

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

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1 **Abstract**

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

23 250 words

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

27 **Introduction**

28 The precautionary principle is an established guideline applied to environmental policy and
29 considered a fundamental tool for sustainable development (Cooney, 2004; Kriebel et al.,
30 2001; Myers, 1993). It is based on the idea of “better safe, than sorry”, in more detail
31 described as “when an activity raises threats of harm to human health or the environment,
32 precautionary measures should be taken even if some cause and effect relationships are not
33 fully established scientifically” (Raffensperger & Tickner, 1999). The precautionary principle
34 is usually applied when decision makers have an obligation to respond while there are
35 indications of a negative impact, which are expected to be serious or irreversible and when
36 there exists scientific uncertainty to the nature and severity of the threat (LILC, 2000; Prato,
37 2005). As this often applies to new developments, which are in potential conflict with species
38 conservation, the precautionary principle has become a common element in environmental
39 impact assessments in relation to endangered species. Nevertheless, the precautionary
40 principle is often criticised for being not entirely “science based” (i.e. even though an activity
41 or development has not been shown to be harmful it might still be prohibited) and is therefore
42 accused to hinder progress or innovation (Kriebel et al., 2001; Sandin et al., 2002).

43 The recent increase of wind energy use in Central Europe and the consequential necessity to
44 evaluate wind farm projects with regard to conservation targets provides a good example how
45 the precautionary principle is applied in the field of endangered species protection. There are
46 three main effects wind turbines may have on wildlife: firstly, increased mortality due to
47 collisions, secondly, habitat fragmentation or reduced population connectivity when animals
48 avoid passing through wind turbine areas, and thirdly, habitat loss due to construction works
49 and avoidance of the disturbed area. Both birds and bats are known to collide with wind
50 turbines causing increased adult mortality (Drewitt & Langston, 2008; Johnson et al., 2002;
51 Kuvlesky et al., 2007; Langston & Pullan, 2003 ; Rydell et al., 2010). Although in most cases

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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

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77 species is lacking. Using the example of capercaillie (*Tetrao urogallus*) in the Black Forest,
78 Germany, we identified areas of different functionality and importance with regard to
79 reproduction, metapopulation persistence and connectivity, which were combined with
80 population-related thresholds to define area categories with different levels of vulnerability
81 and consequential implications for wind power development.

82 **Methods**

83 *Model species*

84 Due to its specific habitat and extensive area requirements, and its high sensitivity to human
85 disturbance, the capercaillie is considered an indicator of undisturbed mountain forest
86 ecosystems rich in structural diversity (Cas & Adamic, 1998; Klaus et al., 1989; Simberloff,
87 1998; Storch, 1995) and an umbrella species for the underlying species community (Pakkala
88 et al., 2003; Suter et al., 2002). The same attributes, along with a limited dispersal capacity,
89 renders the species highly vulnerable to habitat degradation and fragmentation. In Central
90 Europe capercaillie is listed in most national red data books and in Annex I of the EU Birds
91 Directive (EU Directive 79/409/EEC on the Conservation of Wild Birds, 1979), and its
92 presence was one of the main criteria for the designation of special protected areas (SPA) for
93 birds in the Natura 2000 network. However, the proportion of the capercaillie range that is
94 covered by protected areas is far from sufficient to support self-sustaining, viable populations
95 in most countries (Storch, 2007).

96 As the Central European populations are mostly confined to mountain regions, with
97 distributions largely overlapping the areas suitable for wind energy development, capercaillie
98 became a focal species for impact regulations. However, although a wide array of knowledge
99 is available on behaviour and habitat requirements, it is still unclear how the species is
100 influenced by wind turbines. The main impact is expected from turbine construction and

101 operation triggering avoidance behaviour and thus effective habitat loss (González & Ena,
102 2011; Horch et al., 2003; Horch et al., 2006; Langston & Pullan, 2003), but none of these
103 effects have been scientifically proven yet. The only published study on the cantabrian
104 subspecies *T. urogallus cantabricus* shows a significant decrease of capercaillie signs in
105 winter, one year after turbine construction (González & Ena, 2011). As capercaillie is highly
106 sensitive to human presence (Thiel, 2007), road construction in the forefront of wind-turbine
107 erection, followed by an increased human use of the area, is highly likely to reduce habitat
108 suitability (Thiel et al., 2008). Moreover, being a prey species to raptors, the flickering
109 shadows elicited by the turbines blades may affect vigilance behaviour, a hypothesis that
110 requires further research (Lovich & Ennen, 2013). Capercaillie are known to collide with
111 many different man-made structures (Baines & Andrew, 2003; Baines & Summers, 1997;
112 Bevanger & Brøseth, 2004; Catt et al., 1994) and occasional collisions with wind turbines
113 have been reported from Sweden (Göran Rønning, pers. comm.). Despite case studies
114 suggesting negative effects of wind turbines on capercaillie, it is impossible to draw general
115 conclusions at the population level. In case of the small and fragmented Central European
116 capercaillie populations however, any additional impact may affect long-term population
117 viability, which is why the precautionary principle is applied to handle conflicts between wind
118 turbine construction and capercaillie protection.

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120 ***Study area***

121 The study area encompassed the Black Forest (i.e. the ecoregions “Black Forest” and “Baar-
122 Wutach”, Aldinger et al. 1998), a forested mountain range of about 7 000 km² in south-
123 western Germany. It was selected as it hosts the largest Central European capercaillie
124 population outside the Alps (Storch 2007) and, at the same time, is one of the Federal State’s
125 primary regions for wind energy development due to favourable wind conditions along the

126 mountain ridges. The capercaillie population is distributed over 520 km² in the forested
127 regions of the highest altitudes (Braunisch & Suchant, 2006), isolated from neighbouring
128 populations (Storch and Segelbacher 2000) and forms a metapopulation system consisting of
129 four main subpopulation clusters (Segelbacher et al. 2008) (Figure 1a). Since the beginning of
130 the 20th century the population has declined greatly, from an estimated 3'000-4'000 males
131 (Suchant in Lieser and Roth 2001) to a low of 250 males counted in 2003. Since then the
132 population has slightly recovered to approximately 300 males, which translates to a
133 conservatively estimated minimum size of 600 individuals (Braunisch & Suchant, 2006),
134 which exceeds only marginally the estimated size of a minimum viable population (MVP) of
135 500 birds (Grimm & Storch, 2000). Consequently, the loss or isolation of any sub-population
136 is expected to increase considerably the overall extinction risk (Braunisch et al., 2010;
137 Braunisch & Suchant, 2006).

139 *Spatially explicit sources of information*

140 To define the zones where wind turbine construction potentially interfere with the target of
141 capercaillie conservation, we developed a spatially explicit planning concept (in the following
142 referred to as “spatial concept”) that aims at the preservation of a long-term viable capercaillie
143 metapopulation. It is, therefore, not targeted exclusively on areas of current species
144 occurrence and reproduction, but also includes – based on the spatial requirements of a viable
145 population – a network of habitat patches that, due to their size, quality and spatial
146 configuration, meet the species’ demands as regards both habitat suitability and inter-patch
147 connectivity. For this, we combined three main sources of spatial information on (1) species
148 distribution, (2) habitat potential and (3) habitat connectivity obtained from species
149 monitoring and spatial modelling. As they have been already published elsewhere and a

150 detailed description of the methods would be beyond scope we provide only a brief outline

151 here and refer to the appendices and the original publications for more detailed information.

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153 *Species distribution and core areas with reproduction*

154 Data on current capercaillie distribution were obtained from a long-term capercaillie

155 monitoring programme which consists of two components: First, a systematic, annual survey

156 of lekking places, and second, a year-round collation of data from all available sources, such

157 as incidental direct observations and indirect evidence (feathers, faeces) provided by hunters,

158 foresters, bird-watchers as well as data collected in research projects (Braunisch & Suchant,

159 2006). Every five years, the minimum capercaillie distribution was at a scale of 1:25 000

160 based on all available data from the preceding 5-years period (Figure 1a). Capercaillie patches

161 were defined as ‘occupied’ when at least three proofs (direct or indirect) with a maximum

162 distance of 1 km to each other had been recorded within the preceding five years’ period. For

163 the delineation of a capercaillie patch the minimum polygon encompassing these observation

164 points was drawn, aligning the patch boundaries to lines evident on the ground (i.e., forest-

165 field boundaries, trails, streams, etc.) with a deviation of 100 m from the minimum polygon

166 tolerated (for details see: (Braunisch & Suchant, 2006). In addition, locations relevant for

167 reproduction were extracted from the database, i.e. all lekking sites and locations of nests or

168 chicks. For this study, data from a ten-year period (2000-2010) were considered.

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170 *Habitat potential*

171 Areas relevant for long-term occupancy were identified based on the concept of the

172 “Landscape Habitat Potential” (Suchant et al., 2003), which quantifies the capacity of the

173 prevailing landscape conditions to support the natural development of suitable habitat and

174 vegetation structures for a species and, at the same time, to provide sufficient framework

175 conditions for species' inhabitation . We used species presence data (N=1600) from forest
176 patches with continuous occupancy (at least 20 years as identified by the monitoring
177 programme) and an Ecological Niche Factor Analysis (Hirzel et al., 2002; Hirzel et al., 2006)
178 to model the probability of long-term capercaillie presence as a function of the prevailing
179 environmental conditions, notably climate and soil conditions, topographic and land use
180 characteristics forest distribution and fragmentation as well as human infrastructure. The
181 resulting map shows the sites (occupied or non-occupied) which offer suitable landscape
182 framework conditions for long-term capercaillie presence and thus represent the area
183 generally available for a metapopulation (Figure 1b, for details see: Appendix A, Braunisch &
184 Suchant, 2007, 2008).

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186 *Habitat connectivity*

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

200 et al., 2010). The model was evaluated using both data partitioning and independent
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2 201 observation data of dispersing birds.

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9 203 ***Spatial concept: combining spatial information with ecological thresholds***

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12 204 To delineate areas with different importance and functionality for the capercaillie population
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15 205 which then translate into different implications for wind energy development, the three data
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17 206 sources were evaluated with regard to population related target values and combined in a
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20 207 stepwise manner. Thereby we distinguished between areas relevant for capercaillie
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22 208 inhabitation and population connectivity.

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27 210 ***Areas relevant for species inhabitation***

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30 211 Areas relevant for capercaillie inhabitation were classified according to the following criteria,
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32 212 with the letters corresponding to the steps illustrated in Figure 2:

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34 213 (a) *Patch accessibility*: Habitat patches within a metapopulation network must be within the
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37 214 birds' reach. The seasonal movements of adult birds are an average of 1-2 km and median
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39 215 dispersal distances of juveniles are generally less than 10 km (Patthey et al., 2012; Storch
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42 216 & Segelbacher, 2000). Areas with habitat potential were thus only considered if they
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44 217 were within 10 km of the nearest occupied capercaillie patch (Braunisch & Suchant,
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46 218 2006).

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49 219 (b) *Patch size*: Moss et al. (1991) and Moss (1994) quote a minimum patch size of 100 ha as
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51 220 a precondition for capercaillie inhabitation. Only patches achieving this minimum size
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54 221 were deemed relevant for inhabitation, while smaller patches were evaluated for their
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56 222 function as stepping stones (see Figure 2f).

223 (c) *Patch quality*: The capercaillie meta-population in the study area amounts to 600 birds.
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2 224 The area required by a capercaillie population of this size depends on habitat quality.
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4 225 With an average proportion of 30 % suitable habitat, as determined for the capercaillie
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7 226 habitats in the Black Forest, a minimum area of 60'000 ha is required (Suchant &
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10 227 Braunisch, 2004). The area with habitat potential was thus classified into three quality
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12 228 levels: The 60'000 ha with the highest potential formed level 1, the remaining area with
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14 229 moderate and low potential was subdivided using equal habitat potential intervals and
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17 230 attributed to the levels 2 and 3.
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19 231 (d) *Current inhabitation status*: For the final classification of areas with regard to the
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22 232 potential conflict with wind energy development, the areas with habitat potential were
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24 233 intersected with the current capercaillie distribution (Braunisch & Suchant, 2006), and
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27 234 four categories were formed reflecting different levels of importance (Figure 2): A
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29 235 particular emphasis was put on the core areas with reproduction. These were defined by
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31 236 drawing a 1km radius around each lek site and each ascertained location of reproduction
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34 237 as obtained from the monitoring data. The distance of 1 km was chosen because most
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36 238 females breed within 1 km of a lekking site (Wegge & Rolstad, 1986). Furthermore an
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39 239 exclusion zone of 1km is generally advised for capercaillie habitats (LAG-VSW, 2007).
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41 240 To avoid exclusion of wind power in areas irrelevant for capercaillie inhabitation, only
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44 241 areas with habitat potential (level 1-3), within the 1 km radius was classed as first priority
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46 242 (category 1). Second highest priority was given to areas occupied by capercaillie with
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49 243 high or moderate habitat potential (category 2). These were followed by unoccupied areas
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51 244 with moderate potential or occupied areas with low potential (category 3). The remaining
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53 245 areas, which were neither occupied nor served as potential habitats with long-term
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56 246 relevance (i.e. low or no habitat potential) were classed in category 4.
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248 *Areas relevant for metapopulation connectivity*

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

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

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

267 ***Potential conflict areas with wind energy development and management implications***

268 Each location of the study area was thus assigned to one of the four categories. Whereas in
269 category 1-sites there is a high probability that negative effects of wind turbine construction
270 may interfere with both reproduction and population connectivity, a stepwise decreasing
271 conflict potential can be expected for sites of category 2 and 3. In category 2 current

272 distribution areas without ascertained reproduction as well as corridors of secondary
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2 273 importance are concerned, while category 3 sites mainly encompass unoccupied, potential
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4 274 habitats which, however, serve as a buffer zone around core habitats and allow population
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7 275 fluctuations and recolonization processes in the metapopulation system (see Braunisch et al.,
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9 276 2007). In category 4 areas negative effects can largely be ruled out. Applying the
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12 277 precautionary principle, we translated these categories into management recommendations:
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14 278 Representing the core areas of the distribution, wind energy development should be banned
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17 279 from category 1 sites. For sites of the categories 2 and 3 we recommended a mandatory,
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19 280 detailed on-site assessment of the population situation at and around the foreseen turbine
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22 281 locations before deciding whether the project should be declined or whether impacts could be
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24 282 minimized by an optimized planning and adequate compensation measures. No further
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26 283 restrictions are required in category 4 sites. Finally, to provide an applicable planning tool
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29 284 which allows a direct appraisal of prospective turbine sites in the study area, without
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31 285 revealing the precise locations of vulnerable key habitats (i.e. lek sites), the resulting map was
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34 286 intersected with the areas profitable for energy development, i.e. where the average annual
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36 287 windspeed at 100m above ground exceeded 5,25 m/s, as extracted from the wind atlas of
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39 288 Baden-Württemberg (Land Baden-Württemberg 2010).

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42 43 44 290 *Comparison with prevailing guidelines*

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46 291 Existing guidelines for wind energy planning in Germany recommend a radius of 1km around
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48 292 capercaillie reproduction sites from which wind energy development should be banned (LAG-
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51 293 VSW, 2007). We compared the areas under protection resulting from this approach with the
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53 294 areas relevant for capercaillie (i.e. categories 1-3) as obtained by our spatial concept with
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56 295 regards to both, areas irrelevant to capercaillie that would be protected as well as areas with
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58 296 metapopulation functionality that would not fail to receive a protection status.
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2 298 **Results**

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4 299 ***Basic information: Species distribution, habitat potential and connectivity***

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7 300 According to the prevailing climate, topography, land-use and site conditions, 181'770 ha of

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9 301 the study area offered a potential for long-term capercaillie inhabitation, were located within

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11 302 10km distance to inhabited areas and of sufficient size to support capercaillie occupancy. 35%

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13 303 (63'280ha) thereof offered a high, 29% (53'730ha) a moderate and 36% (64'760 ha) a low

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15 304 habitat potential. Capercaillie was distributed over 51'650 ha. Based on the locations of 107

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17 305 lekking sites and 1070 locations of reproduction (nests or chicks) 37'055 ha (72%) thereof

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19 306 were classed as core areas relevant for reproduction. 108 dispersal corridors were calculated

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21 307 between the capercaillie patches. Depending on the landscape structure, corridors often

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23 308 deviated considerably from the straight connection between the patches' centroids and

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25 309 frequently crossed spatially isolated, unoccupied habitat patches, 49 of which were classified

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27 310 as "stepping stones". Detailed results on current distribution status, habitat potential and inter-

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29 311 patch connectivity as well as on model performance and evaluation results can be obtained

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31 312 from (Braunisch et al., 2010; Braunisch & Suchant, 2006; Braunisch & Suchant, 2007).

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35 314 ***Prioritization of areas in relation to regulations for wind energy development***

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37 315 Within the study area 114'880 ha were identified as currently or potentially relevant for

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39 316 capercaillie inhabitation (Figure 2), 48% (54'750ha) thereof were attributed to category 1, the

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41 317 remaining 18% and 34% were classed as category 2 and 3 respectively (Table 1). Of the area

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43 318 currently inhabited by capercaillie 72% fell in category 1, 27% in category 2 and the

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45 319 remaining 1% in category 3. In addition, areas relevant for connectivity (i.e. corridors and

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47 320 embedded stepping-stone habitats) comprised 59'930 ha, with 34%, 39% and 27% thereof

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49 321 falling in the categories 1, 2 and 3 respectively. On the corridors 62 "stepping stone" habitat-

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322 patches with an average size of 45 ha (SD: 27 ha) were identified. The remaining 542'750 ha
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2 323 (76%) of the study area were attributed to category 4.

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4 324 Assuming a predicted average annual windspeed of at least 5.25m/s at 100m above ground
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7 325 level as threshold for profitability, 79'250 ha (11%) of the study area were potentially suitable
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9 326 for wind energy development. Capercaillie conservation aspects had to be considered on 50%
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11 327 of these areas, with 26% being allotted to category 1, 11% to category 2 and 13% to
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14 328 category 3.

19 330 *Comparison with prevailing guidelines*

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21 331 Applying the prevailing recommendations of applying a 1km-buffer zone around the
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24 332 reproduction sites would have resulted in 60'330 ha where turbine construction would be
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26 333 prohibited. According to our spatial concept, 51'289 ha (i.e. 85% thereof) were also classified
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29 334 as relevant for capercaillie (Table 2, Appendix C, Figure C1), the remaining 9'040 ha (15%)
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31 335 however, would be protected although they are neither currently inhabited nor characterized
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34 336 by a function as potential habitat or connectivity element. By contrast, 123'520 ha would not
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36 337 receive any protection status, although relevant for the population, mainly with regard to
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39 338 population connectivity.

44 340 **Discussion**

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46 341 Despite being criticized for various reasons (Sandin et al., 2002), the precautionary principle
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48 342 is an essential element in environmental decision-making and species protection (Kriebel et
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51 343 al., 2001). As illustrated by our case example, it is characterized by four dimensions (Sandin,
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53 344 1999): (1) there are indications of negative effects which might be irreversible (e.g.
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56 345 extinction of the local capercaillie population) (threat dimension); (2) the mechanism and the
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58 346 severity of the impact is unknown (uncertainty dimension) and (3) the decision makers, i.e.
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1 347 the local government, have the obligation to take measures (action dimension), as (4) the
2 348 target species is endangered and under international protection law (command dimension).
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4 349 While the latter two dimensions are usually well-supported by legal framework, the inherent
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7 350 lack of scientific evidence in the former two (Sandin, 1999) provokes the criticism the
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10 351 precautionary principle would “stifle progress without good reason”, thus being “excessively
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12 352 risk-aversive” (Resnik, 2003) if not “unscientific” (Brombacher, 1999; Resnik, 2003). The
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14 353 consequential postulation, that precautionary measures can only be justified if the threats they
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17 354 address are plausible and the measures reasonable (Resnik, 2003; Sandin, 2004) calls for
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19 355 coherent methods to guide action in the face of uncertainty (Raffensperger and Barrett (2001).
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22 356 We addressed this challenge by illustrating how a lack of knowledge about the threat itself
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24 357 may be partially compensated by making best use of the available knowledge on the object at
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26 358 risk: based on a systematic combination of evidence-based spatial information, we qualified
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29 359 the relative importance of sites for metapopulation functionality and translated this
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31 360 information into graduated management implications that strictly protect minimum
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34 361 requirements at the population level, while not being overly restrictive in less relevant sites.
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39 363 ***Plausibility of threat: Potential effects of wind energy on the target species***

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41 364 Wind turbines can threaten wildlife populations by causing un-compensable extra mortality
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43 365 through collisions, by generating habitat loss or disturbance, potentially affecting
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46 366 reproduction or triggering behavioral responses such as changes in habitat use or movement
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49 367 patterns. In capercaillie, as in other grouse species, collisions have been mainly reported with
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51 368 turbine towers, since the species’ flight altitude is usually below the rotor-swept zone.
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53 369 Although collision risks are often underestimated as victims are predated before they are
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56 370 found (Korner-Nievergelt et al., 2011), we consider this impact minor compared to other
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58 371 potential effects.
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372 The surface of the construction area of the wind turbines is usually not large (0.2 - 1 ha,
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2 373 MKULNV, 2012) and therefore not considered a major factor of habitat loss (Drewitt &
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4 374 Langston, 2006; Langston & Pullan, 2003), except in the case of spread out wind parks
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6
7 375 (Langston & Pullan, 2003). Yet, avoidance of otherwise suitable areas close to the turbines
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10 376 can cause indirect habitat loss (Drewitt & Langston, 2008). The presence of the turbines (e.g.
11
12 377 rotor movement, noise, shadow flickering), the increase of human use in the area due to
13
14 378 construction of paths and roads and maintenance personnel may inflict a “disturbance effect”,
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17 379 defined here as any action or object causing a change in animal behaviour or physiology,
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19 380 without necessarily incurring fitness costs. However, such effects have been shown to be
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21
22 381 highly species and site specific, which obstructs their transferability (Drewitt & Langston,
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24 382 2008; Gill et al., 1996; Kuvlesky et al., 2007). Studies on different grouse species also showed
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26 383 diverging results: for capercaillie reduced numbers of males at lekking sites near a newly
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29 384 established wind park have been observed in Austria and reported from Sweden (Göran
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31 385 Rönning, pers. comm.), and also the closely related black grouse (*Tetrao tetrix*) showed
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34 386 dramatic decreases in number of lekking males in a wind park area in Austria (Zeiler &
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36 387 Grünschachner-Berger, 2009). LeBeau et al. (2014) found indications of reduced brood
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39 388 survival of greater sage grouse (*Centrocercus urophasianus*) near wind turbines, and female
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41 389 greater prairie chickens (*Tympanuchus cupido*) seemed to adjust their space use near a wind
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44 390 park in the United States (Winder et al., 2014). On the contrary, no significant effects on
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46 391 habitat use, behaviour or reproduction have been found for willow ptarmigan (*Lagopus*
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48 392 *lagopus*) in Norway (Bevanger et al., 2010) and the closely related red grouse (*Lagopus*
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51 393 *lagopus scotica*) in Scotland (Pearce-Higgins et al., 2009).
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53 394 Finally, there are indications that birds adjust their flight path to fly around wind turbines
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56 395 which can elicit extra energy costs (de Lucas et al., 2004; Dirksen et al., 1998; Farfán et al.,
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58 396 2009; Plonczkier & Simms, 2012). Turbines might even function as a barrier between
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397 roosting, feeding or breeding grounds (Drewitt & Langston, 2006; Farfán et al., 2009;
1
2 398 Langston & Pullan, 2004) and – at the landscape scale - reduce population connectivity
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5 399 (Andrén, 1994; Fahrig, 1997, 2003; Hanski & Gilpin, 1997; Lande, 1993). Due to their
6
7 400 relatively heavy body weight and proportionally small wing size capercaillie, as all members
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10 401 of the grouse family, are considered “poor flyers” (Rayner, 1988), and inter-patch movements
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12 402 mostly occur in a stepwise manner from hilltop to hilltop. Dispersal has been shown to be
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14 403 affected by landscape features, with open areas, roads and settlements reducing the
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17 404 probability of inter-patch dispersal (Braunisch et al., 2010), which makes it likely that turbine
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19 405 constructions may have a similar effect. Since the genetic differentiation between the four
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21
22 406 main subpopulations in the study area (Figure 1a) already suggests isolation effects
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24 407 (Segelbacher et al., 2008), accumulations of turbines placed on the primary connecting
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27 408 corridors may further contribute to reducing metapopulation connectivity.
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31 410 *Reasonability of measures: Spatial prioritization and management implications*

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34 411 Most studies addressing the effects of wind-turbines on wildlife are temporally and spatially
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36 412 restricted, i.e. quantify collision rates (Conway & Danby, 2014; Everaert & Stienen, 2007;
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39 413 Musters et al., 1996) or effects on local habitat use (Leddy et al., 1999; Meek et al., 1993;
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41 414 Reichenbach & Steinborn, 2006; Steinborn & Reichenbach, 2011; Winder et al., 2014).
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44 415 Although a proven impact on single individuals or subpopulations must not necessarily imply
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46 416 a threat at population level, studies addressing effects on the population scale are as scarce as
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49 417 challenging (Bellebaum et al., 2013; Carrete et al., 2009; Schaub, 2012). This may explain
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51 418 why most spatial planning concepts also focus on the protection of local occurrences or even
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54 419 single breeding pairs, e.g. by defining buffer zones around observation locations from which
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56 420 wind energy is banned (Bright et al., 2008; LAG-VSW, 2007). Our concept, by contrast, aims
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58 421 at preserving the spatial requirements of a viable metapopulation, thereby distinguishing
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422 between sites of different functionality, i.e. reproduction, inhabitation and connectivity.
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2 423 Moreover, we provide a graded evaluation of the relative importance of each site in the
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5 424 study area which translates into different levels of restrictions for wind energy development.
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7 425 This evaluation was based on three main criteria: current situation, long-term potential and
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10 426 functionality: Whereas the current species distribution, and particularly the core areas of
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12 427 reproduction are taken into account with high priority, high priority is also given to sites
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14 428 where the prevailing climate, topography and land-use conditions support the natural
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17 429 development of suitable habitat, i.e. sites which have a higher probability of being of long-
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19 430 term relevance to the population (Braunisch & Suchant, 2007). With this approach we do not
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22 431 only indirectly account for fluctuations in distribution area or reproduction sites, thereby
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24 432 preventing a stepwise erosion of temporarily unoccupied but long-term species-relevant sites,
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27 433 we also perform an “ecological cost-benefit assessment”, as secondary habitats which are
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29 434 prone to deteriorate without active habitat management are ranked lower – unless they are
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32 435 crucial for reproduction or metapopulation connectivity.

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36 437 The approach has some methodological challenges, though. While information on habitat
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39 438 potential or corridor locations is based on spatial models evaluating landscape conditions, and
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41 439 thus can be expected to remain valid unless substantial transformations of land-use patterns
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44 440 occur, the information on current capercaillie distribution, mating and reproduction sites is
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46 441 expected to fluctuate over time which calls for a periodical re-assessment. Moreover, since
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49 442 this information is mainly based on voluntary data of ornithologists, hunters and forestry
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51 443 personnel, a consistent data quality has to be secured in the monitoring framework. For
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53 444 prioritization the spatial information was evaluated using target values based on population-
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56 445 related thresholds. These, however, were partly adopted from studies conducted in other
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58 446 regions, which may challenge their transferability. Particularly, population viability analyses

447 strongly depend on local reproduction and survival rates with a high variability in outcome.
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2 448 Although the conditions in the Bavarian Prealps (South-Eastern Germany) largely resemble
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5 449 those in the Black Forest the MVP-results can only represent a rough estimate. While
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7 450 performing a sensitivity analysis (i.e. varying each threshold within the range its potential
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9 451 values) would have been out of scope, as the regional variance is largely unknown, one has to
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12 452 be aware that – if not the relative ranking - so the classification and absolute amount of area
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14 453 attributed to the four categories may have changed with changing the quantitative targets.
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17 454 Approximately 500 birds are considered as an MVP of capercaillie (Grimm & Storch, 2000),
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19 455 which – under the prevailing habitat conditions - require a minimum area of 50'000 ha
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22 456 (Suchant & Braunisch, 2004). According to our concept 54'750 ha is classed as category 1,
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24 457 i.e. a sufficient amount of habitat for an MVP is under strict protection from wind energy
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26 458 development, supplemented by an additional protection of the primary corridors connecting
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29 459 these habitats. The other sites, i.e. category 2 and 3 are mainly situated like buffer areas of
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31 460 stepwise decreasing importance around the highly protected core areas, thus representing a
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34 461 “safety zone” where wind energy is not generally banned, but has to undergo a thorough
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36 462 evaluation process which includes the appraisal of the site-specific conditions in the field.
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39 463 With this approach we assign highest priority (and restrictions) to sites where the plausibility
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41 464 for threat is highest, the uncertainty as regards functional importance for the population is
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43 465 lowest, and thus the justification for precautionary measures is strongest. This graded
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46 466 approach may also enhance the acceptance among planners, authorities and conservationists,
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48 467 as it represents an attempt to avoid either error-minimization bias the precautionary principle
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51 468 is often criticized for (Dorman, 2005): i.e. either being too restrictive (thus minimizing the
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53 469 type-2 error of wrongly rejecting the hypothesis that wind energy poses a threat) or being too
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56 470 permissive in favor of turbine construction (by overemphasizing the minimization of the
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58 471 corresponding type-1 error).

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473 ***Application in wind farm planning***

474 The resulting map allows authorities and planners a rapid and standardized first appraisal at a
475 high resolution. Thereby it does not only indicate where wind turbine construction plans will
476 face restrictions (i.e. category 1) and where no further constraints apply (category 4), but
477 provides a gradated estimation of the planning risk: Whereas in category 1 sites wind energy
478 construction is generally banned, development plans in category 2 and 3 have to be submitted
479 to a systematic, in situ impact assessment following a standardized procedure. It includes (1) a
480 repeated control for lekking activity before and during the mating season, (2) a thorough
481 search for indicators of reproduction (i.e. feathers, faeces and chicks) along transect lines in
482 late summer, as well as the mapping of (3) habitat quality and (4) evidence of species
483 presence at systematically distributed sampling plots using the method described in Storch
484 (2002). Data shall be collected within the capercaillie-relevant areas of the respective category
485 up to 1km distance from the construction site. Based on the resulting local situation in terms
486 of habitat suitability and habitat use in relation to the construction site, potential impacts shall
487 be estimated and the mitigation potential through a modification of the turbine positioning
488 appraised. In addition, the compensability shall be determined and compensation measures
489 quantified. Whereas new evidence of mating or reproduction will lead to the decline of the
490 project, habitat loss may be compensated through habitat improvement measures. These
491 measures should primarily be implemented in areas with habitat potential but low current
492 suitability with regard to forest structure or within corridors. Inside the compensation area –
493 the extent of which is determined by the importance and size of the habitat concerned - target
494 values for structural key parameters (see Suchant & Braunisch, 2004) must be reached and
495 maintained during the operational life of the wind turbine. Given the differences in relative
496 importance between the two categories, projects planned in category 2-sites inherently face a

1 497 higher risk of being rejected than those in category 3 sites, mainly encompassing un-occupied,
2 498 potential habitats or marginal parts of the distribution area where impacts are more likely to
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5 499 be compensable.

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7 500 Although our spatial concept is not legally binding, planners and authorities are currently
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10 501 using it as official planning document. Thereby, the perceived plausibility played a major
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12 502 role for accepting the precautionary concept: While we observed a consistent public
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14 503 agreement for banning turbine construction from the core areas of reproduction, the advice
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17 504 not to construct wind turbines on primary dispersal corridors elicited resistance. Although the
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19 505 majority of corridor areas is per se not suitable for wind energy development (i.e. crossing
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21 506 valleys or settlements where turbine construction is either not profitable or subjected to other
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24 507 restrictions), and population connectivity has been proven to be crucial for metapopulation
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26 508 persistence in the Black Forest (Segelbacher et al., 2008), it is difficult to convince public,
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29 509 planners and authorities that wind turbines should not be constructed in “stepping stone”
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31 510 habitats where the species has not been sighted for many years and the habitat is of low
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34 511 quality. To raise acceptance and promote adequate implementation, the concept was publicly
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36 512 presented and an implementation guideline, as well as the digital map showing the different
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39 513 categories, was made accessible on a website (www.windenergie.fva-bw.de).

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41 514 Our concept refers only to one species though. Although capercaillie counts among the main
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44 515 focal species in relation to wind energy development in Central European mountain forests,
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46 516 and its key habitats largely overlap with those of other conservation relevant species
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48
49 517 (Braunisch et al., 2013), planners usually need to consider a wide range of potentially
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51 518 vulnerable species. Developing similar concepts for species with complementary spatial and
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53 519 functional requirements and integrating them into a single planning tool would facilitate an
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56 520 adequate and timely consideration of conservation targets in the rapidly spreading
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58 521 development.

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523 Conclusions

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

- 536 (1) Precautionary measures should focus on the relevant ecological unit, i.e. target viable
537 populations and not local occurrences or individual animals,
- 538 (2) they should consider population dynamics processes, e.g. fluctuations in occupancy as
539 well as population connectivity, instead of merely relying on a temporal snapshot of
540 occurrence data,
- 541 (3) they should be based on a differentiated risk appraisal, with the estimated probability
542 and severity of threat on the population resulting in graded management implications
543 or restrictions,
- 544 (4) which, however, must ensure at least the minimum requirements of a viable
545 population until further knowledge is available.

546 Since precautionary measures always represent as an interim solution, regular revisions
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2 547 measures based on up-to-date knowledge will be crucial for promoting the precautionary
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4 548 principle as a valuable and justified basis for weighing ecological risks in conservation and
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7 549 landscape planning.

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9 550

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11
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13
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557 **References**

- 1
2 558 Aldinger, E., Hübner, W., Michiels, H. G., Mühlhäußer, G., Schreiner, M., & Wiebel, M.
3 559 (1998). Überarbeitung der standortskundlichen regionalen Gliederung im
4 560 südwestdeutschen Standortskundlichen Verfahren. *Mitteilungen des Vereins für*
5 561 *Forstliche Standortserkundung und Forstpflanzenzüchtung*, 39, 5-72.
- 7 562 Anderson, D., Manes, R., Manville, A., McMahon, S., Robel, R., Roppe, J., . . . Strickland, D.
8 563 (2008). Report on Wind & Wildlife - Key Research Topics.: Wildlife Workgroup of
9 564 the National Wind Coordinating Collaborative.
- 10 565 Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with
12 566 different proportions of suitable habitat: a review. *Oikos*, 71(3), 355-366.
- 13 567 Anthelme, F., Grossi, J. L., Brun, J. J., & Didier, L. (2001). Consequences of green alder
14 568 expansion on vegetation changes and arthropod communities removal in the northern
15 569 French Alps. *Forest Ecology and Management*, 145(1-2), 57-65. doi: 10.1016/s0378-
17 570 1127(00)00574-0
- 18 571 Bach, L., & Rahmel, U. (2004). Summary of wind turbine impacts on bats - assessment of a
19 572 conflict. *Bremer Beiträge für Naturkunde und Naturschutz*, 7, 245-252.
- 20 573 Baines, D., & Andrew, M. (2003). Marking of deer fences to reduce frequency of collisions
22 574 by woodland grouse. *Biological Conservation*, 110, 169-176.
- 23 575 Baines, D., & Summers, R. W. (1997). Assessment of bird collisions with deer fences in
24 576 Scottish forests. *Journal of Applied Ecology*, 34, 941-948.
- 25 577 Bellebaum, J., Korner-Nievergelt, F., Dürr, T., & Mammen, U. (2013). Wind turbine fatalities
26 578 approach a level of concern in a raptor population. *Journal for Nature Conservation*,
28 579 21(6), 394-400. doi: <http://dx.doi.org/10.1016/j.jnc.2013.06.001>
- 29 580 Bevanger, K., Berntsen, F., Clausen, S., Dahl, E. L., Flagstad, Ø., Follestad, A., . . . Vang, R.
30 581 (2010). Pre- and post-construction studies of conflicts between birds and wind turbines
31 582 in coastal Norway (BirdWind). Report on findings 2007-2010.: NINA Report 620. 152
33 583 pp.
- 34 584 Bevanger, K., & Brøseth, H. (2004). Impact of power lines on bird mortality in a subalpine
35 585 area. *Animal Biodiversity and Conservation*, 27(2), 67-77.
- 36 586 Brandt, J. S., Haynes, M. A., Kuemmerle, T., Waller, D. M., & Radeloff, V. C. (2013).
37 587 Regime shift on the roof of the world: Alpine meadows converting to shrublands in
38 588 the southern Himalayas. *Biological Conservation*, 158(0), 116-127. doi:
40 589 <http://dx.doi.org/10.1016/j.biocon.2012.07.026>
- 41 590 Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H., & Bollmann, K. (2013).
42 591 Selecting from correlated climate variables: a major source of uncertainty for
43 592 predicting species distributions under climate change. *Ecography*, 36, 1-13.
- 45 593 Braunisch, V., Segelbacher, G., & Hirzel, A., H. (2010). Modelling functional landscape
46 594 connectivity from genetic population structure - a new spatially explicit approach.
47 595 *Molecular Ecology*, 19, 3664-3678.
- 48 596 Braunisch, V., & Suchant, R. (2006). Das Raufußhühner - Bestandesmonitoring der FVA.
49 597 *Berichte Freiburger Forstliche Forschung*, 64, 55-67.
- 51 598 Braunisch, V., & Suchant, R. (2007). A model for evaluating the 'habitat potential' of a
52 599 landscape for capercaillie *Tetrao urogallus*: a tool for conservation planning. *Wildlife*
53 600 *Biology*, 13(1), 21-33.
- 55 601 Braunisch, V., & Suchant, R. (2008). Using ecological forest site mapping for long-term
56 602 habitat suitability assessments in wildlife conservation - demonstrated for capercaillie
57 603 (*Tetrao urogallus*). *Forest Ecology and Management* 256, 1209-1221.

- 604 Bright, J., Langston, R., Bullman, R., Evans, R., Gardner, S., & Pearce-Higgins, J. (2008).
 1 605 Map of bird sensitivities to wind farms in Scotland: A tool to aid planning and
 2 606 conservation. *Biological Conservation*, *141* (9), 2342-2356.
- 3 607 Brombacher, M. (1999). The precautionary principle threatens to replace science. . *Pollution*
 4 608 *Engineering, (Summer)*, 32–34.
- 5 609 Carrete, M., Sánchez-Zapata, J. A., Benítez, J. R., Lobón, M., & Donázar, J. A. (2009). Large
 6 610 scale risk-assessment of wind-farms on population viability of a globally endangered
 7 611 long-lived raptor. *Biological Conservation*. doi: 10.1016/j.biocon.2009.07.027.
- 8 612 Cas, J., & Adamic, M. (1998). The influence of forest alteration on the distribution of
 9 613 capercaillie leks in the Eastern Alps. *Zbornik* *57*, 5-57.
- 10 614 Catt, D. C., Dugan, D., Green, R. E., Moncrieff, R., Moss, R., Picozzi, N., . . . Tyler, G. A.
 11 615 (1994). Collisions against Fences by Woodland Grouse. *Scotland Forestry*, *67*(2),
 12 616 105-118.
- 13 617 Conway, A. J., & Danby, R. K. (2014). Recent advance of forest-grassland ecotones in
 14 618 southwestern Yukon. *Canadian Journal of Forest Research*, *44*(5), 509-520.
- 15 619 Cooney, R. (2004). The Precautionary Principle in Biodiversity Conservation and Natural
 16 620 Resource Management: An issues paper for policy-makers, researchers and
 17 621 practitioners. *IUCN, Gland, Switzerland and Cambridge, UK.* , xi + 51.
- 18 622 de Lucas, M., Janss, G. F. E., & Ferrer, M. (2004). The effects of a wind farm on birds in a
 19 623 migration point: the Strait of Gibraltar. *Biodiversity and Conservation*, *13*, 395-407.
- 20 624 Dirksen, S., Winden, J. V. D., & Spaans, A. L. (1998). Nocturnal collision risks of birds with
 21 625 wind turbines in tidal and semi-offshore areas. In: *Ratto C.F. and Solari G. (eds),*
 22 626 *Wind Energy and Landscape. Balkema, Rotterdam, The Netherlands.* (pp. 99-107).
- 23 627 Dorman, P. (2005). Evolving Knowledge and the Precautionary Principle. *Ecological*
 24 628 *Economics* *53*, 169–176.
- 25 629 Drewitt, A. L., & Langston, R. H. W. (2006). Assessing the impacts of wind farms on birds.
 26 630 *Ibis*, *148*, 29-42.
- 27 631 Drewitt, A. L., & Langston, R. H. W. (2008). Collision effects of wind-power generators and
 28 632 other obstacles on birds. *Annals of the New York Academy of Sciences*, *1134*, 233-266.
- 29 633 Everaert, J., & Stienen, E. W. M. (2007). Impact of wind turbines on birds in Zeebrugge
 30 634 (Belgium). *Biodiversity and Conservation*, *16*, 3345-3359.
- 31 635 Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction.
 32 636 *Journal of Wildlife Management*, *61*, 603-610.
- 33 637 Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology,*
 34 638 *Evolution and Systematics*, *34*, 487-515.
- 35 639 Farfán, M. A., Vargas, J. M., Duarte, J., & Real, R. (2009). What is the impact of wind farms
 36 640 on birds? A case study in southern Spain. *Biodiversity and Conservation*, *18*, 3743-
 37 641 3758.
- 38 642 Gill, J. A., Sutherland, W. J., & Watkinson, A. R. (1996). A method to quantify the effects of
 39 643 human disturbance on animal populations. *Journal of Applied Ecology*, *33*, 786-792.
- 40 644 González, M. A., & Ena, V. (2011). Cantabrian Capercaillie signs disappeared after a wind
 41 645 farm construction. *Chioglossa*, *3*, 65-74.
- 42 646 Grimm, V., & Storch, I. (2000). Minimum viable population size of capercaillie *Tetrao*
 43 647 *urogallus*: results from a stochastic model. *Wildlife Biology*, *6*(4), 219-225.
- 44 648 Hanski, I., & Gilpin, M. E. (1997). *Metapopulation biology: ecology genetics and evolution.*
 45 649 San Diego: Academic press.
- 46 650 Hirzel, A. H., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-Niche Factor
 47 651 Analysis: How to compute habitat-suitability maps without absence data? *Ecology*,
 48 652 *83*(7), 2027-2036.

- 653 Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., & Guisan, A. (2006). Evaluating the ability
 1 654 of habitat suitability models to predict species presences. *Ecological Modelling*, 199,
 2 655 142-152.
- 3 656 Horch, P., Bruderer, B., Keller, V., Mollet, P., & Schmid, H. (2003). Windenergiekonzept
 4 657 Schweiz - Beurteilung der 40 prioritären Standorte aus ornithologischer Sicht.:
 5 658 Schweizerische Vogelwarte, Sempach.
- 6 659 Horch, P., Graf, R., Liechti, F., Mollet, P., & Schmid, H. (2006). Windenergiestandorte
 7 660 Kanton Luzern. Beurteilung von möglichen Windenergiestandorten im Kanton Luzern
 8 661 bezüglich ihrer Auswirkungen auf Vögel.: Schweizerische Vogelwarte, Sempach.
- 9 662 Johnson, G. D., Erickson, W. P., Strickland, M. D., Shepherd, M. F., Shepherd, D. A., &
 10 663 Sarappo, S. A. (2002). Collision mortality of local and migrant birds at a large-scale
 11 664 wind-power development on Buffalo Ridge, Minnesota. *Wildlife Society Bulletin*,
 12 665 30(3), 879-887.
- 13 666 Klaus, S., Andreev, V., Bergmann, H. H., Müller, F., Porkert, J., & Wiesner, J. (1989). *Die*
 14 667 *Auerhühner* (Vol. 86). Magdeburg: Westarp Wissenschaften.
- 15 668 Korner-Nievergelt, F., Korner-Nievergelt, P., Behr, O., Niermann, I., Brinkmann, R., &
 16 669 Hellriegel, B. (2011). A new method to determine bird and bat fatality at wind energy
 17 670 turbines from carcass searches. *Wildlife Biology*, 17, 350-363.
- 18 671 Kriebel, D., Tickner, J., Epstein, P., Lemons, J., Levins, R., Loechler, E. L., . . . Stoto, T.
 19 672 (2001). The precautionary principle
 20 673 in environmental science. *Environ Health Perspective*, 109, 871-876.
- 21 674 Kuvlesky, W. P., Brennan, L. A., Morrison, M. L., Boydston, K. K., Ballard, B. M., &
 22 675 Bryant, F. C. (2007). Wind Energy Development and Wildlife Conservation:
 23 676 Challenges and Opportunities. *Journal of Wildlife Management*, 71, 2487-2498.
- 24 677 LAG-VSW. (2007). Länder-Arbeitsgemeinschaft der Vogelschutzwarten.
 25 678 Abstandsempfehlungen zu bedeutsamen Vogellebensräumen sowie Brutplätzen
 26 679 ausgewählter Vogelarten. *Berichte zum Vogelschutz*, 44, 151-153.
- 27 680 Lande, R. (1993). Risks of population extinction from demographic and environmental
 28 681 stochasticity and random catastrophes. *American Naturalist*, 142, 911-927.
- 29 682 Langston, R. H. W., & Pullan, J. D. (2003). Windfarms and birds: an analysis of the effects
 30 683 of wind farms on birds, and guidance on environmental assessment criteria and site
 31 684 selection issues.: RSPB/Birdlife International Report. Strasbourg, France.
- 32 685 Langston, R. H. W., & Pullan, J. D. (2004). Effects of wind farms on birds (pp. 89 p.).
 33 686 Strasbourg: Council of Europe Publishing.
- 34 687 LeBeau, C. W., Beck, J. L., Johnson, G. D., & Holloran, M. J. (2014). Short-Term Impacts of
 35 688 Wind Energy Development on Greater Sage-Grouse Fitness. *Journal of Wildlife*
 36 689 *Management, Early Online*.
- 37 690 Leddy, K. L., Higgins, K. F., & Naugle, D. E. (1999). Effects of Wind Turbines on Upland
 38 691 Nesting Birds in Conservation Reserve Program Grasslands. . *Wilson Bulletin*, 111,
 39 692 100-104.
- 40 693 LILC. (2000). *Summary of the workshop on the precautionary principle in wildlife*
 41 694 *conservation*. , University of Cambridge, Cambridge, United Kingdom.
- 42 695 Lovich, J. E., & Ennen, J. R. (2013). Assessing the state of knowledge of utility-scale wind
 43 696 energy development and operation on non-volant terrestrial and marine wildlife.
 44 697 *Applied Energy*, 103, 52-60.
- 45 698 Lynch, M., & Ritland, K. (1999). Estimation of pairwise relatedness with molecular markers.
 46 699 *Genetics*, 152, 1753-1766.
- 47 700 Meek, E. R., Ribbands, J. B., Christer, W. G., Davy, P. R., & Higginson, I. (1993). The
 48 701 effects of aero-generators on moorland bird populations in the Orkney Islands,
 49 702 Scotland. *Bird Study*, 40(2), 140-143.

- 703 MKULNV. (2012). Leitfaden Rahmenbedingungen für Windenergieanlagen auf Waldflächen
 1 704 in Nordrhein-Westfalen (pp. 64).
- 2 705 Moss, R. (1994). Decline of capercaillie (*Tetrao urogallus* L.) in Scotland. . *Gibier Faune*
 3 706 *Sauvage*, 2(11), 217-222.
- 4 707 Moss, R., Picozzi, N., & Catt, D. C. (1991). Capercaillie ecology *Forestry Commission*
 5 708 *Report on Forest Research* (pp. 69).
- 6 709 Musters, C. J. M., Noordervliet, M. A. W., & Ter-Keurs, W. J. (1996). Bird casualties caused
 7 710 by a wind energy project in an estuary. *Bird Study*, 43, 124-126.
- 8 711 Myers, N. (1993). Biodiversity and the precautionary principle. *Ambio*, 22(2-3), 74–79.
- 9 712 Pakkala, T., Pellika, J., & Lindén, H. (2003). Capercaillie *Tetrao urogallus* - ag good
 10 713 candidate for an umbrella species in taiga forests. *Wildlife Biology*, 9(4), 309-316.
- 11 714 Patthey, P., Signorell, N., Rotelli, L., & Arlettaz, R. (2012). Vegetation structural and
 12 715 compositional heterogeneity as a key feature in Alpine black grouse microhabitat
 13 716 selection: conservation management implications. *European Journal of Wildlife*
 14 717 *Research*, 58, 59–70.
- 15 718 Pearce-Higgins, J. W., Stephen, L., Langston, R. H. W., Bainbridge, I. P., & Bullman, R.
 16 719 (2009). The distribution of breeding birds around upland wind farms. *Journal of*
 17 720 *Applied Ecology*, 46, 1323-1331.
- 18 721 Plonczkier, P., & Simms, I. C. (2012). Radar monitoring of migrating pink-footed geese:
 19 722 behavioural responses to offshore wind farm development. *Journal of Applied*
 20 723 *Ecology*, 49, 1187-1194.
- 21 724 Prato, T. (2005). Accounting for Uncertainty in Making Species Protection Decisions.
 22 725 *Conservation Biology*, 19(3), 806–814.
- 23 726 Raffensperger, C., & Tickner, J. (1999). *Protecting Public Health and the Environment:*
 24 727 *Implementing the Precautionary Principle*. . Washington, DC: Island Press.
- 25 728 Rayner, R. M. V. (1988). Form and Function in Avian Flight. *Current Ornithology*, 5, 1-66.
- 26 729 Reichenbach, M., & Steinborn, H. (2006). Windkraft, Vögel, Lebensräume - Ergebnisse einer
 27 730 fünfjährigen BACI-Studie zum Einfluss von Windkraftanlagen und Habitatparametern
 28 731 auf Wiesenvögel.
- 29 732 Resnik, D. (2003). Is the Precautionary Principle Unscientific? *Studies in the History and*
 30 733 *Philosophy of Biological and Biomedical Sciences*, 34, 329-344.
- 31 734 Rydell, J., Bach, L., Dubourg-Savage, M., Green, M., Rodrigues, L., & Hedenström, A.
 32 735 (2010). Bat Mortality at Wind Turbines in Northwestern Europe. *Acta*
 33 736 *Chiropterologica*, 12(2), 261-274.
- 34 737 Sæther, B. E., & Bakke, Ø. (2000). Avian life history variation and contribution of
 35 738 demographic traits to the population growth rate. *Ecology*, 81(3), 642-653.
- 36 739 Sandin, P. (1999). Dimensions of the precautionary principle. *Human and Ecological Risk*
 37 740 *Assessment*, 5, 889–907.
- 38 741 Sandin, P. (2004). The precautionary principle and the concept of precaution. *Environmental*
 39 742 *Values*, 13, 461–475.
- 40 743 Sandin, P., Peterson, M., Hansson, S. O., Rudén, C., & Juthe, A. (2002). Five charges against
 41 744 the precautionary principle. *Journal of Risk Research* 5, 287-299.
- 42 745 Schaub, M. (2012). Spatial distribution of wind turbines is crucial for the survival of red kite
 43 746 populations. *Biological Conservation*, 155(0), 111-118.
- 44 747 Segelbacher, G., Manel, S., & Tomiuk, J. (2008). Temporal and spatial analyses disclose
 45 748 consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao*
 46 749 *urogallus*). *Molecular Ecology*, 17, 2356-2367.
- 47 750 Simberloff, D. (1998). Flagships, umbrellas, and keystones: is single-species management
 48 751 passé in the landscape era? *Biological Conservation*, 83(3), 247-257.

- 752 Steinborn, H., & Reichenbach, M. (2011). Kiebitz und Windkraftanlagen - Ergebnisse aus
 1 753 einer siebenjährigen Studie im südlichen Ostfriesland. *Naturschutz und*
 2 754 *Landschaftsplanung*, 43(9), 261-270.
- 3 755 Stewart, G. B., Pullin, A. S., & Coles, C. F. (2007). Poor evidence-base for assessment of
 4 756 windfarm impacts on birds. *Environmental Conservation*, 34, 1-11.
- 5 757 Storch, I. (1995). *Habitat requirements of capercaillie*. Paper presented at the Proceedings of
 6 758 the 6th International Grouse Symposium.
- 7 759 Storch, I. (2002). On Spatial Resolution in Habitat Models: Can Small-scale Forest Structure
 8 760 Explain Capercaillie Numbers? *Conservation Ecology*, 6(1), 25 p.
- 9 761 Storch, I. (2007). Grouse: Status Survey and Conservation Action Plan 2006-2010. (pp.
 10 762 114p): Gland, Switzerland: IUCN and Fordingbridge, UK: World Pheasant
 11 763 Association.
- 12 764 Storch, I., & Segelbacher, G. (2000). Genetic correlates of spatial population structure in
 13 765 central European capercaillie *Tetrao urogallus* and black grouse *T. tetrix*: a project in
 14 766 progress. *Wildlife Biology*, 6(4), 305-310.
- 15 767 Suchant, R., Baritz, R., & Braunisch, V. (2003). Wildlife Habitat analysis: a multidimensional
 16 768 habitat management model. *Journal for Nature Conservation*, 10, 253-268.
- 17 769 Suchant, R., & Braunisch, V. (2004). Multidimensional habitat modelling in forest
 18 770 management - a case study using capercaillie in the Black Forest, Germany.
 19 771 *Ecological Bulletins*, 51, 455 - 649.
- 20 772 Suter, W., Graf, R. F., & Hess, R. (2002). Capercaillie (*Tetrao urogallus*) and Avian
 21 773 Biodiversity: Testing the Umbrella-Species Concept. *Conservation Biology*, 16(3),
 22 774 778-788.
- 23 775 Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R., & Jenni, L. (2008). Ski tourism
 24 776 affects habitat use and evokes a physiological stress response in capercaillie *Tetrao*
 25 777 *urogallus*: a new methodological approach. *Journal of Applied Ecology*, 45, 845-853.
- 26 778 Thiel, D. K. (2007). *Behavioral and Physiological Effects in Capercaillie (Tetrao urogallus)*
 27 779 *Caused by Human Disturbance*. Dissertation, Universität Zürich, Zürich.
- 28 780 Wegge, P., & Rolstad, J. (1986). Size and spacing of capercaillie leks in relation to social
 29 781 behavior and habitat. *Behavioral Ecology and Sociobiology*, 19, 401-408.
- 30 782 Winder, V. L., McNew, L. B., Gregory, A. J., Hunt, L. M., Wisely, S. M., & Sandercock, B.
 31 783 K. (2014). Space use by female Greater Prairie-Chickens in response to wind energy
 32 784 development. *Ecosphere*, 5(1), 1-9.
- 33 785 Zeiler, H. P., & Grünschachner-Berger, V. (2009). Impact of wind power plants on black
 34 786 grouse, *Lyrurus tetrix* in Alpine regions. *Folia Zoologica* 58, 173-182.
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789 **Tables:**

1
 2 790 Table 1: Size and proportion of the areas (a) relevant for capercaillie inhabitation, (b) relevant
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 4 791 for metapopulation connectivity, (c) with current capercaillie distribution and (d) suitable for
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 7 792 wind energy development that are allotted to the area-categories (1-4) with different
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 9 793 implications for wind turbine construction. Highest priority is given to areas of category 1,
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 12 794 where wind turbine construction is generally banned. In categories 2 and 3 detailed impact
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 14 795 assessments are required, while in category 4 no further restrictions apply. WE: wind energy
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 17 796 development.

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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

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801 Table 2: Metapopulation-based versus observation-based approach: Comparison of the spatial
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 2 802 concept with the currently prevailing recommendations of banning turbine construction within
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 4 803 a 1km-buffer zone around capercaillie reproduction sites. A: Attribution of the area within the
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 6 804 buffer zone (“protected”) to the categories of the spatial concept, B: area outside the buffer
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 8 805 zone (“not protected”) but relevant for capercaillie according to the spatial concept, either for
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 10 806 inhabitation or metapopulation connectivity. An illustration of divergence between both
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 12 807 approaches is provided in Appendix C, Figure C1.
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	(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						

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811 **Figure captions**

1
2 812 Figure 1: Spatially explicit fundamentals integrated in the concept: (A) capercaillie
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4 813 distribution (grey) with core areas of reproduction (black), (B) long-term habitat potential in
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7 814 three classes: high (black), moderate (dark grey), low (light grey) , and (C) corridors
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10 815 consisting of 100 paths (grey) offering the best conditions for inter-patch dispersal between
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12 816 capercaillie patches (black), redrawn from: Braunisch et al. 2010, modified.

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17 818 Figure 2: Stepwise evaluation of areas relevant to capercaillie metapopulation persistence and
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19 819 connectivity. Information on current distribution, long-term habitat potential and dispersal
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22 820 corridors were combined with population-related thresholds as regards patch accessibility (a),
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24 821 patch size (b), patch quality (c), current inhabitation status (d), significance (e) and function
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27 822 (f) for metapopulation connectivity, resulting in four area-categories (1-4) with different
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29 823 implications for wind turbine construction. Thresholds were derived from (a) Storch and
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31 824 Segelbacher (2000), (b) Moss (1991, 1994), (c,f) Braunisch and Suchant (2007), (d)
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34 825 Braunisch and Suchant (2006), (e) Braunisch et al. (2010).

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39 827 Figure 3: Spatial planning concept illustrating four area-categories with different levels of
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41 828 importance for the capercaillie metapopulation and consequential restrictions for wind energy
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44 829 construction (right panel). The categorization resulted from combining different sources of
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46 830 spatial population information with ecological thresholds as described in Figure 2, the
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49 831 successive steps are schematically illustrated (left panel): The current capercaillie distribution
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51 832 (green) and core areas with reproduction (red, A) were intersected with the long-term habitat
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53 833 potential (three levels: high=dark blue, moderate = medium blue, and low=light blue) (B),
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56 834 resulting in a map showing areas relevant for capercaillie inhabitation (C). This was then
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835 combined with the results of a corridor-model (hatched, D) to form the final categories 1-4 (E,

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Figure 1
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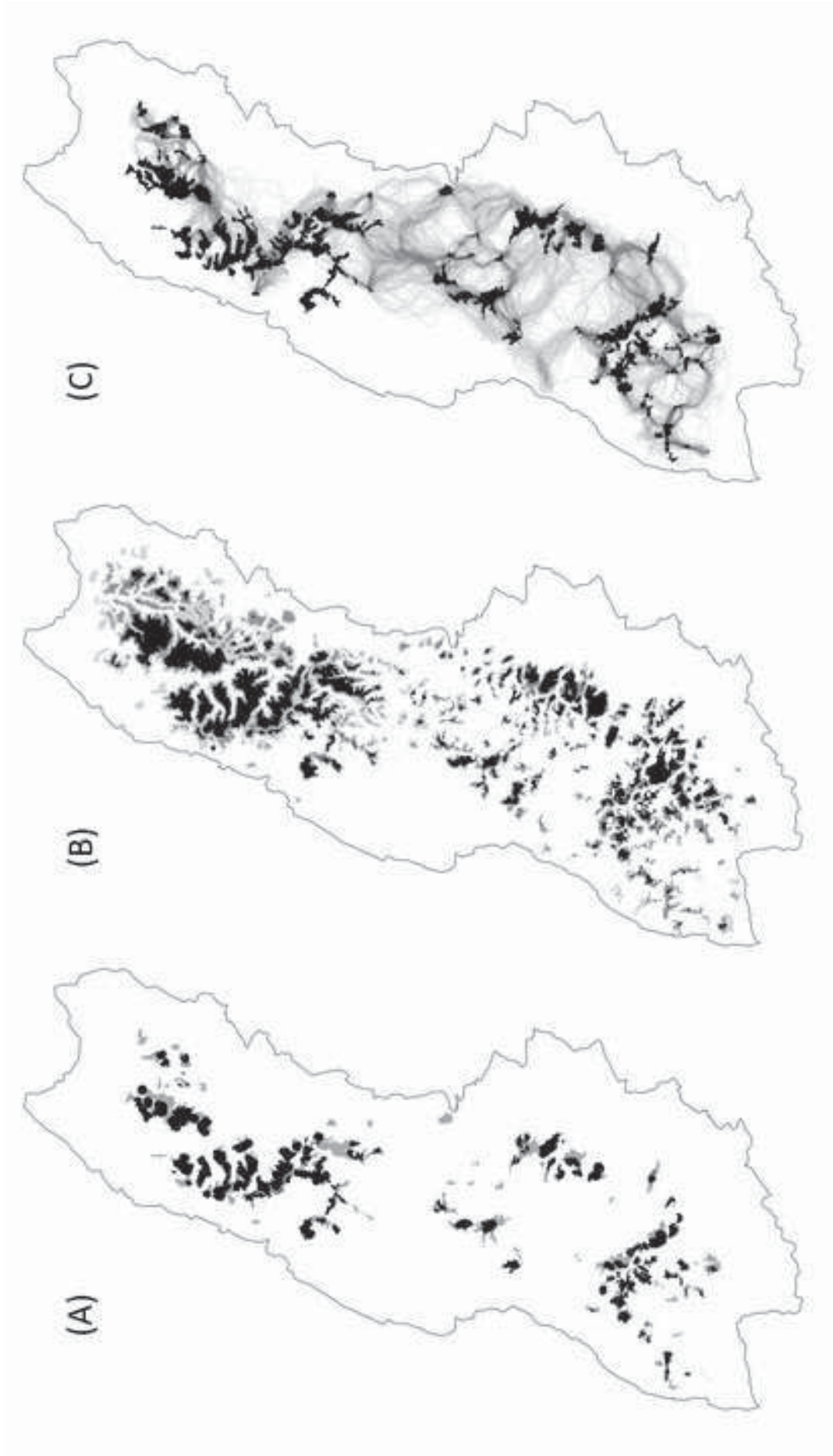


Figure 2
 Click here to download high resolution image

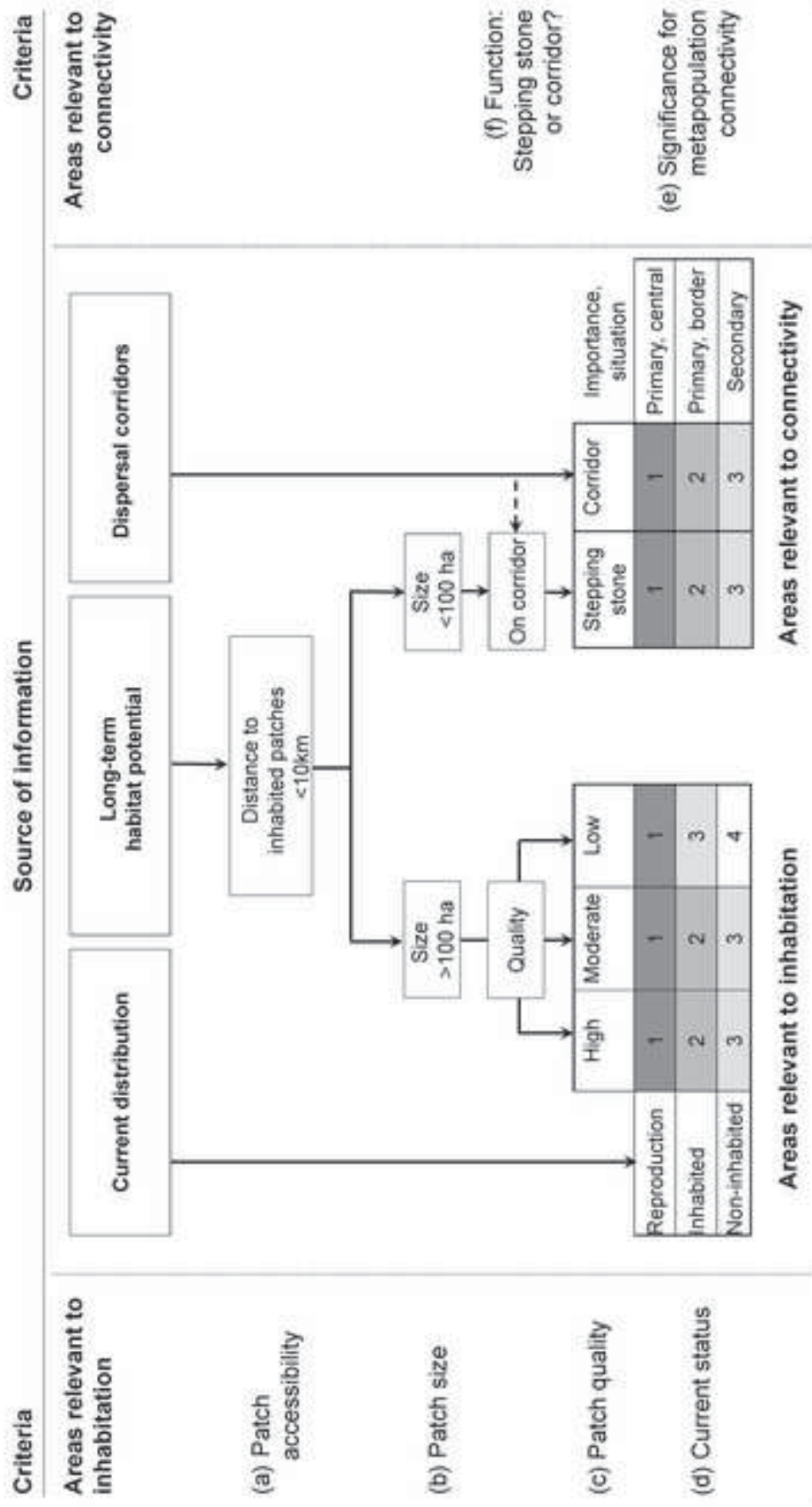
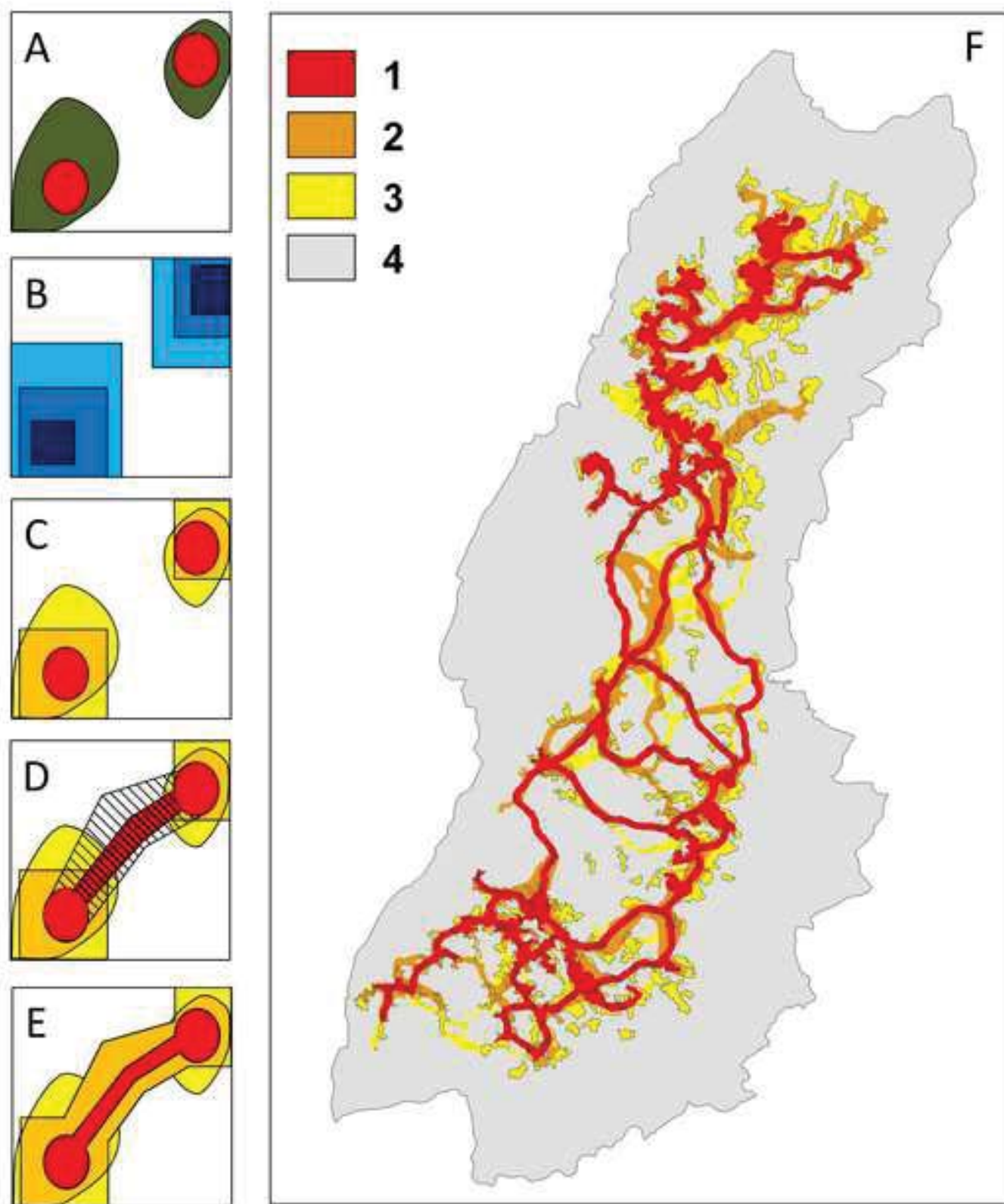


Figure 3
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Appendix A:

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).

References

- Böhner, J., Köthe, R. & Trachinow, C. 1997: Weiterentwicklung der automatischen Reliefanalyse auf der Basis von digitalen Geländemodellen. - Göttinger Geographische Arbeiten 100: 3-21. (In German)
- Box, G.E.P. & Cox, D.R. 1964: An analysis of transformation. - Royal Statistics 26: 211 – 243.
- Braunisch, V. & Suchant, R. 2006: Das Raufußhühner - Bestandesmonitoring der FVA. - Berichte Freiburger Forstliche Forschung 64, 55 – 67. (In German)
- Braunisch, V., Suchant, R. (2008): Using forest soil inventories for long term habitat suitability assessments in wildlife conservation: capercaillie habitats in the Black Forest, Germany. *Forest Ecology and Management* 256, 1209-1221.
- ESRI 1996: Using ArcView GIS: User manual. Environmental Systems Research Institute, Redlands, California, 350 pp.
- Fielding, A.H. & Bell, J.F. 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. - *Environmental Conservation* 24: 38 – 49.
- Hannah, P., J.P. Palutikof & Quine, C.P. 1995: Predicting windspeeds for forest areas in complex terrain. - In: Coutts, M.P. & Grace, J. (Eds.); *Wind and trees*. Cambridge University Press, Edinburgh, U.K, pp. 113-132.
- Hirzel, A.H., Hausser J., Chessel, D. & Perrin, N. 2002: Ecological-niche factor analysis: How to compute habitat- suitability maps without absence data? - *Ecology* 83: 2027-2036.
- Hirzel, A. H., et al. 2006. Evaluating the ability of habitat suitability models to predict species presences. - *Ecological Modelling* 199: 142-152.
- Hutchinson, G.E. 1957: Concluding remarks. - *Cold Spring Harbour Symposium on Quantitative Biology* 22: 415 – 427.

- Mitchell, S.J., Hailemariam, T. & Kulis, Y. 2001: Empirical modeling of cutblock edge windthrow risk on Vancouver Island, Canada, using stand level information. - *Forest Ecology and Management* 154: 117-130.
- Schneider, C. & Schönbein, J. 2003: Klimatologische Analyse der Schneesicherheit und Beschneibarkeit von Wintersportgebieten in deutschen Mittelgebirgen. Gutachten für die Stiftung Sicherheit im Skisport des Deutschen Skiverbandes, 97 pp. (In German)
- Sokal, R.R. & Rohlf, F.J. 1981: *Biometry: The principles and practice of statistics in biological research*. W.H. Freeman and Co., New York, 887 pp.
- Suchant, R., Baritz, R., Braunisch, V., 2003. Wildlife Habitat analysis: a multidimensional habitat management model. *Journal for Nature Conservation* 10: 253-268.
- Wilson, J.D. 1984: Determining a topex score. - *Scottish Forestry* 38/4: 251-256.

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 'Frictionator' 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.

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

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.

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

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 occurring in the respective cell (equation 3).

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

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 $C_{p,i}/A_p$ 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 'Frictionator' 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.

References

- Belkhir K, Castric V, Bonhomme F (2002) IDENTIX, a software to test for relatedness in a population using permutation methods. Université Montpellier II, Montpellier, France.
- 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.
- Emaresi G, Pellet J, Dubey S, Hirzel AH, Fumagalli L (2009) Landscape genetics of the Alpine newt (*Mesotriton alpestris*) inferred from a strip-based approach. *Conservation Genetics* published online.
- Goslee S, Urban D (2007) Dissimilarity-based functions for ecological analysis: The ecodist Package, Version 1.1.2.
- Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3), pp. Updated from Goudet (1995): Fstat version 1991.1992: a computer program to calculate F-statistics. *Journal of Heredity*, 1986, 1485-1486.
- Graf RF, Bollmann K, Suter W, Bugmann H (2005) The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. *Landscape Ecology* 20, 703-717.
- Hirzel AH, Fontanillas P, Braunisch V (2008) Frictionator. Lab of Conservation Biology, Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland.
- Legendre P, Fortin M-J (1989) Spatial pattern and ecological analysis. *Vegetatio* 80, 107-138.
- Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. *Genetics* 152, 1753-1766.
- Mantel N (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research* 27, 209-220.
- McKelvey KS, Schwartz MK (2005) DROPOUT: a program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. *Molecular Ecology Notes* 5, 716-718.
- Piertney SB, Höglund J (2001) Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). *Molecular Ecology Notes* 1, 303-304.
- Sachot S (2002) Viability and management of an endangered capercaillie (*Tetrao urogallus*) metapopulation Thèse de doctorat, Université de Lausanne.
- Segelbacher G, Höglund J, Storch I (2003) From connectivity to isolation: genetic consequences of population fragmentation in capercaillie across Europe. *Molecular Ecology* 12, 1773-1780.
- Segelbacher G, Manel S, Tomiuk J (2008) Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). *Molecular Ecology* 17, 2356-2367.
- Segelbacher G, Paxton RJ, Steinbruck G, Trontelj P, Storch I (2000) Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). *Molecular Ecology* 9, 1934-1935.
- Smouse PE, Long JC, Sokal RR (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35, 627-632.
- Valiere N (2002) GIMLET: a computer program for analysing genetic individual identification data. *Molecular Ecology Notes* 2, 377-379.

Appendix C

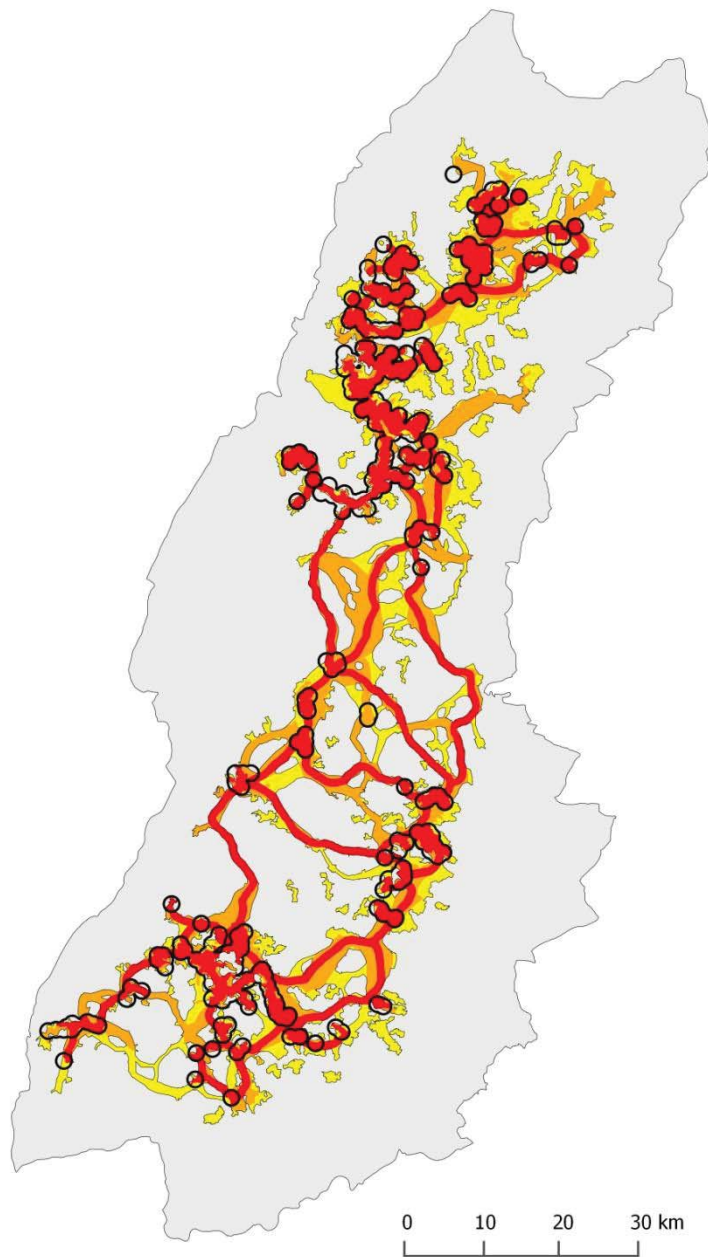


Figure C1: Metapopulation-based versus observation-based approach: Comparison of the spatial concept (four area categories: red: 1, orange: 2, yellow: 3, grey: 4, defined as illustrated in Figure 2) with the area that would fall under protection when following the recommendation of banning wind turbine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