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Source: Wildlife Biology, 6(3) : 179-188

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2000.007

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RENDEZ-VOUS

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Large-scale forest corridors to connect the taiga fauna to Fennoscandia

Harto Lindén, Pjotr I. Danilov, Andrei N. Gromtsev, Pekka Helle, Ernest V. Ivanter & Juri Kurhinen

Lindén, H., Danilov, P.I., Gromtsev, A.N., Helle, P., Ivanter, E.V. & Kurhinen, J. 2000: Large-scale forest corridors to connect the taiga fauna to Fennoscandia. - Wildl. Biol. 6: 179-188.

Finland and Russian Karelia belong to the same biogeographical entity, lying on the same Precambrian bedrock. During the last half century there has been an enormous 'natural experiment', in which forestry in Finland has been very intensive, whereas in Karelia forestry has been negligent leaving large primaeval areas untouched. As a result, Russian forests have a much greater diversity of wildlife. In particular, rare species and species favouring old forests are more abundant in Karelia than in Finland. Typical dominant species in Finland are those characteristic of younger successional stages as well as many vole-dependent small carnivores. Finland is situated on the eastern margin of a vast coniferous taiga. The future of the taiga fauna in Fennoscandia is dependent on the condition of the taiga forests in Russia and on the connectivity of Fennoscandian forest areas to the intact taiga, i.e. connectivity at the border between Russia and Finland. In this paper, we focus our attention on the narrow isthmus between the White Sea and Lake Onega, which is an extremely important connection for the northern element of the taiga fauna. The capercaillie *Tetrao urogallus* may be a good focal species, with its large spatial requirements for lek areas depicting the need for connectivity to maintain viable populations. We suggest that large-scale connections should be planned, 'forest bridges' intruding into Finland and even into Sweden, where the proportion of mature forests would be high enough (as much as 1/3 of the total area) to guarantee the connectivity between subpopulations. We argue that this may not necessarily represent additional costs for forestry, provided that actions are taken for a careful large-scale planning of forest harvesting to satisfy the requirements of these corridors. We believe that large-scale preservation of ecosystems will be a better strategy in the future than species-specific conservation programmes for wildlife species.

Key words: capercaillie, connectivity, Fennoscandia, forestry, game communities, landscape ecology

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Received 15 June 2000, accepted 20 July 2000

Associate Editor: Jon E. Swenson

On a map the outline of Finland forms the figure of a lady - the Maiden of Finland (Fig. 1). You may see her waist, relatively broad hips, flapping long skirt, her head and her raised arm. She may be easily distinguished from the world map depicting the boundaries between countries. What is even more astonishing is that she may be recognised from a satellite photo taken in spring, when snow cover is still present (see Fig. 1). Finland may be seen as a white area surrounded, of course, by the Gulf of Finland and the Gulf of Bothnia, but also by the dark-looking land areas in Russia and even in Sweden (see Fig. 1). Punkari (1985) interpreted this photo as revealing the minor amount of dense, mature forest in Finland compared with neighbouring countries. Finland has extensive open areas: lakes, agricultural land, open marshes, clear-cuttings, thinned stands and settlements. During the period of snow cover these open areas, together with the relatively sparse forests, leave the white impression seen on the satellite photo. This interpretation was followed by a long and intense debate in the Finnish media, in which several forest researchers strongly disagreed with Punkari's views. Much has happened since then, and now we have detailed and reliable data on the amount of forest in Finland and Russia that clearly support Punkari's interpretation. Due to fragmented ownership and small patches of forest regeneration, the resulting mosaic is formed by very small and see-through, transparent fragments (Kurki, Mykrä & Nikula in press) which probably give the white appearance on the satellite photo.

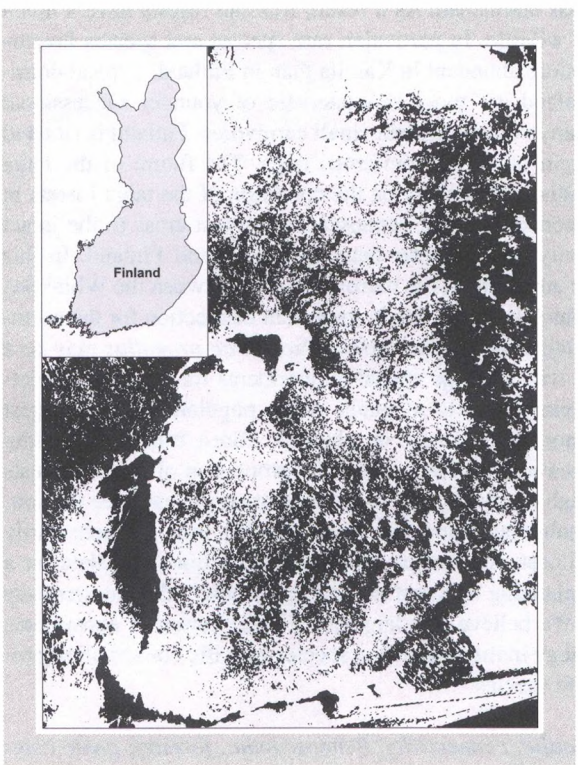


Figure 1. Finland and the neighbouring countries as seen on a satellite photograph published in a Finnish book (Punkari 1985) in the mid-1980s. The outlines of Finland are given in the insert. The Gulf of Bothnia may be seen between Finland and Sweden (to the west), and the Gulf of Finland is north of Estonia (to the south). The eastern border stands out especially clearly as the black area.

The historical experiment

After the Second World War, extensive and efficient forest management practices were introduced in Finland. As a result of rapid management processes, mature forests have nearly disappeared from southern

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Table 1. Abundance ratios of 15 well-investigated wildlife species based mainly on monitoring data from the Finnish Game and Fisheries Research Institute (FGFRI) and the Karelian Research Centre of the Russian Academy of Sciences, Institute of Biology (KRC). The brown bear ratios are assessed from Danilov et al. (1994) based on long-term national monitoring schemes of both countries. The ratio for wild forest reindeer has been estimated from Heikura et al. (1985). All the other ratios are based on winter track censuses performed by FGFRI and KRC, with mammal abundance indices indicating the number of crossing tracks/10 km/24 hours during 1990-1999, and grouse index indicating the number of individuals observed per 10 transect kilometres recalculated from Danilov et al. (1996).

Species	Method and years	Ratio	References
Species more abundant in Karelia (ratio: Karelia/Finland)			
Wolf *Canis lupus*	Snow tracks, 1990-1999	35.2	FGFRI and KRC
Wild forest reindeer *Rangifer tarandus fennicus*	Aerial censuses in Finland, strip surveys in Karelia, in early 1980s	>10	Heikura et al. 1985
Wolverine *Gulo gulo*	Snow tracks, 1990-1999	7.7	FGFRI and KRC
Brown bear *Ursus arctos*	Long-term monitoring in both countries, in the early 1990s	>5	Danilov et al.
Lynx *Lynx lynx*	Snow tracks, 1990-1999	2.2	FGFRI and KRC
Capercaillie *Tetrao urogallus*	Observed birds during winter counts, 1990-1995	1.8	Danilov et al. 1996
Hazel grouse *Bonasa bonasia*	Observed birds during winter counts, 1990-1995	1.6	Danilov et al. 1996
Pine marten *Martes martes*	Snow tracks, 1990-1999	1.3	FGFRI and KRC
Stoat *Mustela erminea*	Snow tracks, 1990-1999	1.2	FGFRI and KRC
Black grouse *Tetrao tetrix*	Observed birds during winter counts, 1990-1999	1.2	Danilov et al. 1996
Species more abundant in Finland (ratio: Finland/Karelia)			
Red fox *Vulpes*	*vulpes* Snow tracks, 1990-1999	4.7	FGFRI and KRC
Mountain hare *Lepus timidus*	Snow tracks, 1990-1999	3.1	FGFRI and KRC
Moose *Alces alces*	Snow tracks, 1990-1999	2.7	FGFRI and KRC
Red squirrel *Sciurus vulgaris*	Snow tracks, 1990-1999	1.3	FGFRI and KRC
Willow grouse *Lagopus lagopus*	Observed birds during winter counts, 1990-1995	1.1	Danilov et al. 1996

on winter track counts (e.g. Danilov et al. 1996), detailed presentation of densities of large predators in both countries (Danilov, Nyholm & Nyholm 1994), and species-specific knowledge (e.g. Heikura, Pulliainen, Danilov, Erkinaro, Markovsky, Bljudnik, Sulkava & Lindgren 1985), we are able to give to all these species such a reliable abundance index that a ratio may be calculated with a relatively high accuracy (Table 1).

Despite the approximate nature of these comparisons, they reveal a clear overall pattern. Rare species in Finland, as well as endangered species (e.g. wolf *Canis lupus*, brown bear *Ursus arctos*, wild forest reindeer *Rangifer tarandus fennicus*), are generally far more abundant in Karelia than in Finland. Species favouring old growth and primaeval forests are common in Karelia, whereas species typical of early successional stages of forests (e.g. moose *Alces alces* and mountain hare *Lepus timidus*) prevail in Finland. Many of the differences in abundance are striking, considering the proximity and biogeographical relatedness of the study areas.

Many vole-dependent small carnivores are more abundant in Finland than in Karelia, hypothetically due to the large areas of clear-cuttings (Henttonen 1989). Modern forestry creates numerous clear-cuttings and abandoned fields with forest plantations, where an abundance of graminids is a characteristic feature. The typical forest-dwelling voles of the genus *Clethrionomys* are replaced by grassland species of the genus *Microtus*, which again may occur in very high densities. As a result, modern forestry probably increases densities of both the voles and their predators. For instance, red fox *Vulpes vulpes* densities are markedly higher in Finland than in Russian Karelia (Fig. 3, see Table 1), and Finnish red foxes are probably also better adapted to living in urban areas.

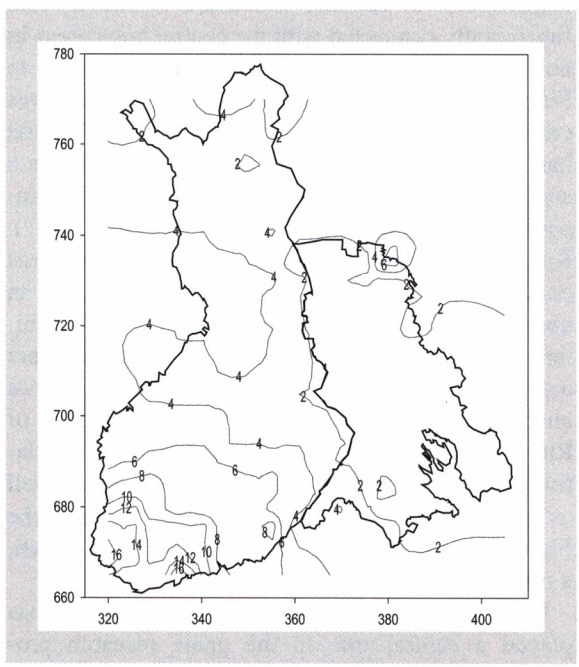


Figure 3. Geographical variation in mean snow track densities of the red fox throughout Finland and Karelia during 1990-1999 (data from the Finnish Game and Fisheries Research Institute and the Karelian Research Centre of the Russian Academy of Sciences, Institute of Biology). The yearly total lengths of track count lines in both countries range within 20,000-25,000 km.

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and central Finland, the remaining mature forests are heavily fragmented and situated in small, scattered patches, and the structural variation in forest landscapes has decreased markedly. The fragmentation in northern Finland is mainly due to forest regeneration processes, whereas in more southern parts of the country also agriculture, human settlements and thousands of lakes increase the fragmentation of forest areas. Kurki (1997) points out that in Finland no good quantitative information about the structure of present forest landscapes is available. Due to small-patterned ownership and generally small cutting areas, the spacing of old forests is very even, leading to the conclusion that there are practically no continuous older forest areas in managed forests (Kurki 1997).

Concurrently, the forests in Russian Karelia have maintained their wildland character; they have not been utilised economically to a large extent. At the border between our two countries, the forests undergoing natural dynamics meet the frontier of intensive forestry (Syrjänen, Kalliola, Puolasmaa & Mattsson 1994). The proportion of 'wild areas' (old and middle-aged forests plus bogs) within the whole area is markedly larger in Karelia than in Finland, 63 vs 52%, respectively (Fig. 2). There are vast, primaeval taiga forests in Karelia, which are essentially and functionally connected with the central taiga areas in northern and central Russia. In contrast, forests in Finland are largely pine-dominated monocultures created for pulp industry purposes. Karelian forests have a high α-diversity, i.e. high diversity within a single habitat patch, where organisms at least in principle utilise common resources (Whittaker 1977). Karelian landscapes of fairly large primaeval forests comprise several tree species of varying ages, an abundance of understorey and rich small-scale habitat variation (e.g. Gromtsev 1999). In Finland, there are about 1.5 million kilometres of ditches in forests and marsh areas, whereas in the northern parts of Russian Karelia there are practically none. A relatively larger proportion of agricultural areas as well as bodies of water impoverish and fragment the Finnish forest landscape; Karelian forests are, again, a treasure of biodiversity.

Large-scale monitoring of game populations has played a central role in the game research programmes for decades both in Finland and Karelia (Lindén, Helle, Helle & Wikman 1996, Danilov, Helle, Annenkov, Belkin, Bljudnik, Helle, Kanshiev, Lindén & Markovsky 1996). We contend that the abundances of our forest game species are on a large scale the best documented in the world. Moreover, the monitoring methods used in our countries are basically identical. As a result, we can reliably compare the structures of game animal communities in these two areas with completely different degrees of forest exploitation. Biogeographically, Finland and Karelia belong to the same entity lying on the same Precambrian bedrock, and, as stated earlier, their comparison reveals the effects of different forest practices. These circumstances provide a unique opportunity, a 'natural experiment', to study the consequences of an ab-rupt change in forest landscapes on the welfare of wildlife species. We have compared the game communities in Russian Karelia to an approximately simi-lar sized area of Finland (see Fig. 2) based on winter track count results published cooperatively for several years (e.g. Helle, Wikman, Helle, Danilov, Bljudnik & Belkin 1999).

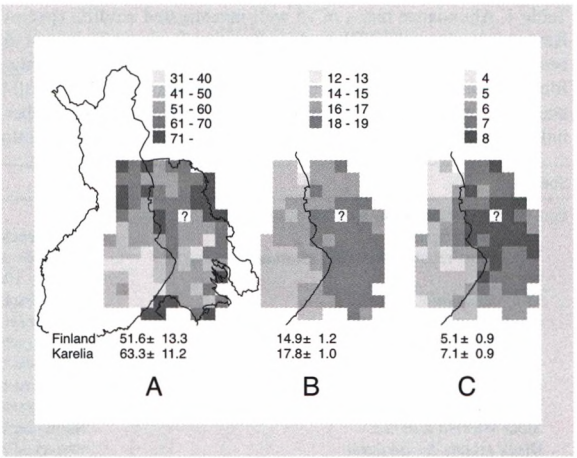


Figure 2. The study areas, including the whole of Russian Karelia and a comparable area in Finland, divided into 50 x 50 km grid squares. In map A the proportions of habitats suitable for the capercaillie are given, including old and middle-aged forests (more than 40-50 years), and also bogs and other unproductive forest lands, are included. The proportions of forest are calculated from data obtained from the Forest Research Institutes in Karelia and Finland. Map B gives the average number of 20 wildlife species (wild boar *Sus scrofa*, polecat *Mustela putorius*, American mink *Mustela vison*, weasel *Mustela nivalis*, otter *Lutra lutra* and the 15 species in Table 1) present each year in the grid squares. Map C gives the average number of eight selected wildlife species that are dependent on forests, i.e. wolf, brown bear, wolverine, capercaillie, hazel grouse, pine marten, lynx and red squirrel. Question marks indicate inadequate information.

Abundance ratios in Karelia and Finland

For 15 well-investigated wildlife species we are also able to provide intercountry abundance ratios. Based

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Bisection of the forests and their fauna at the border

Species richness, measured and expressed as the average number of altogether 20 wildlife species per grid square (50 x 50 km), is markedly higher in Karelia than in Finland (see Fig. 2, map B). The difference in the number of species is about 20%, which is simply explained by the larger number of forest-dwelling species typical of wildland areas in Karelian grid squares (see Fig. 2, map C). Large predators, species favouring old forest stands, and some threatened species are also more abundant in Karelia than in Finland.

The border itself can be distinguished in nature in many ways. There are abrupt changes in the landscape and forest structure, and interestingly enough, also in the composition of the wildlife communities (Fig. 4). A simple community similarity index (e.g. Whittaker 1960, Lande 1996, see the legend of Figure 4) describing the similarity in species composition shows that the wildlife species composition within the grids of each country is quite homogeneous, but there is a sharp and drastic change in similarity at the border.

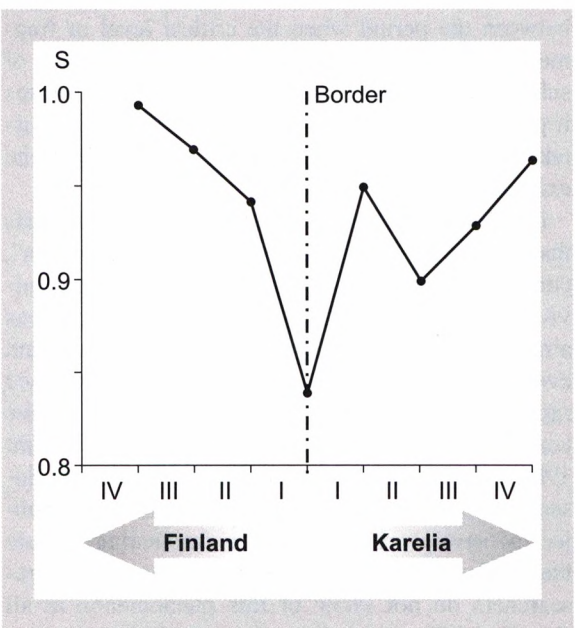


Figure 4. Uniformity in wildlife communities in the study area based on a similarity index of neighbouring grids. 'Border' denotes the grid squares on the boundary, and the Roman numerals identify the first (I), second (II), third (III) and fourth (IV) grid squares from the border into each country. The community similarity index (S) is calculated from the equation S = 2C/(A + B), where C = combined number of species in grids a and b, A = the number of species in grid a, and B = the number of species in grid b.

Along the entire border between the countries there is a broad and forested zone, varying in width from several hundred metres to tens of kilometres, which functions effectively as a huge nature reserve. In fact, no human activity is permitted in this area, and the 'green belt' or 'source zone' is of vital importance to the Finnish fauna. The Finnish forest areas along the eastern border often have more valuable or richer faunal elements than more central parts of the country. For instance, large predator densities in Finland are clearly highest near the eastern border, and large predators also reproduce most successfully in this area (for brown bear, see Kojola & Laitala 2000). Eight bird species inhabiting the eastern nature reserve areas in Finland do not occur at all in the western reserves (Virkkala & Rajasärkkä in press). The quite recently developed index for wildlife richness as a whole reaches its highest values near the border (Lindén, Helle, Vuorimies, Wikman 1999). The border zone seems to be a source area also for many other species than vertebrate wildlife, e.g. rare and threatened insect species living on decaying wood (Siitonen & Martikainen 1994).

The capercaillie as an example

The capercaillie is a character species of the boreal coniferous zone, the taiga forests. The species has traditional lek sites in taiga forests, and leks in continuous old forests support more lekking males than those in fragmented forests (e.g. Wegge & Rolstad 1986). The lekking pattern and seasonal movements of the promiscuous capercaillie have been thoroughly described (e.g. Wegge & Rolstad 1986, Rolstad & Wegge 1989, Hjorth 1994), but to summarise shortly, continuous mature forest areas support both more leks and more lekking cocks than fragmented forest areas. One lek requires an area of at least 3 km^2, and very often 6-8 km^2, especially under more northern conditions. In southern and central Finland the vicinity of the lek for up to one kilometre is strikingly more forested than the areas outside this one-kilometre radius (Lindén & Pasanen 1986, Helle, Helle & Lindén 1994).

An established capercaillie cock is extremely philopatric (see also Rolstad & Wegge 1989: Fig. 3). After recruitment to a particular lek, the cock remains faithful to this lek for the rest of his life. Young cocks even choose their lek from the vicinity of their birth site. The female is the dispersing sex, but even their dispersal distances are modest, some 15 km on

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average (e.g. Koivisto 1956, P. Helle & P. Kumpu, unpubl. data).

Viable capercaillie populations, i.e. active leks in functional connection with each other, need a landscape that is at least 30% forested (forests more than 40-50 years old) (Wegge & Rolstad 1986). Andrén (1994) estimated that in general 30% coverage with a suitable habitat is the critical minimum for several wildlife species; a reduction in the proportion of suitable habitat to less than 30% leads to patch isolation and a rapid decrease in population sizes. In increasingly fragmented forests, it is very likely that leks become isolated, and they lose their functional connectivity with neighbouring leks. These isolated leks may easily become extinct due to additional clear-cutting, hunting or simply during stochastic population declines.

The map sketched in Figure 5 is mainly imaginary based on our understanding of the effects of forest fragmentation on the spatial distribution of capercaillie leks. Much research is needed to verify the actual situation. Presumably the lek populations are relatively close to each other in Russia, in the area of 'viable' populations (average nearest neighbour distances, ANNDs, perhaps 2-5 km, depending on the area). There is probably a rapid change at the border between Russia and Finland, where generally continuous primaeval forests meet fragmented commercial forests. In this area of 'threatened' populations (most of western Fennoscandia), ANNDs are still relatively low (3-10 km) but the isolation process has clearly started, and the lek populations occur in separate clusters. The alternative prediction is that the leks are still relatively near each other, but have only a couple of active cocks per lek, which is often true if fragmentation is caused merely by forestry as is the case, for instance, in eastern Finland. It is very difficult to see any positive future for the remaining European populations situated in the area subject to 'extinctions' (southwestern Finland, southern Sweden and nearly all of central and southern Europe), where human land use has conquered the previously forested areas, and the forests, as well as the existing leks, are distinctly isolated from each other. The leks are solitary or clumped, but these lek aggregations have no functional connectivity with neighbouring lek systems. There may be tens of kilometres separating lekking units (single or clumped leks), and isolated leks in fragmented forests are likely to gradually become extinct. Müller (1990) presented an extremely informative and detailed map of dated disappearances of capercaillie leks in a large but heavily fragmented landscape in Germany. Several decades may lapse between the period when the critical level of fragmentation was exceeded and the final extinction of subpopulations. This long time lag, however, makes it possible to repair at least some of the earlier mistakes, e.g. improving the habitat quality between the existing leks.

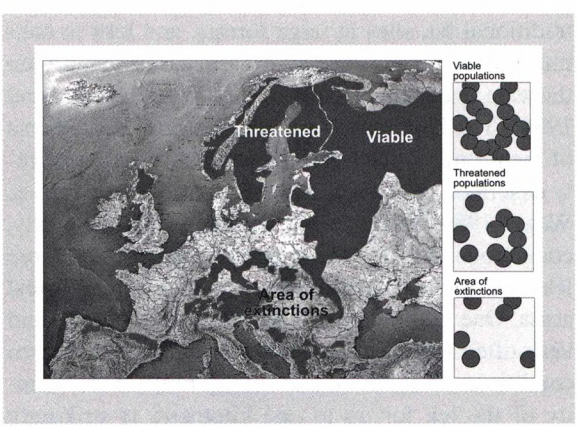


Figure 5. Approximate distribution of the capercaillie in Europe (redrawn from Hjorth 1994). The capercaillie, especially the nominal race *Tetrao urogallus urogallus*, is a typical representative of the Siberian faunal type. In its core area (viable populations), leks are well connected with each other, but in the area containing 'threatened' populations (most of Fennoscandia) the fragmentation process has already isolated many leks from each other, or at least they have lost their connection with the original taiga populations along the eastern border of Finland. In the southern and central Europe (area of extinctions) all remaining lek populations are isolated from the uniform distribution area, and the risk of local extinctions is high. The time to extinction is proportional to the number and size of leks in the restricted areas.

Lindén & Pasanen (1986) presented the hypothesis that abnormally behaving "insane capercaillie cocks", common in heavily fragmented forest areas, are survivors of destroyed leks. This phenomenon was already common in central Europe 100 years ago and even earlier. In Estonia and Finland it increased rapidly after the Second World War, when intensive commercial forestry became a reality (see also Viht 1984). At present, nearly all Finns know about 'insane capercaillie cocks', as they are a favourite subject of newspaper articles. It is fascinating to note that in Russian Karelia local hunters and grouse researchers do not know of this phenomenon at all (Lindén 1997), which strengthens the idea that populations are healthy and viable in Russia whereas they are threatened in Finland. The 'insane cocks' are perhaps the first sign of habitat deterioration. The speculatively increasing number of hybrids between the capercaillie and black grouse *Tetrao tetrix* in Finland may be a more alarming trend, because this phenom-

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enon preceded the extinction of the capercaillie in some areas in central Europe (see also Porkert 1999).

Critical passages for the taiga fauna

Relatively large forest reserves, or wildland areas, occur in the northernmost parts of Finland and huge nature reserves also exist on the Kola Peninsula (Fig. 6). However, these areas are situated too far north when considering the welfare of the taiga fauna. Typical bird species of the taiga include the Siberian jay *Perisoreus infaustus*, the Siberian tit *Parus cinctus*, the three-toed woodpecker *Picoides tridactylus*, and the nominal subspecies of the capercaillie *Tetrao urogallus urogallus*. Populations of all these species have decreased markedly in Finland during recent decades, mainly due to intensive forestry (Väisänen, Lammi & Koskimies 1998).

Three different isthmuses (marked I - III in Fig. 6) connect Fennoscandia to the taiga forests in the east. Isthmuses I and II are too far south to support the above-mentioned northern bird species. Isthmus III, between the White Sea and Lake Onega, is therefore the most suitable 'passage way' for the fauna of the northern taiga element to remain connected with Fennoscandia. We do not only mean the route to follow or the living conditions for individuals, but more importantly we mean the connectivity of subpopulations or metapopulations, especially important for many resident species and the maintenance of gene flow. The relatively narrow isthmus III is not a heavily forested area, but has large fens and tundra-like open landscapes (see Fig. 6). Against this background it is extremely important that there is a very large reserve (4,030 km^2), the Vodlozero National Park (marked with the letter E in Fig. 6), which is really connecting the eastern wildlife to Fennoscandia. There are relatively numerous nature reserves between the Vodlozero Park and the border between Russia and Finland. In Karelia there are more than 150 different nature reserves, with an average size of more than 82 km^2. Furthermore, the amount of old and middle-aged forest and the high α-diversity of the forests in Russian Karelia (Gromtsev 1999), guarantee the welfare of the taiga fauna as far east as the border.

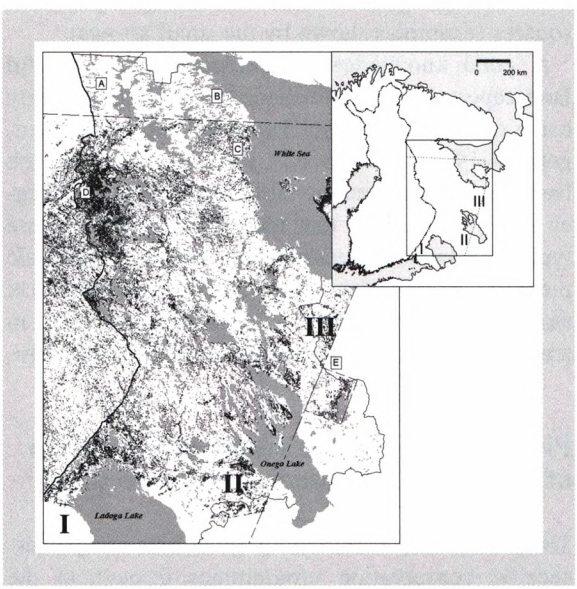


Figure 6. Coniferous forests of high density (density >0.6; age > 100 years) in Karelia and eastern Finland according to the satellite image in 1997 (pixel size: 125 x 125 m, interpreted by P. Litinsky). The dashed line depicts the border of the image. The letters A-E denote the regions of last large fragments of primaeval forests (for short descriptions of these fragments, see Gromtsev 1999). Note the isthmuses I-III, through which the taiga fauna extends into Fennoscandia, and especially isthmus III across which the Siberian fauna (including many northern species) is connected with Finland. Isthmus III is relatively narrow and has extensive open fens, large water bodies and other unforested areas. On the other hand, it has a huge nature reserve, Vodlozero National Park (denoted by the letter E).

Forest bridges across Finland

As mentioned earlier, densities of many forest bird species, large predators and wildlife richness in Finland as a whole are clearly highest near the eastern border, but this situation does not extend deep into the country, possibly due to low forest connectivity. The existing nature reserves in southern and central Finland are so few, small and scattered, that it is quite impossible to guarantee the welfare of wildlife in these reserves. We recommend concentrating different types of reserves into certain restricted areas in Finland to promote connectivity rather than retaining the current scattered pattern.

A large proportion of forests in Finland are state-owned, but most of these forests lie in northern Finland. The only visible exception is the belt of smaller forest patches along the Suomenselkä Ridge (the lower part of the forked arrow in Fig. 7), where one may also find small nature reserves. The forests in this area are relatively barren and only minor agricultural activity occurs in the area.

To protect the essential element of the taiga forests and their fauna in the southern part of Finland, it would be necessary to create a corridor from the east-

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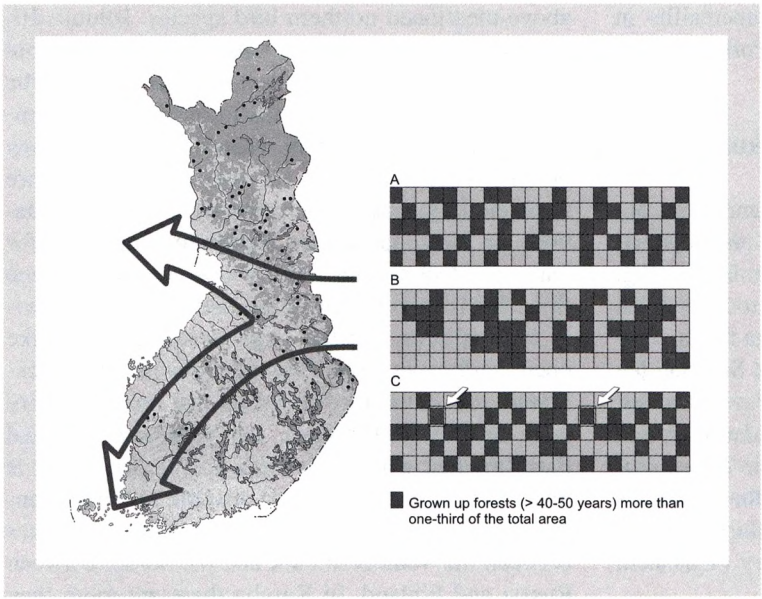


Figure 7. State-owned forests (dark shaded areas) in Finland and the most important nature conservation forests (marked with dots). The large forked arrow on the map indicate the approximate sites of potential large-scale corridors, 'forest bridges', required to guarantee the connectivity with the Russian border. These 'forest bridges' should not be thought of as permanent corridors with protected areas, rather as a flexible system, in which the connectivity of mature forests is ensured by large-scale forestry planning. The 50-km wide corridors may be established following three alternative patterns (A-C). In the three parallelograms which all contain 44 shaded grid squares, each small square covers 10 x 10 km (the standard map sheet in Finland). Pattern A is a relatively good one, but the connectivity is lost in several sites. In pattern B, grid squares with a proportion of mature forest exceeding 1/3 are overaggregated in the middle. Pattern C is the best option as it maintains a continuous connection; however, the small arrows indicate some grid squares of great importance to the corridor and in these sites careful forestry planning is needed.

ern border down to the southwestern part of the country, as indicated by the lower part of the forked arrow in the map (see Fig. 7). We must strongly emphasise that this corridor idea is not a proposal to increase the number of nature reserves; it aims to maintain a certain proportion of mature forests, perhaps 1/3 of the total area, in order to ensure the necessary living conditions for the taiga fauna and the connectivity to the Russian taiga, the capercaillie being a prominent model species in this respect.

It might be considered an important task for Finland to create one 'forest bridge' across the country to Sweden and Scandinavia. Fortunately, the Scandinavian mountains provide a relatively large, continuous forest area, which surely has the capacity to maintain viable populations for very long periods, even under totally isolated conditions. However, it would be possible to break this isolation by 'building a forest bridge across Finland'.

This type of corridor might be a 50-km wide belt. To illustrate this recommendation with examples, we will examine three alternatives in which the basic unit of area is a square of 10 x 10 km, the local map size in Finland (see Fig. 7). All three alternatives include 44 squares in which the proportion of mature forest (more than 40-50 years old) is larger than 1/3 of the total area (see Fig. 7). In other words, considering the total amount of forest cuttings all the three alternatives are approximately equal. Alternative A is a relatively good and continuous pattern, but connectivity is broken at several points. Alternative B is far too clumped or aggregated, whereas alternative C is the best for connecting forest species, as the squares with high forest cover are adjacent to each other. But even in alternative C there is some danger of losing connectivity, e.g. due to extensive harvesting in some squares (examples shown by the small arrows).

A good knowledge of metapopulations, careful landscape analysis and enhancement of connectivity using corridors (see also Hanski & Gilpin 1991, Angelstam 1997, Gustafsson & Hansson 1997), are the basic means to maintain viable populations on a larger scale. We believe that the development of these types of corridors requires only careful, large-scale planning of forestry. With careful planning, i.e. aimed at creating forest connectivity, the costs in terms of reduced yield from the forest should be low.

Protection of species versus preservation of ecosystems or functional connectivity

Today there are hundreds or thousands of species-specific conservation programmes throughout the world. They are extremely valuable and important efforts to save certain key requirements of nature, which are rapidly being lost. The threatened species provide a good illustration of this problem, and studies of threatened species reveal the urgent need to save the diversity of their habitats and habitat complexes on different scales.

However, the protection of species is too often understood only as a national duty. The white-backed woodpeckers *Dendrocopos leucotos* must be saved in

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Finland: only some tens of pairs are left. The 60-75 wolves remaining in Sweden cause anxiety, because the number is considerably lower than the minimum viable population size (MVP) of 500 animals given by experts (Anon. 1999). But there is no need to examine only national figures. The white-backed wood-peckers in Finland live on the edge of their distribution area (Cramp 1985), and they are not of global concern. The same is true for Swedish wolves; if it is possible to create a functional connectivity using the forest bridge idea, the Swedish authorities and scientists may conveniently dispense with their worries of MVP requirements. It is very interesting to note that Pulliainen (1974) already plotted the wandering routes of wolves in Finland in much the same way as we have sketched forest bridges.

Establishing small scattered nature reserves may be a good conservation policy in some cases for several rare and threatened species. However, when we are trying to preserve the viability of the whole wildlife community, we must consider the impact on ecosystem characteristics on large, regional scales. We must be concerned about the conditions of vegetation zones, faunal types and other large entities. In fact, we are then thinking about the needs of biodiversity. The fragmentation of natural areas is perhaps the most worrying threat. Providing large-scale corridors, to maintain the connectivity of wildlife populations, is one of the best tools available to fight the continuous impoverishment of nature.

Acknowledgements - thanks to thousands of hunters in Finland and Russian Karelia for their magnificent field work in counting game animals and their tracks from year to year on a voluntary basis. Numerous scientists in our countries have contributed to this cooperative project in several ways; it is impossible to mention all of them, so we acknowledge them collectively. Bernt-Erik Sæther and Jon Swenson provided valuable comments on the drafts of the manuscript. Financial support was provided by the Academy of Finland (HL, project 7205/1993). This study is a contribution of the Research Program for the Finnish Grouse.

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