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Capercaillie *Tetrao urogallus* - a good candidate for an umbrella species in taiga forests

Timo Pakkala, Jani Pellikka & Harto Lindén

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The capercaillie *Tetrao urogallus* is widely accepted as a species seriously suffering from fragmentation of forests and habitat loss. Foresters as well as conservationists agree on the need and principles for maintaining viable populations, but the proposed management means often differ. The approach currently favoured by Finnish foresters is to manage capercaillie leks and their surroundings using methods that differ from those used in intensive forestry. It may be desirable to prove that forests with capercaillie leks also favour other forest bird species and biodiversity in general. During the last 16 years (1987-2002), forest birds have been censused and capercaillie leks were mapped in the 465-km^2 study area in southern Finland. Most of the study area consists of spruce-dominated mature forests. The remainder of the landscape is a mixture of variously aged forests, agricultural areas, lakes and scattered human settlements with a gradient from an agricultural-forest mosaic to forest-dominated areas. The old-growth forest bird species three-toed woodpecker *Picoides tridactylus*, pygmy owl *Glaucidium passerinum* and red-breasted flycatcher *Ficedula parva* were more abundant within 300 m and 1,000 m radii around capercaillie lek sites than in non-lek control sites. Also the overall species richness of breeding forest birds was higher in the vicinity of capercaillie leks. On a larger scale (100 x 100 km squares), using the wildlife triangle scheme developed in Finland, we show that the density of capercaillie closely coincides with a wildlife richness index describing the total abundance of 15 other forest-dwelling mammal and bird species with diverse ecology and habitat requirements. Capercaillie is a flagship species for foresters, and can be considered a good candidate for an umbrella species for wildlife in taiga forests.

Key words: capercaillie, Finland, lek, species richness, taiga forests, umbrella species

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Biodiversity concerns are now seen as crucial factors in Finnish forestry, also outside nature reserves, i.e. in commercial forests. Foresters and other people earning their living from forestry are often rural people, and hunting is their axiomatic activity or has been a hobby since their youth. This is perhaps why forest professionals in Finland have always been very much aware of the problems involved in game management and game re-

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search. It is much easier to justify radical changes in forest management practices to forest users, using game animals as the target species, than it is using smaller organisms, some of which are even considered forest pests. The proprietor of the largest area of Finnish forests (Metsähallitus) has located and mapped about 3,000 capercaillie leks in Finland in order to develop effective guidelines for forest management to save the viability of these leks (Anon. 1997). The guidelines follow the recommendations given especially by Finnish, Swedish and Norwegian scientists (e.g. Rolstad & Wegge 1987, Rolstad, Wegge & Gjerde 1991, Hjorth 1994, Wegge 1995, Helle, Lindén, Aarnio & Timonen 1999).

In Finland, the capercaillie *Tetrao urogallus* was originally a mythical bird that has kindled numerous superstitious beliefs and the creation of many a fairytale. The capercaillie is one of the most charismatic of game animals, comparable even to large predators and moose *Alces alces*. Only a few decades ago, hunting authorities had the sole responsibility for managing the capercaillie and its habitats, but currently, the capercaillie appears to be a favourite species amongst various interest groups ranging from hunters to conservationists and foresters. The abundance of capercaillie in Finland has declined quite dramatically from the middle of the last century (e.g. Lindén & Rajala 1981, Lindén 2002), especially in the southwestern parts of the country, where numbers have dropped by as much as 70-80%.

For foresters, the capercaillie is a flagship species (*in sensu* Shrader-Frechette & McCoy 1993), a symbol of and a leading element for viable taiga forests. Thus, exclusion of areas containing capercaillie leks from intensive forestry is quite acceptable to the foresters, especially if the capercaillie could serve as an 'umbrella species' (*in sensu* Shrader-Frechette & McCoy 1993), and a large selection of other forest species would benefit from these activities as well.

The spatial requirements of capercaillie leks are extensive, with displaying males jointly using an area of at least 300 ha (e.g. Rolstad & Wegge 1987, 1989, Rolstad, Wegge & Larsen 1988, Storch 1995, 1997, Sjöberg 1996), implying that the management activities for capercaillie will have a strong influence on many other species and the biodiversity in general. In the Swiss Alps, Suter, Graf & Hess (2002) observed that species richness and abundance of mountain birds, especially those restricted to subalpine forests, were higher in the vicinity of capercaillie. They concluded that capercaillie could be a useful umbrella species for conservation purposes. In the German Alps, Fischer & Storch (2001) obtained evidence that good capercaillie habitats correlated with high woodpecker densities. Whether these results can be extrapolated to the situation in Finland remains unclear, because the Finnish boreal forests differ greatly ecologically from those of the Alps, and because associations between species at the scale of forest stands, as found in Europe, may not necessarily hold at larger spatial scales (Storch & Bissonette 2002). Also, for the sake of forest managers and decision makers, the status of an umbrella species must be earned under local conditions.

We focused on two main questions to provide evidence that capercaillie may be suitable as a potential umbrella species for wildlife in the forests of Finland. Firstly, we studied the association between capercaillie leks and forest bird species at local scales. In a 465-km^2 study area in southern Finland, where forest birds were mapped extensively during 1987-2002 (e.g. Pakkala, Hanski & Tomppo 2002), we compared the abundance and richness of forest bird species in the vicinity (300 m and 1,000 m radii) of capercaillie leks with that of the control forest areas further away from the leks. Then we studied which habitat and landscape factors correlated with species richness. Secondly, we compared the densities of capercaillie and other wildlife species within 100 x 100 km areas, using the Wildlife Richness Index (WRI; see Lindén, Helle, Vuorimies & Wikman 1999) obtained from the same census routes, the so-called wildlife triangles that cover all of Finland (concerning method, see Lindén, Helle, Helle & Wikman 1996).

Study area, material and methods

Study area

The study area is located in the municipality of Lammi in southern Finland (61°15'N; 25°00'E; Fig. 1) and covers a total area of 465 km^2. The landscape is a mixture of variously aged forests, agricultural areas, lakes and scattered human settlements with a gradient from a southern agricultural-forest mosaic to northern forest-dominated areas. Forest covers 76% of the study area, and spruce-dominated coniferous or mixed mature forests are the most common forest types.

Breeding bird data and study design

The capercaillie lek sites within the study area were mapped during 1987-2002. The centres of the leks were defined by the locations of the displaying males. The annual data were combined to estimate a weighed centre for each lek during the entire study period. Locations where only solitary displaying males were detected were not included. A total of 41 lek sites were

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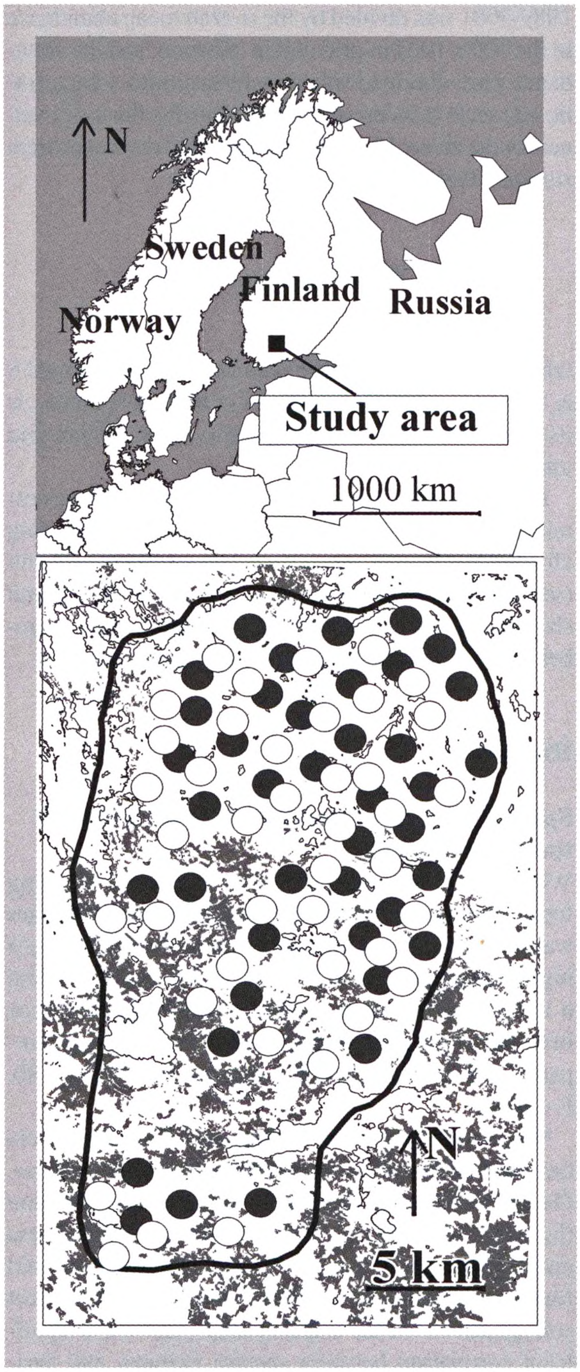

Figure 1. Location of the Lammi study area (encircled) with capercaillie lek positions (●) and control (non-lek) sites (○) during the study period 1987-2002. Lakes are deliminated by thin black lines and agricultural areas by grey shading. Other areas consist mostly of forests.

determined in the study area (see Fig. 1). The study area was also representatively covered with breeding bird censuses (i.e. territory mapping; concerning method see Pakkala et al. 2002), and all parts of the study area were mapped over a period of at least three years during the study period. The annual censuses were conducted between 15 April and 15 July. From these breeding bird data, the presence of 80 forest species was registered within 300 and 1,000-m radii from each lek centre. Species that typically occur in clear-cuts, other open areas, young forest stands, agricultural areas and human settlements were not included (e.g. nightjar *Caprimulgus europaeus*, woodlark *Lullula arborea*, white wagtail *Motacilla alba*, jackdaw *Corvus monedula*, red-backed shrike *Lanius collurio*, scarlet rosefinch *Carpodacus eryhtrinus* and yellowhammer *Emberiza citrinella*). Only the forest population of the swift *Apus apus* was included. The number of territories of three conservationally valuable species in mature forests (i.e. pygmy owl *Glaucidium passerinum*, three-toed woodpecker *Picoides tridactylus* and red-breasted flycatcher *Ficedula parva*) were estimated within 300 and 1,000-m radii of lek centres (see Pakkala et al. 2002). A combined 3-year dataset was randomly selected at each site to standardise the census effort. All censuses were performed by the senior author.

Lek sites were compared with control sites located on forest land 2 km southwest of the above-mentioned lek site at least 1 km from any other lek site, and the proportion of forest land on both study scales (300 and 1,000 m, respectively) had to be > 50%. If these conditions were not met, the location of a control site was moved the minimum distance either clockwise or counterclockwise along the 2 km distance radius in order to fulfill the conditions. The criteria for control sites were thus made rigorous enough to ensure comparability between lek and non-lek (control) sites. Pairwise patterning of lek and control sites also guaranteed general similarity in cover and forest types (see Fig. 1). The breeding bird data of the control sites were gathered using the same methods as used at the lek sites.

Habitat and landscape data

Based on land-use and forestry data, digital topographic maps made by the National Land Survey of Finland and aerial photographs of and field information on the study area, we calculated habitat and landscape area values for the areas around lek and control sites. The following factors were computed within radii of 300 and 1,000 m: water, agricultural land, young forests (< 20 years old, including clear-cuts), middle-aged forests (20-70 years old) on mineral and peat soil, old forests (> 70 years old) on mineral and peat soil, and the number of buildings which describes the general level of human impact. The land-use and forestry data were selected to match the bird census years of the particular leks or control sites.

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Habitat and landscape features were correlated with species richness by calculating Spearman's rank correlation coefficients between areas of land use types, number of buildings and species richness. These data were also used to analyse differences in habitat and landscape features between lek and control sites; median areas of land-use types and number of buildings were compared using Mann-Whitney U-tests.

The proportions of land-use types are intercorrelated. To study the independent effects of habitat and landscape features on species richness, compositional transformations (log (proportion of land-use type/proportion of old forest on mineral soil); Aitchison 1986) were used for areas of land-use types. Proportions of zero were replaced with 0.001 which was an order of magnitude smaller than the smallest proportion observed (Aebicher, Robertson & Kenward 1993). These composites were then correlated with species richness using Spearman's rank correlation.

Wildlife richness index and capercaillie abundances

The relationship between capercaillie and other wildlife species was examined using data from the wildlife triangle scheme (see Lindén et al. 1996) which provides abundance information for about 30 different wildlife species including the capercaillie. Wildlife triangles are census routes of 12 km, which are counted both in winter (January-March) and in August. In winter, the snow tracks crossing the census line are counted, and in summer all grouse species are counted in a 60-m wide main census belt using a 3-man chain (Rajala 1974). The triangle network in Finland is dense and regionally representative (see Fig. 3).

The Wildlife Richness Index (WRI; Lindén et al. 1999), based on information on capercaillie and 15 other species, is a true diversity index accounting for both the number of species and their relative abundance. The 15 other species were mountain hare *Lepus timidus*, red squirrel *Sciurus vulgaris*, wolf *Canis lupus*, red fox *Vulpes vulpes*, stoat *Mustela erminea*, pine marten *Martes martes*, wolverine *Gulo gulo*, lynx *Lynx lynx*, white-tailed deer *Odocoileus virginianus*, moose, wild forest reindeer *Rangifer tarandus fennicus*, roe deer *Capreolus capreolus*, black grouse *Tetrao tetrix*, hazel grouse *Bonasa bonasia* and willow grouse *Lagopus lagopus*. The species group deliberately included ecologically very different species representatives: mammals and birds, predators and their prey and species with different habitat and spatial requirements.

To calculate the WRI for each wildlife triangle, the mean abundance for each species in the triangle in 1989-2001 was divided by the overall mean abundance in the 100 x 100 km grid unit in question, and the abundance ratio obtained was transformed into a $\log_{10}$ (ratio +1) scale (Lindén et al. 1999). Finally, the index values for the above 15 species (capercaillie excluded) were summed using the following equation:

$$WRI_t = \sum_{i=1}^{15} \log_{10}\left(\frac{a_{it}}{a_{ig}}+1\right)$$

where WRI_t is the wildlife richness index in triangle t, a_{it} is the abundance of species i in triangle t, and a_{ig} is its mean abundance in the respective 100 x 100 km grid unit.

In this analysis, mean capercaillie densities were correlated with the WRI values of the other 15 species using all wildlife triangles inside each 100 x 100 km grid unit (see Fig. 3) as separate samples. The 100 x 100 km unit size was chosen to ensure sufficient sample sizes (number of wildlife triangles) in the correlation analysis.

Results

Species richness of forest birds at lek sites and their surroundings

Within a 300-m radius, the mean number of breeding forest bird species (excluding capercaillie) at the lek sites was 41.2 and 36.4 at the control sites; the difference is highly significant ($t = 5.17$, $df = 80$, $P < 0.001$). Within a 1,000-m radius there was an insignificant difference in favour of lek surroundings (mean 59.6 species) compared with control sites (58.1 species; $t = 1.76$, $df = 80$, $P = 0.08$).

We also studied which habitat and landscape factors (see Methods section) correlated with species richness. On the 300-m scale, there was a significant correlation ($|r_s| > 0.22$, $df = 80$, $P < 0.05$) between species richness and middle-aged forest on mineral soil (negative), old forest on mineral soil (positive) and old forest on peat soil (positive). On the 1,000-m scale there was a significant correlation between species richness and agricultural land (negative), old forest on mineral soil (positive) and the number of buildings (negative).

As some of the habitat and landscape variables are intercorrelated, the results should be interpreted within ecologically relevant frames. Old forest on mineral soil was the most common land-use type on both the 300 (46.1% of total area) and 1,000-m scale (39.6%), and it correlated significantly positively with species richness. It can therefore be considered as the most important habitat

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and landscape element. If composite transformations of other habitat and landscape factors ((log (proportion of land use type/proportion of old forest on mineral soil); see Methods section) are used, independent composites can be correlated with species richness. On the 300-m scale, there was a significant ($|r_s| > 0.22$; df = 80, $P < 0.05$) negative correlation between species richness and log (proportion of middle-aged forest on mineral land/proportion of old forest on mineral soil); all other correlations were insignificant. On the 1,000-m scale, there was a significant ($|r_s| > 0.22$; df = 80, $P < 0.05$) negative correlation between species richness and log (proportion of agricultural land/proportion of old forest on mineral soil); all other correlations were insignificant. These results indicate that on the 300-m scale the species richness of forest birds is positively associated with the total area of old forest types. The negative association of middle-aged forests on mineral soil is probably mediated by its strong negative correlation (r_s = -0.71; df = 80, $P < 0.001$) with the proportion of old forest on mineral soil. On the 1,000-m scale, the most important landscape factor associated with species richness seems to be the relation between proportions of old forest types and agricultural land. The number of buildings was negatively correlated with species richness on the 1,000-m scale. If the number of buildings was, however, related to agricultural land sites (number of buildings/area of agricultural land), the correlation between this ratio and species richness was positive (r_s = 0.36; df = 51, $P < 0.01$). The correlation between the number of buildings and species richness was slightly positive, but insignificant, on the 1,000-m scale in non-agricultural land sites (r_s = 0.20; df = 24, $P > 0.1$) which indicates that the general negative effect of the number of buildings is mediated by its strong positive correlation (r_s = 0.74; df = 80, $P < 0.001$) with agricultural land areas.

Lek and control site landscapes differed from each other. On the 300-m scale, median areas of young forests (lek 0.9 ha; control 3.2 ha) and middle-aged forests on mineral soil (lek 5.1 ha; control 7.1 ha) were significantly smaller (Mann-Whitney U-test: $P < 0.05$), and areas of middle-aged (lek 2.0 ha; control 0.8 ha) and old forests (lek 1.9 ha; control 0.8 ha) on peat soil and old forests on mineral soil (lek 14.3 ha; control 10.0 ha) were significantly larger at lek sites than at control sites. On the 1,000-m scale, the median number of buildings (lek 6; control 24) was significantly smaller and median areas of middle-aged forests (lek 26.6 ha; control 17.1 ha) and old forests (lek 19.8 ha; control 12.4 ha) on peat soil larger at lek sites than at control sites. All other differences in habitat and landscape factors were insignificant.

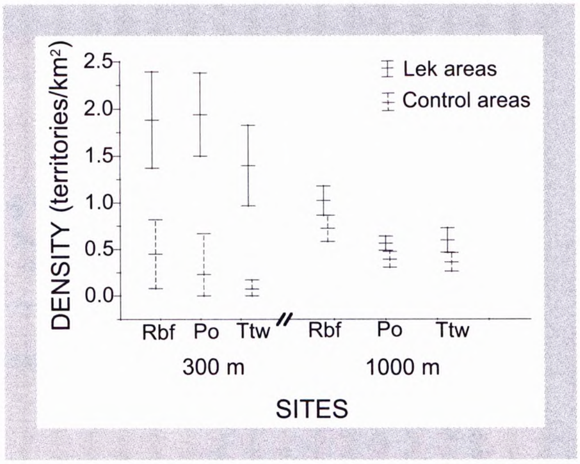

Figure 2. Densities of the three bird species red-breasted flycatcher (Rbf), pygmy owl (Po) and three-toed woodpecker (Ttw) representing mature forests (mean ± 95% confidence levels) at lek and control sites (300 m) and their surroundings (1,000 m). All densities were higher in lek areas than in the respective control areas (two-sample t-test: 300 m: red-breasted flycatcher, t = 4.45; pygmy owl, t = 6.64; three-toed woodpecker, t = 5.89; df = 80 and $P < 0.001$ in all cases; 1,000 m: red-breasted flycatcher, t = 2.85; P = 0.006; pygmy owl, t = 3.08; P = 0.003; three-toed woodpecker; t = 2.90; P = 0.005; df = 80 in all cases).

Densities of three bird species of mature forests: pygmy owl, three-toed woodpecker and red-breasted flycatcher

Densities of the three chosen bird species (red-breasted flycatcher, pygmy owl and three-toed woodpecker), representatives of mature forests, were compared between lek and control sites (300 m) and their surroundings (1,000 m) by two-sample t-tests. Density was calculated as the mean number of territories in the three census years per area of old or middle-aged forests. All comparisons showed that the densities of the three species studied were significantly higher at lek sites and their surroundings than at control areas. The mean densities were 4.2, 8.5 and 19.3 times higher at the 300-m scale and 1.4, 1.4 and 1.7 times higher at the 1,000 m scale, respectively (Fig. 2). We also calculated the densities per area of old forest alone, and the results were the same: the mean densities were significantly higher at lek areas (300 m: 3.7, 8.0 and 23.3 times higher; 1,000 m: 1.4, 1.5 and 1.6 times higher, respectively).

Capercaillie densities vs wildlife richness indices

The correlation between capercaillie densities and WRI varied between r_s = -0.16 and r_s = 0.62 in the 100 x 100 km grid units (Fig. 3). The relationship was slightly negative in four and significantly positive in eight out of 34 units. The mean of the correlation coefficients (r_s = 0.21) differed significantly from zero (one sample t-test: t = 7.252, df = 33, $P < 0.001$).

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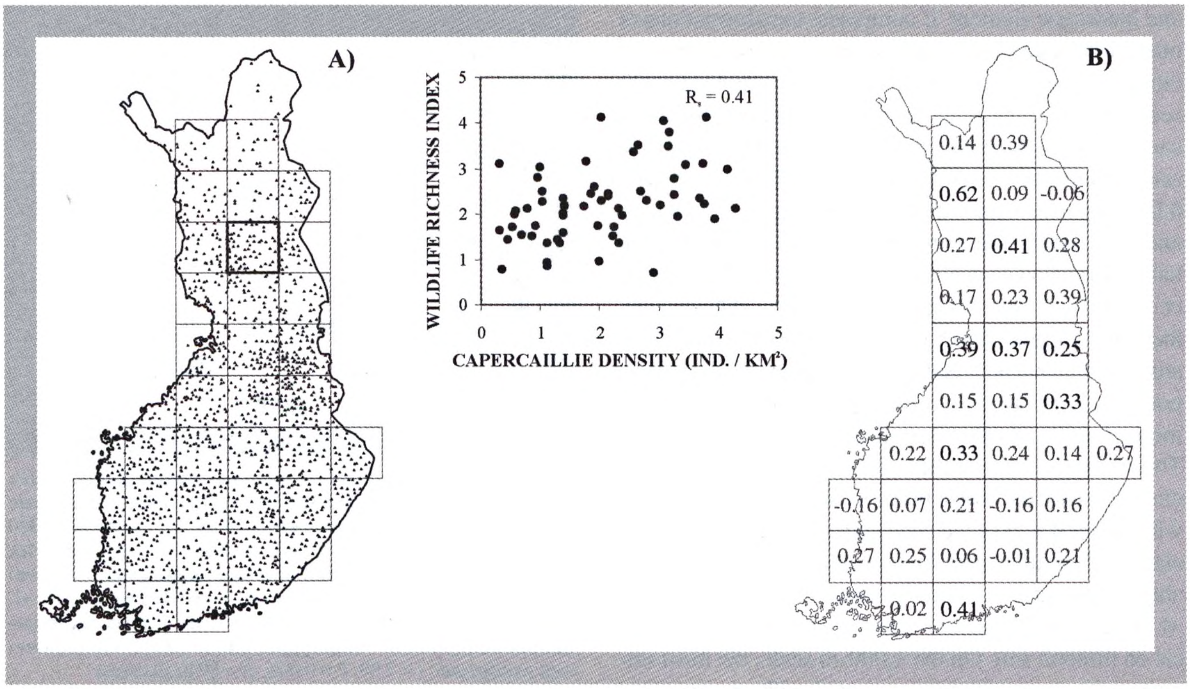

Figure 3. Distribution of the more than 1,500 wildlife triangles in Finland (A) in which both summer and winter censuses are carried out in nearly 1,000 triangles in any given year. The diagram in the middle gives the relationship between capercaillie density and wildlife richness index in a single grid of 100 x 100 km (shown in bold in A). In B) the values of correlation coefficients between capercaillie density and wildlife richness index in the 100 x 100 km grids in Finland are given. Grids of significant correlations ($P < 0.05$) are shown in bold.

The correlation coefficients were highest in the central and northern parts of Finland, whereas the lowest correlations were obtained in the coastal areas, where capercaillie densities were also the lowest.

Discussion

There were significantly higher numbers of forest bird species in the vicinity of capercaillie leks than at control sites. The densities of the three mature forest specialists pygmy owl, three-toed woodpecker and red-breasted flycatcher were significantly higher near leks than in control areas. Our results agree with those of Suter et al. (2002) being, however, even more pronounced and functioning on a larger scale.

On the 300-m scale, the species richness was significantly higher at lek sites than at control sites. This may partly be caused by the occurence of larger areas of old forest at lek sites which correlated positively with species richness. Thus the positions of leks themselves in the forest landscape affected forest bird diversity. On the 1,000-m scale, the difference in species richness was small, and both the habitat and landscape types of lek and control areas were furthermore rather similar which indicates a kind of saturation in species richness and similarity in forest landscape patterning in the study area on this spatial scale.

The habitat and landscape factors measured did not take into account small-scale factors of forest structure, e.g. vertical layering, structure of understorey vegetation and the amount of dead wood which are all important for forest bird diversity (e.g. Virkkala & Toivonen 1999). Because the densities of the three mature forest specialist species were significantly higher in old and middle-aged forests near lek sites, it is probable that some of the key factors causing high bird diversity at capercaillie leks are connected to the elements of forest structure mentioned above.

Capercaillie leks require large, continuous tracts of forests rather than large open bogs, water areas, agricultural land and settlements (e.g. Lindén & Pasanen 1990). The availability of forests rather than the quality of habitats seems to be the most distinctive feature. We have to emphasise that the umbrella species concept presented in this connection primarily concerns permanent lek areas, and not e.g. the year-round home ranges or habitat requirements of individual birds.

The comparison of capercaillie densities with the wildlife richness index revealed that high densities of

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capercaillie were also connected with high wildlife abundance in general, also on a larger spatial scale. This is understandable as capercaillie needs large and continuous forest areas, which have been rapidly decreasing also in Fennoscandia. Many important elements in the fauna of taiga forests require vast forest areas well connected with each other (e.g. Lindén, Danilov, Gromtsev, Helle, Ivanter & Kurhinen 2000). The capercaillie seems to be a relevant umbrella species representing wildlife in general, provided that capercaillie populations are abundant, and the lek network functions. If the landscape structure can not maintain viable populations, the status of capercaillie as an umbrella species will not be valid in these areas.

Foresters are prepared to manage thousands of capercaillie lek areas in Finland and thus invest in the conservation of capercaillie. Large forest areas will be managed following the principals recommended by Fennoscandian grouse experts. These activities aim to increase several small and large-scale diversity elements in the forest structure. Besides being a good candidate for an umbrella species of wildlife, capercaillie is thus also a flagship species of forest management. Managing lek surroundings by taking into account the requirements of capercaillie is, of course, a good step forward, but it must be carried out on a very large scale to guarantee an adequate amount of forested landscapes for capercaillie and other taiga forest fauna.

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