017). When not considering such temporal differences, with responses that can even show opposite directions (i.e. avoidance and attraction during different times of the day or between seasons) in the analysis, e.g. by pooling data from different daytimes or seasons, true responses of wildlife to recreation activities might remain undetected or underestimated.

Habitat-dependent variation

An understanding of the habitat conditions in which human disturbance has the most severe impact on wildlife is considered an important research gap (Sutherland 2007), I attempt to address this question in chapters two and four. Although the results regarding avoidance of recreation infrastructure are to some extent similar to previous studies (Summers et al. 2007, Moss et al. 2014), my thesis reveals how this response can differ under different habitat conditions, and which has implications for novel mitigation measures, i.e. buffering negative effect by habitat management (chapter 2 and 4).

Inter-individual variation

In the third chapter I combined genetic analyses with analyses of faecal stress hormone metabolite levels in capercaillie droppings to study individual heterogeneity of stress responses towards human recreation. By combining genetic and corticosterone analysis I was able to show large differences between individuals. However, where previous studies have already shown that responses of wildlife might vary between different individuals of the same species (Carrete & Tella 2011), my results demonstrate that not only are there differences between individuals, but also show that overlooking these differences might lead to erroneous results and conclusions (chapter 3).

Response types and ecological theories on human wildlife interactions

The combination of different study designs, data collection methods and analysis methods allowed me to reveal a broad spectrum of different sources of variation in the response of wildlife towards human recreation. This has implications for evaluating which of the ecological theories explaining human-wildlife responses apply to the study species.

The risk disturbance hypothesis implies that wildlife responds to human presence, in a similar way as to the presence of predators, with anti-predator behaviour (Frid & Dill 2002) and that these responses are considered to bear costs for the individual (Lima & Dill 1990). The fact that animals can learn in which habitats or areas the risk of encountering a predator - or a human - is particularly high and consequently avoid such areas is defined in the landscape of fear concept (Laundré et al. 2010). I have found both red deer (chapter 1) and capercaillie (chapter 2 and 4) avoid recreation infrastructure, which indicates that both species see humans as potential predators and react with anti-predator behaviour as per the risk disturbance hypothesis (Lima & Dill 1990, Frid & Dill 2002). The reduced use of areas close to recreation infrastructure is likely to indicate the existence of a landscape of fear (Laundré et al. 2010) for both species, which can be, as in the case of in red deer, modulated by a “time of fear”. Because red deer are hunted by humans, it seems obvious that they see humans as a predation risk, and do not seem to habituate to human presence.

The lack of response to human presence in Japanese rock ptarmigan (*Lagopus mutus japonicus*) is explained by the fact that this species has never been hunted (Nakamura 2010, Storch 2013), indicating that it is possible for grouse to habituate to human presence. Because capercaillie have not been hunted in the Black Forest for over 45 years, and are regularly exposed to human recreationists, it could have been expected that they habituate to human presence (Thompson & Henderson 1998, Baudains & Lloyd 2007, Stankowich 2008). However, Thiel et al. (2007) found larger flushing distances in in areas with high recreation pressure, and larger flushing distances were found for black grouse (*Tetrao tetrix*) which were regularly flushed compared to birds not regularly flushed (Baines & Richardson 2007). Even though I cannot compare the response of birds over time, to study whether the response decreased over time (i.e. habituation), the fact that I still found large avoidance distances, combined with the results cited above (Baines & Richardson 2007, Thiel et al. 2007), indicates the limitation of the habituation concept for capercaillie.

The fact that some predator species avoid humans, has been linked to prey species actively seeking human presence to avoid predators (i.e. human shield hypothesis) (Berger 2007, Rogala et al. 2011). However, generalist predators (i.e. red fox (*Vulpes vulpes*) or crows (*Corvus spp.*), which also prey on capercaillie) are often attracted to recreational infrastructure, both for easy movement and food scraps (Macdonald 1980, Storch & Leidenberger 2003), therefore the predator shield hypothesis is not applicable in the case of capercaillie. The increased use of areas by generalist predators might even represent an additional cause for avoidance of areas close to recreation infrastructure. My thesis therefore provides evidence that the risk disturbance hypothesis (Frid & Dill 2002) as well as the landscape of fear concept (Laundré et al. 2010) are applicable for both study species, while also revealing the limitations of habituation to human presence for capercaillie.

Mitigating negative effects of recreation on wildlife

The fact that the response of wildlife to recreation can be modulated by a wide range of factors (Tablado & Jenni 2017) implicates practical options for mitigation measures. Due to the economic importance (Balmford et al. 2015) and the fact that recreation activities are an important ecosystem service (De Groot et al. 2010, Paracchini et al. 2014), managers of nature areas are faced with the challenge of both ensuring attractive possibilities for outdoor recreation activities and the conservation of wildlife. Previous studies have pointed out a variety of options to avoid or mitigate negative effects of recreation activities on wildlife (Steven et al. 2011, Larson et al. 2016). The results of my doctoral thesis reveal new mitigation approaches helping practitioners managing nature areas, but also show limits up to which negative effects of recreation activities on wildlife can be buffered by management.

Temporal restrictions

The first chapter reveals the importance of restricting nocturnal activities: the deer adapted to the diurnal pattern of human recreationists, if recreation activities are performed both during night as well as during day this temporal adaptation is not possible and is therefore highly likely to be detrimental for the deer, as important resources in near recreation infrastructure are no longer accessible. Temporal restrictions can be an important management measure which can help species who can temporally adapt to human presence, it is however important to note that not all species can change their natural behaviour to become nocturnal (e.g. capercaillie). Capercaillie show longer avoidance distances in winter (320 m) compared to summer (145 m) (chapter 2). Therefore it is also an option to restrict the access to recreational infrastructure seasonally (i.e. in winter), to reduce negative effect of recreation infrastructure on wildlife.

Habitat management

Another option is to actively manage the habitats: in chapter two I show that capercaillie show less avoidance to recreation activities when a dense shrub layer along recreational infrastructure is present. Reducing visibility along recreational infrastructure can simultaneously reduce the distance up to which recreation infrastructure is avoided and consequently limit the effective habitat reduction caused by the avoidance of otherwise suitable habitats. By looking at an integrated index of structural habitat suitability in chapter four I reveal that capercaillie show less avoidance of recreational infrastructure in highly suitable habitats (with both good foraging and hiding possibilities), compared to poorly suited habitats. By increasing the structural habitat suitability, it is therefore possible to reduce negative effects of recreation activities. This mitigating effect however is limited, as there seems to be a threshold (i.e., in the case of capercaillie, if more than 50% of the habitat is influenced by recreation activities) above which population densities are affected, independently of the habitat suitability.

Many studies recommend the creation of wildlife refuges in which recreation activities are banned or restricted (Larson et al. 2016). However, defining well-founded, species-specific criteria for the size, amount, distance to infrastructure and quality of such refuges remains a difficult question. My thesis provides some answers on these aspects, which can be combined for systematically planning wildlife refuges.

Case example: designating wildlife refuges for capercaillie in the Black Forest

A frequently recommended mitigation measure to reduce negative effects of recreation activities on wildlife is to designate refuges, with restricted access (Braunisch et al. 2011, Larson et al. 2016, Coppes et al. 2017). In such refuges, human use can be restricted at all times, or only for specific times of the year, for example in the breeding season of a target species (Wilson & Hamilton 2005). Restrictions can also be applied temporally (Steven et al. 2011), for example permitting recreational activities during the day but not during the night. This so called the zonation approach and is often applied in large protected areas such as national parks (Dudley 2008, Solár et al. 2014). Based on the results of my field study, several criteria were defined which can be used to determine suitable locations for wildlife refuges, as well as optimizing wildlife refuges to be beneficial for the target species. Here I present how these results can be combined to systematically locate and optimize wildlife refuges using my model species, the capercaillie in the Black Forest, as a case example. To guide planning and implementation I developed a framework, highlighting the main steps to optimally locate areas suitable for wildlife refuges (Figure 1). First I show how this process can be applied on the scale of the entire Black Forest, to locate areas potentially suitable for designating wildlife refuges. In a second step I combine my results with existing knowledge on the species' ecology as well as with known factors playing an important role in landscape planning, to illustrate how a municipality can prioritize these potential areas to locate the most suitable areas for designating as refuge both from an ecological, and a landscape planning perspective.

Framework

The goal of a wildlife refuge is to create areas in which the target species is disturbed as little as possible by human recreation activities. In an area which is currently intensively used for recreation, designating new refuges would imply the closure of recreation infrastructure. Since this is usually a very unpopular decision, I assume that it generally is easier to designate a refuge in a currently "undisturbed area" compared to an area which is currently intensively used for recreation. After determining the target species, the first step would be to find currently undisturbed areas (i.e. potential refuges) that are relevant for the species (i.e. species distribution area, potentially suitable habitats), while at the same time including factors relevant for landscape planning (Figure 1). For defining "undisturbed", species-specific thresholds (e.g. distance thresholds of avoidance or stress response) have to be taken into account. In a second step these potential refuge areas can be ranked based on a variety of factors, species-specific and from the landscape planning perspective, to find the most suitable locations. If no or little undisturbed areas are found, the effects of recreation activities may be reduced by other management options such as visitor steering, habitat management or by strategically reducing the spatial extent of recreation infrastructure (Figure 1). In the following figure the different steps in this process are outlined in detail using the example of capercaillie in the Black Forest.

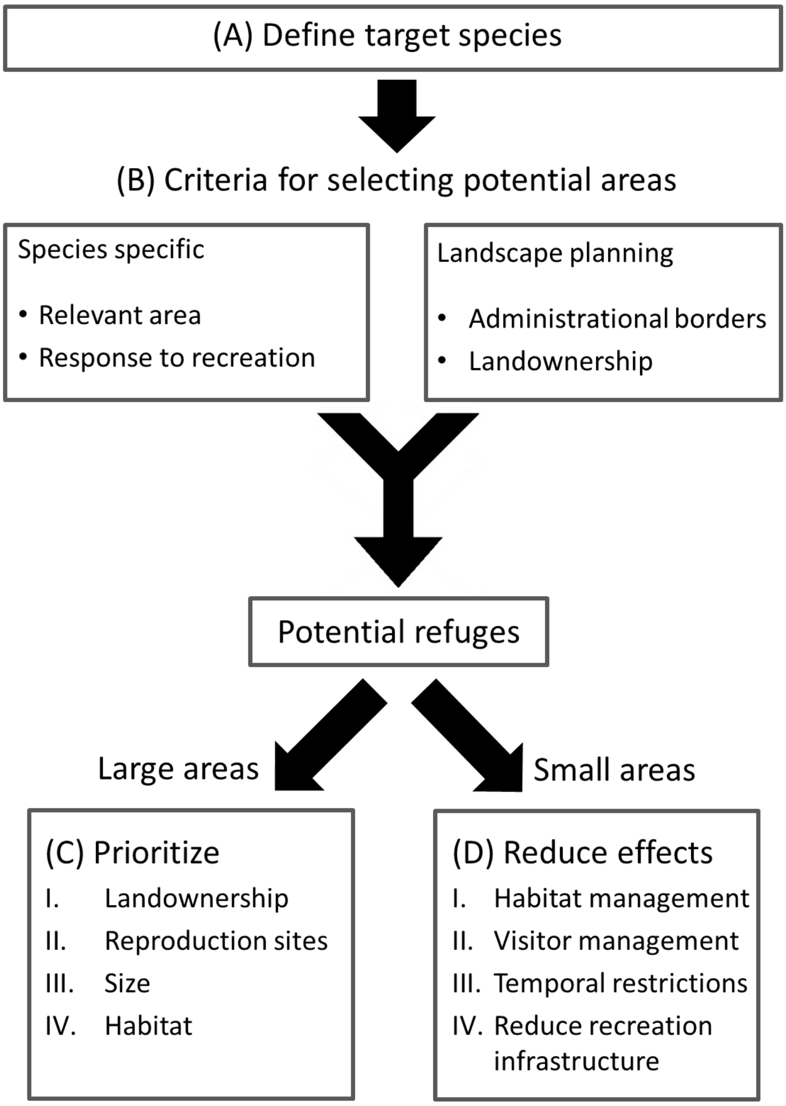

Figure 1: Framework outlining the main steps (B) to systematically determine areas suitable to designate wildlife refuges (potential refuges). Depending on whether large areas or only small areas are available, options for optimal designation or mitigation measures efforts are given (i.e. criteria for prioritizing areas (C) for designating wildlife refuges in the case of large patches or reducing effects of recreation activities (D) in the case of small patches respectively).

(A) Target species - capercaillie

In this case study I apply the framework to the capercaillie population inhabiting the Black Forest, a mountain range in south-western Germany (Figure 2). Recreation and touristic activities have been increasing for the last 30 years in the Black Forest, making it one of the most important economic incomes for the region (Gebhardt 2016). The capercaillie population in the Black Forest has been decreasing over the last decades (Coppes et al. 2016), and is considered to be threatened with extinction (Bauer et al. 2016). During early spring capercaillie males aggregate at lekking sites for mating (Potapov & Sale 2013), and the species is considered an umbrella species for structurally rich, coniferous dominated forests (Suter et al. 2002, Pakkala et al. 2003). Several studies indicate negative effects of recreational activities on capercaillie (chapter 2,3 and 4 of this study) (Summers et al. 2007, Thiel et al. 2011, Moss et al. 2014, Rösner et al. 2014)), which is why minimizing these effects is a key measure for capercaillie conservation in the Black Forest.

(B) Criteria for selecting potential areas

Relevant area

After selection of the target species, determining the region and area relevant to search for wildlife refuges is the next essential step. Due to its sensitivity to recreation activities (Summers et al. 2007, Thiel et al. 2011, Moss et al. 2014, Rösner et al. 2014), and its threatened status in the Black Forest (Bauer et al. 2016, Coppes et al. 2016), the entire capercaillie distribution area (4566.6 km^2) is considered relevant for prospecting for wildlife refuges.

Recreation types – avoidance distance

During summer the main recreation types are hiking and mountain biking with both being facilitated with designated trails. In winter recreational infrastructure includes skiing pistes, cross-country skiing trails, winter hiking trails, snowshoeing trails and back country skiing is also performed both on and off designated trails. To locate all recreation infrastructure, I used the database of the Tourism and Recreation Information System TFIS Baden-Wurttemberg, Germany (www.lgl-bw.de). However, this database only includes data on official trails and no information on snowshoeing trails and back-country skiing areas, therefore I complemented the recreation dataset with data provided by specific user groups on the internet. I included data from websites on which both private persons, as well as official municipal touristic organisation, publish tracks of tours which they advise for recreational purposes: (www.outdooractive.de, www.gpsies.com, www.bergfex.de). Since I found a reduced habitat use of capercaillie within an average distance to recreation activities of 145 meters in summer, and 320 meters in winter, (chapter 2) I used these values to buffer summer and winter recreational infrastructures respectively, to find the areas of the capercaillie distribution which are potentially disturbed by recreation activities as well as areas which are currently undisturbed (i.e. potential refuges) (Figure 2).

Administrational borders and landownership

Because the responsible administrational unit for designating wildlife refuges in the Black Forest is the municipality, and landownership is an important factor influencing the decision of designating a refuge I attributed all resulting potential refuges to their respective municipality and landownership (i.e. state, communal or privately owned).

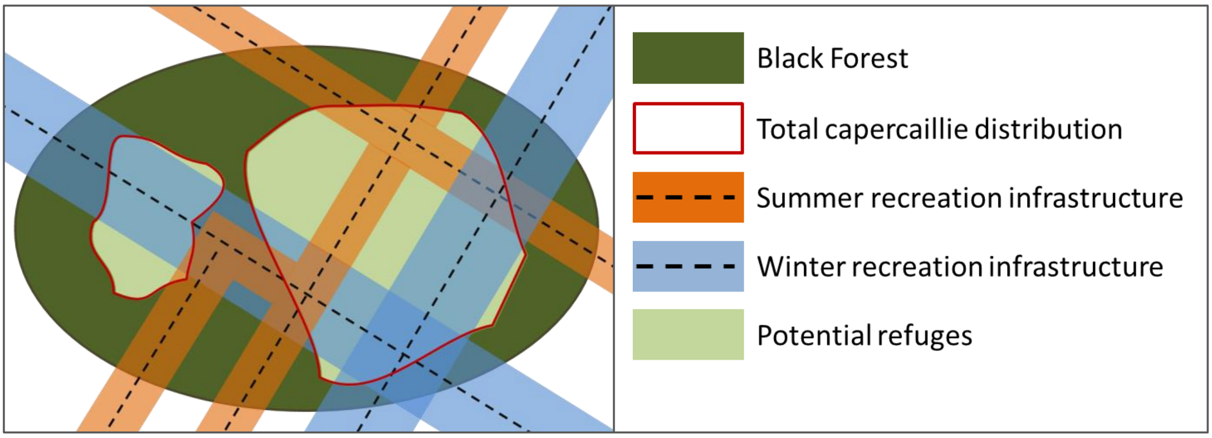

Figure 2: Schematic illustration showing how the potential area for designating refuges within the Black Forest capercaillie distribution were located by applying the avoidance distances (145 and 320m) around summer and winter recreation infrastructure respectively.

The combination of the relevant area (i.e. entire capercaillie distribution in the Black Forest (4566.6 km^2)) with the areas currently potentially disturbed by recreation infrastructure (i.e. within 145 or 320 m of summer and winter recreation respectively) revealed the areas which are currently undisturbed by recreation (Figure 3). After intersecting the undisturbed areas with the municipalities and land ownership, 828 patches, with a total surface of 1492.5 km^2 were located (Figure 3, Table 1). The mean size of these potential refuges was 0.18 km^2 (SD 0.44 km^2, range: 0.001-6.33 km^2). The majority of these areas are on state owned forests (799.5 km^2), followed by private owned forests (361 km^2) and communal owned forests (331.9 km^2, Table 1).

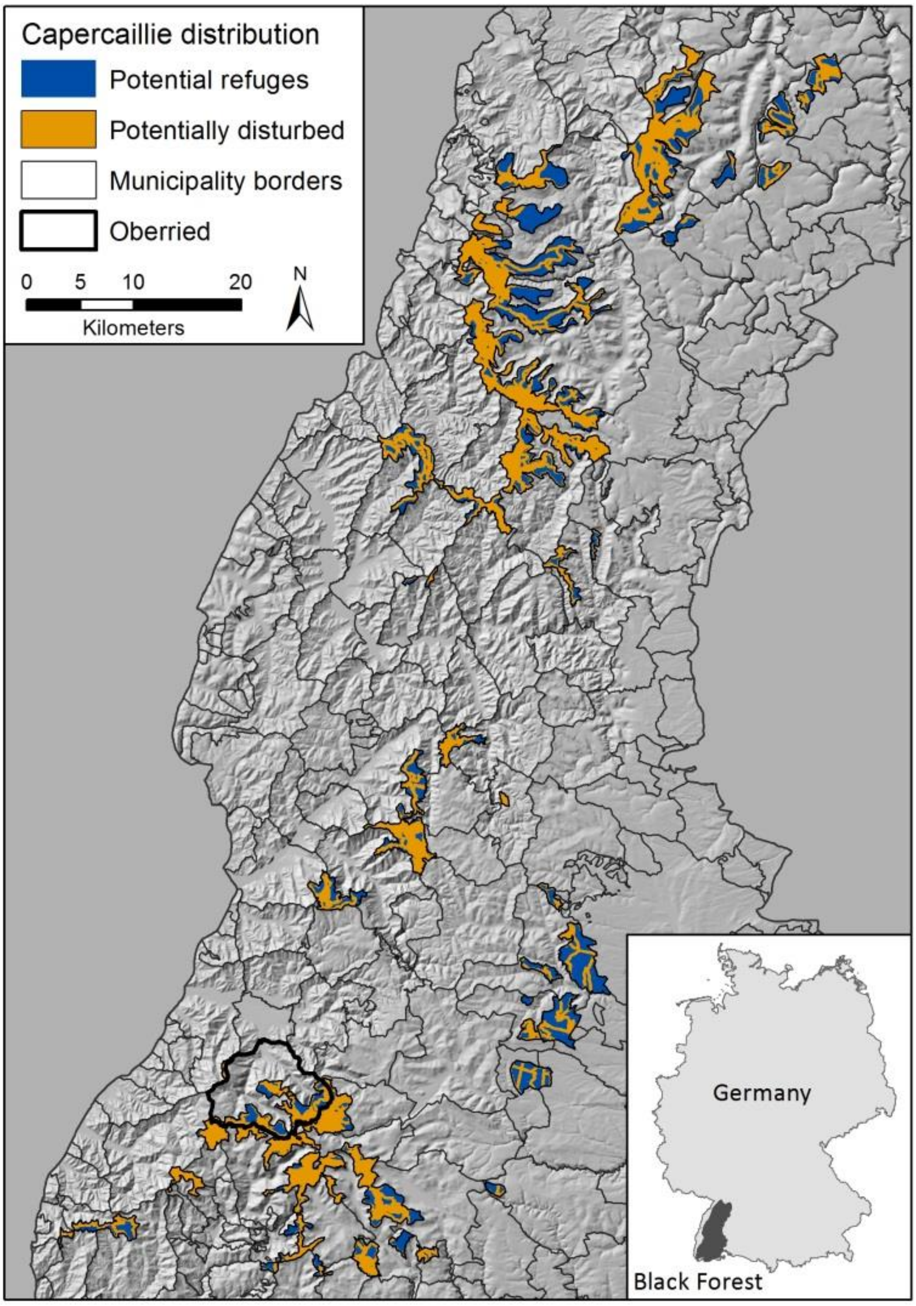

Figure 3: Capercaillie distribution (coloured patches) in the Black Forest and borders of the municipalities (black lines). Parts of the distribution area within 145 m or 320 m of summer and winter recreation infrastructure respectively are considered potentially disturbed (orange). Areas further away are considered potential refuges (blue). The municipality of Oberried (example region of Figure 4) is marked in bold. The inlay map shows the Black Forest within Germany.

Table 1: Area and number of the potential refuges in the Black Forest for capercaillie, which are currently undisturbed by recreation infrastructure (i.e. at least 145 m and 320 m distance to summer and winter recreation infrastructure respectively), total and divided by landownership. The last column shows the proportion of potential refuges of the capercaillie distribution in the Black Forest (4566.6 km^2 (Coppes et al. 2016)).

	Area (km^2)	Number	% of total capercaillie distribution
Total potential refuges	1492.5	828	32.7
Potential refuges in state forests	799.5	309	17.5
Potential refuges in communal forests	331.9	246	7.3
Potential refuges in private forests	361.0	273	7.9

(C) Prioritization

Because there are a large number of potential refuges (Table 1), it is important to prioritize which refuges to designate. Since capercaillie avoid recreation infrastructure for long distances (i.e. on average 320 m in winter (chapter 2)), the refuge should not be too small, else negative effects of the recreation activities will still affect the capercaillie: for example, if a circular area of 0.32 square kilometre is surrounded by a winter recreation trail, the entire area is within 320 meter of this infrastructure. Therefore refuges should be relatively large, to ensure a sufficient area undisturbed by recreation activities. Capercaillie aggregate on group lekking sites during the mating season (Potapov & Sale 2013), and disturbance in such areas is considered to be especially detrimental. Therefore, a species-specific criteria could be to prioritize the designation of refuges in areas where known lekking sites are present. Apart from species-specific, biological criteria for prioritization, one of the most important planning criteria is landownership: as designating a refuge in a private owned forest is unlikely, prioritizing areas in state or communal forest will be more promising for successfully designating a wildlife refuge.

Example: Prioritizing in the municipality of Oberried

To demonstrate how the prioritization works in detail I show the process for one municipality as an example region: Oberried. The municipality of Oberried belongs to the district of Breisgau-Hochschwarzwald and is located in the southern Black Forest (Figure 2). Recreation and tourism is of major economic importance and the municipality includes significant recreational infrastructures such as hiking trails, mountain biking trails, cross-country skiing trails and skiing pistes (Figure 4 panel B). Capercaillie inhabit the forests in the higher altitudes, on an area of ca. 200 km^2 (Figure 4 panel A). The spatial analysis of the recreation infrastructure in the capercaillie habitats, resulted in a total of 37 potential refuges (i.e. >145 m and >320 m away from summer and winter recreation respectively) on a total of 64.7 km^2. The size of the potential refuges varied between 0.002 km^2 and 1.27 km^2.

The majority of the potential refuges are located in state owned forest (42.5 km^2), followed by communal forests (12.5 km^2) and private forests (9.6 km^2). In five of the potential refuges there is a capercaillie lekking site present (Figure 4 panel E). When combining the information on landownership (i.e. preferred designation on state or communal forests, Figure 4 panel C), with the size of the refuges (i.e. goal to designate large refuges, Figure 4 panel D) and the location of lekking sites (Figure 4 panel E), this reveals there are three potential refuges which are over 0.65 km^2, communal or state owned and hold a capercaillie lekking site (Figure 4). When the municipality of Oberried would like to designate a wildlife refuge, based on the above criteria, the largest would be most likely to benefit capercaillie the most (Figure 4 panel F). The municipality might however also rank these or other criteria based on their own experience (for example on habitat suitability) or other requirements.

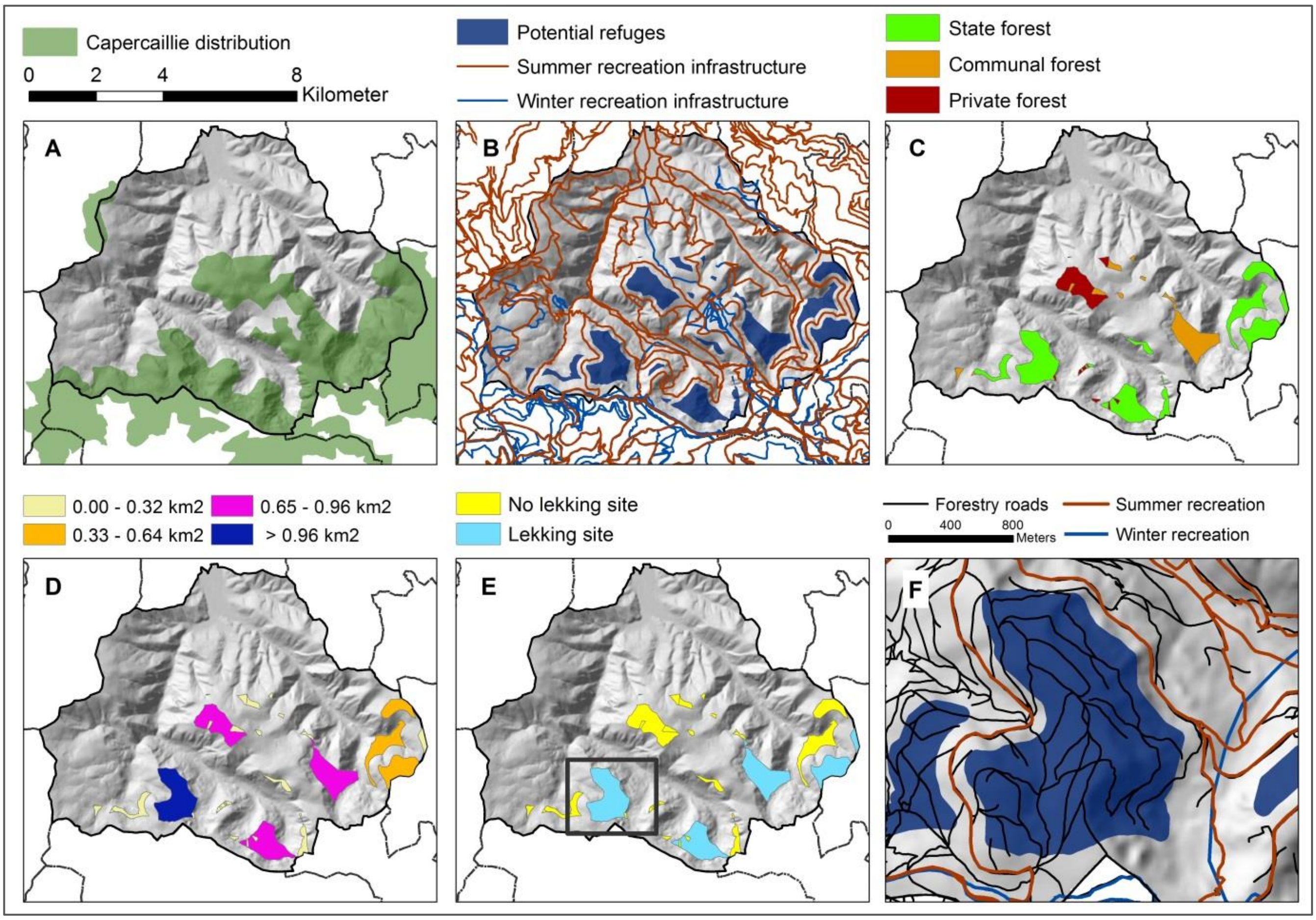

Figure 4: Maps showing the municipality of Oberried and the area inhabited by capercaillie in the municipality (panel A), the recreational infrastructure in the municipality with the remaining “undisturbed areas” (i.e. potential refuges, panel B) as well as the potential refuges depicted based on their landownership (panel C), their area (panel D), and whether there is a capercaillie lekking site in the potential refuge (panel E). The black square in panel E indicates the extent of panel F. Panel F shows a detailed view of the potential refuge with the largest surface, within state owned forests and which also includes a lekking site.

(D) Reducing effects of existing recreation infrastructure

If large part (i.e. >50%) of an area are potentially disturbed by recreation activities, there might be negative effects on capercaillie densities (chapter 4). Since only 32.7 % of the current distribution area is not potentially disturbed (Table 1), negative effects of existing recreation infrastructures should be reduced to minimise adverse impacts on the capercaillie population. My thesis provides several management options to reduce the effects of existing recreation infrastructure on wildlife. The avoidance distance of capercaillie was lower in stands with a dense shrub layer, compared to in more open stands (chapter 2). Therefore the avoidance distance can be reduced by keeping or creating a dense shrub layer along recreational trails, effectively reducing the habitat deterioration caused by recreational activities. Furthermore, keeping a dense shrub layer can additionally reduce the number of people leaving trails, thus reducing disturbance by "off-trail" activities (Coppes & Braunisch 2013). Chapter 4 reveals another option to reduce negative effects of recreation infrastructure on capercaillie: plots close to recreation infrastructure with highly suitable structural habitat suitability (i.e. intermediate canopy cover, intermediate height and high cover of bilberry (*Vaccinium myrtillus*)) were avoided less compared to plots with low structural habitat suitability. Therefore the avoidance of recreational trails by capercaillie can be reduced by improve the structural habitat suitability (chapter 4). Another management option is to restrict nocturnal activities on recreation infrastructure (chapter 1) as well as optimizing visitor steering systems (Freuler & Hunziker 2007, Behrens et al. 2009), or if no other options are available, to close or move existing recreational infrastructure. In this case, my spatial analysis can help determine which recreational infrastructure should optimally be closed or moved to create large areas with little disturbance from recreation infrastructure on capercaillie.

By combining the results of my doctoral thesis with existing knowledge on the capercaillie ecology and factors important for landscape planning, my framework can be applied to systematically locate areas suitable for designating wildlife refuges on a landscape scale. This framework is transferable to other species, given the basic information about their distribution and response towards recreation infrastructure is known.

Outlook

By applying and combining established methods in wildlife research, my doctoral thesis has revealed further insights in the responses of wildlife to recreation activities both for researchers in the field of recreation ecology and practitioners managing nature areas. A methodological drawback from my studies is that I could only analyse recreation activities indirectly by using recreation infrastructure as a proxy. Future studies should directly assess the effects of recreation activities, for example by using an experimental set up, or by including detailed information on the recreational users' spatial and temporal behaviour using visitor counters or transmitters.

For conservation relevant species (i.e. locally threatened or declining), further studies on recreation effects can help to reveal both management options, as well as provide a basis for decisions on the authorisation of new recreation activities. How species behavioural reactions to recreational activities affect fitness and consequently affect population numbers is an important link which must be further studied (Storch 2013). The physiological stress response of wildlife to human presence has been shown in various studies (Arlettaz et al. 2007, Thiel et al. 2011, Rehnus et al. 2014, Arlettaz et al. 2015), the relationship between this stress response and an individual's fitness however also remains underexposed. Although I was able to reveal habitat deterioration due to avoidance of areas with intensive recreational use (chapters 1, 2 and 4), it is difficult to quantify the effect on population scale. It would be important for future studies to look at direct factors of recreation activities and how they influence population dynamic parameters, such as survival, reproduction and mortality (Gill 2007).

For species which are not threatened, but still impacted by recreation activities (e.g. red deer), it would be of interest what the side-effects of the behavioural response are. For deer it has been suggested that the behavioural response (i.e. fleeing or hiding in dense forest patches), causes increased damage to forestry due to bark stripping (Reimoser 1988) or additional deer-car collisions (De Vries 2015). It would be highly relevant to study if and how such indirect effects are caused by recreation activities and might reveal mitigation measures to reduce human-wildlife conflicts. With mitigation measures becoming increasingly important (Sutherland 2007, Buckley 2013), the effectiveness of mitigation measures such as the designation of wildlife refuges must be studied (Sutherland 2007). Future studies should also include social science, on how to inform and steer visitors of nature areas most effectively, to enable both recreation activities, as well as the protection of wildlife. Although there are still many questions to be answered on the effects of recreation activities on wildlife, this should not hinder any actions to mitigate these effects. My thesis highlights that the response of wildlife to recreation activities can be complex and modulated by a variety of factors, which future researchers need to take account in their studies, and practitioners need to consider for designing effective measures.

Summary

Human outdoor recreation activities (i.e. hiking, mountain biking, cross-country skiing) are increasing in numbers, and are economically important in many parts of the world, including the Black Forest. These recreation activities exert pressure on the ecosystems in which they take place and in many cases are a threat to a variety of wildlife species. There are many ways in which wildlife can be impacted by outdoor recreation and tourism: often species react to the presence of humans in a similar way as to the presence of predators, resulting in anti-predator responses. The increase in recreational activities therefore causes an increase in anti-predator costs for wildlife. Some species are attracted to human recreation activities and others have been shown to habituate to human presence, resulting in reduced reactions to humans over time. There are however increasing number of studies indicating negative effects of recreation activities on wildlife. The effects range from fleeing, to changes in vigilance behaviour and reduced use of areas which are intensively used by recreational users (i.e. close to infrastructures such as hiking trails or skiing slopes). Recreation activities have also been linked to changes in bird species composition, reduced densities, and reduced breeding success. Physiological effects include an increased heart rate and increased stress hormone levels in areas close to recreation infrastructure. Previous studies however also revealed that the response wildlife to recreation activities might vary between species, areas and habitats. To provide both possibilities for recreation activities as well as to avoid negative effects on biodiversity, it is important to know the type, extent and source of variation to design effective conservation measures. Using two model species, red deer (*Cervus elaphus*) and capercaillie (*Tetrao urogallus*) I studied how the response of wildlife to recreation activities varies under different environmental conditions. From the results I derived management options to mitigate the effects of recreation activities. In the first chapter I analysed GPS telemetry data of red deer to reveal how they have adapted to the diurnal rhythm of recreationists in their habitats. During the day, when recreationists are present, red deer avoid areas close to the recreation infrastructure, however during night, when no recreationists are present; the deer even prefer these areas. This indicates that the deer have temporally adapted their behaviour to avoid human recreationists. At the same time, I was able to show that the deer preferred to use the wildlife refuges (i.e. areas in which recreational activities are prohibited), compared to other management areas.

In the second chapter I studied how capercaillie spatially avoided recreational infrastructure in the Black Forest, using radio telemetry. The birds showed reduced use of areas close to recreation activities all year around, with higher avoidance distances in winter (320 m) compared to summer (145 m), resulting in an effective habitat reduction. By including detailed vegetation data in the analysis, I showed that this avoidance distance is reduced when a dense shrub layer is present, i.e. when the hiding possibilities are better. When extrapolating the area affected by recreation infrastructure (within the avoidance distances) to the entire capercaillie distribution in the Black Forest, I revealed that a large fraction of the current capercaillie distribution (i.e. up to 20 % in summer and 40 % in winter) is potentially disturbed by recreational activities. This indicates that local-scale avoidance of

recreation infrastructure is likely to cause habitat deterioration on a large scale, possibly negatively affecting the capercaillie population in the Black Forest.

By combining the analysis of faecal corticoid metabolites (FCM) with genetic analyses of capercaillie droppings, I was able to reveal the importance of including information on individual heterogeneity in stress responses when studying the effects of recreation activities on wildlife (chapter three). When comparing generalized additive models which included the information on individual heterogeneity (as a random effect) with those not including this information I showed that the results differed greatly. The models without including the data on individual heterogeneity explained only very little (4.0 % and 5.1 %) of the observed variation in FCM-levels. When including the data on individual heterogeneity the explained variation increased significantly (44.0 % and 45.1 %). At the same time the results of the models changed with additional predictors explaining elevated FCM levels appearing significant. The distance to recreation infrastructure was significantly affecting the FCM-levels, with higher FCM-levels close to recreation infrastructure. In this chapter I have demonstrated that individual heterogeneity can explain most of the observed variance in FCM levels and that ignoring this information can lead to erroneous conclusions.

In the fourth chapter I combined data from 13 different study areas to evaluate the effect of structural habitat suitability (HSI) on the response of capercaillie to recreation activities on local habitat use, as well as regional population densities. Data on structural habitat parameters and capercaillie habitat use (i.e. droppings, feathers) were collected on sample plots. The probability of finding a capercaillie sign on a plot was positively correlated with the HSI. This probability however was reduced close to recreational infrastructure. Interestingly I found an interaction between the HSI and distance to recreational infrastructure on the local habitat use scale: the avoidance of recreational infrastructures was stronger in poor habitat conditions compared to highly suitable habitats. The regional capercaillie density was also positively correlated to the average HSI in an area, however significantly lower densities were found when over 50 % of the area was potentially influenced by recreation activities. On this scale however, no interaction between the average HSI and recreation infrastructure was found. Increasing the structural habitat suitability might therefore reduce negative effects of recreational activities on a local habitat use scale, but not on a population scale. The fact that I found a threshold, indicates that capercaillie can cope to some extent with recreational activities, however when this threshold is exceeded, there are negative effects on the population.

The last chapter synthesizes the results of the previous chapters and shows how these can be applied to mitigate negative effects of recreation on wildlife and systematically designate wildlife refuges, using the example of capercaillie. By applying different research methods, study designs and analysis, my doctoral thesis reveals how the response of wildlife to recreational activities can vary temporally, seasonally, between individuals and under different habitat conditions. I was able to not just generate new insights which are relevant for future researchers in the field of recreation ecology, but also provide results which can be practically applied by practitioners managing nature areas.

Zusammenfassung

In den letzten Jahren verzeichnete man eine starke Zunahme von Freizeitaktivitäten, wie Wandern, Mountainbiking oder Skilanglauf. Diese Aktivitäten sind ein wichtiger wirtschaftlicher Einkommensfaktor. Außerdem wird Erholung als eine wichtige Ökosystemfunktion von Naturgebieten betrachtet. Gleichzeitig üben diese Aktivitäten aber Druck auf die Ökosysteme aus, in denen sie stattfinden. Die negativen Auswirkungen von Freizeitaktivitäten auf die Umwelt sind vielfältig und gelten als Bedrohung für eine Vielzahl von Arten. Freilebende Tiere, von hieran als Wildtiere bezeichnet, reagieren auf die Anwesenheit von Menschen häufig ähnlich wie auf die Präzenz von Prädatoren. Der Anstieg der Freizeitaktivitäten führt daher zu vermehrten, aber unterschiedlichen Reaktionen von Wildtieren: So gibt es auch Arten, die von menschlichen Freizeitaktivitäten oder assoziierten Habitatstrukturen (z.B. Randlinien) oder weggeworfenen Essensresten profitieren. Andere Arten haben sich an die Anwesenheit von Menschen gewöhnt, was zu reduzierten Reaktionen auf den Menschen führt. Es gibt jedoch eine zunehmende Anzahl von Studien, die auf negative physiologische Auswirkungen und Verhaltensänderungen bei Wildtieren durch Freizeitaktivitäten hinweisen. Letztere reichen von Flucht, über die Änderung des Sicherungsverhaltens bis hin zur verminderten Nutzung von Gebieten, die von Freizeitsportlern intensiv genutzt werden (z.B. in der Nähe von Freizeitinfrastrukturen wie Wander- oder Mountainbikestrecken). Am Beispiel von Vogelarten wurde gezeigt, dass Freizeitaktivitäten auch zu einer Veränderung der Zusammensetzung von Artengemeinschaften führen können. Gründe dafür können Verhaltensänderungen sein, die bei einigen Arten zu vermindertem Reproduktionserfolg und erhöhtem Nestverlust führen. Zu den physiologischen Effekten gehören eine erhöhte Herzfrequenz sowie ein erhöhter Stresshormonspiegel in Bereichen nahe der Erholungsinfrastruktur. Frühere Studien haben jedoch auch gezeigt, dass die Reaktionen von Wildtieren auf Erholungsaktivitäten zwischen Arten, Gebieten und Lebensräumen variieren können. Dies erschwert es, effektive Lösungen zu finden, um in Gebieten, die als Wildtierlebensraum und als Erholungsraum genutzt werden, Freizeitaktivitäten zu ermöglichen und gleichzeitig Wildtiere zu schützen.

Anhand von zwei Modellarten (Rothirsch *Cervus elaphus* und Auerhuhn *Tetrao urogallus*) habe ich Gründe für räumliche, zeitliche und individuelle Variabilität in der Reaktion auf Freizeitnutzung innerhalb von Populationen sowie regionale Variabilität zwischen Populationen beleuchtet. Die Ergebnisse sollen Anhaltspunkte für effiziente Managementmethoden und wildtierökologische Fachkonzepte geben, um die Auswirkungen von Erholungssuchenden auf Wildtiere zu reduzieren.

Im ersten Kapitel analysierte ich GPS-Telemetriedaten von Rothirschen, um zu untersuchen, wie sich die Tiere an tageszeitlich unterschiedliche Nutzung ihrer Lebensräume durch Erholungssuchende angepasst haben. Während des Tages, wenn Menschen anwesend sind, vermeiden Rothirsche die Gebiete in der Nähe der Freizeitinfrastrukturen (z.B. Wanderwege, Mountainbikestrecken). In der Nacht hingegen, wenn keine Erholungssuchenden präsent sind, nutzen die Hirsche diese Bereiche bevorzugt. Dies zeigt, dass die Hirsche ihr Verhalten zeitlich angepasst haben, um menschliche Erholungssuchende zu vermeiden und trotzdem die während des Tags nicht verfügbaren Ressourcen nahe der Wege zu nutzen. Gleichzeitig

konnte ich zeigen, dass Hirsche Wildruhezonen (Gebiete in denen Freizeitaktivitäten im Vergleich zu anderen Bereichen eingeschränkt sind) bevorzugt aufsuchen.

Im zweiten Kapitel habe ich untersucht, wie Auerhühner Freizeitinfrastrukturen in Abhängigkeit von der Jahreszeit und der Nutzungsart meiden. Die Vögel zeigten eine verminderte Nutzung von Gebieten in der Nähe von Freizeitaktivitäten mit höheren mittleren Meidungsdistanzen im Winter (320 m) im Vergleich zum Sommer (145 m). Die Gebiete, die näher an den Freizeitinfrastrukturen liegen, stehen den Auerhühnern daher nicht uneingeschränkt zur Verfügung, was effektiv zu einer Lebensraumverschlechterung führt. Zudem konnte ich nachweisen, dass sich die Meidungsdistanz beim Vorhandensein einer dichten Strauchschicht reduziert. Dies zeigt, dass die Vögel weniger Meidung zeigen, wenn Sichtschutz vorhanden ist. Bei der Extrapolation der Meidungsdistanzen auf die gesamte Auerhuhnverbreitung im Schwarzwald konnte ich zeigen, dass große Teile des aktuellen Verbreitungsgebietes innerhalb der oben genannten Meidungsdistanzen liegen. Im Sommer können bis zu 20 % und im Winter bis zu 40 % des derzeitigen Verbreitungsgebietes durch Freizeitinfrastrukturen gestört werden. Dadurch, dass solche großen Flächen betroffen sind, könnte die Meidung von Freizeitinfrastrukturen sich möglicherweise negativ auf die Auerhuhnpopulation im Schwarzwald auswirken.

Durch die Kombination der Analyse von Corticosteroidmetaboliten (Stresslevel) und der genetischen Analyse von Auerhuhnkotproben konnte ich in Kapitel drei die Bedeutung inter-individueller Heterogenität bei der Untersuchung der Auswirkungen von Erholungsaktivitäten auf Wildtiere aufzeigen. Beim Vergleich von generalisierten additiven Modellen, die Informationen zum Individuum enthielten, von dem eine Probe stammte, mit denen, die diese Information nicht enthielten, zeigte sich, dass die Ergebnisse sehr unterschiedlich sein können. Die Modelle ohne die Daten zur inter-individuellen Heterogenität erklärten nur sehr wenig (4.0 % und 5.1 %) der beobachteten Variation der Stresslevel. Bei Einbeziehung der Daten zur inter-individuellen Heterogenität erhöhte sich der Anteil der erklärten Variation signifikant (44.0 % und 45.1 %). Gleichzeitig veränderten sich die Ergebnisse der Modelle: Wurde die Information zum Individuum nicht berücksichtigt, erschienen zusätzliche Prädiktoren signifikant. Die Entfernung zur Erholungsinfrastruktur beeinflusste jedoch in beiden Modellen signifikant die Stresslevel, mit höheren Levels in der Nähe der Erholungsinfrastruktur. Es gelang zu zeigen, dass individuelle Heterogenität den größten Teil der beobachteten Varianz der Stresslevel erklären kann und dass das Ignorieren dieser Information falsche Schlussfolgerungen zur Folge haben kann.

Im vierten Kapitel kombinierte ich Daten aus 13 verschiedenen Untersuchungsgebieten, die über einen Zeitraum von 13 Jahren gesammelt wurden, um die Auswirkungen der strukturellen Habitateignung (Habitateignungsindex HSI) auf die Reaktion von Auerhühnern auf Freizeitaktivitäten zu untersuchen. Hierbei standen die Auswirkungen auf zwei Skalenebenen im Fokus: auf die lokalen Habitatnutzung sowie auf die regionalen Dichten. Daten zu strukturellen Habitat-Parametern und zur Auerhuhn-Habitatnutzung (indirekte Nachweise wie Federn und Kot) wurden an Probepunkten in einem regelmäßigen Raster gesammelt. Die Wahrscheinlichkeit, Auerhuhn-Nachweise zu finden, wurde durch den HSI auf beiden Skalenebenen beeinflusst. An Probepunkten mit einem hohen HSI war die

Wahrscheinlichkeit, einen Auerhuhn-Nachweis zu finden, höher als in Gebieten mit geringem HSI. Diese Wahrscheinlichkeit wurde jedoch in der Nähe von Erholungsinfrastrukturen reduziert. Interessanterweise fand ich eine Interaktion zwischen dem HSI und der Entfernung zur Freizeitinfrastruktur: Die Vermeidung von Freizeitinfrastrukturen ist bei schlechter Habitateignung stärker als bei einer hohen Habitateignung. Auch die Auerhuhndichte war positiv mit dem durchschnittlichen HSI in einem Gebiet korreliert, jedoch wurden signifikant niedrigere Dichten gefunden, wenn mehr als 50 % der Fläche potentiell durch Freizeitaktivitäten beeinflusst waren. Auf der regionalen Ebene wurde jedoch keine Interaktion zwischen dem durchschnittlichen HSI und der Erholungsinfrastruktur gefunden. Eine Erhöhung der strukturellen Habitateignung kann daher negative Auswirkungen von Freizeitaktivitäten auf die lokale Habitatnutzung teilweise reduzieren, dies funktioniert jedoch nicht auf der Populationsebene. Die Tatsache, dass ich einen Schwellenwert gefunden habe, ab dem Freizeitinfrastrukturdichten negative Auswirkungen haben, deutet darauf hin, dass Auerhühner in gewissem Maße mit Freizeitaktivitäten zurechtkommen können. Wird das Maß jedoch überschritten, kann dies negative Auswirkungen auf die lokale Population haben.

Im letzten Kapitel verbinde ich die Ergebnisse der vorhergehenden Kapitel und zeige, wie diese zur systematischen Ausweisung von Wildruhegebieten für Auerhühner angewendet werden können. Durch die Anwendung verschiedener Forschungsmethoden, Studiendesigns und Analysen, zeigt meine Doktorarbeit, wie unterschiedlich die Reaktionen von Wildtieren auf Freizeitaktivitäten zeitlich, je nach Individuum und unter verschiedenen Habitatbedingungen sein können. Ich konnte daher nicht nur relevante Erkenntnisse für zukünftige Forschungstätigkeit generieren, sondern auch Ergebnisse liefern, die von PraktikerInnen angewendet werden können, um negative Auswirkungen von Freizeitaktivitäten auf Wildtiere zu reduzieren.

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Appendix

Supplementary material chapter I

Table S1: Number of locations per individual used for analysis. Number of locations per individual per season and time of the day used for the analysis and the period of tracking. The age was roughly estimated in three classes at the time of tagging (1 = 1-3 years, 2 = 3-5 years, 3 = >5 years old).

		Summer			Winter			
Individual ID	Age	Total	Day	Night	Total	Day	Night	Months tracked
Females								
101	1	818	411	407	2169	1004	1165	29
103	2	525	261	264	671	295	376	22
104	2	341	170	171	999	468	531	16
105	3	348	185	163	945	430	515	18
106	1	485	241	244	1452	633	819	23
107	1	527	263	264	1572	700	872	24
108	1	521	261	260	1637	709	928	24
109	1	518	261	257	1389	605	784	22
110	1	149	75	74	95	35	60	5
111	1	268	135	133	137	126	11	9
Males								
201	3	302	150	152	223	34	189	12
203	1	564	282	282	1847	782	1065	25
204	1	825	413	412	2311	1052	1259	34
205	1	683	348	335	628	241	387	28
206	1	510	253	257	834	358	476	20

Table S2: Models explaining habitat selection within the home range, when not discriminating between different times of the day. Left panel: summer, right panel: winter. Significance levels are indicated with: * p≤ 0.05, ** p≤ 0.01, and *** p≤ 0.001.

	Summer (AUC = 0.624 +- 0.007) STD (Individual): 0.041				Winter (AUC: 0.803 +- 0.008) STD (Individual): 0.462		
Type	Variable	Estimate	SE	Sign.	Estimate	SE	Sign.
	INTERCEPT	0.296	0.102	**	-1.164	0.466	**
Vegetation	CAN_CON	-0.566	0.253	*	0.571	0.471	
	CAN_DEC	-0.575	0.383		0.080	1.010	
	CAN_CONMIX	-0.463	0.253		0.267	0.473	
	CAN_DECMIX	-0.466	0.259		-0.257	0.495	
	SUC_REG_THICK	1.635	0.261	***	0.907	0.479	.
	SUC_POLE	1.011	0.254	***	-0.020	0.472	
	SUC_TREE	0.726	0.252	**	0.672	0.469	
	SUC_OLD	0.594	0.255	*	1.020	0.475	*
	UNDER_CON	0.291	0.063	***			
	UNDER_DEC	1.208	0.159	***			
	UNDER_CONMIX	0.489	0.049	***			
	UNDER_DECMIX	0.063	0.058				
	CANOPY_COVER	-0.024	0.001	***			
	PROTECT_S	-0.005	0.001	***			
Landscape	EASTING	-0.106	0.025	***	-0.492	0.048	***
	SLOPE	0.012	0.003	***	-0.030	0.005	***
	ALTITUDE				0.003	<0.001	***
Human	MGT_CORE	1.564	0.072	***	-0.669	0.092	***
	MGT_REFUGE	1.908	0.083	***	0.447	0.118	***
	ROAD	0.602	0.038	***	1.405	0.094	***
	TOURI_S/W	-0.498	0.116	***	0.722	0.139	***
	HUNT	0.651	0.065	***			
	SETTLE	0.061	0.031	*			
	FEED				1.276	0.056	***

Table S3: Results of the variable selection process to reach the final models presented in Table 3 and 4. The first column shows all variables which were included in the model selection process. Each of the other columns represents one of the six final models: “HRinSA” = home range selection within study area, “inHR” = habitat selection within home range. Variables denominated with a “+” are included in the final model, otherwise the reason for exclusion is indicated: A variable name indicates exclusion due to pairwise correlation (Spearmans R >|0.5|) with this variable, “-“ indicates exclusion during the model selection process based on AIC as described in the methods part, “VIF” indicates this variable is excluded from the model due to a too high variance inflation factor value. Proximity of feeding stations (FEED) was not included in the summer models as no feeding was performed in summer.

Variables tested	HRinSA summer	HRinSA winter	inHR summer day	inHR summer night	inHR winter day	In HR winter night
DHM	-	SETTLE	SETTLE	GREENL	-	-
SLOPE	+	-	+	+	-	+
NORTHING	-	+	+	-	+	+
EASTING	-	+	+	+	+	+
WATER	+	+	+	+	-	+
GREENL	FOREST250	-	FOREST_250	ROAD	-	-
FOREST_250	+	-	+	ROAD	-	-
CANOPY_TYPE	+	-	-	+	+	-
CANOPY_COV	HERB_GRAS	+	+	+	+	VIF
SUCCESSION	+	+	+	+	-	+
UNDER_COV	+	-	-	-	PROTECTION	-
UNDER_TYPE	-	-	+	-	-	-
BILBERRY	+	-	+	+	-	-
HERB_GRAS	+	-	CANOPY_COV	CANOPY_COV	-	-
PROTECTION_S/W	+	+	+	CANOPY_COV	-	+
TOURI_S/W	+	-	+	+	+	+
TOURI_DENS_S/W	TOURI_S/W	TOURI_S/W	TOURI_S/W	TOURI_S/W	TOURI_S/W	TOURI_S/W
ROAD	+	+	-	+	-	+
SETTLE	+	+	-	+	-	-
FEED	Not included	+	Not included	Not included	+	+
HUNT	+	+	+	+	+	+
CONCEPT	+	+	+	+	+	+

Table S4: Final models (provided in Tables 3 and 4) in comparison to the next-best candidate models as obtained during the model selection process. All candidate models with a ΔAIC < 2 to the final model (in bold) as well as the first model with ΔAIC > 2 are shown. Only for the model describing home range selection in the study area during summer (Table 3a) the next four candidate models were not significantly different to the final model (i.e. ΔAIC < 2), so model averaging was applied (Table S5).

Selection of home range in study area: summer

NR	INTERCEPT	BILBERRY	CANOPY TYPE	FOREST250	MGT	HERB_GRAS	HUNT	PROTECT_S	SETTLE	SLOPE	SUCCESSION	TOURI_S	WATER	df	logLik	AIC	delta
2752	**-1.9042**	**-0.0084**	**+**	**0.5254**	**+**	**0.0175**	**-0.0018**	**NA**	**0.0003**	**NA**	**+**	**NA**	**-0.0011**	**18**	**-12087.5**	**24210.9**	**0.00**
3008	**-1.8626**	**-0.0084**	**+**	**0.5256**	**+**	**0.0174**	**-0.0018**	**NA**	**0.0003**	**-0.0033**	**+**	**NA**	**-0.0012**	**19**	**-12086.8**	**24211.7**	**0.71**
4032	**-1.8453**	**-0.0085**	**+**	**0.5595**	**+**	**0.0176**	**-0.0018**	**NA**	**0.0003**	**-0.0043**	**+**	**-0.0002**	**-0.0011**	**20**	**-12086.0**	**24212.0**	**1.05**
3776	**-1.9002**	**-0.0085**	**+**	**0.5501**	**+**	**0.0176**	**-0.0018**	**NA**	**0.0003**	**NA**	**+**	**-0.0001**	**-0.0011**	**19**	**-12087.0**	**24212.0**	**1.06**
2816	**-1.9048**	**-0.0084**	**+**	**0.5257**	**+**	**0.0175**	**-0.0018**	**0.0000**	**0.0003**	**NA**	**+**	**NA**	**-0.0011**	**19**	**-12087.5**	**24212.9**	**2.00**
3072	-1.8618	-0.0084	+	0.5253	+	0.0174	-0.0018	0.0000	0.0003	-0.0033	+	NA	-0.0012	20	-12086.8	24213.7	2.70

Selection of home range in study area: winter

NR	INTERCEPT	EASTING	FEED	HUNT	MGT	NORTHING	PROTECT_W	ROAD	SETTLE	SUCCESSION	TREECOVER	WATER	df	logLik	AIC	delta
2048	**2.9768**	**-1.0539**	**-0.0021**	**-0.0019**	**+**	**-0.2697**	**-0.0100**	**-0.0007**	**-0.0004**	**+**	**-0.0106**	**0.0009**	**17**	**-4140.4**	**8314.9**	**0.00**
1024	3.0491	-1.0648	-0.0020	-0.0019	+	-0.2740	-0.0094	-0.0007	-0.0004	+	-0.0100	NA	16	-4144.9	8321.8	6.91

Selection in home range during summer: day

NR	INTERCEPT	BILBERRY	EASTING	FOREST250	HUNT	MGT	NORTHING	PROTECT_S	WATER	SUCCESSION	TOURI_S	CANOPY_COV	UNDER_TYPE	SLOPE	df	logLik	AIC	delta
8192	**-4.6754**	**-0.0246**	**0.0833**	**1.5835**	**-0.0012**	**+**	**-0.2787**	**-0.0040**	**0.0025**	**+**	**0.0016**	**-0.0128**	**+**	**0.0637**	**22**	**-5997.9**	**12039.8**	**0.00**
8190	-4.6217	-0.0248	NA	1.5719	-0.0012	+	-0.2845	-0.0038	0.0024	+	0.0016	-0.0130	+	0.0639	21	-5999.9	12041.8	2.02

Selection in home range during summer: night

NR	INTERCEPT	BILBERRY	CANOPY TYPE	EASTING	MGT	ROAD	SETTLE	SUCCESSION	TOURI_S	CANOPY COV	WATER	SLOPE	df	logLik	AIC	delta
2048	**2.1902**	**0.0224**	**+**	**-0.4089**	**+**	**-0.0005**	**-0.0003**	**+**	**-0.0009**	**-0.0363**	**-0.0012**	**-0.0416**	**20**	**-3638.5**	**7317.0**	**0.00**
1024	2.0493	0.0212	+	-0.4032	+	-0.0005	-0.0002	+	-0.0011	-0.0368	NA	-0.0414	19	-3643.8	7325.6	8.63

Selection in home range during winter: day

NR	INTERCEPT	EASTING	CANOPY TYPE	MGT	FEED	HUNT	NORTHING	TOURI_W	TREECOVER	df	logLik	AIC	delta
256	**0.4899**	**-0.2306**	**+**	**+**	**-0.0020**	**-0.0010**	**0.2415**	**0.0006**	**-0.0118**	**14**	**-2019.5**	**4066.9**	**0.00**
254	0.5887	NA	+	+	-0.0020	-0.0010	0.2378	0.0005	-0.0114	13	-2023.5	4073.0	6.10

Selection in home range during winter: night

NR	INTERCEPT	EASTING	HUNT	CANOPY COV	MGT	NORTHING	PROTECT_W	ROAD	TOURI_W	SLOPE	SUCCESSION	WATER	df	logLik	AIC	delta
2048	**1.6983**	**-0.9826**	**0.0007**	**-0.0247**	**+**	**-0.2749**	**-0.0131**	**-0.0018**	**-0.0028**	**-0.0999**	**+**	**-0.0021**	**17**	**-1746.3**	**3526.7**	**0.00**
2046	1.8766	-0.9638	NA	-0.0241	+	-0.2827	-0.0133	-0.0019	-0.0029	-0.0936	+	-0.0020	16	-1751.2	3534.4	7.74

Table S5: Model averaging of the model describing home range selection in study area during summer (Table 3a). The table shows the variables included in the five component models (with variable codes described below), as well as the relative importance of the variables.

Component models:

	df	logLik	AIC	delta	weight
1/2/3/4/5/6/8/10/12	18	-12087,47	24210,95	0,00	0,31
1/2/3/4/5/6/8/9/10/12	19	-12086,83	24211,66	0,71	0,22
1/2/3/4/5/6/8/9/10/11/12	20	-12086,00	24212,00	1,05	0,18
1/2/3/4/5/6/8/10/11/12	19	-12087,00	24212,01	1,06	0,18
1/2/3/4/5/6/7/8/10/12	19	-12087,47	24212,95	2,00	0,11

Variable	BILBERRY	CANOPY_TYPE	FOREST250	HERB_GRAS	HUNT	MGT
Term code:	1	2	3	4	5	6
	PROTECT_S	SETTLE	SLOPE	SUCCESSION	TOURI_S	WATER
	7	8	9	10	11	12

Relative variable importance:

	BILBERRY	CANOPY_TYPE	FOREST250	HERB_GRAS	HUNT	MGT
Importance:	1	1	1	1	1	1
N containing models	5	5	5	5	5	5
	SETTLE	SUCCESSION	WATER	SLOPE	TOURI_S	PROTECT_S
Importance:	1	1	1	0,4	0,36	0,11
N containing models	5	5	5	2	2	1

Table S6: Variation inflation factors (VIF) for the variables included in the models presented in Table 3 and 4. For categorical variables the corrected VIF values (VIF^(1/2Df)) are provided.

Selection of home range in study area summer

	VIF	Df	VIF^(1/2Df)
SUCCESSION	87.8297	4	1.7497
PROTECT_S	2.8095	1	1.6762
BILBERRY	1.3562	1	1.1646
CANOPY_TYPE	76.2731	4	1.7191
HERB_GRAS	2.2372	1	1.4957
WATER	1.2261	1	1.1073
FOREST250	4.4706	1	2.1144
SLOPE	1.7117	1	1.3083
MGT	2.8591	2	1.3003
HUNT_	1.2072	1	1.0987
SETTLE	1.6692	1	1.2920
TOURI_S	1.7299	1	1.3153

Selection of home range in study area winter

	VIF	Df	VIF^(1/2Df)
SUCCESSION	11.5638	4	1.3580
PROTECT_W	1.7148	1	1.3095
CANOPY_COV	6.5056	1	2.5506
WATER	1.2278	1	1.1081
EASTING	1.1985	1	1.0948
NORTHING	1.2435	1	1.1151
MGT	2.7752	2	1.2907
HUNT	1.2186	1	1.1039
SETTLE	2.1787	1	1.4760
ROAD	2.2986	1	1.5161
FEED	1.9641	1	1.4015

Selection in home range summer day

	VIF	Df	VIF^(1/2Df)
SUCCESSION	26.0145	4	1.5028
CANOPY_COV	6.0301	1	2.4556
TOURI S	2.2092	1	1.4864
FOREST250	7.5032	1	2.7392
MGT	6.2553	2	1.5815
WATER	1.4176	1	1.1906
HUNT	1.3621	1	1.1671
BILBERRY	1.4868	1	1.2194
PROTECT_S	2.5759	1	1.6050
UNDER_TYPE	3.5834	4	1.1730
SLOPE	1.9711	1	1.4040
NORTHING	1.1644	1	1.0791
EASTING	1.1195	1	1.0581

Selection in home range summer night

	VIF	Df	VIF^(1/2Df)
CANOPY_COV	6.2753	1	2.5051
SUCCESSION	66.9894	4	1.6914
BILBERRY	1.3733	1	1.1719
CANOPY_TYPE	52.3784	4	1.6402
WATER	1.3645	1	1.1681
EASTING	1.0917	1	1.0448
SLOPE	1.8101	1	1.3454
MGT	3.8503	2	1.4008
TOURI_ S	1.8544	1	1.3618
ROAD	2.3282	1	1.5258
SETTLE	2.6390	1	1.6245

Selection in home range winter day

	VIF	Df	VIF^(1/2Df)
CANOPY_COV	8.4449	1	2.9060
CANOPY_TYPE	16.0006	4	1.4142
NORTHING	1.3806	1	1.1750
EASTING	1.0975	1	1.0476
MGT	6.0831	2	1.5705
HUNT	1.5674	1	1.2519
TOURI W	2.0509	1	1.4321
FEED	2.6154	1	1.6172

Selection in home range winter night

	VIF	Df	VIF^(1/2Df)
SUCCESSION	4.6354	4	1.2113
SUCCESSION	1.6708	1	1.2926
NORTHING	1.2164	1	1.1029
EASTING	1.1893	1	1.0906
SLOPE	3.2211	1	1.7947
WATER	1.4825	1	1.2176
MGT	4.9732	2	1.4933
HUNT	1.8869	1	1.3736
TOURI W	1.8581	1	1.3631
ROAD	2.7571	1	1.6605

Table S7: Odd's ratios with 95% confidence interval for the coefficients of the models provided in Table 3 and 4. Odd's ratios were obtained using the Wald chi-square method, the lower (2.5%) and upper (97.5%) boundary of the confidence interval are provided.

Selection of home range in study area summer

	Estimate	2.5%	97.5%
INTERCEPT	0.1578	0.1237	0.2013
SUC_REGTHICK	1.5718	0.9098	2.7154
SUC_POLE	0.9222	0.5420	1.5689
SUC_TREE	1.0318	0.6088	1.7486
SUC_OLD	0.8230	0.4812	1.4077
PROTECT_S	0.9999	0.9981	1.0018
BILBERRY	0.9916	0.9881	0.9950
CAN_CON	0.3773	0.2222	0.6407
CAN_DEC	1.4863	0.6585	3.3549
CAN_CONMIX	0.4213	0.2479	0.7158
CAN_DECMIX	0.4763	0.2765	0.8206
HERB_GRAS	1.0177	1.0162	1.0193
WATER	0.9989	0.9985	0.9992
FOREST250	1.7508	1.4181	2.1616
SLOPE	0.9958	0.9899	1.0017
MGT_CORE	6.8521	6.0446	7.7676
MGT_REFUGE	15.2986	13.1606	17.7839
HUNT	0.9982	0.9981	0.9983
SETTLE	1.0004	1.0003	1.0004
TOURI_S	0.9998	0.9996	1.0001

Selection of home range in study area winter

	Estimate	2.5%	97.5%
INTERCEPT	19.6242	13.6476	28.2182
SUC_REGTHICK	9.1042	5.6333	14.7135
SUC_POLE	2.7893	1.8467	4.2131
SUC_TREE	5.8740	4.0445	8.5312
SUC_OLD	6.6752	4.5287	9.8392
CANOPY_COVER	0.9895	0.9847	0.9943
PROTECT_W	0.9901	0.9863	0.9939
EASTING	0.3486	0.3137	0.3874
NORTHING	0.7636	0.6975	0.8360
WATER	1.0009	1.0003	1.0014
MGT_CORE	0.6076	0.5093	0.7248
MGT_REFUGE	1.6971	1.3290	2.1671
HUNT	0.9981	0.9979	0.9983
FEED	0.9980	0.9978	0.9981
ROAD	0.9993	0.9991	0.9995
SETTLE	0.9996	0.9995	0.9998

Selection in home range, summer during day

	Estimate	2.5%	97.5%
INTERCEPT	0.0093	0.0060	0.0145
CANOPY_COVER	0.9873	0.9834	0.9913
SUC_REGTHICK	11.1557	7.1873	17.3152
SUC_POLE	3.8622	2.5874	5.7653
SUC_TREE	1.9211	1.3011	2.8366
SUC_OLD	2.6691	1.7945	3.9701
BILBERRY	0.9757	0.9695	0.9819
PROTECT_S	0.9960	0.9933	0.9987
UNDER_CON	2.0772	1.7065	2.5286
UNDER_DEC	6.3580	3.9313	10.2827
UNDER_CONMIX	1.9613	1.6795	2.2903
UNDER_DECMIX	1.1589	0.9755	1.3767
WATER	1.0025	1.0020	1.0030
EASTING	1.0869	1.0018	1.1792
SLOPE	1.0658	1.0566	1.0750
NORTHING	0.7568	0.7060	0.8112
FOREST250	4.8705	3.1412	7.5518
MGT_CORE	3.6041	2.6455	4.9101
MGT_REFUGE	3.4858	2.5208	4.8200
TOURI_S	1.0016	1.0012	1.0020
HUNT	0.9988	0.9986	0.9991

Selection in home range, summer during night

	Estimate	2.5%	97.5%
INTERCEPT	8.9371	6.1799	12.9244
CANOPY_COVER	0.9644	0.9600	0.9688
SUC_REGTHICK	1.6449	0.6596	4.1019
SUC_POLE	2.1013	0.8920	4.9500
SUC_TREE	2.0798	0.8904	4.8579
SUC_OLD	1.2245	0.5209	2.8785
BILBERRY	1.0226	1.0162	1.0291
CAN_CON	0.4675	0.2002	1.0915
CAN_DEC	1.4997	0.4474	5.0276
CAN_CONMIX	0.5076	0.2170	1.1876
CAN_DECMIX	0.2646	0.1057	0.6621
WATER_DIST	0.9988	0.9981	0.9995
EASTING	0.6644	0.5965	0.7400
SLOPE	0.9592	0.9479	0.9708
MGT_CORE	3.9398	3.0171	5.1446
MGT_REFUGE	5.6906	4.1367	7.8284
TOURI_S	0.9991	0.9987	0.9996
SETTLE	0.9998	0.9996	0.9999
ROAD	0.9995	0.9993	0.9997

Selection in home range, winter during day

	Estimate	2.5%	97.5%
INTERCEPT	1.6350	0.8231	3.2480
CANOPY_COVER	0.9883	0.9810	0.9960
CAN_CON	43.0125	20.4603	90.4220
CAN_DEC	17.9391	1.2019	267.7520
CAN_CONMIX	30.2577	14.1850	64.5420
CAN_DECMIX	41.2635	16.9385	100.5210
NORTHING	1.2730	1.1013	1.4720
EASTING	0.7940	0.6771	0.9310
MGT_CORE	0.0876	0.0611	0.1260
MGT_REFUGE	0.2281	0.1454	0.3580
HUNT	0.9990	0.9985	0.9990
TOURI_W	1.0006	1.0002	1.0010
FEED	0.9980	0.9978	0.9980

Selection in home range, winter during night

	Estimate	2.5%	97.5%
INTERCEPT	6,8880	4,4850	11,9700
SUC_REGTHICK	0,9760	0,4360	1,7690
SUC_POLE	5,7430	0,2030	0,4710
SUC_TREE	1,7480	1,8960	3,5260
SUC_OLD	12,9440	2,4150	5,7010
PROTECT_W	16,6010	0,9870	1,0010
NORTHING	0,9880	0,6300	0,8630
EASTING	0,7390	0,2870	0,4240
SLOPE_MEAN	0,3550	0,8780	0,9130
WATER	0,9010	0,9960	0,9980
MGT_CORE	0,9980	0,4850	0,9170
MGT_REFUGE	0,7280	3,8220	8,1110
HUNT	4,8310	1,0000	1,0010
TOURI_W	1,0010	0,9970	0,9980
ROAD	0,9970	0,9980	0,9980

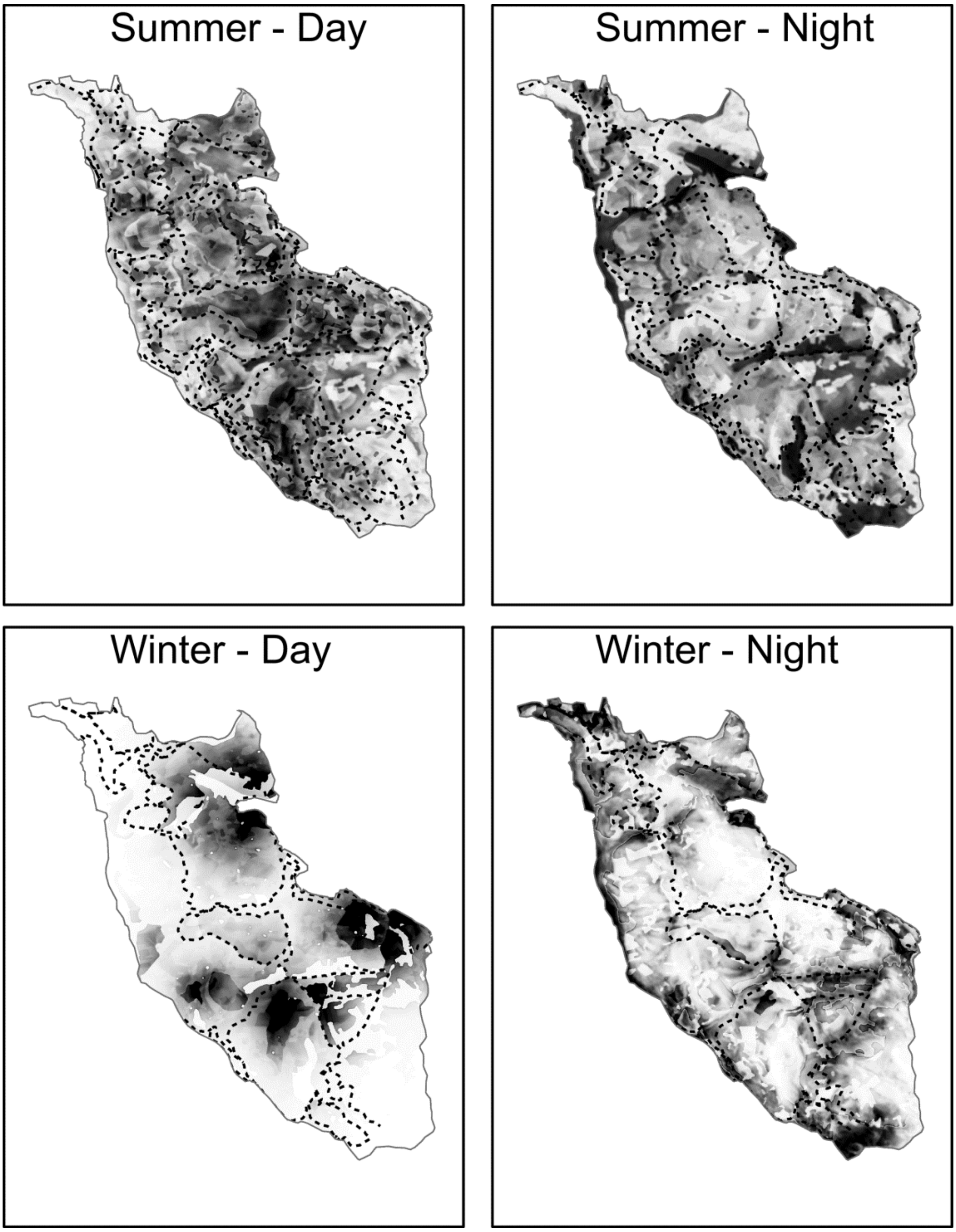

Figure S1: Relative probability of red deer presence in summer (upper panel) and winter (lower panel), during day (left) and night (right). Black and white represent high and low probability of presence respectively. Dashed lines indicate the presence of summer and winter recreation trails, respectively.

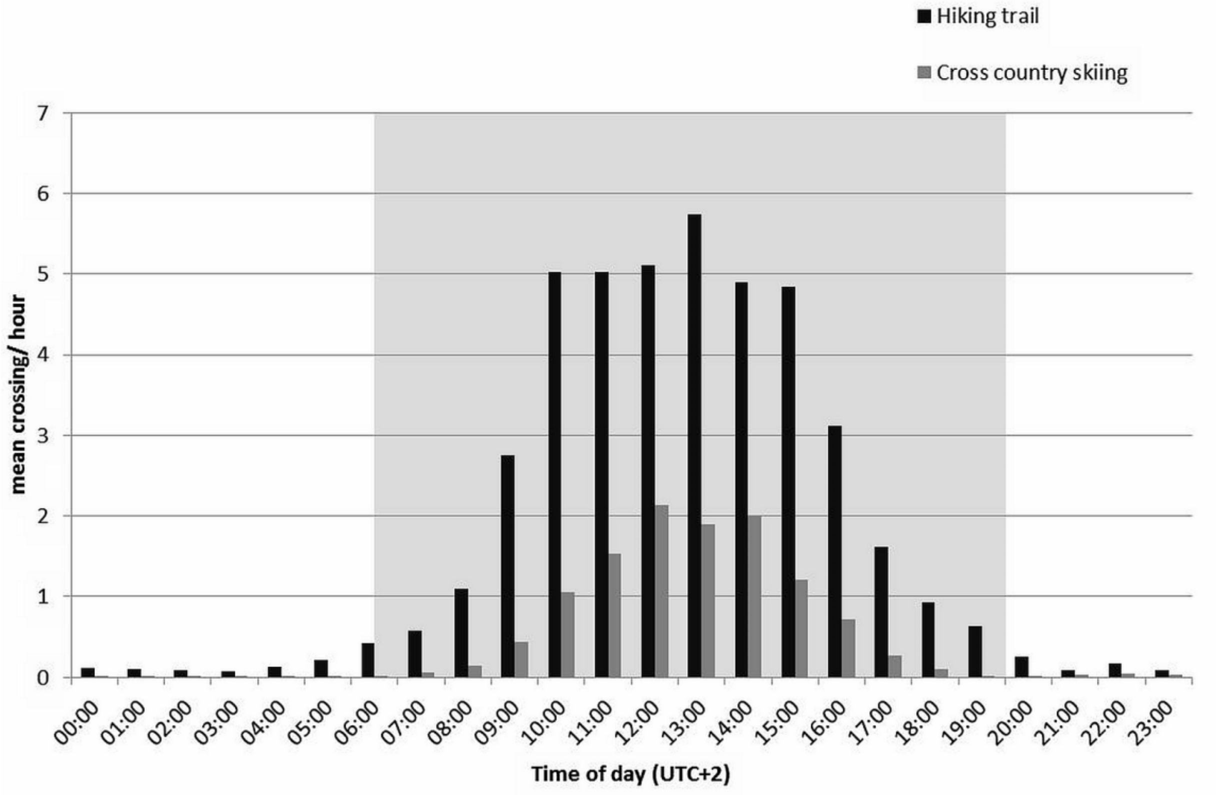

Figure S2: Mean number of visitors per hour present on selected summer (black) and winter (grey) trails, for the different times of the day. The shaded area shows the time between sunrise and sunset for the studied time period. For three months (17.2.2010 14.4.2010) TRAFx Infrared trail counters were placed along three designated hiking trails and three cross country skiing trails within the study area. These count the number of times an individual passed the light sensor. Although we cannot exclude that red deer crossed the sensors, particularly during nighttime, we assume most of these crossings are humans since these were placed along designated recreation infrastructure. Most of the activity on the trails is during the time between sunrise and sunset.

Supplementary material chapter II

Table S1: Univariate models testing for sex specific differences in habitat use with regard to the environmental variables. Positive estimates indicate a relative preference of the respective variable by (males) and vice versa. Only variables which were retained in the final models (Table 3, 4) are shown.

Summer				Winter			
Variable	Estimate	Std.Error	Pr(>|z|)	Variable	Estimate	Std.Error	Pr(>|z|)
Altitude	-0.003	0.025	0.891	Slope	0.024	0.399	0.952
Outer Forestedge	3.189	12.290	0.979	Northing	-0.435	24.244	0.986
Inner Forestedge	-1.818	14.954	0.903	Forestedge	-28.180	136.980	0.837
Road_dist	13.450	9.551	0.888	Temperature_W	-0.072	0.724	0.920
Settlement_dist	-0.209	8.335	0.980	Road_dist	2.204	7.439	0.767
Bike_dist	-1.054	10.707	0.922	Recreation_W	-1.507	17.916	0.933
Restaurant_dist	1.104	5.819	0.850	Parking_dist	0.775	7.338	0.916
Hike_dist	2.272	15.420	0.883	Suc_Regeneration	-1.112	16.509	0.300
Stand_spruce-mix	0.641	8.270	0.938	Suc_Thicket	1.231	17.505	0.944
Stand_beech-mix	2.061	9.870	0.835	Suc_Pole	0.984	17.695	0.956
Structure_2layers	0.022	6.026	0.997	Suc_Tree	0.180	16.647	0.991
Structure_>2Layers	-0.725	9.289	0.938	Suc_Old	0.522	16.755	0.975
Canopy_cover	-0.025	0.240	0.917	Structure_2Layers	-1.071	5.701	0.851
Canopy_cover^2	0.000	0.002	0.925	Structure_>2Layers	-0.878	5.367	0.870
Canopy_gaps	0.192	2.080	0.927	Stand_spruce-mix	1.224	0.003	0.869
Shrub_distr_Single	0.239	30.610	0.994	Stand_beech-mix	-0.720	5.639	0.898
Shrub_distr_Sgroup	2.042	34.860	0.953	Stand_beech	-0.298	8.955	0.973
Shrub_distr_Lgroup	1.677	29.910	0.955	Softwoods	0.003	0.235	0.990
Shrub_distr_Spread	-1.817	20.230	1.000	Shrub_distr_Single	-0.912	5.567	0.870
Shrub_cover	0.020	0.183	0.913	Shrub_distr_Sgroup	-0.946	10.273	0.927
Ground_cover	-0.009	0.131	0.945	Shrub_distr_Lgroup	-0.231	6.087	0.970
Herbs	0.018	0.257	0.945	Shrub_distr_Spread	0.387	13.460	0.977
Grasses	-0.009	0.248	0.971	Bilberry	0.003	0.110	0.981
				Canopy_cover	-0.016	0.237	0.945
				Canopy_cover^2	0.000	0.002	0.957
				Shrub_height	-0.005	0.042	0.899
				Fern	-0.035	0.227	0.876
				Herbs	-0.006	0.176	0.974
				Grass	0.009	0.148	0.952
				Moss	0.022	0.208	0.917

Table S2: Models for homerange selection within the study area (a) and habitat selection within homerange (b) calculated based on a reduced dataset, subsampling the first 25 locations from each individual.

		(a) Winter in study area			(b) Winter in home range		
		SD (Individual): 0.258			SD (Individual): <0.001		
Type	Variable	Estimate	SE	Sign.	Estimate	SE	Sign
	Intercept	-0.708	5.730		0.683	1.342	
Landscape	Slope	-0.075	0.017	***	-0.047	0.014	**
	Forestedge	5.077	0.914	***			
	Temperature_W	-0.160	0.040	***			
	Northing				-1.011	1.049	
Human	Road_dist	-0.228	0.346		-0.901	0.277	**
	Recreation_W	-2.982	0.871	***	1.567	0.696	*
	Parking_dist	2.147	0.346	***	0.961	0.306	**
Vegetation	Shrub_distr_Single	-0.083	0.332		-0.014	0.249	
	Shrub_distr_Sgroup	-1.266	0.448	***	-1.267	0.350	***
	Shrub_distr_Lgroup	0.116	0.505		0.093	0.317	
	Shrub_distr_Spread	-2.045	1.154	.	-3.131	0.748	***
	Bilberry	0.009	0.006		<0.001	0.005	
	Canopy_cover	0.110	0.153				
	Canopy_cover^2	-0.001	0.001				
	Shrub_height	-0.007	0.013				
	Fern	0.003	0.012				
	Herbs	0.012	0.009				
	Grass				0.010	0.008	
	Moss				0.015	0.010	
	Stand_spruce-mix				-0.581	0.309	.
	Stand_beech-mix				-0.484	0.465	
	Structure_2Layers				-0.533	0.236	*
	Structure_>2Layers				-0.004	0.238	
	Softwoods				-0.005	0.014	
	Suc_Thicket				-0.548	1.282	
	Suc_Pole				-1.419	1.263	
	Suc_Tree				-0.058	1.234	
	Suc_Old				-0.087	1.243	

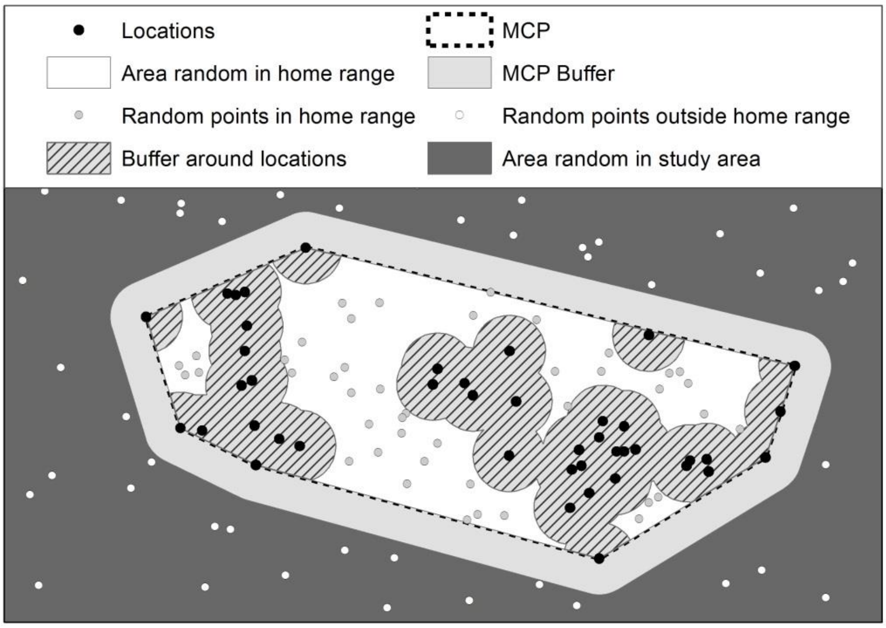

Figure S1: A schematic overview how random locations were generated in the different areas within (grey points) and outside (white points) the homerange. Locations outside the homerange were generated up to a maximum of 3.9 km.

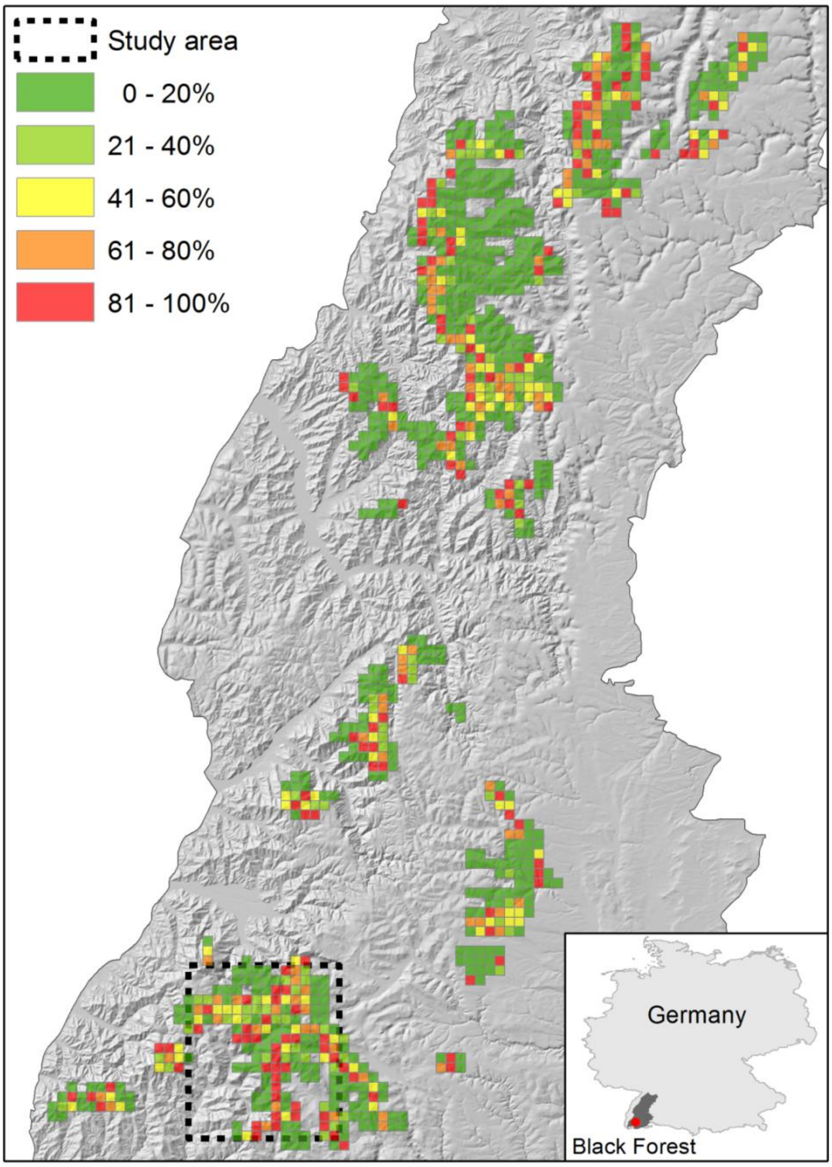

Figure S2: Capercaillie distribution in the Black Forest, Southwestern Germany and proportion of habitat affected by summer recreation. Shown are all 1 km^2 squares with capercaillie presence, with colors indicating the proportion of habitat within the respective square that is located within 145 m distance from mountain bike trails.

Supplementary material chapter III

Table S1: Linear mixed models explaining the FCM levels on both scales model (including individual as a random effect). Codes and descriptions of the predictors are given in Table 1 of the main manuscript. P-values were obtained using the Satterthwaite approximation to degrees of freedom.

	(a) Full local scale (20 m radius)				(b) Full home range scale (400 m radius)			
	Estimate	Std.error	T value	Pr(>|t|)	Estimate	Std.error	T value	Pr(>|t|)
Intercept	6.008	0.261	23.000	<0.001	5.831	0.260	22.513	<0.001
Recr_dist	-0.068	0.033	-2.092	0.037	0.113	0.101	1.124	0.261
Recr_dist^2	-	-	-	-	0.232	0.056	4.153	<0.001
Recr_dist^3	-	-	-	-	-0.177	0.062	-2.866	0.004
PrecDay	0.035	0.047	0.759	0.448	0.068	0.048	1.438	0.151
PrecDay^2	-0.079	0.031	-2.517	0.012	-0.080	0.031	-2.563	0.011
Tmin3D	-0.133	0.046	-2.874	0.004	-0.064	0.042	-1.551	0.122
Tmin3D^2	-0.091	0.030	-3.048	0.002	-	-	-	-
SexM	0.355	0.079	4.510	<0.001	0.323	0.081	4.014	<0.001
Day	-0.070	0.088	-0.804	0.421	-0.071	0.089	-0.803	0.422
Day^2	0.122	0.034	3.569	<0.001	0.122	0.035	3.520	<0.001
Day^3	-0.047	0.028	-1.649	0.100	-0.028	0.029	-0.960	0.337
Day^4	-0.017	0.006	-3.012	0.003	-0.013	0.006	-2.257	0.024
ProbOpen	-0.059	0.052	-1.122	0.262	-0.057	0.046	-1.243	0.214
ProbOpen^2	-0.024	0.028	-0.865	0.387	-0.005	0.021	-0.260	0.795
Day:SexM	0.202	0.070	2.874	0.004	0.171	0.071	2.421	0.016

Table S2: Number of samples per winter season and sex (total sample size = 894 samples). Sex was genetically identified.

	2012/2013	2013/2014	2014/2015	2015/2016
N Female	6	70	100	41
N Male	71	215	286	105
Total	77	285	386	146

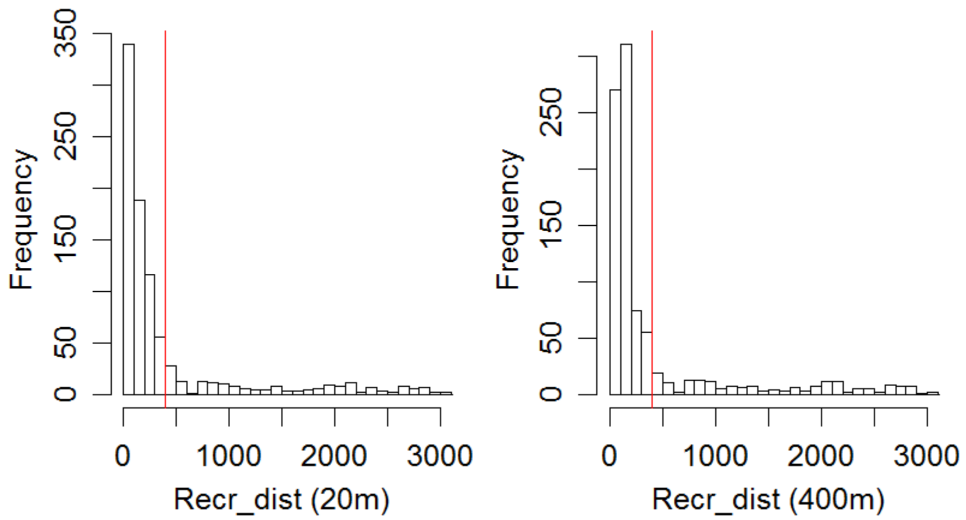

Figure S1: Some samples were collected further than 400 meters away, however capercaillie are most likely not affected by recreation distance over distances more than 400 meters, (Thiel et al. 2011, Coppes et al. 2017). Therefore we truncated the values. Here we show the frequency distribution of the predictor distance to recreation (Recr_dist) for both local (20 m) and home range scale (400 m). For the models we truncated the distance to recreation at 400 m, indicated in red.

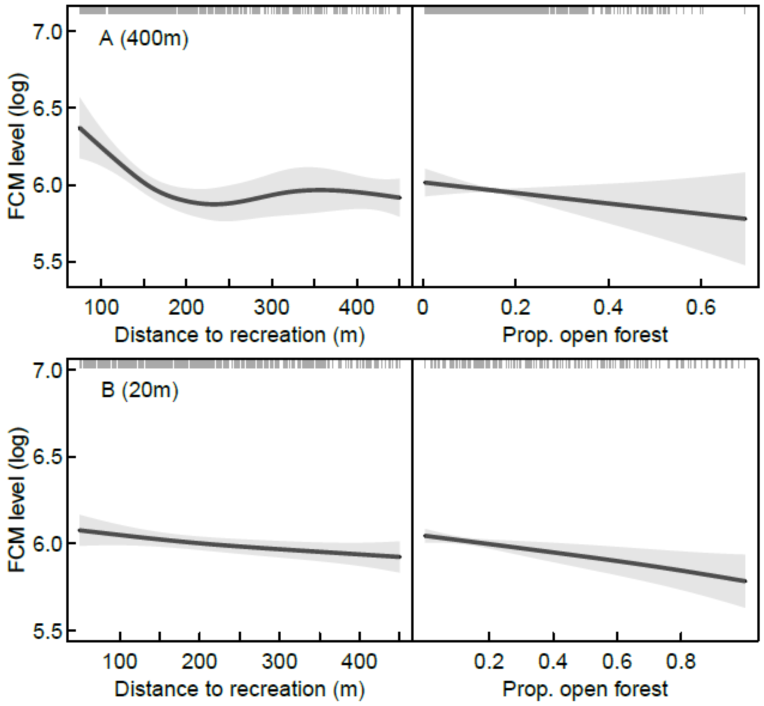

Figure S2: Effect plots showing FCM levels as a function of the environmental predictor variables, measured at the local scale (i.e. panel B within a 20 m radius, below) and the home range scale (i.e. panel A, within a 400 m radius, above). Grey areas indicate the 95% confidence intervals conditional on the estimated smoothing parameters of the model, while holding all other covariates at the mean. Variable codes and descriptions are provided in Table 1.

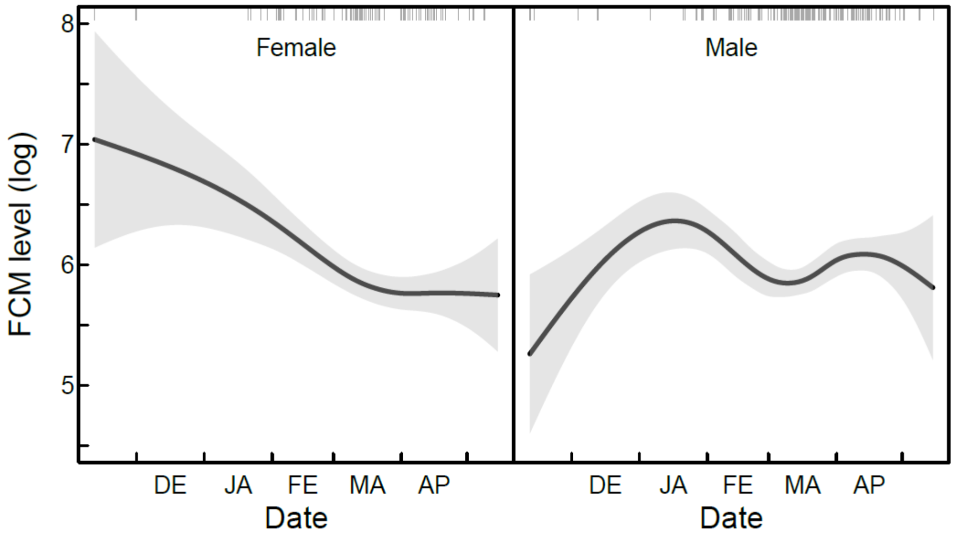

Figure S3: Effect plots displaying the effect of season for female (left) and male (right) birds for the home range scale model including individuals as random effect (effect plots for the local scale model see Fig. 3). Grey areas indicate the 95% confidence intervals conditional on the estimated smoothing parameters of the model, while holding all other covariates at the mean. Differences in effect plots between model including and excluding individual information are provided in the Figs 3 and 4.

Supplementary material chapter IV

Table S1: Results of the generalized linear mixed models relating the percentage of plots with capercaillie signs per area and year to the average habitat suitability (Avg_HSI) and the percent of sample plots located within a distance of 145 m to recreation infrastructure (Recr_area). Descriptions of the predictors can be found in Table 3.

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

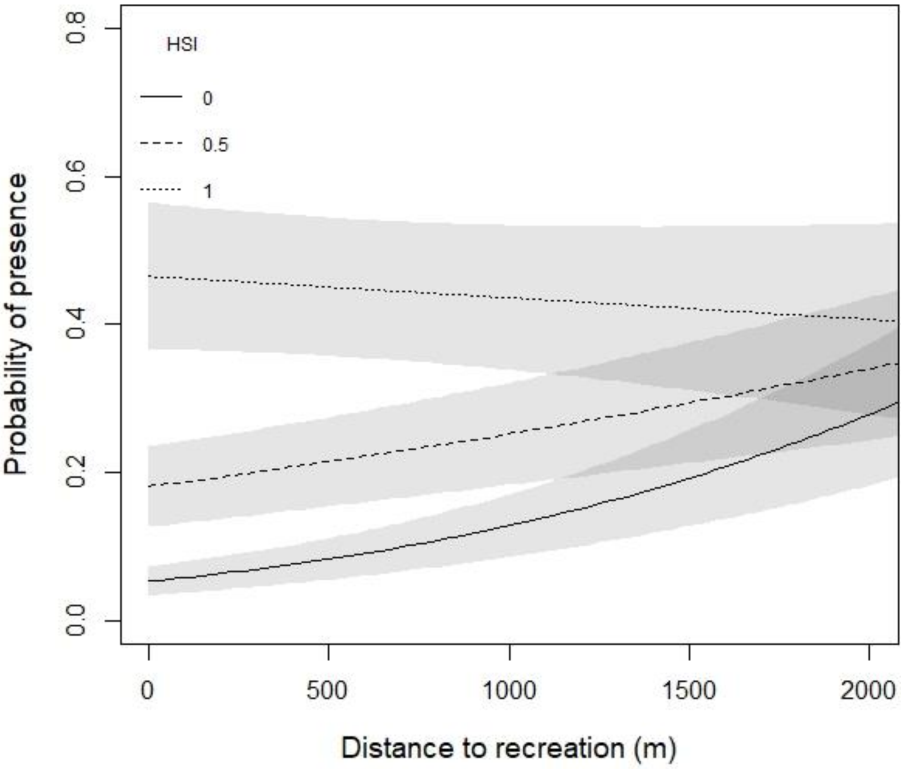

Figure S1: Interaction between habitat suitability (HSI) and distance to recreation infrastructure. The probability of finding a capercaillie sign within different distances to recreation infrastructure is shown for different habitat suitability values (HSI = 0, 0.5, 1) for the “full model”, including all data.