Underpinning the precautionary principle with evidence: a spatial concept for guiding wind power development in endangered species' habitats

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Abstract

The precautionary principle is an essential guideline in decision making, particularly for regulating novel developments with unknown or insufficiently proven environmental impact. However, due to the inherent component of uncertainty it has been widely critized for being "unscientific", i.e. hindering progress without sufficient evidence. The consequential postulation, that precautionary measures are only justified if the addressed threats are plausible and the measures reasonable, calls for methods to guide action in the face of uncertainty. Using the example of species conservation versus wind-farm construction, an expanding development with hypothesized - but unexplored - effects on our model species the capercaillie (*Tetrao urogallus*), we present an approach that aims at compensating the lack of knowledge about the threat itself by making best use of the available knowledge about the object at risk. By systematically combining information drawn from population monitoring and spatial modelling with population ecological thresholds, we identified areas of different functionality and importance to metapopulation persistence and connectivity. We integrated this information into a spatial concept defining four area-categories with different implications for wind power development. Highest priority was assigned to areas covering the spatial and functional requirements of a minimum viable population, i.e. sites where the plausibility for threat is highest, the uncertainty as regards importance for the population is lowest, and thus the justification for precautionary measures is strongest. This gradated approach may also enhance public acceptance, as it attempts to avoid either error-minimization bias (i.e. being too restrictive or permissive) the precautionary principle is frequently criticized for.

250 words

Keywords: capercaillie, dispersal model, habitat model, impact assessment, Tetrao urogallus, wind energy

Introduction

The precautionary principle is an established guideline applied to environmental policy and considered a fundamental tool for sustainable development (Cooney, 2004; Kriebel et al., 2001; Myers, 1993). It is based on the idea of "better safe, than sorry", in more detail described as "when an activity raises threats of harm to human health or the environment, precautionary measures should be taken even if some cause and effect relationships are not fully established scientifically" (Raffensperger & Tickner, 1999). The precautionary principle is usually applied when decision makers have an obligation to respond while there are indications of a negative impact, which are expected to be serious or irreversible and when there exists scientific uncertainty to the nature and severity of the threat (LILC, 2000; Prato, 2005). As this often applies to new developments, which are in potential conflict with species conservation, the precautionary principle has become a common element in environmental impact assessments in relation to endangered species. Nevertheless, the precautionary principle is often criticised for being not entirely "science based" (i.e. even though an activity or development has not been shown to be harmful it might still be prohibited) and is therefore accused to hinder progress or innovation (Kriebel et al., 2001; Sandin et al., 2002).

The recent increase of wind energy use in Central Europe and the consequential necessity to evaluate wind farm projects with regard to conservation targets provides a good example how the precautionary principle is applied in the field of endangered species protection. There are three main effects wind turbines may have on wildlife: firstly, increased mortality due to collisions, secondly, habitat fragmentation or reduced population connectivity when animals avoid passing through wind turbine areas, and thirdly, habitat loss due to construction works and avoidance of the disturbed area. Both birds and bats are known to collide with wind turbines causing increased adult mortality (Drewitt & Langston, 2008; Johnson et al., 2002; Kuvlesky et al., 2007; Langston & Pullan, 2003 ; Rydell et al., 2010). Although in most cases the effects at population-level are unclear (Stewart et al., 2007), increased adult mortality in long lived, slow reproducing species can rapidly affect population numbers (Sæther & Bakke, 2000). Moreover, a wide range of animal species have been shown to avoid areas around wind turbines, effectively causing habitat loss or acting as barriers to movement (Bach & Rahmel, 2004; Drewitt & Langston, 2006; Pearce-Higgins et al., 2009). Yet, the effects of wind turbines on wildlife seem to be highly species and site specific and the mechanisms behind remain poorly understood (Anderson et al., 2008; Kuvlesky et al., 2007). Besides, most studies on this subject are case studies, making it difficult to draw general conclusions. This lack of knowledge induces policy makers to apply the precautionary principle, which usually results in defining buffer zones around sites with ascertained species presence, for example nesting sites, where wind turbines are prohibited (Bright et al. 2008). The extent of this buffer zone is often based on expert opinion (Bright et al. 2008) and is therefore highly debated. Moreover, this approach is static and often based on data collected in a short time-window (e.g. a single breeding season), thus neglecting spatial and temporal fluctuations as well as minimum required areas or functional connectivity at the population level. One may argue that the lack of knowledge precludes a more complex approach. However, even if the effect of wind turbines on a species is unknown, evidence-based information on species' habitat selection and spatial requirements is often largely available or can be generated with relatively low effort from existing data sources. We state that this knowledge should be applied to determine prohibition zones for wind turbine development and advocate that the precautionary principle is used to protect viable populations of species and not only individuals. Here we provide an approach illustrating how a systematic combination of available data and knowledge can be applied to minimize - within the framework of the precautionary principle - the potential impact of wind power development on an endangered species population, even though knowledge about the actual effects of wind turbines on the species is lacking. Using the example of capercaillie (*Tetrao urogallus*) in the Black Forest, Germany, we identified areas of different functionality and importance with regard to reproduction, metapopulation persistence and connectivity, which were combined with population-related thresholds to define area categories with different levels of vulnerability and consequential implications for wind power development.

Methods

Model species

Due to its specific habitat and extensive area requirements, and its high sensitivity to human disturbance, the capercaillie is considered an indicator of undisturbed mountain forest ecosystems rich in structural diversity (Cas & Adamic, 1998; Klaus et al., 1989; Simberloff, 1998; Storch, 1995) and an umbrella species for the underlying species community (Pakkala et al., 2003; Suter et al., 2002). The same attributes, along with a limited dispersal capacity, renders the species highly vulnerable to habitat degradation and fragmentation. In Central Europe capercaillie is listed in most national red data books and in Annex I of the EU Birds Directive (EU Directive 79/409/EEC on the Conservation of Wild Birds, 1979), and its presence was one of the main criteria for the designation of special protected areas (SPA) for birds in the Natura 2000 network. However, the proportion of the capercaillie range that is covered by protected areas is far from sufficient to support self-sustaining, viable populations in most countries (Storch, 2007).

As the Central European populations are mostly confined to mountain regions, with distributions largely overlapping the areas suitable for wind energy development, capercaillie became a focal species for impact regulations. However, although a wide array of knowledge is available on behaviour and habitat requirements, it is still unclear how the species is influenced by wind turbines. The main impact is expected from turbine construction and operation triggering avoidance behaviour and thus effective habitat loss (González & Ena, 2011; Horch et al., 2003; Horch et al., 2006; Langston & Pullan, 2003), but none of these effects have been scientifically proven yet. The only published study on the cantabrian subspecies *T. urogallus cantabricus* shows a significant decrease of capercaillie signs in winter, one year after turbine construction (González & Ena, 2011). As capercaillie is highly sensitive to human presence (Thiel, 2007), road construction in the forefront of wind-turbine erection, followed by an increased human use of the area, is highly likely to reduce habitat suitability (Thiel et al., 2008). Moreover, being a prey species to raptors, the flickering shadows elicited by the turbines blades may affect vigilance behaviour, a hypothesis that requires further research (Lovich & Ennen, 2013). Capercaillie are known to collide with many different man-made structures (Baines & Andrew, 2003; Baines & Summers, 1997; Bevanger & Brøseth, 2004; Catt et al., 1994) and occasional collisions with wind turbines have been reported from Sweden (Göran Rönning, pers. comm.). Despite case studies suggesting negative effects of wind turbines on capercaillie, it is impossible to draw general conclusions at the population level. In case of the small and fragmented Central European capercaillie populations however, any additional impact may affect long-term population viability, which is why the precautionary principle is applied to handle conflicts between wind turbine construction and capercaillie protection.

Study area

The study area encompassed the Black Forest (i.e. the ecoregions “Black Forest” and “Baar-Wutach", Aldinger et al. 1998), a forested mountain range of about 7 000 km² in south-western Germany. It was selected as it hosts the largest Central European capercaillie population outside the Alps (Storch 2007) and, at the same time, is one of the Federal State’s primary regions for wind energy development due to favourable wind conditions along the mountain ridges. The capercaillie population is distributed over 520 km² in the forested regions of the highest altitudes (Braunisch & Suchant, 2006), isolated from neighbouring populations (Storch and Segelbacher 2000) and forms a metapopulation system consisting of four main subpopulation clusters (Segelbacher et al. 2008) (Figure 1a). Since the beginning of the 20th century the population has declined greatly, from an estimated 3’000-4’000 males (Suchant in Lieser and Roth 2001) to a low of 250 males counted in 2003. Since then the population has slightly recovered to approximately 300 males, which translates to a conservatively estimated minimum size of 600 individuals (Braunisch & Suchant, 2006), which exceeds only marginally the estimated size of a minimum viable population (MVP) of 500 birds (Grimm & Storch, 2000). Consequently, the loss or isolation of any sub-population is expected to increase considerably the overall extinction risk (Braunisch et al., 2010; Braunisch & Suchant, 2006).

Spatially explicit sources of information

To define the zones where wind turbine construction potentially interfere with the target of capercaillie conservation, we developed a spatially explicit planning concept (in the following referred to as “spatial concept”) that aims at the preservation of a long-term viable capercaillie metapopulation. It is, therefore, not targeted exclusively on areas of current species occurrence and reproduction, but also includes – based on the spatial requirements of a viable population – a network of habitat patches that, due to their size, quality and spatial configuration, meet the species’ demands as regards both habitat suitability and inter-patch connectivity. For this, we combined three main sources of spatial information on (1) species distribution, (2) habitat potential and (3) habitat connectivity obtained from species monitoring and spatial modelling. As they have been already published elsewhere and a detailed description of the methods would be beyond scope we provide only a brief outline here and refer to the appendices and the original publications for more detailed information.

Species distribution and core areas with reproduction

Data on current capercaillie distribution were obtained from a long-term capercaillie monitoring programme which consists of two components: First, a systematic, annual survey of lekking places, and second, a year-round collation of data from all available sources, such as incidental direct observations and indirect evidence (feathers, faeces) provided by hunters, foresters, bird-watchers as well as data collected in research projects (Braunisch & Suchant, 2006). Every five years, the minimum capercaillie distribution was at a scale of 1:25 000 based on all available data from the preceding 5-years period (Figure 1a). Capercaillie patches were defined as 'occupied' when at least three proofs (direct or indirect) with a maximum distance of 1 km to each other had been recorded within the preceding five years' period. For the delineation of a capercaillie patch the minimum polygon encompassing these observation points was drawn, aligning the patch boundaries to lines evident on the ground (i.e., forest-field boundaries, trails, streams, etc.) with a deviation of 100 m from the minimum polygon tolerated (for details see: (Braunisch & Suchant, 2006). In addition, locations relevant for reproduction were extracted from the database, i.e. all lekking sites and locations of nests or chicks. For this study, data from a ten-year period (2000-2010) were considered.

Habitat potential

Areas relevant for long-term occupancy were identified based on the concept of the "Landscape Habitat Potential" (Suchant et al., 2003), which quantifies the capacity of the prevailing landscape conditions to support the natural development of suitable habitat and vegetation structures for a species and, at the same time, to provide sufficient framework conditions for species' inhabitation . We used species presence data (N=1600) from forest patches with continuous occupancy (at least 20 years as identified by the monitoring programme) and an Ecological Niche Factor Analysis (Hirzel et al., 2002; Hirzel et al., 2006) to model the probability of long-term capercaillie presence as a function of the prevailing environmental conditions, notably climate and soil conditions, topographic and land use characteristics forest distribution and fragmentation as well as human infrastructure. The resulting map shows the sites (occupied or non-occupied) which offer suitable landscape framework conditions for long-term capercaillie presence and thus represent the area generally available for a metapopulation (Figure 1b, for details see: Appendix A, Braunisch & Suchant, 2007, 2008).

Habitat connectivity

To localise the "corridors" between the habitat patches that were most important for maintaining metapopulation connectivity, we developed a model that detected species-specific dispersal patterns from population genetic structure (Braunisch et al., 2010). Pairwise relatedness (Lynch & Ritland, 1999) between 213 individuals of the capercaillie population was correlated with the intervening landscape structures, while controlling for isolation by distance, in order to identify the landscape variables that either promoted or impeded gene flow. The results were used to generate a spatially explicit landscape permeability map that allowed identifying dispersal corridors that offered the relatively best conditions for individual movements between subpopulations. Corridors were calculated between the centroids of all inhabited patches located more than 1km from the next neighbour. First, between each pair of neighbouring patches, 1000 random paths were calculated and path with the highest permeability was retained. Repeating this procedure 100 times resulted in 100 partly overlapping paths forming a corridor (Figure 1c, for details see: Appendix B, Braunisch et al., 2010). The model was evaluated using both data partitioning and independent observation data of dispersing birds.

Spatial concept: combining spatial information with ecological thresholds

To delineate areas with different importance and functionality for the capercaillie population which then translate into different implications for wind energy development, the three data sources were evaluated with regard to population related target values and combined in a stepwise manner. Thereby we distinguished between areas relevant for capercaillie inhabitation and population connectivity.

Areas relevant for species inhabitation

Areas relevant for capercaillie inhabitation were classified according to the following criteria, with the letters corresponding to the steps illustrated in Figure 2:

(a) *Patch accessibility*: Habitat patches within a metapopulation network must be within the birds' reach. The seasonal movements of adult birds are an average of 1-2 km and median dispersal distances of juveniles are generally less than 10 km (Patthey et al., 2012; Storch & Segelbacher, 2000). Areas with habitat potential were thus only considered if they were within 10 km of the nearest occupied capercaillie patch (Braunisch & Suchant, 2006).

(b) *Patch size:* Moss et al. (1991) and Moss (1994) quote a minimum patch size of 100 ha as a precondition for capercaillie inhabitation. Only patches achieving this minimum size were deemed relevant for inhabitation, while smaller patches were evaluated for their function as stepping stones (see Figure 2f).

(c) *Patch quality:* The capercaillie meta-population in the study area amounts to 600 birds. The area required by a capercaillie population of this size depends on habitat quality. With an average proportion of 30 % suitable habitat, as determined for the capercaillie habitats in the Black Forest, a minimum area of 60’000 ha is required (Suchant & Braunisch, 2004). The area with habitat potential was thus classified into three quality levels: The 60’000 ha with the highest potential formed level 1, the remaining area with moderate and low potential was subdivided using equal habitat potential intervals and attributed to the levels 2 and 3.

(d) *Current inhabitation status:* For the final classification of areas with regard to the potential conflict with wind energy development, the areas with habitat potential were intersected with the current capercaillie distribution (Braunisch & Suchant, 2006), and four categories were formed reflecting different levels of importance (Figure 2): A particular emphasis was put on the core areas with reproduction. These were defined by drawing a 1km radius around each lek site and each ascertained location of reproduction as obtained from the monitoring data. The distance of 1 km was chosen because most females breed within 1 km of a lekking site (Wegge & Rolstad, 1986). Furthermore an exclusion zone of 1km is generally advised for capercaillie habitats (LAG-VSW, 2007). To avoid exclusion of wind power in areas irrelevant for capercaillie inhabitation, only areas with habitat potential (level 1-3), within the 1 km radius was classed as first priority (category 1). Second highest priority was given to areas occupied by capercaillie with high or moderate habitat potential (category 2). These were followed by unoccupied areas with moderate potential or occupied areas with low potential (category 3). The remaining areas, which were neither occupied nor served as potential habitats with long-term relevance (i.e. low or no habitat potential) were classed in category 4.

Areas relevant for metapopulation connectivity

The areas relevant for metapopulation connectivity were obtained from the corridor model (Braunisch et al., 2010). A distinction was made between ‘stepping stone habitats’ and ‘corridors’ (see Figure 2):

(e) *Relative significance for metapopulation connectivity*: The corridor model (Braunisch et al. 2010) provided a raster map, showing the relative suitability of the landscape for inter-patch movement between subpopulations. In homogeneous landscapes, this resulted in broad corridors, whereas narrow corridors where obtained where the landscape conditions provided only one suitable connection (Figure 1c). Moreover, most habitat patches were connected by several possible pathways. To preserve a functional network connecting all inhabited capercaille patches, the primary connection that offered the relatively best conditions for dispersal between the core areas with reproduction of neighboring habitat patches was selected. A central band of 1km minimum width was delineated and assigned to category 1. The remaining corridor area was classed as category 2. Secondary corridors of minor quality and importance were assigned to category 3.

(f) *Function – stepping stone or corridor:* Patches with moderate to high habitat potential smaller than 100 ha (see 2.4.1.b) located on a corridor were classed as ‘stepping stones’, and assigned to the corresponding category of the corridor.

Potential conflict areas with wind energy development and management implications

Each location of the study area was thus assigned to one of the four categories. Whereas in category 1-sites there is a high probability that negative effects of wind turbine construction may interfere with both reproduction and population connectivity, a stepwise decreasing conflict potential can be expected for sites of category 2 and 3. In category 2 current distribution areas without ascertained reproduction as well as corridors of secondary importance are concerned, while category 3 sites mainly encompass unoccupied, potential habitats which, however, serve as a buffer zone around core habitats and allow population fluctuations and recolonization processes in the metapopulation system (see Braunisch et al., 2007). In category 4 areas negative effects can largely be ruled out. Applying the precautionary principle, we translated these categories into management recommendations: Representing the core areas of the distribution, wind energy development should be banned from category 1 sites. For sites of the categories 2 and 3 we recommended a mandatory, detailed on-site assessment of the population situation at and around the foreseen turbine locations before deciding whether the project should be declined or whether impacts could be minimized by an optimized planning and adequate compensation measures. No further restrictions are required in category 4 sites. Finally, to provide an applicable planning tool which allows a direct appraisal of prospective turbine sites in the study area, without revealing the precise locations of vulnerable key habitats (i.e. lek sites), the resulting map was intersected with the areas profitable for energy development, i.e. where the average annual windspeed at 100m above ground exceeded 5,25 m/s, as extracted from the wind atlas of Baden-Württemberg (Land Baden-Württemberg 2010).

Comparison with prevailing guidelines

Existing guidelines for wind energy planning in Germany recommend a radius of 1km around capercaillie reproduction sites from which wind energy development should be banned (LAG-VSW, 2007). We compared the areas under protection resulting from this approach with the areas relevant for capercaillie (i.e. categories 1-3) as obtained by our spatial concept with regards to both, areas irrelevant to capercaillie that would be protected as well as areas with metapopoulation functionality that would not fail to receive a protection status.

Results

Basic information: Species distribution, habitat potential and connectivity

According to the prevailing climate, topography, land-use and site conditions, 181’770 ha of the study area offered a potential for long-term capercaillie inhabitation, were located within 10km distance to inhabited areas and of sufficient size to support capercaillie occupancy. 35% (63’280ha) thereof offered a high, 29% (53’730ha) a moderate and 36% (64’760 ha) a low habitat potential. Capercaillie was distributed over 51’650 ha. Based on the locations of 107 lekking sites and 1070 locations of reproduction (nests or chicks) 37’055 ha (72%) thereof were classed as core areas relevant for reproduction. 108 dispersal corridors were calculated between the capercaillie patches. Depending on the landscape structure, corridors often deviated considerably from the straight connection between the patches’ centroids and frequently crossed spatially isolated, unoccupied habitat patches, 49 of which were classified as “stepping stones”. Detailed results on current distribution status, habitat potential and inter-patch connectivity as well as on model performance and evaluation results can be obtained from (Braunisch et al., 2010; Braunisch & Suchant, 2006; Braunisch & Suchant, 2007).

Prioritization of areas in relation to regulations for wind energy development

Within the study area 114’880 ha were identified as currently or potentially relevant for capercaillie inhabitation (Figure 2), 48% (54’750ha) thereof were attributed to category 1, the remaining 18% and 34% were classed as category 2 and 3 respectively (Table 1). Of the area currently inhabited by capercaillie 72% fell in category 1, 27% in category 2 and the remaining 1% in category 3. In addition, areas relevant for connectivity (i.e. corridors and embedded stepping-stone habitats) comprised 59’930 ha, with 34%, 39% and 27% thereof falling in the categories 1, 2 and 3 respectively. On the corridors 62 “stepping stone” habitat-patches with an average size of 45 ha (SD: 27 ha) were identified. The remaining 542’750 ha (76%) of the study area were attributed to category 4.

Assuming a predicted average annual windspeed of at least 5.25m/s at 100m above ground level as threshold for profitability, 79’250 ha (11%) of the study area were potentially suitable for wind energy development. Capercaillie conservation aspects had to be considered on 50% of these areas, with 26% being allotted to category 1, 11% to category 2 and 13% to category 3.

Comparison with prevailing guidelines

Applying the prevailing recommendations of applying a 1km-buffer zone around the reproduction sites would have resulted in 60’330 ha where turbine construction would be prohibited. According to our spatial concept, 51’289 ha (i.e. 85% thereof) were also classified as relevant for capercaillie (Table 2, Appendix C, Figure C1), the remaining 9’040 ha (15%) however, would be protected although they are neither currently inhabited nor characterized by a function as potential habitat or connectivity element. By contrast, 123’520 ha would not receive any protection status, although relevant for the population, mainly with regard to population connectivity.

Discussion

Despite being criticized for various reasons (Sandin et al., 2002), the precautionary principle is an essential element in environmental decision-making and species protection (Kriebel et al., 2001). As illustrated by our case example, it is characterized by four dimensions (Sandin, 1999): (1) there are indications of negative effects which might be irreversible (e.g. extinction of the local capercaillie population) (threat dimension); (2) the mechanism and the severity of the impact is unknown (uncertainty dimension) and (3) the decision makers, i.e.

the local government, have the obligation to take measures (action dimension), as (4) the target species is endangered and under international protection law (command dimension). While the latter two dimensions are usually well-supported by legal framework, the inherent lack of scientific evidence in the former two (Sandin, 1999) provokes the criticism the precautionary principle would “stifle progress without good reason”, thus being “excessively risk-aversive” (Resnik, 2003) if not “unscientific” (Brombacher, 1999; Resnik, 2003). The consequential postulation, that precautionary measures can only be justified if the threats they address are plausible and the measures reasonable (Resnik, 2003; Sandin, 2004) calls for coherent methods to guide action in the face of uncertainty (Raffensperger and Barrett (2001). We addressed this challenge by illustrating how a lack of knowledge about the threat itself may be partially compensated by making best use of the available knowledge on the object at risk: based on a systematic combination of evidence-based spatial information, we qualified the relative importance of sites for metapopulation functionality and translated this information into gradated management implications that strictly protect minimum requirements at the population level, while not being overly restrictive in less relevant sites.

Plausibility of threat: Potential effects of wind energy on the target species

Wind turbines can threaten wildlife populations by causing un-compensable extra mortality through collisions, by generating habitat loss or disturbance, potentially affecting reproduction or triggering behavioral responses such as changes in habitat use or movement patterns. In capercaille, as in other grouse species, collisions have been mainly reported with turbine towers, since the species’ flight altitude is usually below the rotor-swept zone. Although collision risks are often underestimated as victims are predated before they are found (Korner-Nievergelt et al., 2011), we consider this impact minor compared to other potential effects.

The surface of the construction area of the wind turbines is usually not large (0.2 - 1 ha, MKULNV, 2012) and therefore not considered a major factor of habitat loss (Drewitt & Langston, 2006; Langston & Pullan, 2003), except in the case of spread out wind parks (Langston & Pullan, 2003). Yet, avoidance of otherwise suitable areas close to the turbines can cause indirect habitat loss (Drewitt & Langston, 2008). The presence of the turbines (e.g. rotor movement, noise, shadow flickering), the increase of human use in the area due to construction of paths and roads and maintenance personnel may inflict a "disturbance effect", defined here as any action or object causing a change in animal behaviour or physiology, without necessarily incurring fitness costs. However, such effects have been shown to be highly species and site specific, which obstructs their transferability (Drewitt & Langston, 2008; Gill et al., 1996; Kuvlesky et al., 2007). Studies on different grouse species also showed diverging results: for capercaillie reduced numbers of males at lekking sites near a newly established wind park have been observed in Austria and reported from Sweden (Göran Rönning, pers. comm.), and also the closely related black grouse (*Tetrao tetrix*) showed dramatic decreases in number of lekking males in a wind park area in Austria (Zeiler & Grünschachner-Berger, 2009). LeBeau et al. (2014) found indications of reduced brood survival of greater sage grouse (*Centrocerus urophasianus*) near wind turbines, and female greater prairie chickens (*Tympanuchus cupido*) seemed to adjust their space use near a wind park in the United States (Winder et al., 2014). On the contrary, no significant effects on habitat use, behaviour or reproduction have been found for willow ptarmigan (*Lagopus lagopus*) in Norway (Bevanger et al., 2010) and the closely related red grouse (*Lagopus lagopus scotica*) in Scotland (Pearce-Higgins et al., 2009).

Finally, there are indications that birds adjust their flight path to fly around wind turbines which can elicit extra energy costs (de Lucas et al., 2004; Dirksen et al., 1998; Farfán et al., 2009; Plonczkier & Simms, 2012). Turbines might even function as a barrier between roosting, feeding or breeding grounds (Drewitt & Langston, 2006; Farfán et al., 2009; Langston & Pullan, 2004) and – at the landscape scale - reduce population connectivity (Andrén, 1994; Fahrig, 1997, 2003; Hanski & Gilpin, 1997; Lande, 1993). Due to their relatively heavy body weight and proportionally small wing size capercaillie, as all members of the grouse family, are considered “poor flyers” (Rayner, 1988), and inter-patch movements mostly occur in a stepwise manner from hilltop to hilltop. Dispersal has been shown to be affected by landscape features, with open areas, roads and settlements reducing the probability of inter-patch dispersal (Braunisch et al., 2010), which makes it likely that turbine constructions may have a similar effect. Since the genetic differentiation between the four main subpopulations in the study area (Figure 1a) already suggests isolation effects (Segelbacher et al., 2008), accumulations of turbines placed on the primary connecting corridors may further contribute to reducing metapopulation connectivity.

Reasonability of measures: Spatial prioritization and management implications

Most studies addressing the effects of wind-turbines on wildlife are temporally and spatially restricted, i.e. quantify collision rates (Conway & Danby, 2014; Everaert & Stienen, 2007; Musters et al., 1996) or effects on local habitat use (Leddy et al., 1999; Meek et al., 1993; Reichenbach & Steinborn, 2006; Steinborn & Reichenbach, 2011; Winder et al., 2014). Although a proven impact on single individuals or subpopulations must not necessarily imply a threat at population level, studies addressing effects on the population scale are as scarce as challenging (Bellebaum et al., 2013; Carrete et al., 2009; Schaub, 2012). This may explain why most spatial planning concepts also focus on the protection of local occurrences or even single breeding pairs, e.g. by defining buffer zones around observation locations from which wind energy is banned (Bright et al., 2008; LAG-VSW, 2007). Our concept, by contrast, aims at preserving the spatial requirements of a viable metapopulation, thereby distinguishing between sites of different functionality, i.e. reproduction, inhabitation and connectivity. Moreover, we provide a gradated evaluation of the relative importance of each site in the study area which translates into different levels of restrictions for wind energy development. This evaluation was based on three main criteria: current situation, long-term potential and functionality: Whereas the current species distribution, and particularly the core areas of reproduction are taken into account with high priority, high priority is also given to sites where the prevailing climate, topography and land-use conditions support the natural development of suitable habitat, i.e. sites which have a higher probability of being of long-term relevance to the population (Braunisch & Suchant, 2007). With this approach we do not only indirectly account for fluctuations in distribution area or reproduction sites, thereby preventing a stepwise erosion of temporarily unoccupied but long-term species-relevant sites, we also perform an "ecological cost-benefit assessment", as secondary habitats which are prone to deteriorate without active habitat management are ranked lower – unless they are crucial for reproduction or metapopulation connectivity.

The approach has some methodological challenges, though. While information on habitat potential or corridor locations is based on spatial models evaluating landscape conditions, and thus can be expected to remain valid unless substantial transformations of land-use patterns occur, the information on current capercaillie distribution, mating and reproduction sites is expected to fluctuate over time which calls for a periodical re-assessment. Moreover, since this information is mainly based on voluntary data of ornithologists, hunters and forestry personnel, a consistent data quality has to be secured in the monitoring framework. For prioritization the spatial information was evaluated using target values based on population-related thresholds. These, however, were partly adopted from studies conducted in other regions, which may challenge their transferability. Particularly, population viability analyses strongly depend on local reproduction and survival rates with a high variability in outcome. Although the conditions in the Bavarian Prealps (South-Eastern Germany) largely resemble those in the Black Forest the MVP-results can only represent a rough estimate. While performing a sensitivity analysis (i.e. varying each threshold within the range its potential values) would have been out of scope, as the regional variance is largely unknown, one has to be aware that – if not the relative ranking - so the classification and absolute amount of area attributed to the four categories may have changed with changing the quantitative targets. Approximately 500 birds are considered as an MVP of capercaillie (Grimm & Storch, 2000), which – under the prevailing habitat conditions - require a minimum area of 50’000 ha (Suchant & Braunisch, 2004). According to our concept 54’750 ha is classed as category 1, i.e. a sufficient amount of habitat for an MVP is under strict protection from wind energy development, supplemented by an additional protection of the primary corridors connecting these habitats. The other sites, i.e. category 2 and 3 are mainly situated like buffer areas of stepwise decreasing importance around the highly protected core areas, thus representing a “safety zone” where wind energy is not generally banned, but has to undergo a thorough evaluation process which includes the appraisal of the site-specific conditions in the field. With this approach we assign highest priority (and restrictions) to sites where the plausibility for threat is highest, the uncertainty as regards functional importance for the population is lowest, and thus the justification for precautionary measures is strongest. This gradated approach may also enhance the acceptance among planners, authorities and conservationists, as it represents an attempt to avoid either error-minimization bias the precautionary principle is often criticized for (Dorman, 2005): i.e. either being too restrictive (thus minimizing the type-2 error of wrongly rejecting the hypothesis that wind energy poses a threat) or being too permissive in favor of turbine construction (by overemphasizing the minimization of the corresponding type-1 error).

Application in wind farm planning

The resulting map allows authorities and planners a rapid and standardized first appraisal at a high resolution. Thereby it does not only indicate where wind turbine construction plans will face restrictions (i.e. category 1) and where no further constraints apply (category 4), but provides a gradated estimation of the planning risk: Whereas in category 1 sites wind energy construction is generally banned, development plans in category 2 and 3 have to be submitted to a systematic, in situ impact assessment following a standardized procedure. It includes (1) a repeated control for lekking activity before and during the mating season, (2) a thorough search for indicators of reproduction (i.e. feathers, faeces and chicks) along transect lines in late summer, as well as the mapping of (3) habitat quality and (4) evidence of species presence at systematically distributed sampling plots using the method described in Storch (2002). Data shall be collected within the capercaillie-relevant areas of the respective category up to 1km distance from the construction site. Based on the resulting local situation in terms of habitat suitability and habitat use in relation to the construction site, potential impacts shall be estimated and the mitigation potential through a modification of the turbine positioning appraised. In addition, the compensability shall be determined and compensation measures quantified. Whereas new evidence of mating or reproduction will lead to the decline of the project, habitat loss may be compensated through habitat improvement measures. These measures should primarily be implemented in areas with habitat potential but low current suitability with regard to forest structure or within corridors. Inside the compensation area – the extent of which is determined by the importance and size of the habitat concerned - target values for structural key parameters (see Suchant & Braunisch, 2004) must be reached and maintained during the operational life of the wind turbine. Given the differences in relative importance between the two categories, projects planned in category 2-sites inherently face a higher risk of being rejected than those in category 3 sites, mainly encompassing un-occupied, potential habitats or marginal parts of the distribution area where impacts are more likely to be compensable.

Although our spatial concept is not legally binding, planners and authorities are currently using it as official planning document. Thereby, the perceived plausibility played a major role for accepting the precautionary concept: While we observed a consistent public agreement for banning turbine construction from the core areas of reproduction, the advice not to construct wind turbines on primary dispersal corridors elicited resistance. Although the majority of corridor areas is per se not suitable for wind energy development (i.e. crossing valleys or settlements where turbine construction is either not profitable or subjected to other restrictions), and population connectivity has been proven to be crucial for metapopulation persistence in the Black Forest (Segelbacher et al., 2008), it is difficult to convince public, planners and authorities that wind turbines should not be constructed in “stepping stone” habitats where the species has not been sighted for many years and the habitat is of low quality. To raise acceptance and promote adequate implementation, the concept was publicly presented and an implementation guideline, as well as the digital map showing the different categories, was made accessible on a website (www.windenergie.fva-bw.de).

Our concept refers only to one species though. Although capercaillie counts among the main focal species in relation to wind energy development in Central European mountain forests, and its key habitats largely overlap with those of other conservation relevant species (Braunisch et al., 2013), planners usually need to consider a wide range of potentially vulnerable species. Developing similar concepts for species with complementary spatial and functional requirements and integrating them into a single planning tool would facilitate an adequate and timely consideration of conservation targets in the rapidly spreading development.

Conclusions

The precautionary principle is a vital element to decision making in the field of conservation management, but public acceptance will strongly depend on the coherence of argumentation underlining the plausibility of threat and the reasonability of the measures (Resnik, 2003). We thus strongly advocate including scientific knowledge when defining precautionary measures, if not available on the threat itself, so on the object at risk. We illustrate this on the example of capercaillie conservation versus wind farm construction. By systematically combining information drawn from population monitoring and spatial modelling with ecological thresholds we delineated zones representing the spatial and functional minimum requirements of a viable population (category 1) plus a necessary safety interval (categories 2 and 3) with different importance for preserving population persistence and connectivity and consequential implications for wind energy development. From this exercise we draw the following general recommendations for applying the precautionary principle in this field:

(1) Precautionary measures should focus on the relevant ecological unit, i.e. target viable populations and not local occurrences or individual animals,

(2) they should consider population dynamics processes, e.g. fluctuations in occupancy as well as population connectivity, instead of merely relying on a temporal snapshot of occurrence data,

(3) they should be based on a differentiated risk appraisal, with the estimated probability and severity of threat on the population resulting in gradated management implications or restrictions,

(4) which, however, must ensure at least the minimum requirements of a viable population until further knowledge is available.

Since precautionary measures always represent as an interim solution, regular revisions measures based on up-to-date knowledge will be crucial for promoting the precautionary principle as a valuable and justified basis for weighing ecological risks in conservation and landscape planning.

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Tables:

Table 1: Size and proportion of the areas (a) relevant for capercaillie inhabitation, (b) relevant for metapopulation connectivity, (c) with current capercaillie distribution and (d) suitable for wind energy development that are allotted to the area-categories (1-4) with different implications for wind turbine construction. Highest priority is given to areas of category 1, where wind turbine construction is generally banned. In categories 2 and 3 detailed impact assessments are required, while in category 4 no further restrictions apply. WE: wind energy development.

Area	relevant for inhabitation		relevant for connectivity		current distribution		suitable for WE	
Category	ha	%	ha	%	ha	%	ha	%
1	54‘747	47,66	20‘250	33,79	37‘055	71,74	20‘783	26,22
2	20‘816	18,12	23‘262	38,81	14‘067	27,24	8‘639	10,90
3	39‘313	34,22	16‘421	27,40	528	1,02	9‘997	12,61
4	-	-	-	-	-	-	39‘835	50,26
Total	114‘876	100,00	59‘933	100,00	51‘650	100,00	79‘254	100,00

Table 2: Metapopulation-based versus observation-based approach: Comparison of the spatial concept with the currently prevailing recommendations of banning turbine construction within a 1km-buffer zone around capercaillie reproduction sites. A: Attribution of the area within the buffer zone (“protected”) to the categories of the spatial concept, B: area outside the buffer zone (“not protected”) but relevant for capercaillie according to the spatial concept, either for inhabitation or metapopulation connectivity. An illustration of divergence between both approaches is provided in Appendix C, Figure C1.

	(A) Protected		**(B) Not protected, but relevant**					
	total		total		for inhabitation		for connectivity	
	area (ha)	(%)	area (ha)	(%)	area (ha)	(%)	area (ha)	(%)
Relevant	**51‘289**	**85.01**	**123‘520**	**100.00**	**54‘321**	**43.98**	**69‘198**	56.02
thereof:								
category 1	42‘726	70.82	32‘272	26.13	0	0.00	32‘272	26.13
category 2	4‘426	7.34	39‘653	32.10	17‘738	14.36	21‘915	17.74
category 3	4‘138	6.86	51‘595	41.77	36‘583	29.62	15‘012	12.15
Not relevant (cat. 4)	**9040**	**14.99**						

Figure captions

Figure 1: Spatially explicit fundamentals integrated in the concept: (A) capercaillie distribution (grey) with core areas of reproduction (black), (B) long-term habitat potential in three classes: high (black), moderate (dark grey), low (light grey) , and (C) corridors consisting of 100 paths (grey) offering the best conditions for inter-patch dispersal between capercaillie patches (black), redrawn from: Braunisch et al. 2010, modified.

Figure 2: Stepwise evaluation of areas relevant to capercaillie metapopulation persistence and connectivity. Information on current distribution, long-term habitat potential and dispersal corridors were combined with population-related thresholds as regards patch accessibility (a), patch size (b), patch quality (c), current inhabitation status (d), significance (e) and function (f) for metapopulation connectivity, resulting in four area-categories (1-4) with different implications for wind turbine construction. Thresholds were derived from (a) Storch and Segelbacher (2000), (b) Moss (1991, 1994), (c,f) Braunisch and Suchant (2007), (d) Braunisch and Suchant (2006), (e) Braunisch et al. (2010).

Figure 3: Spatial planning concept illustrating four area-categories with different levels of importance for the capercaillie metapopulation and consequential restrictions for wind energy construction (right panel). The categorization resulted from combining different sources of spatial population information with ecological thresholds as described in Figure 2, the successive steps are schematically illustrated (left panel): The current capercaillie distribution (green) and core areas with reproduction (red, A) were intersected with the long-term habitat potential (three levels: high=dark blue, moderate = medium blue, and low=light blue) (B), resulting in a map showing areas relevant for capercaillie inhabitation (C). This was then

combined with the results of a corridor-model (hatched, D) to form the final categories 1-4 (E, F).

Figure 1

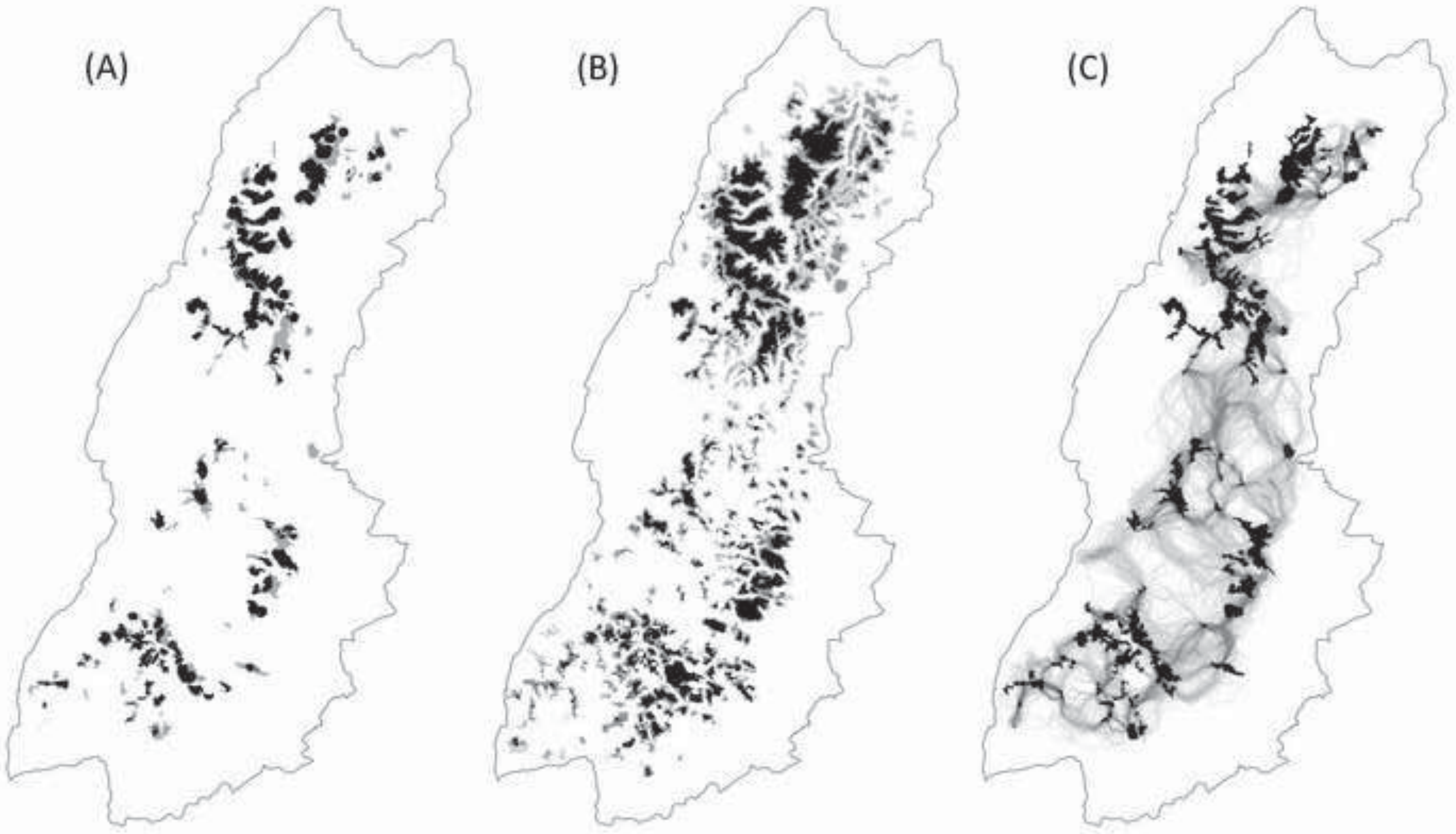

Figure 2

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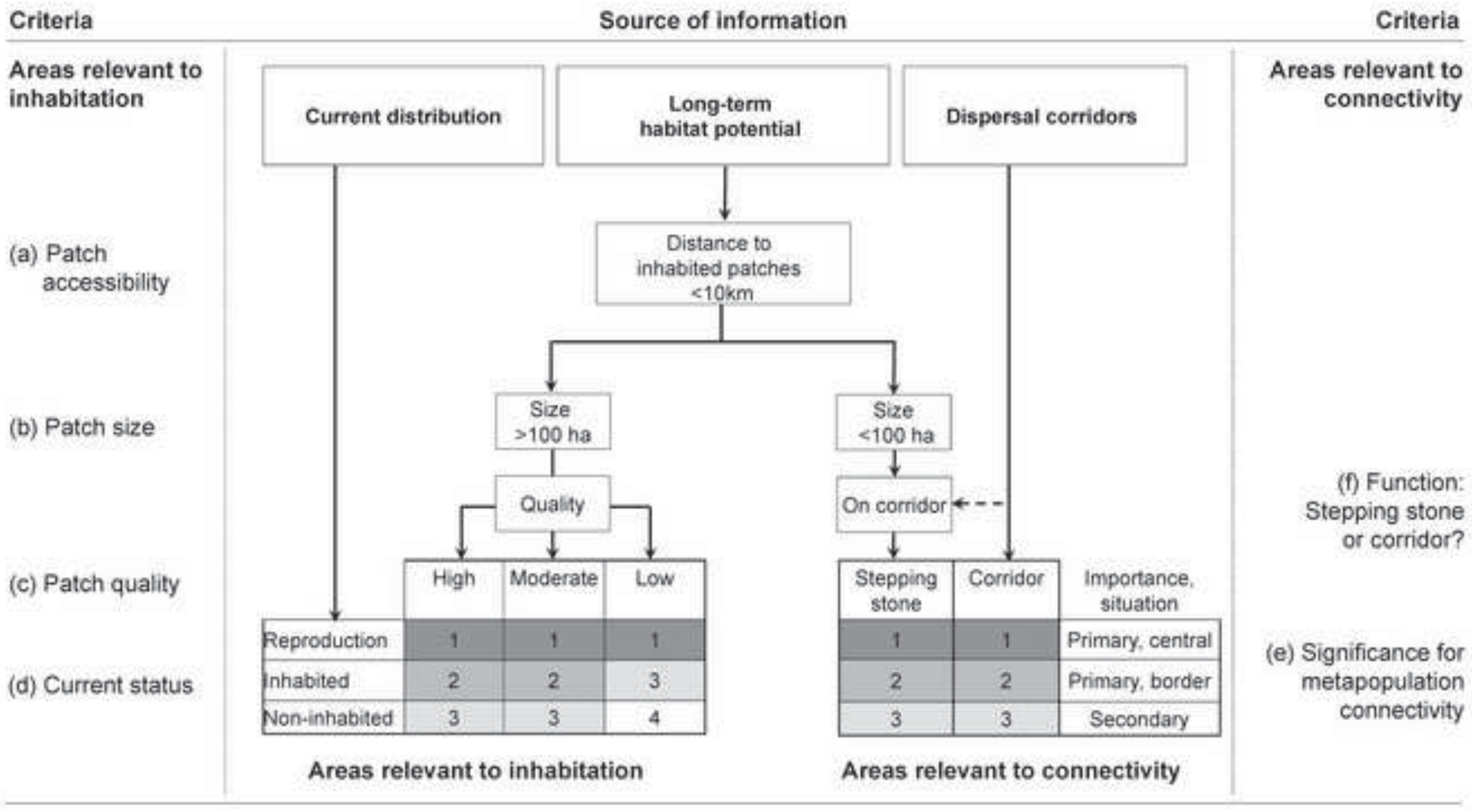
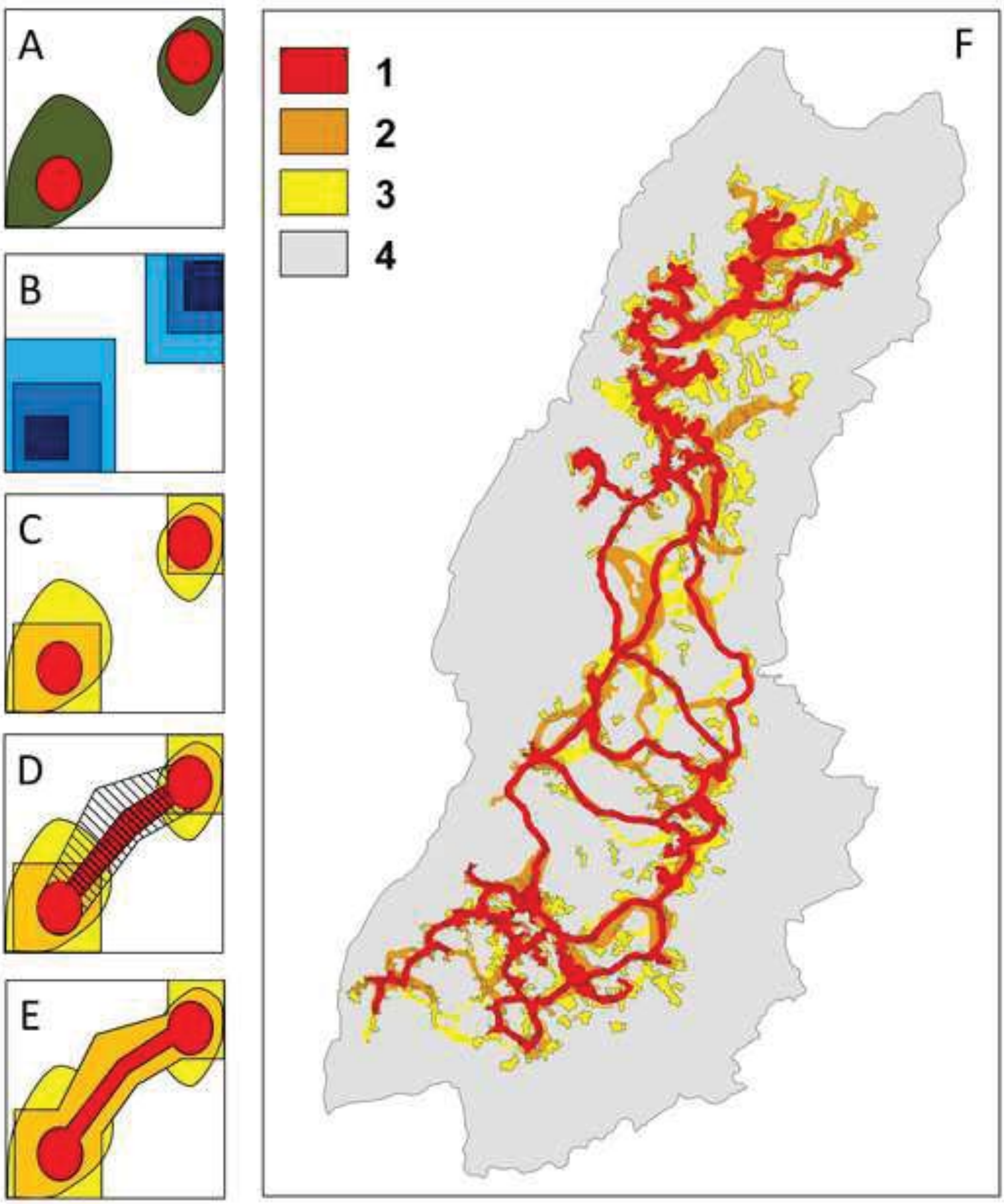


Figure 3



Appendix A:

Habitat potential: A model for evaluating the 'habitat potential' of a landscape for capercaillie Tetrao urogallus

This model identified areas relevant for long-term capercaillie occupancy, i.e. the area generally available for a capercaillie metapopulation. The methodology was based on the concept of the "Landscape Habitat Potential" (Suchant et al. 2003), which quantifies the capacity of the prevailing landscape conditions to support the natural development of suitable habitat and vegetation structures for a species and, at the same time, to provide sufficient framework conditions for species' inhabitation.

Methods, cited from: *Braunisch, V., Suchant, R., 2007. A model for evaluating the 'habitat potential' of a landscape for capercaillie Tetrao urogallus: a tool for conservation planning. Wildlife Biology 13, 21-33.*

Capercaillie data

For our analyses, we randomly sampled 1,600 presence points [from the monitoring database (Braunisch & Suchant 2006)], with at least 300 m between points to reduce bias from spatial autocorrelation. The proportion of records selected from each Black-forest subregion (south, north, east) corresponded to the mean proportion of cocks counted in each area. In addition, to restrict the landscape analyses to areas with 'stable' subpopulations of birds, we included only records from patches that had been consecutively mapped as 'inhabited' since 1988.

Landscape and land use variables

The variables tested in the model […] were subdivided into two categories. 'Landscape' variables are environmental factors that are expected to affect the composition and structure of forests and other vegetation. They therefore define the natural potential of the landscape for the development of suitable habitat. 'Land use' variables in contrast, describe the current distribution of forest and human land use features and therefore may define the area that is available for use by capercaillie. The landscape variables included characteristics of climate, soil conditions, as well as topography. […] We compared three climate variables: the (1) 'average annual temperature', the (2) 'duration of the vegetation period' and the (3) 'number of days with snow >10 cm', the latter calculated according to Schneider & Schönbein (2003). In addition, the 'potential sunshine duration' and the 'potential solar radiation' during the vegetation period (April to September) were modelled after Böhner et al. (1997).

[…] Soil texture, soil type, humus type, nutrient status and hydrological regime were evaluated with respect to their potential to support selected capercaillie habitat structures, including ground vegetation dominated by bilberry *Vaccinium myrtillus*, nutrient-poor forest types dominated by conifers or pines, bogs and wet forests. The variables were then aggregated into a soil condition index using an expert model (Braunisch & Suchant 2008).

Topographic exposure was determined using the topex-index (Wilson 1984), which qualifies a point's position relative to the surrounding terrain. The topex-to-distance index employed here was calculated as the sum of angles to the ground within a fixed distance, measured for each of the eight cardinal directions (Mitchell et al. 2001). A distance of

2’000 m was chosen because Hannah et al. (1995) found this topex to be strongly correlated with the probability of windfall events, which favour open forest structures.

Land use variables describe the availability and spatial distribution of existing land use features (forest, forest fragmentation, agricultural areas), including the distribution of possible sources of disturbance (settlements and linear infrastructures). A distinction was made between ‘forest’ in general, which grouped all available forest categories, and ‘coniferous and mixed forest’, which excluded purely deciduous forest.

As a measure of forest fragmentation, we calculated a 200-m wide forest-agricultural border zone, which included a 100-m buffer on either side of the forest edge. As intensive agriculture (arable fields, orchards and grassland) is very rare in the Black Forest and the map of ‘intensive agriculture’ would have neglected the minimum criteria for statistical normality, it was pooled with non-intensively used grassland and pastures.

[…] Two different maps were constructed for linear infrastructures. On the first map, depicting the fragmentation effect of roads, we pooled all road categories (e.g. main roads, county roads, rural roads) and railways. On the second map, highlighting the disturbance effect of roads, the different road categories were weighted according to average traffic density.

We prepared raster maps with a 30 x 30 m grid for all variables. […] To determine the spatial scale at which a variable performed best, we calculated the mean value for each variable within circular moving windows of 10, 100, 500 and 1,000 ha. These scales correspond to the size of an average forest stand (10 ha), the size of a small (100 ha) and large (500 ha) individual capercaillie home range, and to the average size of an occupied habitat patch in the study area (1,000 ha). As multinormality was required, all variables were normalised using the Box-Cox standardising algorithm (Box & Cox 1964, Sokal and Rohlf 1981). Maps were prepared in ArcView (ESRI 1996) and converted to IDRISI.

Statistical methods

Modelling approach

Multivariate approaches to modelling habitat suitability or to predicting species presence (e.g., logistic regression) usually require presence-absence data. The ecological niche factor analysis (ENFA, Hirzel et al. 2002), based on Hutchinson’s (1957) concept of the ecological niche, compares the conditions of sites with proved species presence against the conditions of the whole study area, requiring only presence data. All predictor variables included in the model are transformed to an equal number of uncorrelated and standardised factors. The first factor explains the species’ marginality (M = the difference between the average conditions within areas with species presence and those in the entire study area), which defines the location of the species’ niche in relation to the range of available conditions. It also explains part of the specialisation (S = the difference between the standard deviation SD of the conditions where the species is present and the SD of conditions in the entire study area), which defines the niche breadth. The subsequent factors explain the rest of the specialisation.

Variable and scale selection

Initially an ENFA was performed including all variables at all spatial scales. Then we calculated a multi-scale model including all variables, each at the scale it performed best and compared this with four single-scale models, including all variables at the same scale (10, 100, 500, 1,000 ha).

To obtain a simple final model without losing too much information, we selected the best of the aforementioned models and reduced the initial set of variables using the following criteria: a variable was only included in the final model if it made a sufficient contribution to marginality or specialisation (> 0.2), if it showed the same algebraic sign in the coefficient value of the marginality factor (indicating avoidance or preference) at all spatial scales and if it was ecologically plausible. In addition, if bivariate correlation between any two remaining variables exceeded a threshold of 0.7, the variable with the lower contribution to specialisation and marginality was discarded.

Landscape model of 'habitat potential'

[…] We calculated an index to 'habitat potential' using the 'area-adjusted median algorithm with an extreme optimum' for the marginality part of the first factor […] (Braunisch et al. 2008). The number of significant factors retained for the calculation of 'habitat potential' was chosen according to the broken-stick model (MacArthur 1960, Hirzel et al. 2002). Indices of 'habitat potential' ranged from 0 (unsuitable for capercaillie) to 100, with low values representing suboptimal areas. […] For model evaluation we applied a 10-fold area-adjusted frequency cross validation (Fielding & Bell 1997). The model quality was quantified using the continuous Boyce index (Hirzel et al. 2006).

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Appendix B:

Inter-patch connectivity: Model identifying the most important connections between capercaillie patches

This model used spatial and genetic data of a highly fragmented population of capercaillie (*Tetrao urogallus*) in the Black Forest, Germany, to investigate effects of landscape structure on gene-flow and to parameterise a spatially explicit corridor model.

Methods, cited from: *Braunisch, V., Segelbacher, G., Hirzel, A., H., 2010. Modelling functional landscape connectivity from genetic population structure - a new spatially explicit approach. Molecular Ecology 19, 3664-3678, shortened.*

Capercaillie samples and population genetic structure

Analyses were based on feather samples from 213 individuals (males=117, females=96) collected across the study area between 1999 and 2004. […] DNA was extracted from individual feather samples using a DNeasy DNA extraction kit (Quiagen) and genotyped at 10 microsatellite loci (TUT1-TUT4, TUT10, BG4-BG6, BG15 and BG18; Segelbacher *et al.* 2000; Piertney & Höglund 2001) as described in detail by Segelbacher et al. (2008). Allele sizes were determined by reference to two standard samples run simultaneously, the ROX 350 Ladder (Applied Biosystems), and a capercaillie individual previously genotyped at the same loci (Segelbacher *et al.* 2003a). All samples were genotyped at least twice and the reliability of identifying individuals, the error rates due to allelic drop out and potential genotyping errors were estimated using the softwares GIMLET (Valiere 2002) and DROPOUT (McKelvey & Schwartz 2005). We used the inter-individual relatedness coefficient, developed by Lynch and Ritland (1999) and calculated using the software IDENTIX (Belkhir *et al.* 2002), as a measure for gene-flow within the population.

Landscape variables

We tested landscape variables either related to land cover or topography. Land cover variables were obtained from Landsat 5 images and the ATKIS road map, distinguishing six categories, namely coniferous and mixed forest, purely deciduous forest, forest edges, roads, settlements and agricultural land. […] Land cover categories that were too scarce for a separate evaluation (< 5% of the total area) were pooled together in an 'others' variable. The continuous topographic variables (i.e., altitude, topographic exposure and slope) were converted into dichotomous maps, with the thresholds for classification chosen according to the variable's known impact on capercaillie habitat selection (Sachot 2002; Graf *et al.* 2005; Braunisch & Suchant 2007). For each variable, raster maps with a 120 x 120 m cell size were prepared, with cell values of 1 or 0 indicating the presence or absence of the respective feature. Consequently, each cell in the study area was characterised by one unique land cover category and three topographic attributes […].

Model generation

The model calibration occurred in three steps: (i) the analysis of landscape-structure effects on relatedness; (ii) the generation of landscape permeability maps and (iii) the corridor calculation.

(i) Effect of landscape structure on relatedness

The first aim was to test whether, in addition to geographic distance, landscape structures affected inter-individual relatedness, and to identify the variables that promote or hinder dispersal. […]

First, the pairwise geographic distance (D_p) between the sampling locations of all p possible pairs of individuals was calculated […]. Then we assessed the proportion of each landscape feature within rectangular landscape strips connecting all pairs, as proposed by Emaresi et al. (2009). […] We compared different strip-shapes, two with a fixed width of 1, 5 and 11 cells (F1, F5 and F11, corresponding to 120, 600 and 1320-meters) and two strips with a length:width ratio of 5:1 (R5) and 11:1 (R11). Strip statistics were calculated using the 'Frictionnator' programme (Hirzel *et al.* 2008).

Isolation by distance was quantified by calculating Mantel regressions (Mantel 1967; Legendre & Fortin 1989) between relatedness *REL* and D_p. We then investigated whether extra information could be extracted from the residuals (R) of these models (equation 1) by using them in mantel regressions with each of the landscape variables. Mantel regressions were performed in R (R Development Core Team 2006) with the package 'ecodist' 1.1.2 (Goslee & Urban 2007), significance was assigned on the basis of 1000 randomisations.

$$REL_p \propto \beta_1 D_p + \beta_0 + R_p \qquad \text{(equation 1)}$$

where:

REL_p is the relatedness coefficient between individuals of the p^{th} pair,
D_p is the geographic distance between them,
β_i are the regression coefficients and
R_p is the residual value.

(ii) Landscape permeability map

In order to create a map quantifying the relative landscape permeability of each cell in the study area, we calculated multiple mantel regressions (Mantel 1967; Smouse *et al.* 1986) for each combination of land cover and topography variables (significant in the univariate models) that could occur in any grid cell within the study area (equation 2). For this purpose, the datasets of both sexes were randomly and equally partitioned into a calibration and a validation subset using only the former for model generation. […] Multiple mantel regressions were performed using Fstat (Goudet 2001), with significance assigned after 1000 randomisations.

$$R_p \propto \sum_{i=1}^{n} \alpha_i \frac{C_{p,i}}{A_p} + \alpha_0 + \varepsilon_p \qquad \text{(equation 2)}$$

where:

R_p: residuals of the regression of relatedness and geographic distance, for the p^{th} pair of individuals
n: number of features considered
α_i: regression coefficient of the variable V_i
α_0: constant term of the regression
$C_{p,i}$: the number of cells in the strip between the p^{th} pair of individuals with occurrence of the feature V_i
A_p: the total number of cells in the strip between individuals of the p^{th} pair.
ε_p: error term

Assuming the effect of each variable or variable combination on relatedness to be a correlate of species specific landscape permeability, we then computed the permeability value (*P*) of each cell (*x)* by summing the effects of the variables occuring in the respective cell (equation 3).

$$P(x) = \sum_{i=1}^{n} \alpha_i O_{x,i} \qquad \text{(equation 3)}$$

where:
$P(x)$ is the permeability value of cell x,
α_i are the coefficients computed in equation 2 and
$O_{x,i}$ is equal to 1 if the feature i occurs in cell x and is equal to 0 otherwise.

O may thus be seen as $C_{p,i}/A_\mathrm{p}$ computed for a single cell. Consequently, the permeability value of each cell equals the sum of the significant correlation coefficients of the multiple Mantel regression model based on the variable combination given in this cell. The non-significant correlation coefficients were set to zero.

(iii) Maximum permeability path (MPP) and MPP-corridors

We developed an alternative approach to the least-cost-path method to localise the best connection between any pair of points: First, 1000 random paths are calculated between the pair of points in question and the best path (maximum permeability path, MPP) retained. […] Repeating this procedure *n*-times (with *n* being user-defined) results in *n* partly overlapping MPP replicates forming a corridor. The path selection routine was included in the 'Frictionnator' software (Hirzel *et al.* 2008).

Corridors for conservation planning

Finally, to locate the areas with the relatively best conditions for inter-patch dispersal, we calculated corridors between all capercaillie patches located more than 1 km from the next neighbour. Corridors consisted of 100 MPP-replicates between the patches' centroids in the Delaunay triangulation network. As the replicates are calculated independently, the number of paths passing through a grid-cell of the study area can be regarded as an indicator of the cell's relative importance for inter-patch connectivity.

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Appendix C

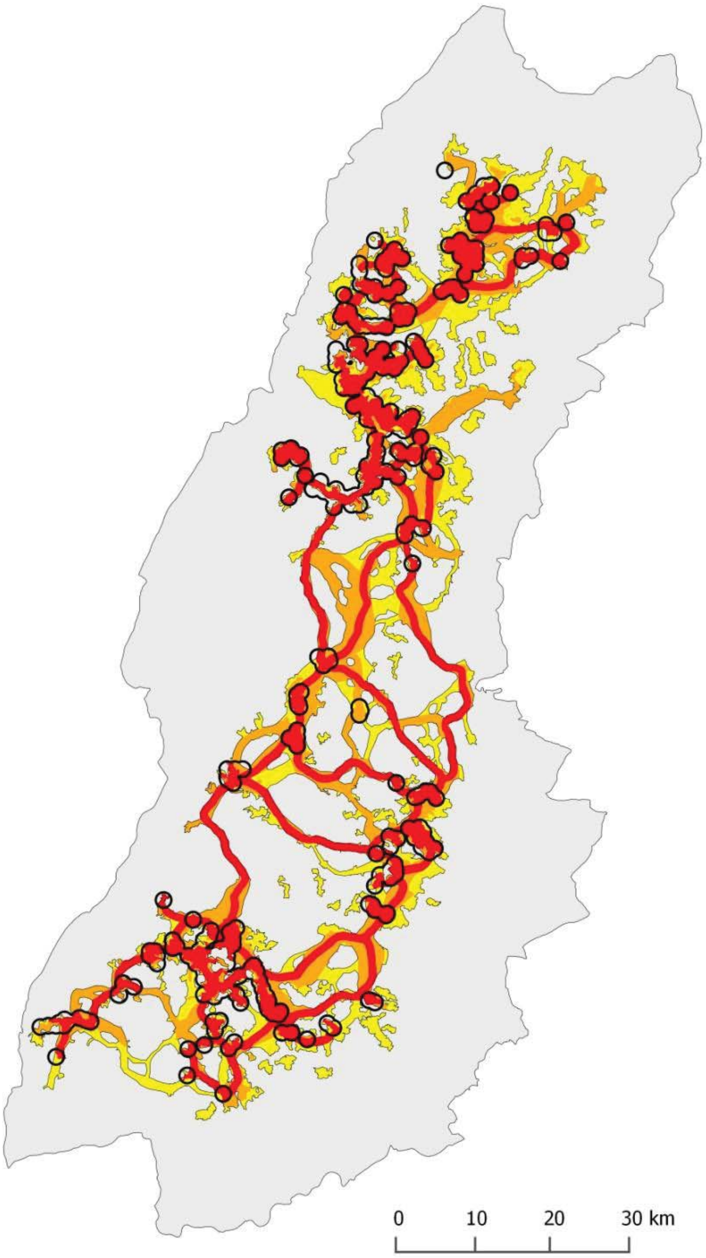

Figure C1: Metapopulation-based versus observation-based approach: Comparison of the spatial concept (four area categories: red: 1, orange: 2, yellow: 3, grey: 4, defined as illustrated in Figure 2) with the area that would fall under protection when following the recommendation of banning wind turbine construction within a 1km-buffer zone around capercaillie reproduction sites (black) (LAG-VSW 2007).