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Capercaillie (*Tetrao urogallus*) Habitat Characteristics in North-Boreal Finland

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This study aimed to identify tools for taking capercaillie habitats into consideration in forest management. This would provide new alternatives for ecologically more sustainable forest management. Capercaillie summer and winter locations, from wildlife monitoring counts (1998–2004) in northern Finland, and reference, non-capercaillie locations were combined with forest planning data, and the area proportions of different landscape classes in an 800-m radius circle surrounding capercaillie and reference locations were compared. Thinning stands (in summer and winter) and spruce mires (in summer) were more abundant in capercaillie habitats than in reference landscapes, whereas e.g. seedling stands, mature stands and waste land areas were less abundant. The relative habitat use was highest in mean tree diameter (DBH) classes from 10.5 to 14.5 cm in summer habitats of adult capercaillie in heath forests, whereas in peatland forests, in brood habitats and in winter habitats it peaked in diameter classes 14.5 to 18.5 cm. The tree layer density was positively associated with the relative habitat use. A trend of lower habitat use was detected in the largest diameters (17–40 cm) in comparison to middle-sized diameters (10–16 cm) in heath forests, but not in peatland forests. Relatively young managed forests (age 30–40 years or more) can form suitable capercaillie habitats in north-boreal forests. However, this suitability is not necessarily permanent. Understorey management, longer rotations and multicohort forest management are suitable tools for capercaillie habitat management, because they can increase the available cover close to the ground, canopy cover, overall forest cover at the landscape scale and bilberry cover.

Keywords grouse; forestry; forest management; thinnings; landscape composition

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1 Introduction

The capercaillie (*Tetrao urogallus*) is known to have umbrella and indicator species characteristics, and a 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 species is adapted to natural boreal forests (e.g. Hjorth 1970), which differ from the present managed forests in many respects. For example, the average age of forests has been relatively high and an uneven-aged stand structure has been common in natural north-boreal forests (e.g. Pennanen and Kuuluvainen 2002). Capercaillie densities declined remarkably throughout its whole range during the 20th century (e.g. Wegge 1979, Lindén and Rajala 1981, Hjorth 1994, Beshkarev et al. 1995, Catt et al. 1998). The main reasons for the decline of capercaillie and other grouse species are changes in forest structure due to forest management (habitat loss, habitat degradation, forest fragmentation), increased predator densities, excessive hunting and adverse climatic changes (e.g. Helle and Helle 1991, Storaas et al. 1999, Kurki et al. 2000, Ludwig et al. 2006). In Finland, the reduction of capercaillie density was about 50% from the 1960s to the end of 1980s, but in the 1990s this trend stopped (Helle et al. 2003).

At the beginning of the 2000s more than 95% of forest land in Finland is managed and more than 50% of forests are less than 60 years old (Finnish Statistical… 2005). Since the beginning of the 1950s, when clear-cuts replaced diameter-based selective fellings (Leikola 1984), forests have typically been managed as single-cohort stands (see e.g. Oliver and Larson 1990) using clear-cut, seed-tree cut, clearing, harrowing or other site preparation, artificial regeneration and thinnings. Thinnings commonly include the clearing and thinning of seedling stands, the first commercial thinning (age 30–50 years) and 1 to 2 later thinnings. Stands are clear-cut commonly at the age of 80 to 120 years. Despite the clear-cuts, the growing stock volume (Finnish Statistical… 2005) and proportion of forested areas (i.e. closed canopy, Löfman and Kouki 2001) started to increase in the 1970s due to tree growth in young managed forests and in 4.9 million hectares of drained peatland forests, which make up 55% of Finnish peatlands (Finnish Statistical… 2005).

The positive association between old or mature forests and the presence of capercaillie has been widely documented (e.g. Hjorth 1970, Wegge and Rolstad 1986, Lindén and Pasanen 1990, Storch 1993, Swenson and Angelstam 1993, Helle et al. 1994, Kurki et al. 2000), but relatively young forests have also been found to be suitable for the species (Rolstad 1989, Rolstad and Wegge 1990, Storch 1993, Miettinen et al. 2005, 2008). Large areas of clear-cutting reduce the quality of capercaillie habitats (e.g. Rolstad and Wegge 1987), but opinions about the effects of thinning have varied from beneficial in dense forests (Rolstad 1989, Klaus 1991, Storch 1993) to neutral (Rolstad and Wegge 1989, Gjerde 1991) and degrading due to the simplified tree-species composition (Seiskari 1962) or stand architecture (Lindén et al. 2000).

Effective capercaillie habitat management is challenging because several scales, seasons and stages of the species life cycle have to be taken into consideration. The home ranges are large, about 100 hectares or more (Rolstad 1988, Rolstad et al. 1988), and the area used by a lekking population covers several thousands of hectares (Hjorth 1994, Hjeljord et al. 2000). There are also differences, for instance, in habitat use between the sexes (Rolstad and Wegge 1990). The species is unable to use potentially suitable patches that are small and isolated (e.g. Storch 2002), and thus the role of large scales increases when the proportion of suitable areas is low (e.g. Rolstad and Wegge 1989, Quevedo et al. 2006). Capercaillie lek management guidelines are available for the landscape scale (Valkeajärvi and Ijäs 1987, Helle et al. 1999, Rolstad and Andersen 2003), but small-scale habitat quality also needs more attention (Graf et al. 2005).

This study aimed to identify tools for taking capercaillie habitats into consideration in forest management. This would provide new alternatives for ecologically more sustainable forest management. We examined the landscapes surrounding capercaillie observations and reference, non-capercaillie points in north boreal Finland to identify, which characteristics of forest are abundant in the capercaillie habitats and which are not. We studied the habitat use e.g. in the light of mean tree diameter and tree layer density within heath

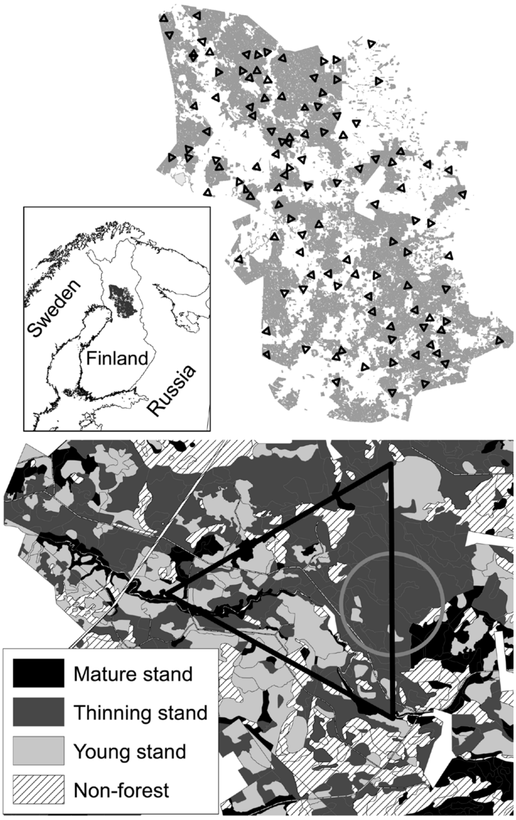

Fig. 1. The study area, wildlife triangles and the studied landscapes. The wildlife triangles and state-owned forests in the study area are shown in the top right. Each side of a wildlife triangle is 4 km in length and the radius of a circle representing the studied landscape around a capercaillie observation and reference sites is 800 metres.

and peatland forests. We also linked the results with the forest management practice and outlined suitable methods for managing capercaillie habitats in commercially managed forests.

2 Materials and Methods

2.1 Study Area

The study area is located in northern Finland (Fig. 1), and most of the area belongs to the north boreal vegetation zone (Ahti et al. 1968). 'Forestry land' covers 94% of the total land area, and the cover of 'forest land' (potential mean annual increment of trees >1 $\mathrm{m^3ha^{-1}}$) is 61%. The landscape is relatively flat, mainly lying between 170 m and 400 m asl. The forests are mostly in commercial use and the forest structure has changed considerably during the 20th century due to loggings and other human activities. Based on the landscape data, Scots pine (*Pinus sylvestris*) is the dominant tree species in 63% and Norway spruce (*Picea abies*) in 10% of the total area. Birches (*Betula* spp.) or other species are dominant in 3% of area and 24% of area is treeless. Old-growth forest covers 0.3%, mature forests 11%, advanced thinning stands 5%, young thinning stands 30%, seedling stands 13% and stands in the regeneration stage 2% of the area. The proportion of scrubland is 15%, waste land 17%, water areas 5% and other open areas 2% (landscape class descriptions are presented in Section 2.3).

2.2 Species Data, Comparative Data and Landscape Data

The capercaillie data of this study originated from wildlife triangle censuses carried out in 1998–2004. The basic unit of this nationwide monitoring programme is a randomly located triangle-shaped transect with 4 km side length (total 12 km) (Lindén et al. 1996). Summer counts are carried out in August, which is a key time for counting tetraonid birds, since the young are still together with their parent(s). A three-man chain is used in summer counts, and each observer counts 10 m belt in his/her both sides. The distance between observers is 20 m. The width of the census belt is consequently 60 m. Winter counts are performed in January to March. In the winter counts one census line is counted (i.e. only one observer is required). All grouse individuals observed from the census line, irrespective of the distance, are included. Volunteer hunters carry out the fieldwork, and the programme is jointly run by the Finnish Game and Fisheries Research Institute and the Hunters' Central Organization.

The capercaillie summer data were from years 2000–2003 and included 174 observations (78 males, 35 females with a brood and 61 single females), while the capercaillie winter data were from years 1998–2004 and included 110 observations (66 males and 44 females). In some cases several individuals were detected in the same location. They were recorded as one observation to avoid pseudoreplication. The location of each observation was digitized in a GIS database together with information on the year, season, sex and age.

Reference data were collected by placing random points (191 for summer and 154 for winter) along census lines of wildlife triangles that had been counted during 2000–2003 (summer) or during 1998–2004 (winter). The reference points could not be located on water or closer than 800 m from a capercaillie observation. Furthermore, capercaillie observations and reference points were excluded if the cover of landscape data within the 800 m buffer zone surrounding them was less than 70%.

Because habitat selection differs between males, broods and single females (e.g. Rolstad 1989), we analysed these categories separately. In the late-summer triangle counts (see Helle and Lindström 1991) the probability of detection was about 60% for single adults but close to 100% for broods (Brittas and Karlbom 1990), which increases the weight of broods in the pooled data. Birds may also have moved when the three-man group approached (Brittas and Karlbom 1990) and locating the observations on a map may also include some error. These errors are, however, relatively small (e.g. Brittas and Karlbom 1990). In addition, due to capercaillie site fidelity, the observations from subsequent years may not have been completely independent (see e.g. Alldredge and Griswold 2006). Some individuals may still have been present in recently clear-cut areas, and some individuals may have been observed during successive years. The proportion of potentially repeated observations was low, however, since less than 15% of observations were within 1 km of the observation of same sex in the previous year.

Landscape data for the study consisted of the forest planning data of Metsähallitus, the state-owned forest enterprise. These included state-owned areas, which covered about 44% of the study area, and represented the beginning of the year 2003. Within the 800-meter buffer zones around the capercaillie observations and reference points the mean proportion of state-owned forest was 95.0%. Forest stands and other habitats in forest planning data are delineated on the basis of tree and soil characteristics. Field inventories for the data had been carried out at various times during the 1990s, but the data had been updated annually following various forest management procedures. For instance, areas undergoing regeneration cuttings are updated at the latest 6 months after the cuttings. The size of a stand is commonly 0.5 to 100 ha, and soil features and some other general features are defined for each forest stand. Tree layer characteristics are defined in a detailed manner; each tree species and cohort is defined separately. In this study, we used mean diameter and stand density index (SDI) to describe the stand structure. Mean diameter was the breast height diameter (DBH) of the dominant tree species in the dominant cohort. The stand density index was calculated based on the basal area and mean diameter ($SDI = 70.8191GD^{-0.395}$, G = Basal Area (m^2ha^{-1}), D = Mean tree diameter (cm), McTague and Patton 1989).

2.3 Methods

We investigated the landscape composition within an 800 m buffer zone (about 200 ha) around each location (capercaillie observations and reference, non-capercaillie points). 800 m buffer zone roughly corresponds to the home range size of the capercaillie (e.g. Rolstad 1988, Rolstad et al. 1988). The proportion of each habitat type surrounding the capercaillie locations was compared with the respective proportion within landscapes surrounding the non-capercaillie, reference points. This difference of area proportions was used to represent the capercaillie habitat use, and will be called as ‘relative habitat use’. The habitats of males, single females and broods (in summer) were studied as pooled summer and winter sets, but also separately. Mann-Whitney-U-test was used for statistical tests, where we tested the observed landscape class proportion differences against the random utilization. A high or low relative habitat use indicates a preference for or avoidance of the habitat type (e.g. Swenson and Angelstam 1993, Storch 1997).

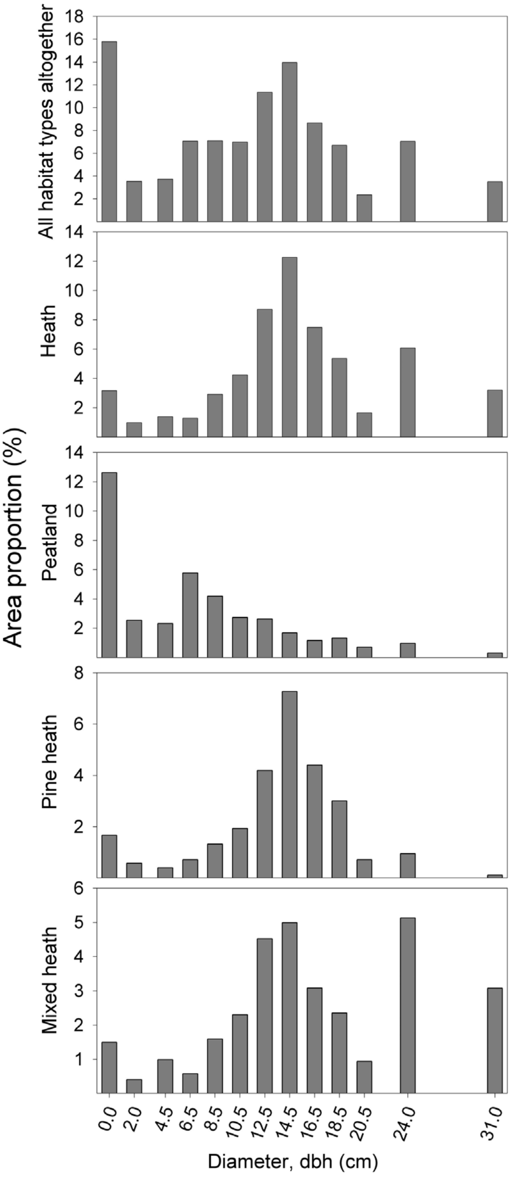

Fig. 2. The proportions of different mean tree diameter classes within different habitat categories in the study material (capercaillie habitats and reference landscapes altogether).

First we examined capercaillie summer and winter habitats using the main land use and cover classes (see e.g. Finnish Statistical… 2005): water, human habitation, waste land, scrubland, spruce mire, pine mire, clear-cut, seed-tree stand, seedling stand, young thinning stand, advanced thinning stand and mature stand. As the proportion of old-growth stands was very low (0.3%), these were included with mature stands. In seedling stands, for instance, the average tree diameter at breast height (DBH) is commonly less than 8 cm, while in young thinning stands it is 8 to 16 cm, and in advanced thinning stands 17 to 23 cm. We also studied the relative habitat use in each development stage of forest separately in pine-dominated forests and other types of forests (most of those spruce-dominated).

In the next step, we studied the relative habitat use of capercaillie in 13 diameter classes: 0 (treeless, or average tree diameter <1 cm at 1.3 m height), 2 (1–3 cm), 4.5 (4–5 cm), 6.5, 8.5, 10.5, 12.5, 14.5, 16.5, 18.5, 21.5 (20–23 cm), 25 (24–26 cm) and 31 cm (27–35 cm). We examined all habitat types altogether, but also heath forests (mineral soil), peatland forests, pine heaths and mixed heaths separately. The amount of area falling to each diameter class varied between the habitat types (Fig. 2); in peatland forests the small diameter classes were most abundant, whereas in heath forests the middle-sized diameter classes were the most common. The heaths were divided to pine heaths and mixed heaths according to proportion of pine of total timber volume (≥95% or <95% of pine). This corresponds also the site productivity classification (e.g. Finnish Statistical… 2005): herb-rich and fresh forest types had mostly less than 95% of pine, whereas dry or barren types had nearly always 95% or more pine. Seed-tree stands were excluded from these analyses due to their low tree density (<50 trees/ha). We also linked the relative habitat use of capercaillie with the forest management practice. According to forest planning data, the average tree diameter after the first commercial thinning was 15.9 cm (SD = 2.55, n = 2357) in heath forests and 14.2 cm (SD = 3.95, n = 324) in peatland forests. Respectively, the average tree diameter after the thinning of a seedling stand was in heath and peatland forests in most occasions 6 or 7 cm.

In the third section we extended the comparison of capercaillie summer habitats and reference landscapes to the tree layer density, which was represented by SDI. First, the average SDI's were compared between capercaillie habitats and reference landscapes. Second, capercaillie habitat

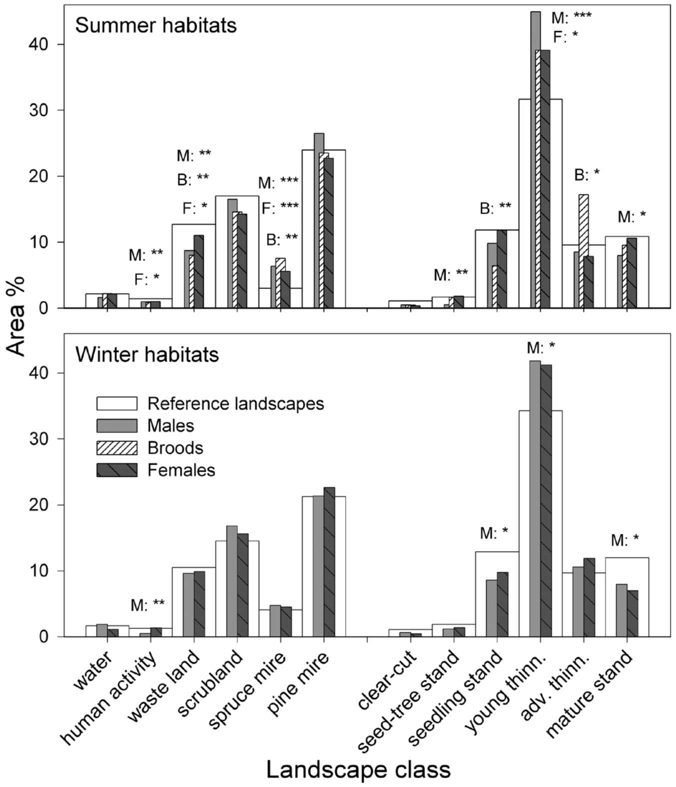

Fig. 3. Landscape class proportions in the surrounding landscapes, which represent the capercaillie summer and winter habitats and reference landscapes. Statistical significance of differences from Mann-Whitney U-tests: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

use was studied separately in heath and peatland forests as divided to two diameter classes (stand mean diameter, DBH, 10–16 cm and 17–40 cm), which both were divided to 10 density classes. SDI is constant in larger diameters (whereas e.g. total timber volume or basal area or tends to be higher in larger diameters, the same concerns SDI in young forests), which enables this combination of several diameter classes for the analysis. We used t-test to compare the averages of relative habitat use between diameter classes 10–16 cm and 17–40 cm in heath and peatland forests. Furthermore, we studied the relative habitat use of capercaillie and mean SDI as the functions of mean tree diameter more closely. We analysed the relationship between relative habitat use of capercaillie and mean SDI within the 13 diameter classes using Pearson correlation.

3 Results

3.1 Capercaillie Habitat Use within Basic Landscape Classes

Spruce mires were more abundant in capercaillie summer habitats than in reference landscapes (Fig. 3). The proportion of spruce mires was about 3% in the reference landscapes, but in capercaillie summer habitats it varied from 5.5% for single female habitats to 7.5% for brood habitats. Young thinning stands were more abundant (39–45%) in the capercaillie summer (male, female and pooled) and winter (male and pooled) habitats than in the reference landscapes (30–35%). Advanced thinning stands were significantly more abundant in brood habitats (17.2%) than in reference landscapes (9.6%). Mature stands were less abun-

Table 1. The average proportions of forest development classes according to the dominant tree species in capercaillie habitats and reference landscapes within an 800 m radius. Statistical significance of differences between capercaillie habitats and reference landscapes from Mann-Whitney U-tests: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ° = $p < 0.1$.

Tree species	Landscape class	Class proportion (%) Reference landscapes	Capercaillie habitats	Brood habitats	Male habitats	Female habitats
SUMMER HABITATS						
Pine	Clearcut or seed-tree stand	1.7	1.1 **	1.5	0.4 ***	1.8
	Seedling stand	10.1	8.4	5.0 **	8.3	10.4
	Young thinning stand	29.9	38.7 ***	37.1	40.9 ***	36.6 *
	Advanced thinning stand	8.7	8.2 °	14.2	7.2 *	6.1 *
	Mature stand	6.4	3.0 *	4.6	2.0 **	3.4 °
Spruce or birch	Clearcut or seed-tree stand	1.1	0.5	0.6	0.6	0.4
	Seedling stand	1.7	1.4	1.4	1.5	1.4
	Young thinning stand	1.7	3.1 **	2.0	4.0 ***	2.5 °
	Advanced thinning stand	0.8	1.8 **	3.0 *	1.2	1.8 *
	Mature stand	4.5	6.2	4.9	6.0 °	7.2
WINTER HABITATS						
Pine	Clearcut or seed-tree stand	1.8	1.2	–	1.1	1.3
	Seedling stand	10.9	7.4 *	–	6.5 *	8.6
	Young thinning stand	32.2	38.6 *	–	39.3 *	37.6
	Advanced thinning stand	8.8	9.8	–	9.3	10.6
	Mature stand	6.2	3.8 *	–	4.0 *	3.5
Spruce or birch	Clearcut or seed-tree stand	1.1	0.7	–	0.8	0.5
	Seedling stand	2.0	1.7	–	2.0	1.2
	Young thinning stand	2.1	3.0	–	2.5	3.7
	Advanced thinning stand	0.9	1.3	–	1.3	1.3 °
	Mature stand	5.8	3.7	–	3.9	3.5

dant in male summer (8.0%) and winter (7.6%) habitats than in reference landscapes (10.9% and 11.6%, respectively). Seedling stands were less abundant in capercaillie summer (brood) and winter (male and pooled) habitats than in the reference landscapes. Also waste land areas in summer (male, female, brood and pooled) as well as human habitation areas in summer (male, female and pooled) and winter (male) were less abundant than in the reference landscapes.

In pine forests, young thinning stands were more abundant in male and single female summer habitats than in reference landscapes, but advanced thinning stands (males and females) and mature stands (males: significant; females: trend) were less abundant (Table 1). In spruce- or birch-dominated forests, young thinning stands were more abundant in male summer habitats and advanced thinning stands in brood and single female summer habitats. In pine forests, young thinning stands were more abundant in male winter habitats, whereas seedling stands and mature stands were less abundant than in reference landscapes.

3.2 Capercaillie Habitat Use within Tree Diameter Classes

In heath forests the highest relative habitat use was found in the middle-sized diameter classes. In most cases the relative habitat use peaked in slightly larger diameter classes in the winter habitats than in the summer habitats. In peatland forests the relative habitat use was less variable than in heath forests. In the overall landscapes (i.e. all habitat types altogether) the diameter class 0 cm (~ treeless) was less abundant and the diameter class 10.5 cm was more abundant in capercaillie summer habitats than in reference landscapes

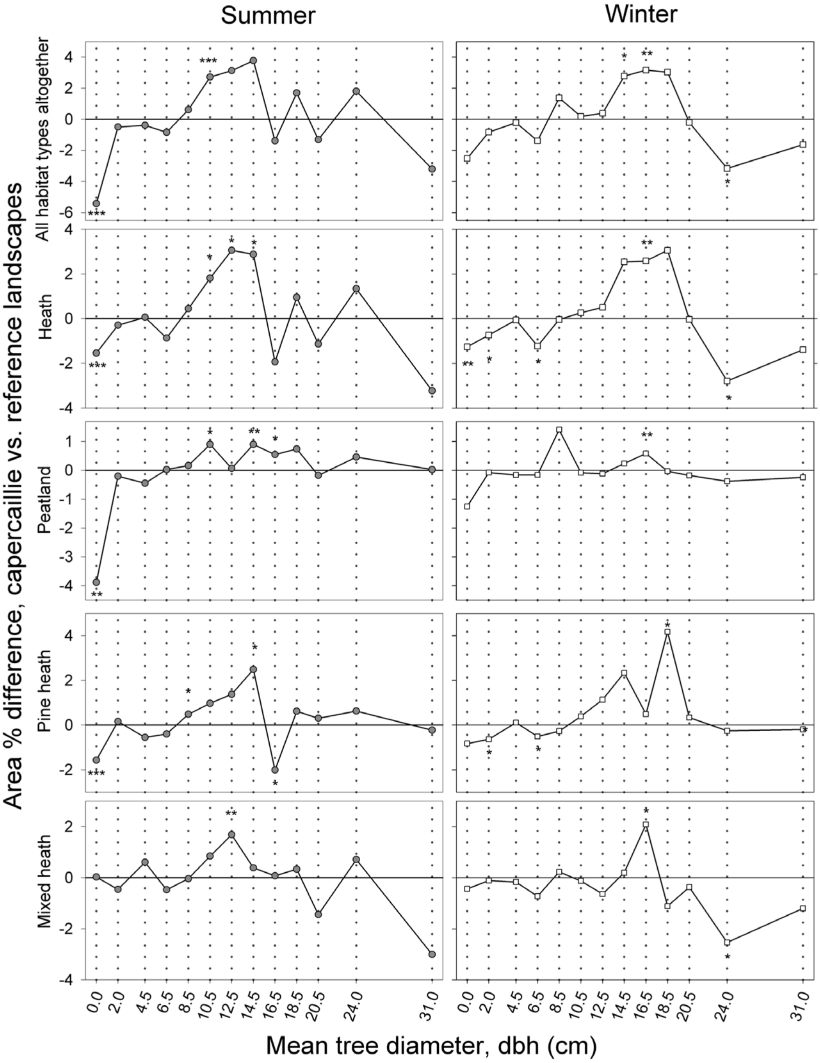

Fig. 4. Relative habitat use of capercaillie (males, single females and broods pooled) at summer in 13 mean tree diameter classes on the left. Respectively, relative habitat use of capercaillie at winter on the right. Statistical significance of differences from Mann-Whitney U-tests: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

(Fig. 4, row 1 left). Respectively, diameter classes 14.5 and 16.5 cm were more abundant and diameter class 24.0 cm was less abundant in the winter habitats (Fig. 4, row 1 right).

In heath forests diameter classes 10.5, 12.5 and 14.5 cm were abundant in the capercaillie summer habitats (Fig. 4, row 2 left). Respectively diameter class 16.5 cm was more abundant and diameter classes 0, 2.0, 6.5 and 24.0 cm were less abundant in the winter habitats (Fig. 4, row 2 right). In peatland forests diameter classes 10.5, 14.5 and 16.5 cm were more abundant and treeless areas were less abundant in the summer habitats (Fig. 4, row 3 left) and diameter class 16.5 cm was more abundant in the winter habitats (Fig. 4, row 3 right). In pine heaths diameter classes 8.5 and 14.5 cm were more abundant and diameter classes 0 and 16.5 cm less abundant in the summer

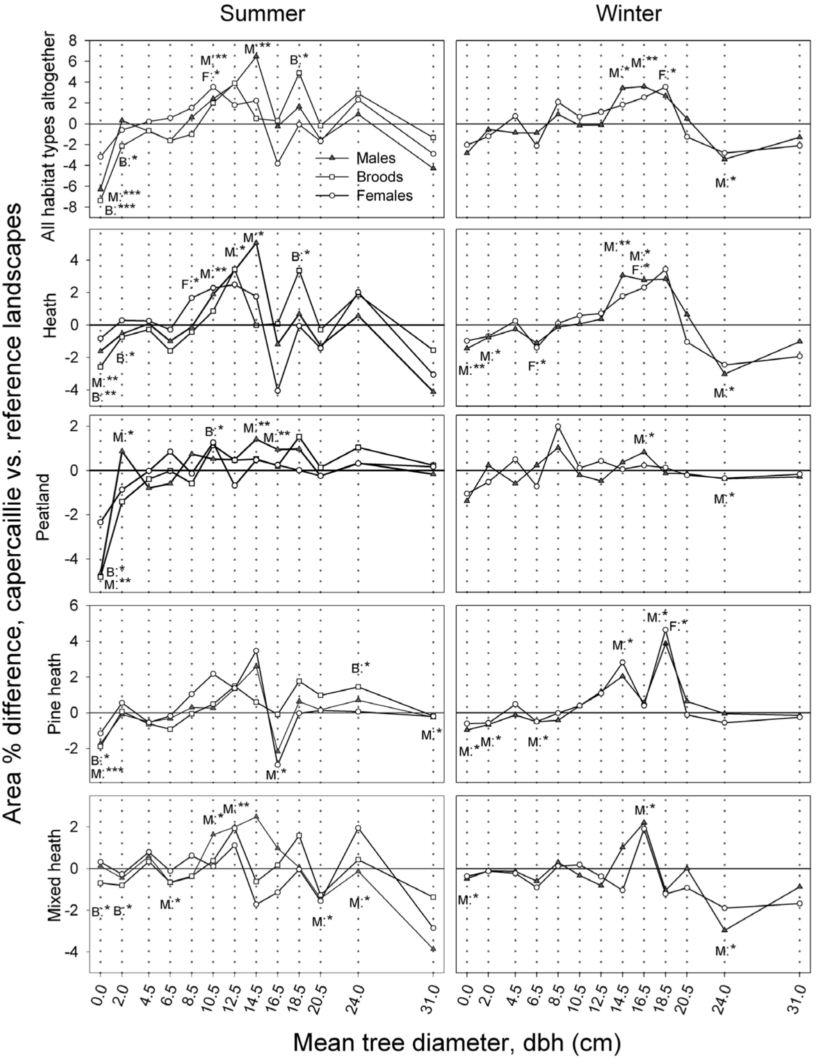

Fig. 5. Relative habitat use of capercaillie males, broods and single females at summer in 13 mean tree diameter classes on the left. Relative habitat use of capercaillie males and females at winter on the right. Statistical significance of differences from Mann-Whitney U-tests: *** = p < 0.001, ** = p < 0.01, * = p < 0.05.

habitats (Fig.4, row 4 left). Respectively diameter class 18.5 cm was more abundant and classes 2.0 and 6.5 cm were less abundant in the capercaillie winter habitats (Fig. 4, row 4 right). In mixed heaths diameter class 12.5 cm was more abundant in the summer habitats (Fig. 4, row 5 left) and diameter class 16.5 cm was more abundant and class 24.0 cm less abundant in the winter habitats (Fig. 4, row 5 right).

In the overall landscapes diameter class 10.5 was more abundant in male and single female summer habitats than in reference landscapes, class 14.5 cm was more abundant in male summer habitats and class 18.5 cm in brood habitats (Fig. 5, row 1 left). Diameter classes 14.5 and 16.5 cm were more abundant in male winter habitats than in the reference landscapes and diameter class 18.5 cm was more abundant in female winter habitats, but the diameter class 24.0 cm was less abundant in the male winter habitats (Fig. 5, row 1 right). In heath forests, peatland forests, pine heaths and mixed heaths males, single females and broods showed relatively similar patterns both within summer (Fig. 5, rows 2–5 left) and winter (Fig. 5, rows 2–5 right).

3.3 Capercaillie Habitat Use within Tree Layer Density Classes

The mean SDI (which represents the tree layer density, and be interpreted as canopy cover at the forests stand scale and as overall forest cover at the larger scales) was 230.68 in the pooled capercaillie habitats and 199.63 in the reference landscapes (Mann-Whitney U-test, $p<0.001$). The difference was found also between reference landscapes and male ($SDI=239.52$, $p<0.001$) and between brood habitats and reference landscapes ($SDI=244.01$, $p<0.001$), but between habitats of single females and reference landscapes ($SDI=211.72$, $p=0.328$) difference was not found.

In heath forests indications of high capercaillie relative habitat use were detected in two highest SDI-classes in the diameter class 10 to 16 cm (Fig. 6), whereas indications of low relative habitat use were found only at low SDI-classes in diameter classes 10 to 16 cm and 17 to 40 cm. In peatland forests indications of high relative habitat use were found at moderate and high SDI-classes in both diameter classes, whereas the only low relative habitat use was detected in the second SDI-class in the diameter class 10 to 16 cm. In heath forests a trend of higher relative habitat use in the diameter class 10 to 16 cm than in the diameter class 17 to 40 cm ($t=1.773$, $p=0.093$) was found, but this was not detected in peatland forests ($t=0.145$, $p=0.886$).

In peatland forests the relative habitat use of capercaillie and SDI were correlated in the pooled capercaillie data when those were studied as functions of stand mean diameter ($r_p=+0.768$, $p=0.002$) (Fig. 7). This was detected in male, single female and brood habitats (all $r_p>+0.592$, $p<0.034$). In heath forests this relationship was not found in the pooled data ($r_p=+0.294$, $p=0.330$), male or single female habitats, whereas in the brood habitats the correlation was found ($r_p=+0.591$, $p=0.033$). In heath forests the relative habitat use of capercaillie was in accord with SDI in small and middle-sized diameter classes, but in large diameters the habitat use was lower than could be expected based on SDI.

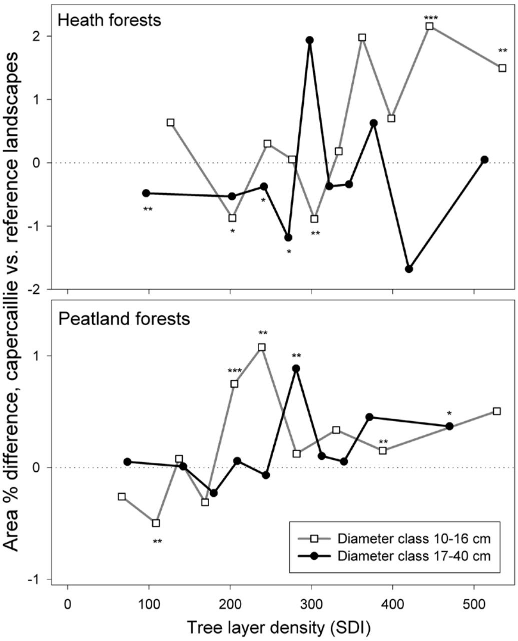

Fig. 6. Relative habitat use of capercaillie within 10 stand density classes in tree diameter classes 10–16 cm and 17–40 cm in heath forest and peatland forest. The asterisks indicate higher or lower class relative abundance in relation to reference landscapes. Statistical significance of differences from Mann-Whitney U-tests: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

4 Discussion

4.1 Characteristics of Capercaillie Habitats

Young thinning stands were more abundant in nearly all types of capercaillie habitat than in the reference landscapes, although in brood habitats ($p<0.14$) and in single female winter habitats ($p<0.09$) this difference showed only a trend. Heath forests were, on average, more abundant in

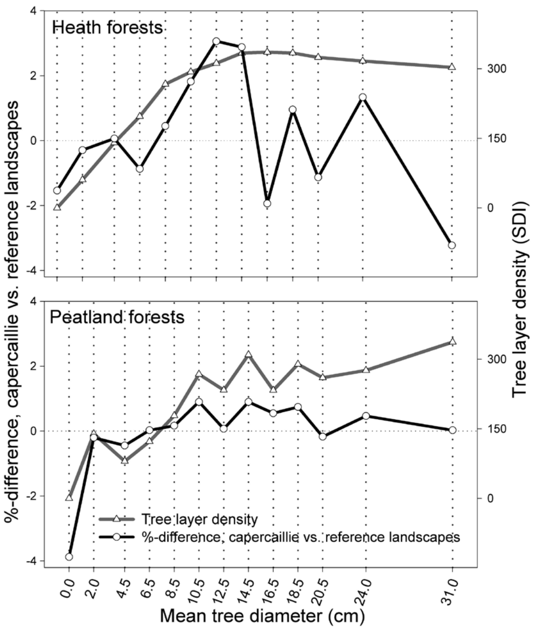

Fig. 7. Mean SDI (Stand Density Index, represents the tree layer density) and relative habitat use of capercaillie as functions of mean tree diameter in heath and peatland forests.

capercaillie habitats than in reference landscapes beginning about from average tree diameter 8 cm. In peatland forests the relative habitat use was quite high even in smaller diameter classes. Based on the forest planning data, a stand commonly reaches mean diameter of 8 cm at the age of 30 to 40 years in the study area. At 8 cm mean diameter SDI – which can be interpreted as canopy cover in stand scale and overall forest cover in larger scales – had almost reached the highest level (see Fig. 7). The age of 30 to 40 years is consistent with the findings of Seiskari (1962), which is slightly lower than Rolstad's (1989) estimate (> 40–50 years). According to findings of Swenson and Angelstam (1993), in turn, capercaillie selects forests 90 years old or older but uses forests 20 year old or older according to their availability. Recently lekking site formations in thinning forests (Rolstad et al. 2007, Valkeajärvi et al. 2007) and positive relationship between thinning stand proportion and capercaillie lekking site surroundings (Miettinen et al 2005) have been detected in the boreal forests. An age of 30 to 40 years corresponds also well with the ending of the capercaillie population decline in Finland in the 1990s (Helle et al. 2003), since the large forest age-classes were clear-cut in the 1950s and 1960s (Leikola 1984).

Our study was representative of state-owned forests in northern Finland, which are commonly quite low in productivity. Therefore our findings cannot be directly applied, for instance, to southern Finland, where for example the average timber volume in older forests is twice as high as in northern Finland (Finnish Statistical…2005). On the other hand, capercaillie density in the 2500 km^2 study units was positively associated with young thinning stand proportion also in the southern and central Finland (Miettinen et al. 2008). Thus relatively young managed forests can obviously provide at least moderately suitable habitats for the capercaillie throughout the country.

In northern Finland the male, brood and pooled capercaillie summer habitats showed higher average overall forest cover than the non-capercaillie, reference landscapes, but the habitats of single females did not show this pattern. The importance of overall forest cover for the capercaillie has been noted in several earlier studies, and it is positively associated with factors such as grouse breeding success (e.g. Wegge and Rolstad 1986, Lindén and Pasanen 1990, Picozzi et al. 1992, Storch 1993, Helle et al. 1994, Helle and Nikula 1996, Kurki et al. 1997, Kurki et al. 2000). Single females, however, are probably somewhat less demanding in their habitat selection than broods or males (Rolstad and Wegge 1990). The relative habitat use of capercaillie was high in densely or moderately stocked forests. Respectively, in all stages of stand development the relative habitat use was quite low in the sparsely stocked stands. This follows the Storch's (1995) expression that forest age or successional stage alone does not guarantee the capercaillie habitat quality; at the forest stand scale species needs moderate or high canopy cover.

A strong positive relationship between old or mature forests and capercaillie abundance or habitat use has traditionally been observed (e.g. Wegge and Rolstad 1986, Lindén and Pasanen 1990, Storch 1993, Helle et al. 1994, Kurki et al.

2000), but in northern Finland capercaillie showed a different pattern in the use of mature forests (see also Seiskari 1962, Miettinen et al. 2005, 2008). In winter habitats the tree species composition could potentially provide an explanation for the low relative use of mature forests. Capercaillie need pine needles for winter food (e.g. Seiskari 1962) and almost 91% of thinning stands were pine-dominated in the study area. But only 50% of mature stands were pine-dominated. The relative habitat use was very low also in mature pine forests, however. This suggests that the tree species composition cannot explain the observed pattern. Probably that explains the capercaillie habitat selection only when the pine proportion is low over larger areas (see e.g. Miettinen et al. 2008). Also e.g. moulting could explain the low abundance of mature forests around capercaillie observations. Rolstad and Wegge (1990) noted that in midsummer (June–July), only broods prefer old forests, but they detected a positive association between males and old forests during all the other months. Thus, in August the species habitat selection should not be exceptional.

The study units were large (200 ha), and thus the broad-scale spatial structure (Legendre et al. 2002) could be the most potential explanation for the low relative use of mature forests. The proportions of mature forests and seedling stands were positively associated in the study material ($r_p = +0.11$, $p = 0.034$, $n = 365$). However, the proportion of young thinning stands was negatively associated with that of seedling stands ($r_p = –0.28$, $p < 0.001$) as well as clear-cut and seed-tree stands ($r_p = –0.32$, $p < 0.001$). Also the proportions of mature and young thinning stand were negatively associated ($r_p = –0.55$, $p < 0.001$). Most landscapes include mature forests, but those rarely contain enough mature forests for capercaillie home ranges (Mykrä et al. 2000). Eventually, small patches of mature forests can become useless for the capercaillie if other suitable patches are not adjoined (e.g. Dunning et al. 1992, Andrén 1994). We performed an a posteriori analysis limited to wildlife triangles in which mature forests mainly formed large patches (>100 ha). Mature forests were abundant in capercaillie habitats (37.9%, $n=21$) and in reference landscapes (34.4%, $n=33$), but the difference was not significant (Mann-Whitney U-test, $Z=–1.172$, $p>0.7$). This suggests that the main reason for the low relative use of mature forests would be found from the forest stand scale.

Habitat overstocking (i.e. too high tree densities) is most likely in productive sites, in young stands and in multicohort stands due to greater (absolute) density of stems. In this study from the north-boreal region clear indication of habitat overstocking was not observed. Overstocking of the capercaillie habitat has been observed in, for example, in the mountainous forests of central Europe. There two-thirds of the pole-stage and older forests as well as multicohort forests have been estimated too dense to be optimal for capercaillie, whereas mature managed forests were selected (Storch 1993). Also in southern Norway signs of capercaillie habitat overstocking have been detected in managed forests (Rolstad 1989, Gjerde 1991). In the south-boreal zone moderate capercaillie densities were found from the multicohort forests (Swenson and Angelstam 1993). In south-boreal forests the suitability of forest for the capercaillie can be relatively constant after a certain threshold in forest development (e.g. Rolstad 1989, Rolstad and Wegge 1990). In the low-productive north-boreal forests, in turn, mature single-cohort forest could be too open for the capercaillie. Instead, younger stages or multicohort tree layer structure – as in the natural old-growth forests – could fit better for the species.

Capercaillie stays most of the time on the ground during the snow-free period (e.g. Seiskari 1962). Therefore, the physical properties of forest stands close to the ground can explain why the young thinning stands were more abundant in capercaillie habitats than in reference landscapes, but mature stands were not. The species avoids open areas where cover from predators is lacking, and dense areas where it cannot escape from predators (Rolstad and Wegge 1990). Small-scale variation in forest density is beneficial (Rolstad and Wegge 1990, Gjerde 1991) because it allows capercaillie to either hide or escape from predators (e.g. Rolstad 1989). Capercaillie may therefore favour forests with mixed tree species (e.g. Helle et al. 1990). The capercaillie is also known to prefer a relatively limited visibility (20–50 m) at lekking sites (Valkeajärvi and Ijäs 1986), and the horizontal cover has been found to be inversely associated with losses of grouse nests (Ludwig 2007). Our findings suggest that capercaillie need two types of cover. Canopy cover (vertical direction) provides protection against avian predators, whereas cover close to the ground (horizontal or intermediate directions) is needed against mammalian predators (e.g. Kvasnes and Storaas 2007).

The understorey cohort was available in forest planning data in 1.1% of the stands (range 0.6–1.6% in the national forest inventories in northern Finland, Kuusela et al. 1986). Small amounts of understorey may not be recorded in the forest planning data, since the greatest weight in forest inventories has been placed on the dominant tree cohort. This 1.1% is also divided between e.g. forests of different ages and soil types. Therefore we did not study directly the effect of tree layer diversity on the capercaillie habitat use. Indirect evidence was available, however. In young forests (young thinning stands) the tree crowns reach close to ground and can provide both canopy cover and cover close to the ground. But in later stages forest management reduces the canopy diversity (e.g. Lilja and Kuuluvainen 2005) and trees are naturally pruned (spruce less than pine or birch). The relative habitat use of capercaillie reduced significantly in large diameter classes in heath forests, but not in peatland forests. In peatland forests the canopy has been found to be more multilayered than in heath forests (Sarkkola et al. 2004, Hotanen et al. 2006). Even though there are probably also other differences between mature heath and peatland forests, this difference suggests that the cover close to the ground would be an important characteristic of the capercaillie habitat.

The effects of first commercial thinning on the capercaillie habitat use may vary depending on the habitat type and season. In heath forests at summer the relative habitat use of adult capercaillie peaked below the average stage of first commercial thinning within the study area (15.9 cm), in tree diameter classes from 8.5 to 14.5 cm. In brood habitats, in turn, it peaked later, in diameter class 18.5 cm. Also in winter habitats or in peatland forests (where the average of mean tree diameter is 14.2 cm after the first commercial thinning) the relative habitat use peaked after the average stage of first commercial thinning, in diameter classes from 14.5 to 18.5 cm. Probably the first commercial thinning reduces the summer habitat quality of capercaillie in a managed north boreal heath forests. But in structurally diverse peatland forests the first commercial thinning or thinning of a seedling stand could even benefit the species by reducing the number of stems. During the winter, in turn, the habitat needs of capercaillie may be slightly different, and at winter they may prefer older forests for other reasons (e.g. stronger branches in feeding trees).

The relative habitat use of capercaillie decreased at the diameter classes of 6.5 cm and 16.5 cm in heath forests. After the thinning of a seedling stand (6.5 cm) the habitat use increased again in the next diameter class, however. This as well as the moderate habitat use increase also after the first commercial thinning suggest the presence of a short-term effect, perhaps due to the presence of cutting residues. Those can restrict grouse movement (specifically the small chicks) or alter the field layer vegetation. Management of residues (collection, piling or breaking) could inhibit the abovementioned effects. The residue piles could also increase the cover on the ground against the predators (Kortland 2006). The possible ecological and economical benefits (e.g. value of residues as an energy source) of the thinning residue management deserve to be studied more closely in the future – and evaluated carefully in comparison to the costs of residue management.

Our findings fit well together with the view that thinnings degrade capercaillie habitats mainly due to the degradation of stand architecture (Lindén et al. 2000). The role of thinning strength is probably substantially low in relation to the effects of degraded stand architecture. Cautious thinnings (low thinning frequency and/or strength) would lead to higher canopy cover, but in unthinned, dense forests the single-cohort tree layer structure becomes probably even more pronounced since the available resources (e.g. light) are not available for the non-dominant cohorts (see e.g. Oliver and Larson 1990). The effects of degraded stand architecture are probably more pronounced in the heath forests, but eventually this concerns also the ditched peatland forests where the canopy diversity first increases over 20 to 30 years (Hotanen et al. 2006), but later becomes more homogeneous (Sarkkola et al. 2004).

The low reproductive output has in most occasions been the main reason behind the population decline of capercaillie (e.g. Moss et al. 2000) and other grouse species. For example the survival of black grouse (*Tetrix tetrix*) adults in Finland has increased since the 1960s, but brood survival has followed an opposite trend (Ludwig 2007). Broods need abundant food within relatively small areas, whereas adult birds can easily move over longer distances to seek food. The bilberry (*Vaccinium myrtillus*) is known as an important field layer dwarf-shrub species for the capercaillie (e.g. Storch 1993). It is an excellent food source and provides cover for the chicks. It also hosts several herbivorous invertebrate species that are an important food source for the small chicks (Storch 1993, Sjöberg 1996, Wegge et al. 2005). Capercaillie breeding success has been found to increase with increasing bilberry cover (Baines et al. 2004), although only in relatively small (< 25%) cover proportions. In Finland the percentage cover of bilberry reaches up to at least 50% (Salemaa 2001, Lakka and Kouki 2009), but it is unknown whether an increase in cover above 25% benefits the capercaillie.

The availability of bilberry berries could explain why the relative habitat use peaked after the first commercial thinning in brood habitats. At August chicks can use the berries, but during the midsummer, which is more critical for their survival, their food resources depend on the coverage of bilberry. Bilberry coverage decreases drastically after a clear-cut, but recovers moderately within a few decades (Salemaa 2001). A high tree layer density limits the cover of bilberry (e.g. Ihalainen et al. 2005), and thinnings as well as other selective cuts should benefit the bilberry due to the increased amount of light (e.g. Atlegrim and Sjöberg 1996). Quite low coverages of bilberry have been found, however, in advanced thinning stands (Lakka and Kouki 2009) and after thinnings (Miina et al. 2009). That could be caused by e.g. thinning residues and logging roads.

The proportion of spruce mires was two- or nearly threefold higher in capercaillie summer habitats than in reference landscapes. This is in accord with the findings of Rolstad (1989) and Wegge et al. (2005), and suggests that spruce mires are specifically suitable capercaillie summer habitats, especially for the broods. Most moderately or densely stocked peatland forests were also more abundant in capercaillie habitats than in reference landscapes. The tree layer diversity may increase their quality as the capercaillie habitats, but moist forests can also provide a good availability of insect food for capercaillie (Stuen and Spidsø 1988). Ditching evidently reduces the reproductive output of grouse, even though the actual mechanisms are still unclear (Ludwig et al. 2008). The ditch restoration has probably the same effect. The restoration, however, may not always be necessary in stocked forests (Sarkkola et al. 2008) if also the thinning strength is kept low. The peatland forests could have a huge potential in the capercaillie habitat management, and therefore it would be important to explore carefully the ecological and economical impacts of the reduced intensity of ditch restorations within different thinning regimes in the peatland forest management.

4.2 Capercaillie Habitat Management in Commercially Managed Finnish Forests

The characteristics of old natural forests, such as large trees and decaying dead trees, are already mimicked in Finnish forest management to provide habitats for invertebrates and woodpeckers, among other species. Capercaillie, in turn, needs bilberry (e.g. Storch 1993) and several types of forest cover. At the landscape scale overall forest cover is crucial for the species (see also e.g. Rolstad and Wegge 1987). At the forest stand scale species obviously needs both canopy cover and cover close to the ground (horizontal cover). The availability of these characteristics in commercially managed forests can be upgraded in many ways. In spruce mires these features are well available, and thus those deserve a special attention. Understorey management, longer rotations and selective cuts are tools, which are available for the forest owners to manage capercaillie habitats in commercial forests.

Understorey management would need only small modifications to the normal forest management practice. The visibility of 20–50 m, which capercaillie is known to prefer at lekking sites (Valkeajärvi and Ijäs 1986), could be used as a coarse goal, but it is also known that the variation in the visibility (cover close to the ground) is beneficial for the species (e.g. Rolstad 1989). If the understorey is thin, as it commonly is in northern Finland and/or low-productive sites, it would be preferable to save whatever is present. If the understorey is very dense, pre-clearings evidently increase the productivity of the first commercial thinning (e.g. Kärhä 2006). However, e.g. <1000 understorey trees/ha, in small groups, can provide suitable cover for the grouse without 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 if the understorey trees are not too old (e.g. > 60 years, Hyppönen et al. 2002). It can also accelerate the start of the next rotation (Aarnio et al. 2002) and therefore also increase the overall forest cover. If the groups of understorey trees could be utilized reasonably in the forest regeneration, even trials of understorey (spruce) planting could be considered for example at capercaillie lekking sites.

Longer rotations would increase the overall forest cover and improve connections between suitable patches (see for example the percolation theory, e.g. Gardner et al. 1987). It is well known that capercaillie habitat management calls for spatial planning to aggregate the suitable patches if the overall forest cover is low (e.g. Rolstad and Wegge 1987). Large-scale spatial planning is challenging in Finland, however, due to the large numbers of small forest holdings. In the most forested landscapes, in turn, reduced management unit size would benefit capercaillie, because that would increase the variation in the habitat types (Rolstad and Wegge 1987). Longer rotations would probably increase also the bilberry availability, which would especially benefit grouse broods (e.g. Baines et al. 2004). The rotation length is, however, tightly connected to economical profitability, which is the main goal of most forests owners (e.g. Karppinen 1998). 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 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 can help to combine the ecological and economical goals of forestry to some degree, 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.

Selectively cut forests (multicohort- or uneven-aged forests) can provide temporally quite stable moderate canopy cover (e.g. Oliver and Larson 1990) and cover close to the ground. Selective cuts don't reduce the amount of insect food for the chicks either as the clear-cuts do (Stuen and Spidsø 1988, Kvasnes and Storaas 2007). Therefore selective cuts can provide a valuable alternative between the single-cohort management and avoidance of all cuts in the multiobjective forestry. In the light of capercaillie habitat management it would be preferable to replace the clear-cuts by selective cuts or use long rotations specifically in spruce mires, which can provide, for example, suitable brood habitats for the species. After all, the multicohort forest management model, where longer and varying rotations are used and most clear-cuts are replaced by selective cuts, partial cuts and group selection methods (e.g. Bergeron et al. 2002, Kuuluvainen 2008), would obviously be consistent with the habitat needs of the capercaillie.

5 Conclusions

Bilberry availability and overall forest cover are well known as characteristics of the capercaillie habitats. At the scale of a forest stand capercaillie obviously needs two types of cover; canopy cover and cover close to the ground (horizontal cover). The managed north-boreal forest attains an appropriate habitat structure for the capercaillie relatively early, within 30 to 40 years. However, our results suggest that the habitat quality is not necessarily guaranteed in the older managed forests in northern Finland due to low cover close to the ground. Understorey management, which necessitates only small changes to today's general forest management practices, can be used to increase this type of cover. In the long term, longer rotations would increase the overall forest cover, improve the connectivity between suitable patches and increase the bilberry cover. Multicohort forest management would, in addition, increase the cover close to the ground. The replacement of clear-cuts by selective cuts or the use long rotations would probably provide the best impact on the capercaillie population in spruce mires, which can provide, for example, plenty of insect food for the small chicks. In future, ecological and economical benefits and costs of thinning residue management and reduced ditch restoration intensity deserve to be studied carefully. Overall forest cover, canopy cover and cover close to the ground deserve to be studied also in relation to the habitat use of other species. This would help to evaluate the role of these forest characteristics in a wider ecological context.

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