Defining spatial priorities for capercaillie Tetrao urogallus lekking landscape conservation in south-central Finland

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Source: Wildlife Biology, 18(4) : 337-353

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/11-073

Wildl. Biol. 18: 337-353 (2012)
DOI: 10.2981/11-073

Current management

Defining spatial priorities for capercaillie *Tetrao urogallus* lekking landscape conservation in south-central Finland

Saija Sirkiä, Joona Lehtomäki, Harto Lindén, Erkki Tomppo & Atte Moilanen

Effective wildlife management requires knowledge about the areas th at are most important within the distribution range or specific management unit of the focal species. Using the spatial conservation planning tool, Zonation, and spatial data on Finnish forests, we present a fast and relatively simple way to objectively prioritise large areas for our focal species, the capercaillie *Tetrao urogallus*. We constructed the capercaillie lekking landscape prioritisation using published knowledge on the species' habitat and connectivity requirements, and validated the results via comparison to capercaillie lekking-site data. The results show that connectivity considerations both at the home range and the population scale are essential in prioritisation of areas suitable for capercaillie lekking sites. In addition, inclusion of negative connectivity to agri-urban areas further enhances the congruence between the known lekking sites and the areas of high priority (48.7% of known leks falling into the best 20% priority category). We conclude that our approach can be used in several stages of spatial wildlife conservation planning: as a preliminary analysis to find areas subjected to more detailed inventories and modelling, in combination with other analytical tools, or as the main instrument enabling informative use of readily available data in operational large-scale land-use planning. The advantages of our approach include: 1) the ability to execute relatively simple and objective analyses covering wide spatial extents at a high resolution, 2) the possibility to incorporate several ecologically realistic species-specific connectivity components into the analyses, and 3) the potential to help managers target wildlife surveys or conservation and management operations.

Key words: boreal forest, capercaillie, connectivity, game management, grouse, lekking site, spatial conservation planning, Tetrao urogallus, Zonation

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Received 9 August 2011, accepted 24 May 2012

Associate Editor: Hans Christian Pedersen

Capercaillie *Tetrao urogallus* is a characteristic species of the boreal coniferous zone. Along with many other forest grouse species, the capercaillie has been declining and its populations are small throughout much of its range (Storch 2000, 2007). In Finland, the populations of capercaillie have decreased dramatically from the 1960s to 1990s, after which the declining trend has levelled off (Lindén & Rajala 1981, Helle et al. 2003, Sirkiä et al. 2010a). Only a fraction of the original capercaillie population remains in the southern parts of the country, where human impacts have been greatest. As a consequence, the capercaillie is categorised as near-threatened (NT) in the whole country and regionally threatened (RT) in southern and central Finland (Rassi et al. 2001, 2010). It has been suggested that the declines have been mostly anthropogenic, associated with changing land-use practices (especially intensified agriculture and forestry) leading to habitat loss, fragmentation and deterioration (e.g. Storch 2000, 2007). However, the exact mechanisms behind the decline are hard to identify statistically (Sirkiä et al. 2010a).

According to many studies, research and management of the capercaillie should consider several spatial scales (e.g. Storch 1997, 2002, Graf et al. 2005, 2010, Miettinen et al. 2008, 2009, Sirkiä et al. 2010b). In addition to forest-stand scale management (Miettinen et al. 2009, 2010), lekking-site preservation at the landscape scale (at scales covering hundreds of hectares; see Lindén & Pasanen 1987, Helle et al. 1994, Sirkiä et al. 2011a) might be of importance for the species (e.g. Wegge & Rolstad 2002, Sirkiä et al. 2010b). Even thousands of hectares of forest at the surrounding landscape might be of importance in securing the persistence of a lekking population (Sirkiä et al. 2011a). At an even larger scale, dispersal of young females might cover areas up to 1,000 km^2 (Rolstad et al. 1991). Large-scale spatial planning might help recognise the areas suitable for long-term capercaillie population persistence, especially in southern and central Finland (Lindén et al. 2000, Miettinen et al. 2008, Sirkiä 2010).

The variety of methods by which wildlife conservation areas nowadays could be prioritised is overwhelming. Methods range from simple GIS-map overlays (e.g. Brown et al. 2009) to more complicated ecological modelling exercises, including modelling of habitat value or potential (e.g. Braunisch & Suchant 2007) and spatially explicit species distribution models that account for potential human-wildlife conflict zones (e.g. Jensen et al. 2008, Braunisch et al. 2011). Alternative methods do not necessarily rule each other out; in fact, outputs of ecological models can be used as inputs for simple site ranking (e.g. Jensen et al. 2008), for more complicated optimisation (e.g. Newbold & Eadie 2004) as well as for systematic conservation planning using spatial prioritisation tools (e.g. Carroll et al. 2010).

Systematic conservation planning and conservation prioritisation are frameworks that aim at well-informed allocation of limited conservation resources, while not forgetting a balance between conservation and the needs of other land uses (Margules & Sarkar 2007, Moilanen et al. 2009, Nelson et al. 2009, Moilanen et al. 2011). The idea is to base management decisions on transparent quantitative analysis (Margules & Pressey 2000). Spatial conservation prioritisation focusses on the distribution and condition of environment types and on the distributions and population sizes of species as well as on allocation and scheduling of alternative conservation actions. To be able to prioritise areas where the species of interest are most likely to persist in the long-term, it is important to account for not only local habitat quality and quantity, but also (multiple) species-specific connectivity requirements (Margules & Pressey 2000, Lehtomäki et al. 2009, Rayfield et al. 2009).

Here, we used a spatial conservation prioritisation approach and software, Zonation (see e.g. Moilanen et al. 2005, 2011), to create a spatial prioritisation for capercaillie in south-central Finland. With the inclusion of several connectivity components, we aimed to especially focus on lekking sites and the surrounding male home ranges that have been shown to be important for the species throughout much of the year, but especially during the lekking season in spring (see e.g. Wegge & Larsen 1987, hereafter referred to as 'lekking landscapes'). We also identified areas that are least suitable for lekking landscapes, and where management for capercaillie might thus be ineffective. We based the prioritisation on a combination of high-resolution forest coverage data and information from literature about capercaillie habitat and connectivity requirements. Priority maps were validated via comparison to independent capercaillie lekking-site data. Our overall aim was to introduce a practical tool for large-scale management for capercaillie lekking landscapes in Finland. We expect that methods similar to those employed here could have potential for landscape-scale land-use planning and wildlife management elsewhere in the boreal forest zone.

Material and methods

Focal species and study area

The capercaillie is a resident taiga species following closely the distribution of Scots pine *Pinus sylvestris*. In Finland, capercaillie is found almost in the entire country (Lindén 1983). The extent of a capercaillie male home range is several 100 ha, although some males spend most of the year close to their lekking sites (Wegge & Larsen 1987, Rolstad et al. 1991, Storch 1995). During natal dispersal, movements of young birds may cover tens or even hundreds of square kilometres (Rolstad et al. 1991). Because of its broad spatial requirements, the capercaillie may function as an umbrella species and its conservation would also favour other forest-dwelling species (Suter et al. 2002, Pakkala et al. 2003).

The selected study area covered south-central Finland (Fig. 1), approximately covering the hemi-boreal, southern and middle boreal forest vegetation zones, excluding only the northern Karelia and Kainuu areas (Hämet-Ahti 1981). Our study area corresponds to the area covered by the Forest Biodiversity Programme for south-central Finland (so called METSO programme; Finnish Government 2008, see also Lehtomäki et al. 2009). (As a curiosity, 'metso' stands for capercaillie in Finnish, stemming from the word 'metsä' meaning forest). The aims of the METSO programme are to halt the declining trends of forest habitat types and species, and to enhance the overall state of biodiversity in Finland, especially through voluntary, forest-owner driven conservation and species-friendly forest management. Such actions could also improve the current state of capercaillie populations in the southern parts of Finland. The area covered by the METSO programme closely corresponds to the local threat categorisation of capercaillie in south-central Finland (RT; see Rassi et al. 2001, 2010).

Within our study area there are approximately 18 million hectares of forest land covered by the Multi-source National Forest Inventory (MS-NFI) data (see below). Forests are primarily dominated by Scots pine and Norway spruce *Picea abies* with birches *Betula* spp. and some other deciduous trees also being present. The relative coverage of forests dominated by pine, spruce and deciduous trees is approximately 60, 30 and 10% of the forest area, respectively. Other land cover types within our study area include lakes, treeless mires, agricultural areas and human settlements. Human population densities are highest in the southern parts of the country, with a long history of agriculture and related land uses.

Spatial prioritisation using Zonation

'Zonation' is a spatial prioritisation framework and software used across large landscapes (Moilanen et al. 2005, 2009, 2011). It identifies areas that are important for retaining high habitat quality and connectivity for multiple biodiversity features, such as species or habitats, simultaneously (e.g. Kremen et al. 2008, Lehtomäki et al. 2009). It can use input data derived from several different sources, such as remotely sensed habitat databases, empirical data sets or statistical species distribution models, and it can handle large-scale high-resolution data with grid layers up to tens of millions of elements in size (Lehtomäki et al. 2009, Arponen et al. 2012). This allows for ecologically realistic conservation problems to be solved in a manner relevant for operational land-use planning (e.g. Gordon et al. 2009, Thomson et al. 2009, Carroll et al. 2010). The operational principle of Zonation can be summarised as maximal retention of weighted range-size normalised feature richness (Moilanen et al. 2011). The main output of Zonation is a hierarchical prioritisation through the

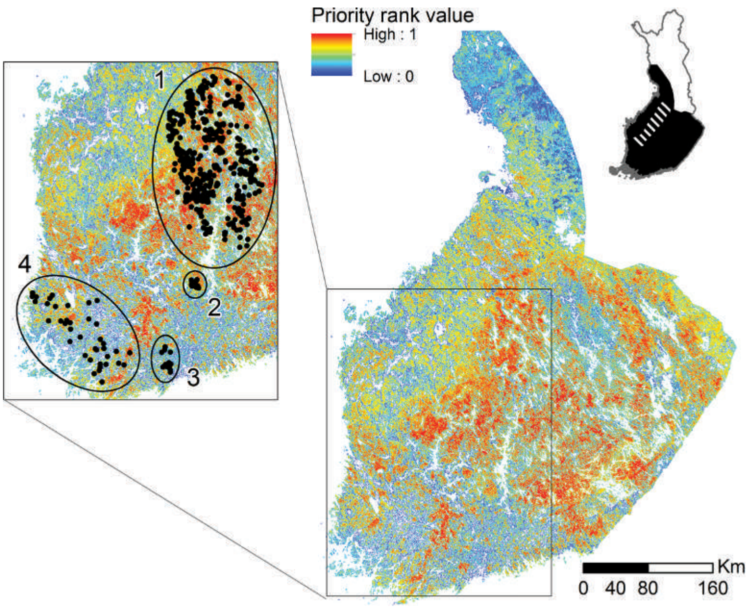


Figure 1. Our study area covers south-central Finland and corresponds to that covered by the Forest Biodiversity Programme for south-central Finland. The Suomenselkä watershed area is indicated with white stripes. The map shows the Zonation output for the scenario S6 including local habitat quality and all four different connectivity considerations (see Table 1 and text for further explanation). The priority ranking has been visualised according to the colour scale indicated in the panel, and areas without data (e.g. lakes and treeless mires) are marked with white. Survey regions (1-4) from which lekking-site data are available are shown in a separate box, lekking sites (N = 448) are indicated with black dots.

full landscape, based on occurrence levels of biodiversity features in cells, connectivity and other considerations.

The ecologically based model of conservation value - analysis setup

We built the prioritisation analyses based on expert opinion and published knowledge on capercaillie ecology. Specific components included in the analysis were 1) local habitat quality, 2) internal connectivity of the capercaillie population and lekking sites, including the home ranges of the males, and 3) avoidance of nearby human-impacted areas, each of which is explained below. As a special component of habitat quality, local-scale habitat heterogeneity was emphasised as an indicator of more natural-like conditions hosting more abundant resources for the capercaillie.

A typical conservation prioritisation process involves several stages starting from data acquisition or extraction and ranging through data pre-processing to the actual prioritisation analysis with suitable software. Following prioritisation, the resulting priority maps need to be further interpreted to facilitate on-the-ground action. The prioritisation work flow employed in our study is summarised in Figure 2.

In the prioritisation analyses, we compared six different combinations of how local habitat quality and connectivity components were treated and weighted in the analysis (scenarios S1-S6; described in Table 1 and Fig. 2). These analyses were built in an incremental manner so that new elements complicating the analysis setup (and making it more realistic) were added one by one on top of the old ones (see 'Zonation prioritisation' in Fig. 2). Here, we present two scenarios including local habitat quality only (S1-S2; see Table 1 and Fig. 2) and two scenarios including both local habitat quality and connectivity (S5-S6; see Table 1 and Fig. 2). The differences between the scenarios are described below.

There are some common analysis settings that were used in all analyses. Conservation value was aggregated according to the additive benefit function analysis variant, with parameter value $z = 0.25$ (Moilanen et al. 2005, Moilanen 2007), which in this case implies additive contributions of habitat quality and connectivity components.

Zonation starts from the full landscape retained for conservation, and it then iteratively removes grid cells, minimising loss of conservation value at each iteration round. During this ranking process, we only removed cells from the edge of the remaining areas so as to maintain additional structural connectivity. Due to the large dimensionality of our data (approximately 18 millions of grid cells with data), we removed 1,000 cells at each ranking iteration round before range-size normalisation was reapplied as per the Zonation meta-algorithm (Moilanen 2007, Moilanen et al. 2009).

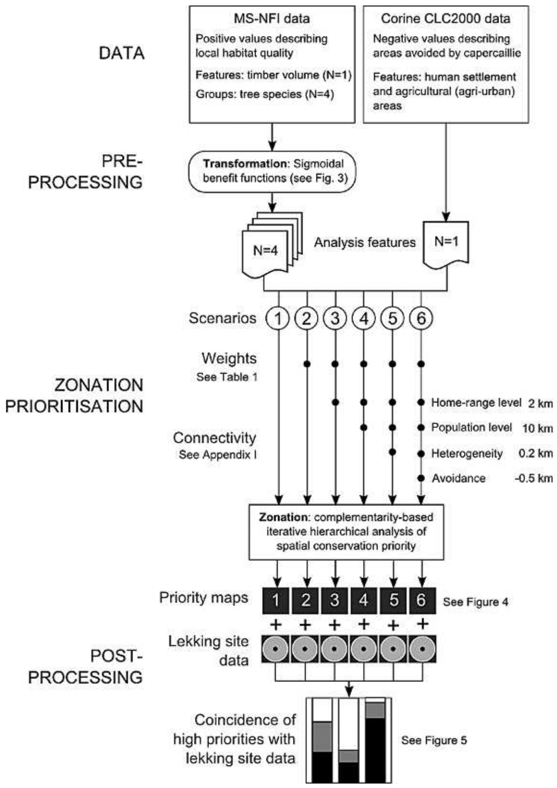


Figure 2. Schematic of the analysis setup. The analysis utilises different software environments. Pre-processing and output post-processing was mainly done with ArcGIS 10 (ESRI 2011). Timber volume benefit functions were created with GDAL (Geospatial Data Abstraction Library) and its Python bindings (OSGF 2011), and priority rank calculations from the lekking-site buffers were performed with the Geospatial Modelling Environment. The Zonation analysis variants are summarised in section 'Zonation prioritisation': each variant (scenarios S1-S6) is indicated by an arrow and analysis features included in the variant are indicated by circles on the top of arrows. Each of the six Zonation analysis variants produces a set of results including a priority map, like the one shown in Figure 4. Each of the priority maps is then overlaid with buffers created from the capercaillie lekking-site data (see 'Lekking-site data' in Material and methods) and an average priority is calculated for each buffer. Finally, the performance of the analysis variants can be compared by examining the mean ranks of habitat surrounding the lekking sites.

Table 1. Input features and their weighting in analyses S1-S6. NA = the feature was not applied in the scenario.

Features	Scenarios					
	S1	S2	S3	S4	S5	S6
Local habitat quality						
Pine forest	1.0	3.0	3.0	3.0	3.0	3.0
Spruce forest	1.0	1.0	1.0	1.0	1.0	1.0
Birch forest	1.0	0.0	0.0	0.0	0.0	0.0
Other deciduous	1.0	0.0	0.0	0.0	0.0	0.0
Agri-urban areas	-1.0	-1.0	-1.0	-1.0	-1.0	-1.0
Home range connectivity	NA	NA				
Pine forest	-	-	7.5	7.5	7.5	7.5
Spruce forest	-	-	2.5	2.5	2.5	2.5
Birch forest	-	-	0.0*	0.0*	0.0*	0.0*
Other deciduous	-	-	0.0*	0.0*	0.0*	0.0*
Population level connectivity	NA	NA	NA			
Pine forest	-	-	-	3.0	3.0	3.0
Spruce forest	-	-	-	1.0	1.0	1.0
Birch forest	-	-	-	0.0*	0.0*	0.0*
Other deciduous	-	-	-	0.0*	0.0*	0.0*
Mixed forest connectivity	NA	NA	NA	NA		
Pine forest	-	-	-	-	3.0	3.0
Spruce forest	-	-	-	-	1.0	1.0
Birch forest	-	-	-	-	0.0**	0.0**
Other deciduous	-	-	-	-	0.0**	0.0**
Negative connectivity to agri-urban areas	NA	NA	NA	NA	NA	Yes***

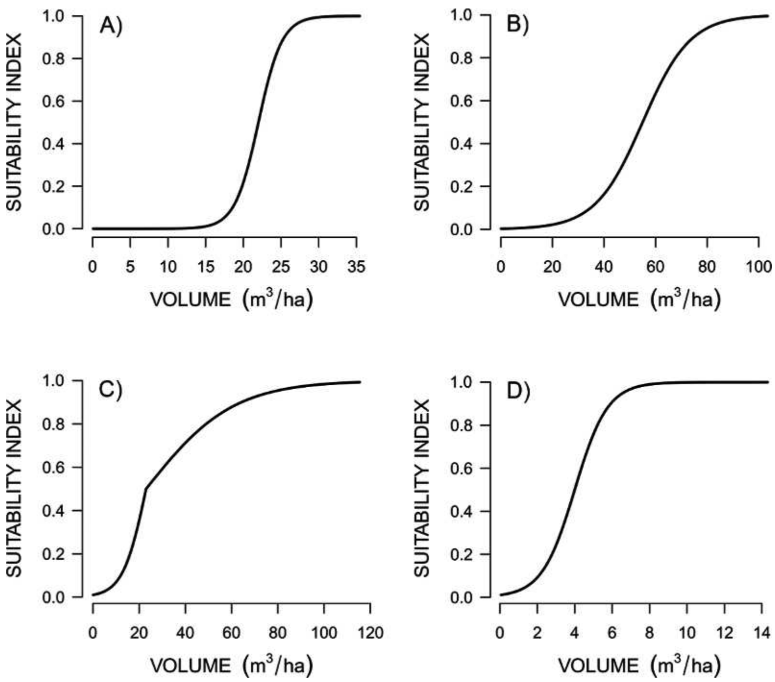
*Although weighted as zero, the presence of birch and other deciduous trees influenced within-forest connectivity calculations for pine and spruce (at 2-km and 10-km spatial scales for home range and population levels, respectively). For the connectivity matrix, see Appendix IA.
**Although weighted as zero, the presence of birch and other deciduous trees influenced the calculations for local forest heterogeneity for pine and spruce forests (matrix connectivity at the narrow, 200-m, spatial resolution). For the connectivity coefficients, see Appendix IB.
***In S6, negative interactions were defined between agri-urban areas (source) and all of the above feature layers (targets), both for habitat quality and connectivity-transformed analysis features (Rayfield et al. 2009). The mean distance of the negative connectivity response was set to 500 m.

Local habitat quality

We defined 'local habitat quality' as forest suitability for capercaillie lekking landscapes in a focal grid cell, and it was designed to include a wide range of suitable forest maturity classes. Earlier studies have described preferred capercaillie habitat for the lekking sites and broods as mature forest (age 60-70 years or more; Wegge & Rolstad 1986, Rolstad & Wegge 1987, 1989a). More recent studies have revealed that lekking sites can also exist in less mature forests (age 30-40 years; Rolstad et al. 2007, Valkeajärvi et al. 2007). In addition, young thinning forest (minimum age 30-40 years) has a positive effect on large-scale capercaillie density in Finland (Miettinen et al. 2008, 2009). When considering lekking site persistence through decades, the amount of forest > 40 years old (mean timber volume > 60 m^3/ha) has a positive influence (Sirkiä et al. 2011a) while the amount of more mature forest (age 51-70 years or more, mean timber volume > 152 m^3/ha) does not seem to have a significant effect (Sirkiä et al. 2011b).

We derived local habitat quality for the capercaillie lekking landscapes from GIS-layers derived from the MS-NFI in Finland, using timber volume as a proxy for local habitat suitability. The data was from year 2005, and the original cell resolution of 25 × 25 m was aggregated to 100 × 100 m (Tomppo 2006, Tomppo et al. 2008). To come up with an ecologically meaningful index of the local habitat quality, we devised a sigmoid-shaped function for each dominant tree species (pine, spruce, birch and other deciduous trees). These benefit functions translate the tree species-specific average timber volume in cell i into an index value S_i according to shapes given in Figure 3, with a value $S_i = 0$ indicating no value for the capercaillie and $S_i = 1$ indicating maximal local quality. These indices represent expert opinion about what is known about suitability of the range of

Figure 3. Sigmoid benefit functions scaling forest suitability by timber volume for different main tree species: A) birch, B) pine, C) spruce and D) other deciduous trees. Note different horizontal scales.



different forest maturity classes for the capercaillie lekking landscapes.

These indices are simplifications, lacking many aspects of capercaillie habitat use, especially outside the lekking season. However, highly detailed data that correspond to all phases of the capercaillie life cycle are not nationally available at such a high resolution; indeed, one aim of this work was to test the suitability of the MS-NFI data for wildlife landscape prioritisation. Note that these transformations define relative forest quality within stands of each dominant tree species, but that a further differential weighting is applied in the analysis to account for the preferences of the capercaillie between tree species (see Table 1). We did not consider the age of forest stands as in the MS-NFI data, forest age is generally positively correlated with stand volume (e.g. Peltola 2003). Moreover, it is currently thought that forest age *per se* is not the most important determinant for the capercaillie lekking sites; in managed boreal forests of present-day Finland, overall forest cover seems to better explain the presence of the species (Miettinen et al. 2008, Sirkiä et al. 2011a,b).

Each benefit function was constructed so that it gives $S_i = 0.5$ at a timber volume equivalent to the reported mean timber volumes of 'young thinning forests' for pine, spruce, birch and other deciduous trees (55, 23, 22 and 4 m^3/ha, respectively; source: MS-NFI 10, available at: http://www.metla.fi/metinfo/vmi/), calculated over young thinning forests in southern Finland (see Fig. 3). This ensures that the relative availability of different forest types is taken into account when calculating the indices. Equally, the benefit functions give the highest index value ($S_i = 1$) at a timber volume equivalent to the reported mean timber volume of 'mature forests' for the four separate tree species layers (97, 109, 29 and 8 m^3/ha for pine, spruce, birch and other deciduous trees, respectively; see Fig. 3 and http://www.metla.fi/metinfo/vmi/). To conclude, although the index describing local habitat quality only achieves its maximum with the mean timber volume for mature forest, relative forest suitability starts to increase already from low volumes, following the flexibility of capercaillie in its habitat use at the lekking sites and the surrounding male home ranges (see also Sirkiä et al. 2011a, Wegge & Rolstad 2011) and leaving room for possible positive or negative effects of forest thinning (Miettinen et al. 2008). To come up with more specific timber volume limits for forest suitability within capercaillie lekking landscapes, more research is needed.

Cells that have zero timber volume might be fresh clear-cuts, agri-urban areas, lakes or treeless mires. We extracted the distribution of agri-urban areas from the freely available Corine CLC2000-database (see e.g. Härmä et al. 2004). We extracted six land-use classes describing 'human settlement' (including buildings, industrial areas, roads, airports and harbours) and four classes of 'agricultural areas' (fields, fruit tree and berry bush cultivations, pastures and small-scale agricultural mosaics) into a single analysis feature layer to describe land uses that cause disturbance for the capercaillie. To model avoidance by the capercaillie, we included agri-urban areas as a negatively weighted local habitat quality layer in all the scenarios (see Table 1 and Fig. 2), and additionally, a negative connectivity influence was specified to spread out from agri-urban areas in S6 (see below). We set lakes and treeless mires to no data (white colouration in Fig. 1).

Connectivity

First, we discuss connectivity for the capercaillie and how it is generally applied in Zonation. After that, we describe the four different connectivity components applied in the analysis.

Connectivity can be assumed to be relevant for the capercaillie because earlier studies have shown that factors operating at broad landscape scales influence its occurrence (e.g. Rolstad et al. 1991, Graf et al. 2005, 2010, Braunisch & Suchant 2007, Sirkiä et al. 2010b). For instance, the area surrounding the lekking site is known to be different from the average Finnish landscape up to distances of 1-1.5 km (Lindén & Pasanen 1987, Helle et al. 1994, Miettinen et al. 2005; see, however, Sirkiä et al. 2011a for even longer distances). Lekking sites are situated inside larger forest patches with a higher forest cover percentage than in the landscape on average (Lindén & Pasanen 1987, Helle et al. 1994). Therefore, it is likely that forest connectivity influences the long-term viability of capercaillie lekking populations (see also Segelbacher & Storch 2002, Segelbacher et al. 2003).

In landscape ecological studies, connectivity is sometimes taken to imply structural connections between landscape elements via for example corridors. In such a setting it is possible to disrupt connectivity by e.g. clear-cutting connecting forest areas. In our analysis, we employ a metapopulation-type connectivity measure which is built upon a declining-by-distance dispersal kernel (for more detailed description on how Zonation implements this type of connectivity, see e.g. Lehtomäki et al. 2009). This kernel specifies how the connectivity between two areas (here grid cells) declines as a function of distance; if the mean distance parameter of the kernel is high, cells further away influence the connectivity of the focal cell.

In the prioritisation process, forest cells with extremely low timber volume (i.e. clear-cuts) automatically get low priority in the analysis due to low local habitat quality (see above). When connectivity requirements are included, the analysis gives higher priority to those cells that are both of high local quality (relatively high volume of trees preferred by the capercaillie) and are in the close vicinity of other high quality cells.

Cells that are not forest, i.e. agri-urban and no data areas (e.g. lakes and treeless mires) reduce connectivity by reducing the fractions of cells that generate a positive connectivity influence. In principle connectivity may extend infinitely far, but due to the declining-by-distance nature of the kernel, connectivity effects become negligible over long distances. With the longest mean distance scale used in the analyses (10 km kernel), cells located further than 30 km away from each other have minor effects on each other's connectivity.

In summary, we incorporated four different connectivity components into our analyses (see 'Zonation prioritisation: Connectivity' in Fig. 2). First, from the scenario S3 onwards, we accounted for the male home-range level connectivity by incorporating forest connectivity at a 2-km scale (mean distance of the declining-by-distance dispersal kernel; see Table 1 and Appendix IA). The mean distance between capercaillie lekking sites is 2 km (Wegge & Rolstad 1986, Sjöberg 1996), and the median distance between the male summer habitats and lekking sites is similarly approximately 2 km (Rolstad et al. 1991). During winter, males usually stay in the close vicinity of leks (Wegge & Larsen 1987). Thus, the 2-km spatial scale is relevant for those ecological phenomena that influence the number of males at leks, thereby influencing also lekking-site persistence (Rolstad & Wegge 1989b).

Second, to account for longer-distance population level connectivity, we included, from scenario S4 onwards, a second set of analysis features transformed by a 10-km scale connectivity kernel. The 10-km distance roughly covers the seasonal movements of females with a brood, and the maximum seasonal movements of males (measured in habitats under a heavy forestry influence in Varaldskogen, Norway; Rolstad et al. 1991, see also Sjöberg 1996). Thus, the 10-km spatial scale probably includes many of the spatial interactions that influence the size of a lekking population (males and females throughout the year; Wegge & Rolstad 2002), also roughly corresponding to the mean dispersal distance of the capercaillie (see

Braunisch & Suchant 2007 and the references within).

Note that both home-range scale and population scale connectivity computations accounted for the fact that forests with different dominant tree species can nevertheless help each other's connectivity. Connectivity within a landscape mosaic of several nominally different, but ecologically partially similar forest types, was computed using the matrix connectivity technique of Lehtomäki et al. (2009). Pairwise habitat similarity coefficients applied in matrix connectivity computations are explained in Appendix IA.

Third, in scenarios S5-S6, we wanted to emphasise the presence of locally mixed forest. We assumed that the stand architecture of mixed forest more resembles multi-cohort natural-like forest, which in turn provides abundant cover and food for capercaillie throughout the year (see e.g. Miettinen et al. 2009). Preference for mixed forests was again incorporated into the analysis by the matrix connectivity technique (Lehtomäki et al. 2009), with coefficients selected for preference of mixed forest at a localised 200-m spatial scale (see Appendix IB and Fig. 2). A single forest cell almost always includes several tree species which all add to the priority value of that cell (section 'Local habitat quality' above). With the 200 m mixed forest connectivity, we therefore set 'an additional' preference for those coniferous forest cells that are close to other forest cells that include some deciduous trees amongst conifers (see Appendix IB).

Lastly, in scenario S6, we included avoidance of nearby agri-urban areas via negative connectivity interactions, as described in Rayfield et al. (2009). Prior studies performed at broad spatial scales suggest that agri-urban areas have a negative influence on capercaillie abundance especially in southern Finland (Miettinen et al. 2008, Lindén et al. 2010, Sirkiä et al. 2010b). It has also been shown that increasing forest fragmentation by agricultural areas increases the predation risk of capercaillie in the remaining forest habitat (Rolstad 1991, Kurki et al. 2000, Storch et al. 2005). The impact of fragmentation may negatively influence birds up to 200-600 m into the forest (Rolstad 1991, see however Storch et al. 2005). In addition, according to expert opinion, birds at lekking sites start to get disturbed by approaching humans when they are on average 500 m away (Ruddock & Whitfield 2007). Therefore, we selected a 500-m spatial scale (kernel mean distance) for the negative connectivity influence. In S6, this additional negative influence was applied to all analysis features representing local habitat quality or connectivity either at the home range, population scale or mixed forest resolution (see Table 1).

Weighting of the components of the ecological model

Weighting sets the relative level of importance for different elements in the prioritisation process. Weights are determined mainly by subjective preferences (following the aims of the prioritisation) and are therefore frequently based on expert opinion. Here, these preferences were strongly shaped by earlier publications dealing with the capercaillie and lekking sites.

With respect to tree species, the capercaillie prefers coniferous forests, especially at lekking sites (e.g. Rolstad & Wegge 1987, 1989a). The proportion of pine-dominated forest stands has been found to have a positive relationship with landscape-scale capercaillie density (Miettinen et al. 2008). The capercaillie is also dependent on pine needles as a winter feed (e.g. Seiskari 1962, Gjerde & Wegge 1989, Andreev & Lindén 1994). Spruce is somewhat less important, although it may provide cover especially during snowless winters (Lindén 1989), and add important structural variability to local habitat. Thus, from S2 onwards (S1 being a baseline analysis with equal weight for all the tree species; see Table 1), we selected the weights for tree species so that primary lekking site and feeding habitat, pine forest, was given a weight of 3, and spruce forest a weight of 1 (see Table 1).

Birch and other deciduous trees were weighted as zero as local habitat, but they were weighted highly in the connectivity measures to express the positive influence of deciduous trees on connectivity and to model higher naturalness of mixed forests compared to monoculture (on a scale of 200 m). Although coniferous forest seems to be the primary habitat for capercaillie leks, deciduous trees and small, forested or open bogs may also be present, especially in the landscape connecting primary habitat patches. Rolstad & Wegge (1987) found that at the lekking sites, the proportion of deciduous trees could be up to 36%. From S3 onwards, the analysis feature layers for birch and other deciduous trees were therefore included to influence the connectivity of pine and spruce forests.

Weights for the home-range scale (2-km) connectivity-transformed features were 7.5 and 2.5 for pine and spruce dominated forests, respectively (see Table 1). Weights for the population scale (10-km) connectivity-transformed features as well as for the connectivity component emphasising the presence of mixed forest at 200-m spatial scale were lower: 3 for pine forest and 1 for spruce forest (see Table 1). This emphasis on home-range scale connectivity was justified because our main interest lies in the lekking landscapes, where the forest surrounding the lekking site up to an approximately 1.5-km distance seems to be the main driver of lekking-site quality (e.g. Wegge & Rolstad 1986, Helle et al. 1994, Miettinen et al. 2005). The weight for the feature describing distributions of agri-urban areas was set to -1, indicating that these areas are highly undesirable for the capercaillie (see Table 1).

Lekking-site data

We used lekking-site data to validate the priority maps, including the material from the southwestern and central Finland study areas used in Sirkiä et al. (2011a,b), supplemented by more recent data from the central Finland, Uusimaa and Hämeenlinna regions. These data were collected by the Finnish Game and Fisheries Research Institute (Survey region 1 in Fig. 1), by local experts (Survey region 2 in Fig. 1), by the Centre for Economic Development, Transport and the Environment of Uusimaa (Survey region 3 in Fig. 1), and by questionnaires and interviews from local game management personnel, land owners and hunters (Survey region 4 in Fig. 1). We checked the data carefully and updated them so that only those lekking sites that were known to have been active in the year 2000 or later were included. In total, we used 448 lekking sites with known locations to evaluate the prioritisation outcome (see Fig. 1). As we cannot guarantee an equal search effort for lekking sites in all four survey regions, we refrain from comparing the results between survey regions. However, comparisons between different scenarios are justified.

Using ArcGIS 10 software (ESRI 2011), we created 500-m buffers surrounding each lekking site, and for the area covered by the buffers (78.5 ha each), we calculated the mean Zonation rank of each scenario S1-S6 analysis (see Fig. 2) using the Geospatial Modelling Environment (version 0.5.3 Beta; available at: www.spatialecology.com). Note that the buffers could overlap with each other to a varying degree, which, however, was an uncommon situation because the leks were usually further apart, as the average nearest neighbour distance for leks was 3.16 km. The chosen buffer size should adequately represent the lekking-site location in the sense that possible movements of the lekking sites (e.g. because of loggings) from one forest patch to another rarely exceed the distance of 500 m (e.g. Rolstad 1989, Valkeajärvi & Ijäs 1991).

Results

General patterns

Figure 1 shows the results for the most realistic analysis variant that includes local habitat quality as well as all four connectivity components (S6; see Table 1). Regions close to the eastern border of Finland, ridges in the southeastern Finland and the large, forested watershed area extending from the southwestern Finland towards northeastern Finland (hereafter referred to as Suomenselkä; inset in Fig. 1) stand out as high priority areas for capercaillie lekking landscapes. Ridge and watershed areas are mostly pine-dominated heath forests, reflecting the preferred lekking-site habitat in scenarios S2-S6. Additional high priority areas extend from the southeastern ridges towards the central Finland, roughly between the two large lakes visible in white in Figure 1. Apart from being dominated by coniferous tree species, the high priority areas are concentrated in the more continuous forest landscapes of south-central Finland.

The lowest ranked areas are mostly situated in the southernmost Finland, close to the Baltic Sea coast line and around big lakes (see Fig. 1). Generally, these areas either have heavy human impacts (with low forest cover and high proportion of agri-urban land use) or they are dominated by deciduous trees (e.g. in the surroundings of lakes). The northernmost part of our study area appears as consistently low rank in all scenarios, likely because of lower forest timber volumes, stemming from lower soil productivity and a shorter growing season in the north. Another possibility is that the distinctively nutrient rich, alkaline soil types of the so-called 'Lapland triangle' (overlapping the northern parts of our study area; e.g. Rassi et al. 2001) create specific forest vegetation characteristics (e.g. forests dominated mostly by deciduous trees) valued lower in our analyses. However, with respect to weighting of tree species in the analysis, we tested several different weighting options without any major changes in the main results.

Differences between the scenarios

Figure 4 shows, in more detail, the priority rankings for the Uusimaa region, the southernmost province of Finland with the capital Helsinki at the coast. Scenarios S1, S2 and S6 are shown; S3, S4 and S5 are omitted because of relatively small changes happening between them.

Scenario S1 based on local habitat quality proposes a very fragmented pattern of priorities compared to other scenarios (see Fig. 4A). In S2, higher weight was given to coniferous forests, concentrating high rank areas closer to the coast line, but again prioritising the landscape in a fragmented manner (see Fig. 4B). The long peninsula in the western part of the province as well as the national park in the middle starts to stand out as a high priority area.

Scenario S6 reveals areas of high local quality that also are well connected, and not in the immediate proximity of agri-urban areas (see Fig. 4C). When compared to S1, it is evident that although the proportion of total forest area in the province is rather high (> 60% of the land area according to the Uusimaa regional council information service), the areas defined as most suitable for capercaillie lekking landscapes under S6 are few and fairly isolated from each other. Regions close to the peninsula in the west, some national parks and specific areas in the eastern and northern parts of the province stand out as of high priority, and the rest of the province has a very low priority ranking (see Fig. 4C). In the whole province, approximately 89,000 ha of land fall into the best 20% priority category according to scenario S6. Note that this figure has been cut from the prioritisation result for the whole study area, and the top 20% areas correspond to roughly 13% of the total land area of the province (Uusimaa regional council information service).

Validation of priorities with lekking-site data

We divided the mean priority ranks calculated from the 500-m buffers surrounding the lekking sites (N = 448) into five evenly spaced categories: the first category included the lowest 20% mean priorities (ranks 0.0-0.2), the next one ranks 0.21-0.4 and so forth (Fig. 5). Only one lekking site under scenario S6 falls into category 0.0-0.2, in the other scenarios no lekking sites were surrounded with such low rank areas. Also the next category (mean priority 0.21-0.4) is very small, including only 2.9% of lekking sites under S1 and ~ 0.5% under the other scenarios (S2, S5 and S6). Under the S1, S2 and S5 scenarios, most of the lekking sites have a mean priority between 0.61 and 0.8 in the surrounding landscape (52.5, 58.9 and

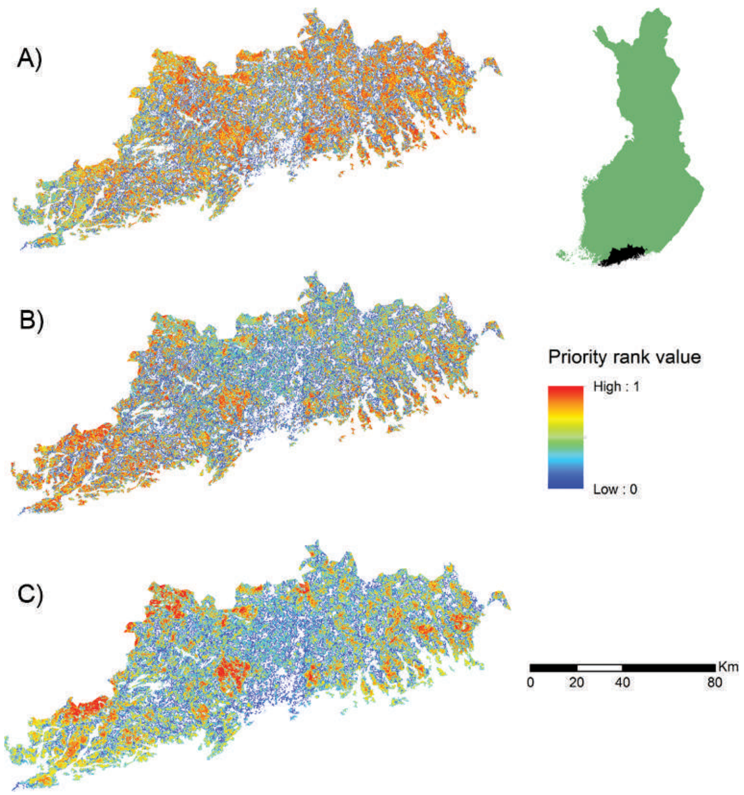


Figure 4. Zonation outputs for A) scenario S1, B) scenario S2 and C) scenario S6 in the Uusimaa province. S1 and S2 include local habitat quality information only, S2 giving higher weight to coniferous tree species. S6 includes the weighted habitat quality as well as all four connectivity components. Colours are as in Figure 1.

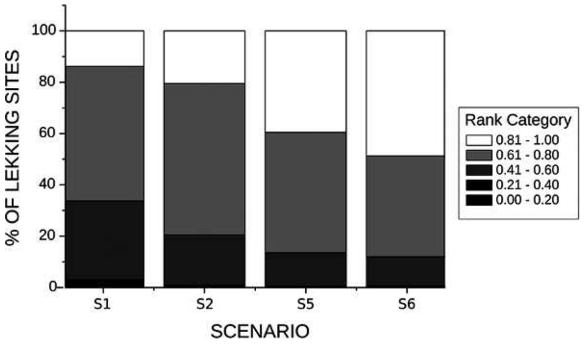


Figure 5. The percentage of lekking sites falling into the five rank categories according to scenarios S1, S2, S5 and S6 (see Table 1 and Fig. 2). The results for scenarios S3 and S4 were very similar to those of S5 and are therefore omitted from the figure. Priority ranks were calculated as the mean rank inside a 500-m buffer surrounding each lekking site.

46.9% of lekking sites fall into this category, respectively). Scenario S6 clearly produces the best correspondence with the lekking-site data, with half of the lekking sites (48.7%) belonging to the highest rank category 0.8-1.0. Under scenarios S1, S2 and S5, the proportion of leks within this category is only 13.8, 20.5 and 39.5%, respectively, demonstrating high effects of forest connectivity. This is also reflected in the mean priorities surrounding all lekking sites, those being 0.66, 0.70, 0.76 and 0.78 under scenarios S1, S2, S5 and S6, respectively. As before, results for the scenarios S3 and S4 closely resembled those of S5 and are therefore omitted.

Discussion

Considering the wide range of methods used to prioritise wildlife conservation areas, specific advantages of our approach are: 1) the ability to perform relatively simple and objective analyses covering wide spatial extents at high resolutions, 2) the possibility to incorporate several ecologically realistic species-specific connectivity components into the analyses, and 3) the potential to help managers target future surveys or conservation and management operations towards the high priority areas. Our approach could be used in different phases of spatial conservation planning: as a preliminary analysis to locate areas for data collection and further modelling, or as the main instrument enabling operational land-use planning and decision making (see e.g. Lehtomäki et al. 2009).

Data limitations and subjective choices are always present and must be considered when evaluating the outcome of any site prioritisation exercise. Here, our aim was to utilise nationally available large-scale high-resolution data to come up with an operationally useful measure of lekking landscape quality for the capercaillie. The indices used for local habitat quality are thus inevitably rough simplifications. For instance, small peat lands and open bogs which frequently occur in the proximity of the lekking sites (Lindén & Pasanen 1987, Rolstad & Wegge 1987) were excluded from the analyses. However, these and other smaller-scale structures within the forest stands (e.g. ground vegetation structure) are probably important only at a very local scale (see, however, Storch 1993). In the end, we are confident that at broader spatial extents our analyses correspond to the main relevant characteristics of capercaillie lekking landscapes. Preliminary evaluations suggest that areas identified as high priority in scenario S6 correspond well to areas judged as valuable also by local experts. In fact, the outcome of this analysis has already been successfully used by the Centre for the Economic Development, Transport and the Environment in the Uusimaa region to locate previously unknown lekking sites for the capercaillie (A. Pummila, pers. comm.).

Braunisch & Suchant (2007) argue that many wildlife habitat modelling and/or prioritisation methods do not incorporate aspects of potentially suitable habitat, but only include those habitats that are currently available. Concerning our results, it is of course possible that some high priority areas will lose value because of forest fragmentation and/or climate change (e.g. Virkkala 1987, Virkkala & Rajasärkkä 2011). Besides including such considerations into future prioritisation analyses, there are also plans to test the potential of greenbelt or corridor solutions to find those forests that are potentially of value in increasing connectivity between high priority areas at the national scale (see also Lindén et al. 2000).

High priority areas and implications for land-use planning

According to the yearly wildlife triangle counts performed in Finland (Lindén et al. 1996), areas of high capercaillie abundance roughly coincide with the areas we identified as high priority for capercaillie lekking landscapes (see Fig. 1). Especially regions close to the eastern border and the Suomenselkä watershed area (see inset in Fig. 1) have fairly strong capercaillie populations, whereas the lake-rich area of central Finland has clearly lower capercaillie abundance (Helle & Wikman 2010). It is interesting that our high priority areas also, at least partially, coincide with the proposed 'forest bridges' or greenbelts, aiming at guaranteeing connectivity of Finnish forests (and forest fauna) towards forests of Russia (Lindén et al. 2000). Forests close to the Russian border seem to be important not only for the capercaillie, but for wildlife species richness and abundance in general (Lindén et al. 1999). This suggests that forests on the Russian side of the border may act as a possible source habitat for wildlife (see also Kouki & Väänänen 2000, Virkkala & Rajasärkkä 2007). This pattern arises from the difference in forest-use histories between Fennoscandia and Russia (see e.g. Angelstam et al. 1995, Uuttera et al. 1996), and it is possible that intensifying forest management on the Russian side of the border might negatively affect wildlife also in neighbouring Finland. For example, Helle et al. (2003) compared grouse abundances between eastern Finland and Russian Karelia in 1964-2002, and found similarly declining trends on both sides of the border.

Compared to the rest of south-central Finland, there is a fairly high proportion of state-owned forests and forest reserves in the Suomenselkä watershed area (see Fig. 7 in Lindén et al. 2000), creating large continuous forest areas. In addition to the capercaillie, other forest wildlife is also relatively abundant in this region, including wild forest reindeer *Rangifer tarandus fennicus*, brown bear *Ursus arctos* and wolf *Canis lupus* (see Heikkinen & Kojola 2010). Overall, the strong wildlife populations of Suomenselkä positively influence wildlife species richness and abundance across the entire region (Pellikka et al. 2006).

In the Uusimaa province, capercaillie abundance has been steadily low during the whole period of wildlife triangle counting (1988-2010; Helle & Wikman 2010). In 2010, the abundance was 2.9 birds/km^2 of forest, while the average value for the whole country was 3.7 (Helle & Wikman 2010). It is evident that the current forested areas in the province are alarmingly small and fragmented. The situation is similar in the adjacent province of southwestern Finland, where the persistence of capercaillie lekking sites was found to be connected to the amount of forest surrounding the lekking site on a 3-km radius (Sirkiä et al. 2011a); a finding underlining the importance of large and continuous forest areas for leks (see also Helle et al. 1994, Lindén et al. 2000). According to our scenario S6, in Uusimaa there are only a few forest areas remaining that are large and connected enough to support a viable network of lekking sites (see Fig. 4C; Lindén et al. 2000). The isolated structure of the remaining larger forest tracts begins to resemble the heavily fragmented landscapes of central Europe. There is a well-documented example of capercaillie lekking site and subpopulation extinctions from isolated forest tracts in Germany (Müller 1990). To prevent further negative capercaillie population trends in southernmost Finland, large-scale greenbelt programmes and local land-use planning operations should be combined to enhance the physical and functional connectivity between the existing forest areas.

Lekking-site data and limitations of the validation

Another potential application of our prioritisation results is to concentrate future lekking-site surveys towards the high priority areas, working down from the highest priorities in scenario S6 (see Fig. 5). In fact, we cannot guarantee that lekking sites were randomly searched for in the first place. It is also highly unlikely that the search effort was equal in all four survey regions, thus, comparisons between the survey regions should be made with caution. However, the increasing proportion of lekking sites falling under the top 20%-rank category, when moving towards scenario S6 (see Fig. 5), clearly shows that the elements we have considered important for the capercaillie and its lekking sites are indeed functionally relevant. Strictly taken, this result only holds for regions from which we were able to obtain lekking-site data (see Fig. 1), but there is little reason to expect that the capercaillie would behave differently in other provinces of south-central Finland.

The inclusion of the weighting scheme directing higher value towards coniferous forests (difference between the scenarios S1 and S2; see Fig. 5) adds approximately seven percentage units of lekking sites to the top category (priority 0.8-1.0), and further inclusion of the connectivity considerations almost doubles the amount of lekking sites falling in this category (from 20.5% in S2 to 39.5% in S5; see Fig. 5). Our connectivity considerations cover spatial extents up to 30 km (the negative-exponential connectivity response has declined to negligible levels at longer distances), so higher priority areas under the scenarios S5 and S6 may cover lekking-site networks rather than single leks (see also Lindén et al. 2000). Areas of high priority might also include more mesic, spruce-dominated areas good for broods, as young males tend to recruit to leks that are fairly close to where they have hatched (i.e. natal dispersal distances are usually < 10 km; Braunisch & Suchant 2007 and the references in it). In Switzerland, inclusion of variables describing landscape structure also improved predictions of capercaillie occurrence at the forest-stand scale (Graf et al. 2010). In a study conducted in Germany, a habitat suitability model built strictly on forest-stand scale variables correctly reflected small-scale habitat preferences for the capercaillie, but had limited potential to predict population abundance at larger scales (Storch 2002).

Conclusions

Large-scale human land use, including forestry and expansion of agri-urban areas, as well as negative effects of climate change continue to threaten wildlife and wildlife habitats in the boreal forest zone (e.g. Virkkala & Rajasärkkä 2011). Here, we have presented one possible solution of how to objectively prioritise important areas for capercaillie lekking sites over large spatial extents. Moreover, by comparing the prioritisation output to lekking-site data, we have shown that elements such as home-range and population-scale connectivity are essential in achieving a sensible prioritisation outcome. Spatial conservation prioritisation can be useful in finding the most important areas for wildlife conservation. Also the low-priority end of the priority ranking can be of operational value: targeting intensive forestry and other environmentally damaging activities to the low-rank areas would facilitate ecological impact avoidance, in this case from the perspective of the capercaillie.

The capercaillie has several qualities that makes it a suitable candidate for spatial prioritisation. First, there are plenty of published studies on its habitat requirements, landscape-level connectivity effects and other ecological characteristics. Second, thanks to the frequent National Forest Inventories, data on the primary habitat features are available for many countries in Europe. Third, there are indications that the capercaillie can be considered as an umbrella species (Suter et al. 2002, Pakkala et al. 2003), making the high priority areas potentially valuable also for many other forest-dwelling species. Unfortunately, analyses based on a single species can never represent the requirements of all forest biodiversity. Thus, in the future, our plan in Finland is to include habitat and connectivity requirements of several wildlife species into a single analysis to come up with 'wildlife landscapes', and validate the results using the wildlife richness index (see e.g. Lindén et al. 1999, Pellikka et al. 2005, 2006). We think that analyses similar to the one developed here might have high potential for wide application in the boreal forest context, to help in recognising important wildlife areas and to support operational large-scale land-use planning and biodiversity conservation.

Acknowledgements - a warm thanks to Pentti Valkeajärvi, Arto Pummila, Ilmari Häkkinen and Markku Milonoff who provided us with the majority of the lekking-site data. Saija Sirkiä and Joona Lehtomäki thank the University of Helsinki Science Foundation for funding. Atte Moilanen acknowledges support from the Academy of Finland Center-of-Excellence program 2006-2011 (grant 213457) and the ERC-StG project GEDA (grant 260393).

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Appendix I. Coefficients used in the connectivity calculations

A) Habitat similarity coefficients used in the connectivity calculations for the home range (2-km spatial scale) and population level (10-km spatial scale) connectivity (multi-feature matrix connectivity; Lehtomäki et al. 2009). Coefficients are given between forests dominated by birch (BI), spruce (SP), pine (PI) and other deciduous trees (OT). A coefficient of 1.0 indicates that the two forest types contribute fully to each other's connectivity. All values on the diagonal are 1.0 because each forest type contributes fully to its own connectivity. A coefficient of 0.0 would indicate that the forest types have no effect on each other's connectivity. Cells with similar dominant tree species (e.g. spruce and pine) also contribute to each other's connectivity, but less than if both cells had the same tree species in them (i.e. coefficient is less than but close to 1.0). Cells with dissimilar tree species (e.g. pine and birch) contribute only little to each other's connectivity (coefficients more than 0.0 but not close to 1.0). Here we use 'similar' and 'dissimilar' in the context of what kind of tree species composition is most often associated with capercaillie lekking landscapes according to expert opinion. Note that the contributions do not have to be symmetrical, i.e. habitat type 1 can be better connected to habitat type 2 than the other way around.

B) The coefficients used in the matrix connectivity emphasising the presence of heterogeneous mixed forest (200-m spatial scale). Here, the contributions are symmetrical and always 1.0 at minimum, with a special emphasis on mixes between 1) pine and other tree species and 2) spruce and other tree species. The exact numbers are based on expert opinion.

	BI	SP	PI	OT
A)				
BI	1.0	0.6	0.3	0.8
SP	0.5	1.0	0.8	0.5
PI	0.3	0.7	1.0	0.2
OT	0.9	0.5	0.3	1.0
B)				
BI	1.0	1.5	2.0	1.0
SP	1.5	1.0	2.0	1.5
PI	2.0	2.0	1.0	2.0
OT	1.0	1.5	2.0	1.0