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Habitat suitability modulates the response of wildlife to human recreation

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ABSTRACT

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

1. Introduction

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

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

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

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

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

2. Methods and materials

2.1. Study areas

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

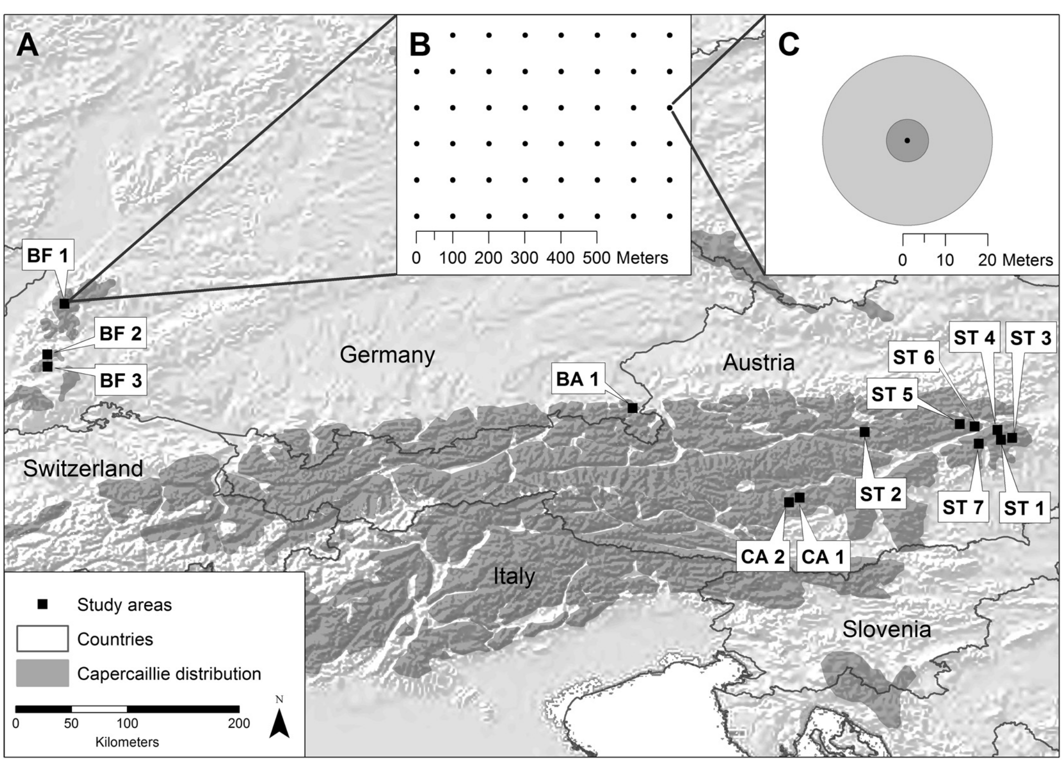

Fig. 1. The study areas (black squares) in Germany and Austria (panel A) in relation to the capercaillie distribution (dark grey) (Coppes et al., 2015). In each study area, data were collected using a systematically distributed grid of sample plots (panel B); signs of capercaillie presence were collected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