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Capercaillie (*Tetrao urogallus* L.) habitats in managed Finnish forests – the current status, threats and possibilities

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Academic Dissertation

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Capercaillie (*Tetrao urogallus* L.) habitats in managed Finnish forests – the current status, threats and possibilities

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ABSTRACT

The aim of this study was to provide applicable knowledge for taking capercaillie into consideration in forest management and thus progress ecologically sustainable forestry. Capercaillie is a respected game species, but it also has indicator and umbrella species characteristics. Therefore capercaillie is closely linked to many other species.

The study focused on the question: which structural characteristics of forest are important for the capercaillie? To gain a thorough view of capercaillie habitat needs, various capercaillie habitats were studied at several spatial scales in Finland in 1990s and 2000s. Species data were mostly from the wildlife monitoring counts. Forest planning data from Metsähallitus and data from the national forest inventories formed the landscape data.

At large spatial scale (2500 km^2 study units) the capercaillie population density was positively associated with the proportion of young thinning stands throughout the country. The association between capercaillie and young thinning stands was also positive at smaller scales in summer habitats, winter habitats and lek surroundings in northern Finland, where also the stand density was found to be positively associated with capercaillie in the summer habitats. The positive relationship between capercaillie and mature forests was found at the beginning of 1990s, but later this association was weak. The managed boreal forests become suitable for the capercaillie within 30 – 40 years, and so the large areas clear-cut in 1950s and 1960s in Finland became suitable for the capercaillie mostly in the 1990s. But the habitat quality may also decrease in the later successional stages of forest. The short-term effects of thinnings on the capercaillie microhabitat quality can vary depending on the stand characteristics and season, and between adult birds and broods, but in the long term low cover on the ground may be the factor, which reduces the habitat quality in older managed forests especially in the low-productive areas and sites.

Overall forest cover at the landscape scale, canopy cover and cover on the ground are important forest characteristics for the capercaillie. Longer rotations, understorey management and selective cuts are suitable methods to increase the capercaillie habitat availability and quality in the managed Finnish forests. Capercaillie habitat management calls also for spatial planning and preserving the availability of pine specifically in southern Finland. Also the costs and benefits of cutting residue management and possibilities to reduce the ditch restoration intensity in peatland forest management deserve a careful evaluation in the future. Furthermore, the connections between the abovementioned forest characteristics and other species deserve also to be studied.

Keywords: boreal forest, grouse, forestry, thinnings, successional stages, wildlife triangle

Miettinen, J. 2009. Metson (*Tetrao urogallus* L.) elinympäristöt talousmetsissä – nykytila, uhat ja mahdollisuudet. Dissertationes Forestales 90. 32 s.
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TIIVISTELMÄ

Tämän tutkimuksen tavoitteena oli tuottaa soveltamiskelpoista tietoa siitä, miten metson elinympäristöt voidaan ottaa huomioon metsänhoidossa, ja siten edistää ekologisesti kestävää metsätaloutta. Metso on arvostettu riistalaji, mutta sillä on myös indikaattori- ja sateenvarjolajin ominaisuuksia. Siten se on läheisesti kytkeytynyt myös moniin muihin lajeihin.

Tutkimus keskittyi kysymykseen: mitkä metsän ominaispiirteet ovat metsolle tärkeitä? Jotta saavutettaisiin kokonaiskuva metson elinympäristövaatimuksista, erilaisia metsohabitaatteja tutkittiin useilla mittakaavoilla Suomessa 1990- ja 2000-luvuilla. Lajiaineistot pohjautuivat pääosin riistakolmiolaskentoihin. Maisema-aineistoina käytettiin Metsähallituksen kuviotietoaineistoa ja valtakunnan metsien inventoinnin (VMI) aineistoja.

Metsotiheyden ja nuorten kasvatusmetsien osuuden välillä havaittiin positiivinen yhteys suurella mittakaavatasolla (2500 km^2 tutkimusyksiköt) läpi koko Suomen. Metson ja nuorten kasvatusmetsien välillä oli positiivinen yhteys myös metson kesä- ja talvielinympäristöissä sekä soidinympäristöissä Pohjois-Suomessa, jossa havaittiin myös positiivinen yhteys metsän tiheyden ja metson kesäisen elinympäristövalinnan välillä. Metson ja uudistuskypsien metsien välillä positiivinen yhteys havaittiin 1990-luvun alussa, mutta sen jälkeen tämä yhteys oli heikko. Boreaalinen talousmetsä kehittyy metsolle soveliaaksi nopeasti, 30 – 40 vuodessa. Nykymuotoisen metsätalouden alkuaikoina, 1950- ja 1960-luvuilla avohakatut laajat alueet palasivat lajin kannalta käyttökelpoisiksi pääosin 1990-luvulla. Mutta elinympäristön laatu voi myös laskea talousmetsän myöhemmissä kehitysvaiheissa. Harvennushakkuiden lyhyen aikajänteen vaikutus metson elinympäristön laatun voi vaihdella riippuen metsikön ominaispiirteistä ja vuodenajasta, sekä aikuisten lintujen ja poikueiden välillä, mutta pidemmällä aikajänteellä vähäinen peitteisyys maanpinnan läheisyydessä voi olla tekijä, joka laskee elinympäristön laatua metsikkötasolla vanhemmissa talousmetsissä erityisesti vähätuottoisilla alueilla ja karuilla kasvupaikoilla.

Maisematason metsäpeitteisyys, metsikkötason peitteisyys (latvuspeitto) sekä peitteisyys maanpinnan läheisyydessä ovat metsolle tärkeitä metsän rakennepiirteitä. Pidemmät kiertoajat, alikasvoksen hoito ja eri-ikäisrakenteisen metsänkasvatuksen käyttö ovat soveliaita menetelmiä metson elinympäristöjen tarjollaolon ja laadun parantamiseksi talousmetsissä. Alueellinen suunnittelu metsolle suotuisten laikkujen yhdistämiseksi sekä männyn tarjollaolon turvaaminen lajin talviravinnon turvaamiseksi ovat tarpeen erityisesti Etelä-Suomessa. Myös hakkuutähteiden käsittelyn hyödyt ja kustannukset, sekä kunnostusojitusten toistuvuuden ja laajuuden vähentämisen mahdollisuudet ansaitsevat jatkossa tulla huolellisesti arvioiduiksi. Lisäksi metsolle tärkeiden metsän rakennepiirteiden ja muiden lajien välisien yhteyksien selvittäminen tarjoaa mielekkään jatkotutkimuskohteen.

Asiasanat: boreaalinen metsä, kanalintu, metsätalous, harvennus, kehitysvaihe, riistakolmio

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Kempele, May 2009

Janne Miettinen

LIST OF ORIGINAL ARTICLES

I Miettinen, J., Helle, P. & Nikula, A. 2005. Lek area characteristics of capercaillie (*Tetrao urogallus*) in eastern Finland as analysed from satellite-based forest inventory data. Scandinavian Journal of Forest Research 20(4): 358-369.

II Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. 2008. Large-scale landscape composition and capercaillie (*Tetrao urogallus*) density in Finland. Annales Zoologici Fennici 45(3): 161-173.

III Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. Changes in landscape-scale habitat selection of capercaillie (*Tetrao urogallus*) in managed north-boreal forest. Manuscript submitted.

IV Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. Capercaillie (*Tetrao urogallus*) habitat characteristics in north-boreal Finland. Manuscript submitted.

In regard to the entire thesis, most of the work done in articles I-IV was carried out by Janne Miettinen, with a notation that in articles I-II Ari Nikula contributed the landscape data and in articles III-IV carried out most work with the landscape data. All the co-authors of separate articles have participated in writing by commenting on the text, and thereby improving the manuscripts.

TABLE OF CONTENTS

1 INTRODUCTION

1.1 Background

Finland is committed under international agreements to sustainable use of its environmental resources (Ministry of Agriculture and Forestry, 2000). The protected areas provide important habitats for many threatened species, but most forests are – and most likely will be – in commercial use. Therefore nature reserves alone can not secure the forest biodiversity, but the nature reserves and commercially used forests have to be considered as a whole (Lindenmayer & Franklin 2002). Some threatened or declined species, which have been earlier considered as old-growth specialists, have been found to survive also in young commercially used forests if suitable microhabitats are available (Martikainen 2001). Ecologically sustainable forest management is thus a central part of maintaining the biodiversity and sustainable use of environmental resources.

The capercaillie (*Tetrao urogallus* L.) is one of the most appreciated game species in Finland. Therefore capercaillie habitat management is tightly connected to the recreational use of forests. But capercaillie also has umbrella species and indicator species characteristics. For example, other grouse species the black grouse (*Tetrao tetrix* L.) and the hazel grouse (*Bonasa bonasia* L.) nest on the ground and spend most of the snow-free season on the ground like the capercaillie, but have either smaller home ranges (hazel grouse) or less specific habitat needs (black grouse) than the capercaillie. Vital capercaillie population indicates the well-being of many other forest dwelling species (e.g. Storch 2000, Suter et al. 2002, Pakkala et al. 2003). Forest areas, which have suitable characteristics for the capercaillie, are known suitable also for many other species. Therefore capercaillie habitat management is closely linked also to the ecological sustainability of forestry.

1.2 Capercaillie ecology

Capercaillie densities have declined remarkably throughout its whole range (e.g. Wegge 1979, Lindén & Rajala 1981, Hjorth 1994, Beshkarev et al. 1995, Catt et al. 1998). In Finland the density of capercaillie decreased by about 50% from the 1960s to the end of 1980s, but in the 1990s the decreasing trend stopped (Helle et al. 2003). Most commonly suggested reasons for the decline are unfavorable changes in forest structure mediated by forest management (habitat loss, habitat degradation, forest fragmentation), increased predator populations, excessive hunting and adverse changes in the climate (e.g. Helle & Helle 1991, Storaas et al. 1999, Kurki et al. 2000, Storch 2000, Moss et al. 2001, Ludwig et al. 2006). The factors affecting the grouse populations are also strongly connected; for example the changes in forest structure cause strengthened populations of rodents, which support dense populations of small predators, which in turn affects the grouse populations especially when the rodent densities are low (alternative prey hypothesis, Henttonen 1989).

Capercaillie is a dimorphic species (Koskimies 1958), and there are differences between the sexes in the habitat use. For example, the female capercaillie is found to use younger forests than the male (e.g. Rolstad 1989). Seasonal home ranges of the species are large (e.g. Rolstad & Wegge 1989), and several types of habitats are needed in the course of the year. Capercaillie has been characterized as a habitat specialist with close affinity to old conifer forests rich in bilberry (*Vaccinium myrtillus* L.) (Rolstad & Wegge 1987, Klaus et al. 1989, Picozzi et al. 1992, Storch 2000). The importance of old or mature forests for capercaillie has been observed in numerous studies in Finland (e.g. Seiskari 1962, Lindén & Pasanen 1990, Helle et al. 1994, Kurki et al. 2000) and elsewhere (e.g. Hjorth 1970, Wegge & Rolstad 1986, Rolstad & Wegge 1989, Picozzi et al. 1992, Storch 1993, Swenson & Angelstam 1993), but also quite young managed forests have been found suitable for the species (Seiskari 1962, Rolstad 1989, Rolstad & Wegge 1990, Storch 1993).

During winter capercaillie's primary need is the needles of pine (*Pinus sylvestris* L.) for food, and it spents the daytime mostly feeding in the trees (e.g. Seiskari 1962). When a suitable snow cover is available capercaillies spend the long winter nights snow-roosting, but if not, they roost in the trees or under the lower branches of spruce (*Picea abies* (L.) Karst.) (Lindén 1989). The weather conditions are important for winter survival of the capercaillie. Winter survival is positively associated with long winter, early snowfall and even coldness of winter in the northern Finland, but with warm and short winter in the southern Finland, where snow-roosting is possible only occasionally (Lindén 1981a).

In March capercaillie males shift close to the lekking areas. Lekking site and the surrounding daytime home ranges (day territories or living sectors) of the cocks (e.g. Wegge & Rolstad 1986, Wegge & Larsen 1987, Hjorth 1994) form a lekking area. Several studies have shown that the day territories, which males use for resting and feeding, extend up to about 1 km from the lek centre (e.g. Wegge & Rolstad 1986, Lindén & Pasanen 1987, Rolstad & Wegge 1987, Helle et al. 1994). At the lekking site territory-holding males (age 3 years and over) have their territories encompassing about 1 – 3 hectares (Hjorth 1970, 1994, Valkeajärvi & Ijäs 1991). The quality of the surrounding areas (day territories) seems to be even more important than the lekking site itself for the viability of the lek: the greater the proportion of mature coniferous forests, the larger and more vital the leks are (Lindén & Pasanen 1987, Rolstad 1989, Picozzi et al. 1992).

According to the fragmentation theory, a minimum of 30% of suitable habitats in the lek area could be used as a limit for the existence of leks (Andrén 1994). If loggings reduce the proportion of mature forests in a large area below this level, the area becomes, according to Rolstad & Wegge (1987), unable to maintain local leks. When single leks disappear, the lek network over a wider area thins out and eventually the lekking populations may become isolated from each other (i.e. population changes as a metapopulation) – a phenomenon familiar in the development of capercaillie populations in Central and Southern Europe (Klaus et al. 1989, Grimm & Storch 2000). Similar observations have been made in some parts of Fennoscandia (Hjorth 1994, Lindén et al. 2000).

Summer is perhaps the most critical part of the capercaillie's annual cycle. Females use most of their time for egg laying, incubating and brood caring between May and July. Nest losses and especially the chick mortality are high. Most of the chicks die before the age of two months (e.g. Lindén 1981a, Wegge & Kastdalen 2007). Mammal predators, for example red fox (*Vulpes vulpes*), pine marten (*Martes martes*) and raccoon dog (*Nyctereutes procyonoides*), cause most of the nest and chick losses (Storch 1991, Wegge & Kastdalen 2007). Even 89% mortality during the first year has been found (Lindén 1981b). The small chicks are dependent on the insect food (protein) during the three first weeks of their life because they do not have ability to digest plant food before that (Marcström 1960). Female leads the brood to the areas where food is available and warms up the chicks if needed. The thermoregulation ability of chick is dependent on the chick weight, and larger chicks can use more time for feeding (Sjöberg 1996). During cold weather chicks need lots of additional energy for maintaining the body temperature and therefore the growth may be reduced (Lindén et al. 1984). An important factor for the growth and survival of chicks is the habitat quality. The importance of bilberry (*V. myrtillus*) for the capercaillie has been emphasized (e.g. Storch 1993, 1994). Bilberry is a field layer shrub species, which is a direct food source for the capercaillie (shoots, leaves, berries), provides cover for chicks and hosts several herbivorous invertebrate species that are an important food source for the chicks (Storch 1993, Sjöberg 1996, Wegge et al. 2005). Baines et al. (2004) found also a positive relationship between bilberry cover and capercaillie breeding success in region where the average bilberry cover is low. The growth rate of chicks has also been found higher in unditched wet forest than in ditched ones, most probably due to reduced field layer vegetation in dense ditched forests (Sjöberg 1996). Also the reproductive output of e.g. black grouse (*T. tetrix*) has been higher in unditched forests (Ludwig et al. 2008).

1.3 Boreal forest dynamics, Finnish forests and forest management

The forest development under natural conditions is known to vary depending on several aspects, e.g. soil characteristics, tree-species composition and disturbances. The events leading to death of trees are called as disturbances. The frequency, extent and severity vary, and they can be divided to small and large disturbance agents according to their size and severity (e.g. Oliver & Larson 1990). Fire has been considered as a major disturbance agent in the natural boreal forest, and the role of windfall, snowbreaks, insects and fungi and other smaller disturbance agents has been estimated relatively low. For example ASIO-model divides areas to four classes according to fire frequency (Angelstam & Rosenberg 1993). For example in northern Fennoscandia the fire frequency was estimated about 100 years (Zackrisson 1977, Haapanen & Siitonen 1978), but since that more detailed views about fire severity, frequency and variation have been presented. Today human prevents the fires, but e.g in the 19^{th} century most forest fires were caused by human, and therefore the frequency of forest fires has probably been overestimated. In boreal forests the average of natural fire intervals has been hundreds of years (e.g. Pitkänen et al. 2002, Wallenius 2002), and in north-boreal Finland the average time between fires has been estimated as 350 years, and 1200 years if the effect of human is excluded (Wallenius et al. 2008). There is also stochastic variation in the fire frequency, and large pines (*P. sylvestris*) survive quite commonly from the fires (Kuuluvainen 2002). The fire frequency should be, however, higher in southern Finland (e.g. Wallenius et al. 2008) since the climate is less humid there than in the northern part of the country.

Human influence has considerably changed forest stand and landscape structure in Finland. It is obvious that the low fire frequency and high tree survival lead to manifold proportion of old forests and higher stand-scale structural variation in natural forests than in commercially managed forests, where forests are clear-cut after every 100 years (see e.g. Pennanen & Kuuluvainen 2002). Finnish forests were, however, utilized also before the 20^{th} century and the modern forestry. For example slash-burn cultivation and tar burning reduced markedly the amount of available timber (Heikinheimo 1915). Thus the availability of timber was low specifically in southern Finland at the beginning of 20^{th} century (Berg & Leikola 1995). The ‘modern era of forestry’ based on clear-cuts and artificial regeneration began in the 1950s, and replaced the earlier diameter-based selective fellings (Leikola 1984). During the 1950s and 1960s a high proportion of old forests were clear-cut and regenerated, primarily with pine (*P. sylvestris*), using large management units especially in northern Finland. Since then, the annual proportion of clear-cuts has decreased to 0.85% of the forest land area, and the size of management units has reduced. Due to the large regeneration areas the total growing stock volume of the forests decreased in 1950s and 1960s, but started to increase in the 1970s due to the growth of young forests (see e.g. Finnish Forest Research… 1992, 2005, Löfman & Kouki 2001).

The proportion of forests is high in Finland and 66.8% of land area and 60.1% of total area (33.8 million hectares) is forest land. Most forests are in commercial use, and the proportion of strictly conserved areas (national parks etc.) is 3.2% of the forest land area. The proportion of conserved areas is high in scrubland (32.1%) and wasteland (40.6%). About 90% of the conserved forest land locates in the northern parts of country (Finnish Forest Research… 2005).

Forests in Finland, as in the most of boreal region, are mostly managed using single-cohort forest management. During each rotation site preparation (clearing, harrowing etc.), regeneration (planting, sowing or seed-trees) and several thinnings are typically done. Thinnings include commonly 1 – 2 thinnings of seedling stand (age approximately 5 – 10 years and 15 – 25 years), first commercial thinning (30 – 50 years) and 1 – 2 later thinnings. Stands are clear-cut commonly at the age of 70 – 120 years depending e.g. on the region, site and tree species (Metsätalouden kehittämiskeskus Tapio 2006). The annual amount of clear-cuts is about 180 000 hectares. This includes about 30 000 ha of seed-tree cuts (Finnish Forest Research… 2005), where about 20 – 50 trees/ha are left for some years to produce seedlings. The first commercial thinning is commonly done in about 15 cm average tree diameter, when most trees are suitable for pulpwood and the thinning is therefore economically profitable. During the last years the clearing of small saplings before the thinnings has become common. The amount of thinnings has increased during the last decade, but the estimated need of first commercial thinnings is still clearly higher (250 000 ha/year) than the amount of thinnings done (183 000 ha/year) (Finnish Forest Research… 2005).

About 55% of about 9 million peatland hectares has been drained (Finnish Forest Research… 2005), and these areas have changed or are changing to growing forests. Most ditching was done in the 1960s and 1970s, and after the end of 1980s the establishment of new ditches has practically ceased (Finnish Forest Research… 2005). Old ditches need commonly restoration after about 20 years (Heikurainen 1980). Since year 1992 the annual amount of ditch restorations has been 70 000 – 80 000 hectares, whereas the official goal was 110 000 hectares (Finnish Forest Research… 2005).

1.4 Forestry and capercaillie habitat needs

Capercaillie has complex habitat needs, and therefore it is a challenging species when adapting forest management to its requirements. There are remarkable differences in the habitat use between sexes and between the seasons (e.g. Rolstad & Wegge 1990). The year-round home range of an individual capercaillie is commonly more than 100 hectares (Rolstad 1988, Rolstad et al. 1988), and the area used by a lekking population is even several thousand hectares (Hjorth 1994, Hjeljord et al. 2000). Effective habitat management for capercaillie has to include several scales (e.g. Rolstad 1989, Storch 2000). If the proportion of suitable habitat is low, as e.g. in central or southern Europe, the large scale is a primary concern in the capercaillie management (e.g. Storch 2002, Quevedo et al. 2006), because a large proportion of suitable area can be useless for the species because those mostly locate as small units embedded in an unsuitable matrix (e.g. Andrén 1994). There, according to the model of Rolstad and Wegge (1989), coarse-grained landscape would be preferable in the light of capercaillie's spatial habitat needs than fine-grained one. Also in Finland the minimum home range needs of capercaillie need also attention, even though >50% of land area consists of thinning stands or mature stands (Finnish Forest Research… 2005) and forested areas quite commonly cluster as larger patches (percolation theory, e.g. Gardner et al. 1987).

The small-scale habitat quality (microhabitat quality) needs also more attention (Graf et al. 2005). Many effects of forest management on the capercaillie habitats and populations are fairly well-known. The negative effects of clear-cuts (e.g. Rolstad & Wegge 1987) on capercaillie populations are evident, ditching is known to reduce the reproductive output of grouse (Ludwig et al. 2008, black grouse) and bilberry is known important for the capercaillie (e.g. Storch 1993, 1994). But there are still many open questions. The estimates of minimum age of forest, which is suitable for the capercaillie, have varied within the boreal region from 30 – 50 years (e.g. Seiskari 1962, Rolstad 1989) to 70 – 90 years (Swenson & Angelstam 1993). When these estimates are compared with the common rotation lengths in managed boreal forests (70 – 120 years) the potential of managed forests as capercaillie habitats appears to be very different between the extremes. Also the evaluations concerning the effect of thinnings on the capercaillie habitat quality have varied. Those have been seen as beneficial in naturally dense forests (Rolstad 1989, Klaus 1991, Storch 1993) or neutral (Rolstad & Wegge 1989, Gjerde 1991), but also as degrading due to simplified tree-species composition (Seiskari 1962) or stand architecture (Lindén et al. 2000). How the thinnings affect capercaillie habitat quality, determines largely the habitat quality in the future because nearly all the potential habitats are already, or will be, thinned in managed forests, which form more than 95% of forest land area in Finland. Furthermore, enough attention may not have been paid to the 'bilberry hypothesis' in Finland (Lindén 2002), because bilberry has been and is very abundant (Salemaa 2001). The cover of bilberry reduces drastically due to clear-cuts, but recovers at least moderately within a few decades (Salemaa 2001, Lakka & Kouki 2009). The reproductive output of capercaillie has been found to be positively associated with bilberry cover in Scotland, but the data range exceeded only up to ground cover 20 – 25% (Baines et al. 2004) and it is unknown if the further increase would benefit the species.

2 OBJECTIVES OF THE RESEARCH

The aim of this study is to provide applicable knowledge for taking capercaillie into consideration in forest management, and thus promote the ecologically sustainable forestry. This study focuses on the question: which structural characteristics of forest are important for the capercaillie? This knowledge can help to detect the threats and possibilities concerning the species habitats and enable efficient capercaillie habitat management. To achieve this goal, many types of capercaillie habitats are studied in several spatial and temporal scales.

The study belongs to the field of forest ecology, and the study approach is landscape ecological because the species in the focus, capercaillie, has large home ranges. Although the scale of results is landscape scale, the results are discussed also in the forest stand scale (see e.g. Swenson & Angelstam 1993), which represents the microhabitat scale for the capercaillie. The tree layer characteristics within the capercaillie habitats are in the main focus, but also other forest characteristics e.g. the field layer structure and predators, which both are known to affect the reproductive output of grouse (e.g. Baines et al. 2004), are taken into consideration. The results are discussed in the light of rich available knowledge about the capercaillie and Finnish forests, taking into consideration also the economical viewpoint of forestry. Based on this I form a synthesis, which aims to a comprehensive view about the relationship between capercaillie habitat needs and forestry. Finally, suitable methods for managing capercaillie habitats in commercially managed forests are outlined.

3 MATERIALS AND METHODS

Capercaillie habitats were studied using several approaches: capercaillie lekking site surroundings (I), capercaillie densities (II, III) and capercaillie habitat selection (III, IV) were examined. Capercaillie densities were studied also in the scale of whole Finland (II), but otherwise the study areas located in northern Finland in north-boreal (II-IV) or in Eastern Finland in the transition zone between mid- and north-boreal vegetation zones (Ahti et al. 1968). The capercaillie lekking site locations originated from the local hunters and Metsähallitus (I). Data on location of individual capercaillie and density data were derived from the wildlife triangle counts (II – IV). Capercaillie data were in all studies combined with the landscape data, which based on the national forest inventories (I, II) or on forest planning data of Metsähallitus (III, IV).

Wildlife triangle counts started in the large scale in 1989. The basic unit of this nation-wide monitoring program is a triangle-shaped transect, with a 4 km side length (total 12 km) (Helle & Lindström 1991, Lindén et al. 1996). The triangles are counted twice a year, winter counts in January – March and summer counts in August, which is the prime time for counting grouse since the young are still in broods together with their parent(s). In the three-man line-transect method, the person in the middle walks along the line and the other two at the distance of 20 m from him/her. The width of the census belt is 60 m. The field work is performed by voluntary hunters and the program is run jointly by the Finnish Game and Fisheries Research Institute and the Hunters’ Central Organization. The detection probability of single adults in the wildlife triangle counts is about 60% and for broods up to 100% (Brittas & Karlbom 1990). The individuals may also move when the counters approach. This shift, however, is nearly always small (Brittas & Karlbom 1990).

Landscape data in the two first articles (I, II) based on the national forest inventory (NFI) (e.g. Tomppo 1991, 1996, Tomppo et al. 1998). Forest planning data from Metsähallitus was used in the last two papers (III, IV). It includes detailed information of forest stands, e.g. soil features and tree layer characteristics for each tree species. The basic units in forest planning data, stands, are divided according to tree layer and soil characteristics. Field inventories in the Metsähallitus forest planning data were made at various times in the 1990’s, but the data are updated annually for different forest management procedures. For example, regeneration cuttings are updated not later than 6 months after the cutting. The forest planning data correspond to the situation in the beginning of the year 2003, but it was also modified to represent the situation at the beginning of 1990s (III) based on the known management history and tree layer characteristics, e.g. average tree diameter and age.

The landscape classification was very similar in papers II, III and IV. The classes of forest were mature stand, advanced thinning stand, young thinning stand, seedling stand (advanced seedling stand in paper II) and clear-cut. The classification followed the forest stand development classes used e.g. in the national forest inventories (Finnish Forest Research… 2005), where the mean tree diameter is > 23 cm in the mature stands, 17 – 23 cm in advanced thinning stands, 8 – 16 cm in young thinning stands and < 8 cm in seedling stands. In papers III and IV other landscapes classes were wasteland, scrub land, water and human habitation. In paper II waste land, scrubland and water were combined as one class (naturally open). In paper I the classification based on the soil type and total timber volume. The classes were water, open areas (e.g. fields, settlements and roads), open bogs (timber volume 0 – 4 m^3ha^{-1}), clear-cuts (mineral soils, timber volume 0 – 4 m^3ha^{-1}), advanced seedling stands (mineral soils, timber volume 5 – 35 m^3ha^{-1}), thinning forests (mineral soils, timber volume 36 – 100 m^3ha^{-1}), peatland forests (peatland, timber volume 36 – 100 m^3ha^{-1}) and mature forests (all types of soils, timber volume > 100 m^3ha^{-1}). The thinning forests included mostly young thinning stands, and the mature forests included mostly advanced thinning stands and mature stands. The limit between thinning stands and mature stands (100 m^3ha^{-1}) located between the average timber volumes of young and advanced thinning stands (68 and 128 m^3ha^{-1}) in the study region (Finnish Forest Research… 2005).

In the large-scale study (II) capercaillie density was studied in relation to landscape class proportions in 50 km x 50 km grid cells. In other studies capercaillie habitats were compared to available landscapes (I, III) or to non-capercaillie landscapes (IV). Circle-shaped landscapes were used to represent the capercaillie habitats (I, III, IV). Mann-Whitney-U-test (I, IV) and T-test (III) were used to study the differences between the capercaillie habitats and comparative landscapes depending on the variable distributions. Logistic regression was used to predict if the location was a capercaillie lekking site or a comparative location (I), and linear regression to study the relationship between landscape variables and the number of capercaillie cocks in the lek (I). Correlation analyses were performed between the landscape class proportions and capercaillie density (II, III). Dutilleul's (1993) adjustment was used in the large-scale study (II) to remove the effects of spatial autocorrelation on the p-values (e.g. Legendre 1993, Legendre et al. 2002).

4 RESULTS AND DISCUSSION

4.1 Young thinning stands are suitable for the capercaillie

Young thinning stands were more abundant in the capercaillie summer habitats than in the available landscapes or in the reference, non-capercaillie landscapes in northern Finland at the beginning of 2000s in 800 m study scale (III, IV). This was found also in the capercaillie winter habitats (IV). Thinning stands were also abundant in capercaillie lek surroundings, and were positively associated with the number of cocks in the lek (I). Also other recent studies in the boreal region have consistently shown a similar pattern, e.g the formation of new leks in young forests (Rolstad et al. 2007, Valkeajärvi & Ijäs 2007). Young thinning stands form quite commonly large units, which can promote their use as capercaillie habitats (see e.g. Rolstad & Wegge 1987). The proportion of young thinning stands was, however, also positively associated with capercaillie density in 2500 km^2 grid cells (50 km x 50 km) throughout Finland (II). Even though also other factors affect the regional capercaillie density (e.g. predators and hunting), this finding – together with the ceased capercaillie decline at the 1990s (Helle et al. 2003) – largely confirms that the young thinning stands can be considered at least moderately suitable for the capercaillie.

The smallest diameter classes (average tree diameter at breast height, DBH) were less abundant in capercaillie habitats than in reference landscapes, but approximately by diameter 8 – 9 cm stands became more abundant in capercaillie summer and winter habitats than in reference landscapes in all studied landscape types; pine heath, mixed heath and peatland forest (IV). Even in the north-boreal region this stage is reached in 30 – 40 years, which is in agreement with Seiskari's (1962) findings. Rolstad and Wegge (1990) suggested the threshold age of 40 – 50 years in the south-boreal region. According to results by Swenson and Angelstam (1993) capercaillie would prefer forests, which are 70 or even 90 years old in south-boreal Sweden (but would use 20 years old or older forests according to their availability, however). Based on the limit of 30 – 40 years managed boreal forests have a high potential as capercaillie habitats, because even in the ordinary forest management practice forest stand is potentially suitable for the species the major part of the rotation period, which is about 70 – 120 years (Metsätalouden kehittämiskeskus Tapio 2006). In a forested landscapes where the age distribution is relatively even, this would mean that most of the area is at any point of time potentially suitable for the species.

In northern Finland the average SDI (McTague & Patton 1989; represents the stand-scale overall forest cover, i.e. canopy cover) was higher in capercaillie male summer habitats and brood habitats than in reference landscapes (IV). The proportion of forest land, which includes forests of all ages, was also positively associated with capercaillie density in southern and central parts of Finland (II). The overall forest cover at the landscape-scale has been found important for the capercaillie also earlier in several occasions (e.g. Seiskari 1962, Wegge & Rolstad 1986, Lindén & Pasanen 1990, Picozzi et al. 1992, Storch 1993, Helle et al. 1994, Helle & Nikula 1996, Kurki et al. 2000). In northern Finland the SDI and Relative Abundance Index (RAI, represents the relative difference of landscape class proportions between capercaillie habitats and reference landscapes) were positively associated in the capercaillie summer habitats (IV). In nearly all studied diameter classes the RAI was low in most sparsely stocked stands and significantly higher in moderately or highly stocked stands (IV). This shows the capercaillie need of overall forest cover also at the microhabitat scale (i.e. canopy cover at the forest stand scale). This is in agreement with Storch's (1995) view that the age or successional stage alone does not guarantee the capercaillie habitat quality.

4.2 The role of mature managed forests

A strong positive relationship between old or mature forests and capercaillie has been consistently detected in many earlier studies (e.g. Hjorth 1970, Wegge & Rolstad 1986, Lindén & Pasanen 1990, Picozzi et al. 1992, Storch 1993, Helle et al. 1994, Kurki et al. 2000). This association was also found in northern Finland at the change of the 1980s and 1990s (III), but after that the relationship between mature forests and capercaillie was weak, absent or even reverse throughout the Finland (I – IV). In the lekking site surroundings in eastern Finland mature forests were more abundant than in the comparative landscapes (I). On the other hand, in this study the landscape classification based on the total timber volume, and therefore the densest young thinning stands were fell to the landscape class 'mature forests'. Furthermore, the number of cocks in the lek was not positively associated with the proportion of mature stands (I). The proportion of mature managed forest was even negatively associated with the regional capercaillie density in central Finland (II) and local density change in northern Finland (III), where mature forests were also less abundant in the male summer and winter home ranges than in the reference landscapes (IV).

The weak relationship between mature managed forests and capercaillie in the landscape scale is evident, but what explains this result? First, the broad-scale spatial structure can affect the results (Legendre et al. 2002). Capercaillie may not use even highly suitable patches if those are smaller than the minimum home range needs of species (Storch 1993, see also Dunning et al. 1992, Andrén 1994). In Finland, where the mature forest proportion is about 10% with slight variation only (II), those alone rarely form patches, which are large enough for the species (Mykrä et al. 2000). At all studied scales mature forest proportion was positively associated with clear-cut and seedling stand proportions (I – IV). During the previous decades the proportion of mature forests has been slightly higher (Finnish Forest Research… 2005) and they obviously formed larger units. In the larger patches the minimum requirements of capercaillie are better met (Rolstad & Wegge 1989). On the other hand, the results changed only slightly even if only large mature forest patches were studied (IV) or methods, which should be able to filter the confusing intercorrelations, were used (II, III). This suggests that the explanation is in the forest stand scale.

Tree-species composition could explain the winter habitat selection of capercaillie (Seiskari 1962). In northern Finland pine, which provides the winter food for the capercaillie, is less abundant in mature forests than in thinning forests. Almost 91% of thinning stands in the study area are pine-dominated, but in mature stands less than 50% (IV). In southern and central Finland the capercaillie population density was positively associated with the pine forest proportion (II). On the other hand, in northern Finland this association was not found (II). There the mature pine-dominated forests were not abundant in capercaillie winter habitats either (IV). This suggests that tree species composition can't explain the habitat selection of capercaillie in northern Finland. The seasonal variation in capercaillie habitat selection (e.g. due to molting and berry eating) could, in turn, explain the observed low abundance of mature forests based on the species locations at August. Rolstad and Wegge (1990) found that during midsummer (June-July) only the broods prefer old forests, but they detected a positive association between the males and old forests during all the other months. Therefore during August the habitat selection of capercaillie should not be exceptional.

Capercaillie stays mostly on ground during the snow-free season (e.g. Seiskari 1962, Pulliainen 1979), and therefore the physical properties of forest stand at the height of field layer can explain the weak association between capercaillie and mature forests. The species is adapted to natural boreal forests (e.g. Hjorth 1970), but there are structural differences between the natural old-growth (multicohort) forests and the mature managed (single-cohort) forests, which can make a significant difference. Mature forests without an understorey were less abundant in male summer habitats than in reference landscapes in northern Finland, but mature forests with an understorey were not (IV). The average stand structure of mature forests may have changed considerably e.g. from the end of the 1980s to the beginning of the 2000s specifically in northern Finland. This could explain why in northern Finland the positive association between capercaillie and mature forests was found at the beginning of 1990s, but not any more at the beginning of 2000s (III). At the beginning of 2000s most mature forests have been thinned, but earlier a significant proportion of mature forests may have been unmanaged for very long time, and thus had old-growth forest characteristics.

Multicohort forests are too dense for the capercaillie e.g. in central Europe (Storch 1993), but in the south-boreal Sweden Swenson and Angelstam (1993) found moderate capercaillie densities in multicohort forests. In central Europe two-thirds of the pole-stage and older forests were considered too dense to be optimal for the capercaillie (Storch 1993). Also in Norway cues about overstocking of capercaillie habitat have been detected (Rolstad 1989, Gjerde 1991). But in north-boreal region of Finland signs of capercaillie habitat overstocking were detected only in diameters 10 – 16 cm (mostly in peatland forests) and in young thinning stands with an understorey (IV). It is quite obvious that the needs of capercaillie are quite similar everywhere. But the forests can be very different. For example the average timber volume in advanced thinning stands and mature stands in southern Finland is twice higher than in northern Finland (Finnish Forest Research… 2005). Therefore the capercaillie habitat overstocking is probably more common in the southern parts of country. Also in multicohort forests and young successional stages the habitat overstocking should be more common due to high density of stems.

It has been hypothesized that after a certain threshold in forest succession the suitability of forest for capercaillie would be relatively constant (Rolstad 1989, Rolstad & Wegge 1990). This assumption could hold true in e.g. south-boreal forests due to more vigorous bush layer, but not necessarily in managed north-boreal forests. An important aspect is that capercaillie needs different types of cover against different predators. Overall forest cover at the stand-scale (i.e. canopy cover, vertical cover) provides cover against most avian predators, whereas cover on the ground (horizontal cover) is needed specifically against the mammalian predators and perhaps against goshawk (*Accipiter gentilis*, Kvasnes & Storaas 2007). Species avoids open areas where the cover against predators is lacking, and dense areas where it can't escape from the predators (Rolstad & Wegge 1990). In the lekking sites capercaillie is known to prefer horizontal visibility of 20-50 m (Valkeajärvi & Ijäs 1986), and the horizontal cover has been found to be inversely associated with losses of grouse nests (Ludwig 2007). Small-scale variation in forest density is beneficial for the capercaillie (Rolstad & Wegge 1990, Gjerde 1991) because it can allow capercaillie to either hide or escape from predators (e.g. Rolstad 1989). The microhabitat variation could be one reason, why the tree-species mixture is common characteristic of capercaillie habitats (Rolstad 1989, Helle et al. 1990).

The diversity of forest stand tree and bush layer is lowered due to management in boreal forests (e.g. Lilja & Kuuluvainen 2005). The amount of understorey is also generally low (Uotila & Kouki 2005) and especially the pines and birches (*Betula sp.*) prune naturally. In young single-cohort forest the tree crowns can provide canopy cover and cover on the ground, but in older single-cohort forest the dominant cohort of trees can provide only little cover on the ground especially in the low-productive pine forests. The canopy is more multilayered in peatland forests than in heath forests (Sarkkola et al. 2004, Hotanen et al. 2006), which could explain, why the RAI reduced in relation to SDI in the largest diameter classes in heath forests, but not significantly in peatland forests in capercaillie summer habitats in northern Finland (IV). The generally low cover on the ground in northern regions could also explain why in Northwestern Russia the shrub cover was higher in brood locations than in comparative ones (Wegge et al. 2005).

4.3 The role of thinnings

Thinnings can upgrade the capercaillie habitat quality in dense forests (Gjerde 1991, Storch 1993), but in northern Finland the habitat use of capercaillie reduced in all studied categories (males, broods and single females) in the diameter class of 16.5 cm in heath forests (IV). According to forest planning data from northern Finland, this diameter class largely represents the stage that follows the first commercial thinning (IV). After the next thinning, in turn, the diameter is commonly approximately 19 – 20 cm. Reduction in the RAI after the thinning of a seedling stand (6.5 cm diameter class) and first commercial thinning (16.5 cm) could also, at least partly, be caused by the cutting residues, which obviously hinders the capercaillie movement. In the winter habitats RAI peaked in slightly larger diameter classes (14.5 – 18.5 cm), but reduced in the following diameter classes (18.5 and 20.5 cm). In peatland forests, where the diameter class 14.5 cm represents coarsely the stage that follows the first commercial thinning, the peak of habitat use located in diameter classes 16.5 cm in summer and winter habitats.

Thinnings probably reduce the capercaillie habitat quality mainly by degrading the stand architecture, as Lindén et al. (2000) have suggested. In other words, in the long term the thinning method is probably more significant for the capercaillie microhabitat quality than the thinning strength in the ordinary Finnish management practice. The growth of individual trees increases due to thinnings (e.g. Peltola et al. 2002), but thinnings tend to reduce amount of smaller trees and thus the cover on ground. However, peatland forests – which have more diverse tree layer structure than heath forests (Sarkkola et al. 2004, Hotanen et al. 2006) – probably have a better tolerance towards this type of microhabitat degradation. In winter, in turn, capercaillie may prefer larger feeding trees. The typical 2 – 4 thinnings during the rotation tend to reduce the tree size variation also in ditched peatland forests, even though there the tree layer diversity first increases 20 – 30 years after ditching (Hotanen et al. 2006). Canopy cover increases again after thinnings due to tree growth, but the cover on the ground does not necessarily recover (e.g. understorey removed). Especially in pine forests also the natural tree pruning can reduce substantially the cover on the ground. In the low-productive sites cautious thinnings would maintain higher canopy cover, but on the other hand moderate thinning could provide more growth resources for the understorey. Also thinning of a seedling stand can have many-sided effects on the capercaillie microhabitat quality. First that may reduce or end the capercaillie habitat overstocking (but cutting residues could reduce the habitat use for few years). In the longer time scale, however, the reduced tree size variation leads to the low cover on the ground.

4.4 Peatland forests

In northern Finland peatland forests were more abundant in capercaillie habitats than in reference landscapes if they were at least moderately stocked (IV). The abundance of spruce mires was also two to three times higher in the capercaillie male, brood and single female habitats in August than in reference landscapes (IV). This agrees with the findings of Rolstad (1989) and Wegge et al. (2005). The tree layer is diverse in peatland forests (e.g. Sarkkola et al. 2004, Hotanen et al. 2006), but obviously also the availability of insect food (Stuen & Spidsø 1988, Wegge et al. 2005) makes spruce mires very suitable also for the broods. Most of stocked peatland forests in Finland are ditched, however. Ditching has been found to reduce the reproductive output of grouse even though the actual mechanisms are still unclear (Ludwig et al. 2008). Ditches do not necessarily hamper physically the adult birds or older chicks, but small chicks could drown to deep wet ditches. Ditching also decreases the amount of insect food for the chicks (Stuen & Spidsø 1988). On the other hand, in ditched peatland the overall forest cover starts to increase due to enhanced tree growth, the tree layer is diverse (e.g. Sarkkola et al. 2004) and eventually also the field layer vegetation becomes similar as in the heath forests (Vanha-Majamaa & Reinikainen 2000). Later also the groundwater starts to increase again, which obviously increases the amount of insect food for the chicks (Stuen & Spidsø 1988). Old ditches, which are filled with *sphagnum*-moss, may not be a direct threat for the chicks, but finally the degrading effects are obviously repeated due to ditch restoration. Peatland forests may have generally a high potential as capercaillie habitats, but at least the spruce mires can provide very suitable capercaillie summer habitats, also for the broods. Therefore those deserve special attention in the capercaillie habitat management.

4.5 Brood habitats

Brood habitats need special attention because reproductive output is in most occasions the main reason behind the population decline of capercaillie (e.g. Moss et al. 2000) and other grouse. For example, black grouse (*T. tetrix*) adult survival has increased in Finland since beginning of the 1960s, but the brood survival has decreased (Ludwig 2007). In northern Finland capercaillie broods preferred slightly later successional stages than the adult birds during August (IV). Capercaillie juvenile density was also higher in the wildlife triangles, where within 3 km radius advanced thinning stands were abundant, but adult density was not (III). The better food availability could explain this difference. Broods need abundant food within relatively small areas, whereas adult bird can easily move over longer distances to seek food. Bilberry (*V. myrtillus*) is a dwarf-shrub, which is considered the most important field layer species for the capercaillie (e.g. Storch 1993). It is a direct food source for the species and it provides cover especially for the chicks. It also hosts several herbivorous invertebrates that are a crucially important food source for the chicks during their first weeks (Storch 1993, Sjöberg 1996, Wegge et al. 2005). Capercaillie breeding success has been found to increase with increasing bilberry cover up to cover about 20% (Baines et al. 2004), but above that proportion the effects are unknown. However, in Finland the bilberry cover proportions can reach up to 50% (e.g. Lakka & Kouki 2005). Bilberry cover decreases drastically due to clear-cut, but recovers moderately in a few decades (Salemaa 2001). Thinnings and other selection cuttings should benefit bilberry due to increased amount of light (Atlegrim & Sjöberg 1996) because high density of trees is known to limit the amount of berries (e.g. Ihalainen et al. 2005). In managed forests the overall cover of bilberry generally increases towards older successional stages (Uotila & Kouki 2005), but some small cues of reduced bilberry cover have also been found in the stage, which correspond the advanced thinning stands (Lakka & Kouki 2005). The cutting residues are one potential explanation for this, because those can suppress the dwarf-shrubs. The sprouts, which are not left below the cutting residues, should get more sunlight in thinned forest and thus be more vigorous and produce more berries. But eventually the capercaillie population may be more dependent on the bilberry cover than berries because the cover largely determines the availability of insect food (Lakka & Kouki 2009), which the chicks need during the critical first weeks of their life.

If the amount of available food is high, the brood daily movement distances obviously reduce, which has been found to increase the chick growth and survival of e.g. willow grouse chicks (*Lagopus lagopus*, Erikstad 1985). If the amount of suitable brood habitat is low in the larger scale, the predation obviously increases exponentially due to increased search efficiency of predators (Storaas et al. 1999). Higher amount of suitable habitats, in turn, would reduce the search efficiency of predators. Increased amount of food would lead to smaller movement distances of broods, which would obviously reduce the amount of olfactory cues for the predators. Smaller movement distances could also reduce the chick probability of getting wet or drowned into ditches. Also the adverse weather conditions and strengthened predator populations, which can reduce the reproductive success of capercaillie and other grouse (e.g. Moss et al. 2001), can be linked with the habitat quality. In suitable habitats the chicks can find enough food easily, and thus stay dry and warm better. This promotes their growth and survival (Sjöberg 1996). In suitable habitats the predators can't detect the chicks, or the poorly flying young chicks can find lower branches and thus avoid e.g. the red fox (*V. vulpes*) or the raccoon dog (*N. procyonoides*). The bilberry availability alone may not be able to explain the capercaillie population decline in Finland (Lakka & Kouki 2009). In future, however, it would be intriguing to explore if high bilberry cover and cover on the ground can be found within the same forest stands.

5 FURTHER VIEWS AND RESEARCH NEEDS

Based on the results, the cutting residues probably cause a short-term reduction in the capercaillie habitat use initially after the thinning (IV). The residues can hinder the movement of small chicks especially. But the residues can also shade the dwarf-shrubs and thus reduce their cover proportion. Eventually dwarf-shrubs, for example the bilberry, may be replaced e.g. by grasses or mosses. To avoid these effects the residues could be collected and used for energy, or those can be placed to the logging tracks. On the other hand, the residues could also be piled, when those could provide cover against the predators (Kortland 2006). In future, the effects of cutting residues as well as the costs and benefits of their management deserve to be studied more closely.

Also new alternatives for the peatland forest management deserve to be evaluated carefully. There are more than five million hectares of ditched peatland in Finland (Finnish Forest Research… 2005), and based on several results (IV, Stuen & Spidsø 1988, Wegge et al. 2005) those have a huge potential as habitats of capercaillie. Reduced ditch restoration would benefit the water ecosystems in many ways (e.g. Simola 1983), but could also lead to increased capercaillie survival and reproductive output. The tree growth increases in most cases after the ditch restoration (e.g. Kojola et al. 2008), but in densely stocked peatland forest the evaporation is high and can therefore maintain the suitable (low) groundwater level. Therefore the ditch restoration may not always be necessary in stocked forests (Finnish Forest Research… 2006, Sarkkola et al. 2008) if also the thinning strength is kept low. The ditch restoration alone may not either increase the tree growth considerably without an additional fertilization. This increases the alternative cost of the intensive management schedule and makes the less intensive management option more competitive.

In southern and central Finland the proportion of pine-dominated forests is low, quite commonly below 30% (II), and there the availability of winter food (pine needles) can become as a critical factor for the capercaillie. The large age classes of Finnish forests are largely pine-dominated, and therefore the pine forests will be quite abundant during the next decades. But beginning from the 1990s the amount of pine planting has reduced and replaced by spruce (Finnish Forest Research… 2005). One significant reason for this is the dense moose (*Alces alces*) population in Finland, which has led to large damages in the pine plantations (e.g. Nikula et al. 2008). But so far the needed quantities – how high proportion of pine forests or how high stand-scale pine proportion capercaillie needs and can those compensate each other – are unknown. Furthermore, the needles of damaged pines provide very suitable winter food for the capercaillie (e.g. Lindén 1989), but it is not yet known if the capercaillie needs high proportions of pine, or can the smaller amount of damaged trees provide the needed winter food resource.

Soil scarification aims to improved establishment of seedlings, but reduces the amount of bilberry together with increased sunlight after clear-cuts (e.g. Salemaa 2001). Bilberry obviously recovers relatively well from the clear-cuts and ordinary soil treatments (e.g. Salemaa 2001), but in future the increasing use of wood as a source of energy can lead to drastic reduction in the amount of dwarf-shrubs. If the soil is scarified after the stumps are collected (for fuel), the roots of dwarf-shrubs, which form the basis for the field layer recovery, can be destroyed much more extensively. In thinning forests or multicohort forests, in turn, the effect of stump collection could be even beneficial for the capercaillie. The collection of stumps or the tree-with-root system could mimic one of the natural disturbance agents, windfall, promote the establishment of understorey and improve the access to the mineral soil. Grouse need stones for their digestive system to break the food that consists largely of hard pieces of plants. Typically mineral soil and stones are available only in the clear-cuts and roads. In clear-cuts the snow cover is thick and predation risk high. In roads, in turn, predation and car-collides increase the risk of death, but under the canopy cover the snow cover is less thick and the risks are lower. Specifically during the winter the availability of stones may be limited, which could reduce the grouse fitness and lead to reduced survival and reproductive output. This has not been shown yet, however.

6 MANAGING CAPERCAILLIE HABITATS IN COMMERCIAL FORESTS IN FINLAND

The results showed that forest cover is important for the capercaillie in all scales. In the landscape scale that can measured as a proportion of forested areas, and in the forest stand scale this means the age about 30 years or more and at least moderate tree density. The importance of old trees for the capercaillie (e.g. Picozzi et al. 1992) or for the entire forest biodiversity (e.g. Esseen et al. 1997) has been emphasized in many occasions. But the results of this work and e.g. the earlier finding that horizontal cover is inversely associated with losses of grouse nests (Ludwig 2007), emphasize the role of smaller, non-dominant trees, which can provide cover on the ground for the capercaillie. Pine (*Pinus sylvestris*) provides winter food for the capercaillie, and the proportion of pine forests was positively associated with capercaillie density in southern and central Finland. Spruce (*Picea abies*), in turn, can have a considerable effect on the capercaillie habitats due to its long crown, which can provide effectively cover on the ground against the predators.

The most suitable methods for capercaillie habitat management change regionally as well as between successional stages and site types. In young and dense forests forest management can first benefit capercaillie (see e.g. Storch 1993), but can later lead to reduced cover on the ground at least in the low-productive sites. At the beginning of 2000s the proportion of young forests (seedling stands) is high in Finland (Finnish Forest Research… 2005) and the large-scale overall forest cover will increase to some degree during the next decades if the forest use does not change markedly. This, however, does not necessarily benefit the capercaillie population markedly if the microhabitat quality reduces in the older managed forests. In northern Finland the role of cover on the ground is probably higher than in southern Finland. In north the forests are low-productive and the ordinary forest management can make the capercaillie microhabitats too open-structured more commonly. According to the model of Rolstad and Wegge (1987) in the most forested landscapes small patch size would benefit the capercaillie due to increased variation in the habitat types. Also the finding, that the lekking site surroundings included more mature forests and thinning forests, but also included more edge of mature forest than the comparative landscapes in eastern Finland (I) fits well together with this model. Therefore reducing the size of forest management units would benefit capercaillie in the highly forested landscapes. Respectively in landscapes, where the overall forest cover is low, the suitable patches need to be either large or clustered to form suitable capercaillie home ranges. In southern Finland the proportions of forest land and pine forests are low (II), and for example in the south-coast area the area occupied by human activity increased from 29% to 36% from the 1970s to the 1990s (Finnish Forest Research… 1976, 2005). Therefore especially in southern Finland capercaillie habitat management needs to include large-scale spatial planning to form patches large enough for the species and preserving the availability of pine forests. But spatial planning, where relatively large planning units are needed (e.g. Kurttila 2001), is challenging in Finland due to the large numbers of small forest holdings. In the long term, however, it is possible to increase the amount and quality of available habitats in the commercially managed forests. For this, longer rotations, selective cuts and understorey management are suitable methods.

6.1 Longer rotations and selective cuts

The multicohort forest management model (e.g. Bergeron et al. 2002, Kuuluvainen 2008) has been suggested to improve the ecological sustainability of forestry in boreal forests. In this method varying rotations, which reach up to several hundreds of years, are used, and most clear-cuts are replaced with selective cuts, partial cuts and group selection methods. This would obviously be consistent with the habitat needs of the capercaillie. But also smaller increase in the rotation length would significantly increase the availability of capercaillie habitats. For example, in a landscape, where the proportion of forest land is 80%, the average proportion of potentially suitable habitats for the capercaillie is about 40% if the limit for suitability is 35 years and average rotation is 70 years, and the proportion of each age class is equal. If the rotation is 120 years, the proportion of potentially suitable capercaillie habitat is about 57%. Longer rotations would mean increased proportion of suitable (micro)habitats, improved connections between the suitable patches (according to the percolation theory, see e.g. Gardner et al. 1987) and higher availability of bilberry (which is more abundant in older forests, e.g. Lakka & Kouki 2009).

The rotation length is, however, tightly connected to economical profitability, which is the main goal of most forests owners (e.g. Karppinen 1998). The maximization of net profit has replaced the maximal timber production as the main goal of forestry, and thus the tendency has been towards shorter rotations. Delayed clear-cutting sharply reduces the net profit of forest owners, especially if interest rates are high, since the committed capital is high in mature forest. On the other hand, thinning from the top has been found to be an optimal method for later thinnings (e.g. Hyytiäinen et al. 2005, Pukkala 2006). It is included in the latest national forest management recommendations, and leads to an optimal rotation up to 20 years longer than thinning from below (Metsätalouden kehittämiskeskus Tapio 2006). This longer optimal rotation bases on the higher thinning incomes. Those base on price difference between the timber qualities (saw-wood vs. pulp- or fuel wood), which can change over time. Thinning from top helps to combine the ecological and economical goals of forestry, but rotations comparable to the natural fire regime (e.g. Kuuluvainen 2008) would call for higher price for older/larger trees, subsidies for the ecologically sustainable forestry, or forest owner's willingness to accept the reduced net profit.

In a selectively cut forest (multicohort forest, uneven-aged forest) the canopy cover remains relatively high quite constantly (e.g. Oliver & Larson 1990). Therefore replacing some clear-cuts by selective cuts would increase the overall forest cover at the larger scales. Selective cuts can reduce the canopy cover to some degree, but not the cover on the ground (Kvasnes & Storaas 2007). Those don't reduce the amount of insect food for the chicks either, as the clear-cuts do (Stuen & Spidsø 1988, Kvasnes & Storaas 2007). From the viewpoint of capercaillie habitat management, the longer rotations or the shift from clear-cuts to selective cuts would have the highest beneficial effect in spruce mires because those are important capercaillie habitats in many respects. Especially in spruce mires the selective cuts can provide a valuable alternative between the clear-cut and avoidance of all cuts.

6.2 Understorey management

In many cases the management of understorey (or other non-dominant cohorts) would need only small modifications to the ordinary forest management practice. The visibility of 20-50 m, which capercaillie is known to prefer at lekking sites (Valkeajärvi & Ijäs 1986), could be used as a coarse goal, but it is also known that the variation in the visibility (cover on the ground) is beneficial for the species (e.g. Rolstad 1989). If the understorey is thin, it would be preferable to save whatever is present. Pre-clearings are increasingly used to support the mechanized logging. If the understorey is very dense, pre-clearings increase the productivity of the first commercial thinning (e.g. Kärhä 2006), and end also the capercaillie habitat overstocking (e.g. Storch 1993). However, e.g. <1000 understorey trees/ha, in small groups, could provide suitable cover for the grouse without a significant reduction in the productivity of thinning (Kärhä 2006) or in the growth of dominant trees (Saksa et al. 2002). The understorey also has great potential in forest regeneration (Hyppönen et al. 2002) if the understorey trees are not too old (e.g. > 60 years). It can also accelerate the start of the next rotation (Aarnio et al. 2002) and therefore increase also the overall forest cover at the larger scales. Even trials of understorey (spruce) planting could be considered to a limited extent, for example at capercaillie lekking sites depending on the forest owner's willingness. More knowledge is needed, however, e.g about the needed understorey density before large invests in understorey management can be recommended.

7 CONNECTIONS TO OTHER SPECIES AND ECOLOGICAL SUSTAINABILITY

The indicator or umbrella species characteristics of capercaillie are obvious since the vital capercaillie population indicates the well-being of many other forest dwelling species (e.g. Storch 2000, Suter et al. 2002, Pakkala et al. 2003). The forest characteristics, which were found as features of suitable capercaillie habitats, were also consistent with many known characteristics of natural boreal forests (e.g. Kuuluvainen 2008). These characteristics of forest stand and landscape provide a basis for the further studies. Linking these characteristics with other species or groups of species (e.g. Wildlife Richness Index, Pellikka 2005) would provide a fruitful insight to evaluate their role in a wider context (for the entire biodiversity). If these associations are clear, that would provide a solid basis to use these forest characteristics as indicators of ecological sustainability of forestry.

8 CONCLUSIONS

This work supports the conception that managed boreal forest reaches appropriate capercaillie habitat structure relatively early, in 30 – 40 years in Finland. The large Finnish forest age classes – i.e. the large areas clear-cut in 1950s and 1960s – became largely suitable for the capercaillie in the 1990s. This could largely explain also the ceased capercaillie population decline. Managed forests are therefore for most of the rotation potentially suitable for the capercaillie, and have in this respect a high potential as capercaillie habitats. But the results also suggest that in managed Finnish forests the habitat quality is not necessarily guaranteed in the later successional stages. Also the expanding human land-use is a threat for the capercaillie especially in the southern Finland.

Some characteristics of the old forests, e.g. large trees or decaying dead trees, are already mimicked in the forest management to provide habitats for the invertebrates and woodpeckers. Capercaillie, in turn, is associated with some other characteristics of old natural forest: overall forest cover at the landscape scale, canopy cover and cover on the ground. Especially in southern Finland capercaillie habitat management calls for preserving the availability of pine and spatial planning. In the long term, longer rotations can be used to increase the overall forest cover. Understorey management, which would need only small changes to the ordinary management practice, can be used to maintain enough cover on the ground. The use of multicohort forest management (selective cuts) would, in turn, increase the overall forest cover at the landscape scale and provide cover on the ground. In the light of capercaillie habitat management longer rotations or replacing the clear-cuts by selective cuts were most beneficial in spruce mires, which are important brood habitats.

Reducing the extent and frequency of ditch restorations in peatland forest management can provide effective tools to upgrade the capercaillie habitats in managed forests. Also cutting residue management may possess a high potential in the habitat management. The possibilities to use these methods, as well as their costs and benefits, deserve to be studied carefully. Furthermore, studying the overall forest cover, canopy cover and cover on the ground in relation to a larger group of species would provide a good opportunity to find, if these characteristics are the ones, which link the capercaillie to the welfare of other species.

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