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Changes in Landscape-Scale Habitat Selection of Capercaillie (*Tetrao urogallus*) in Managed North-Boreal Forest

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We studied changes in habitat selection of capercaillie in northern Finnish boreal forests at two spatial scales during two time periods, 1989–1992 and 2000–2003. We studied capercaillie densities and their changes between the study periods in relation to the landscape class proportions within 3-km buffer zones around the wildlife triangle center points. Furthermore, we compared the landscape class proportions in 800-meter buffer zones around capercaillie wildlife triangle count observations and around the counted wildlife triangle transects using t-tests and compositional analysis. At the local population scale (3 km) the change in adult density between the study periods was associated positively with the proportion of young thinning stands in 2003 and reversely with the mature stand (1992 and 2003) and clear-cut (1992) proportions. Capercaillie juvenile and pooled densities during 2000–2003 were positively associated with the advanced thinning stand proportion in 2003. At the capercaillie home range scale (800 m) habitats were rich in mature stands during 1989–1992 in relation to available habitats, but not during 2000–2003 when young thinning stands were more abundant in relation to available habitats. Relatively young managed forests can be suitable for capercaillie, but mature managed forests as capercaillie habitats may have deteriorated between the study periods. Spatial planning may help to form suitable areas that are large enough for the species, but the highest potential may lay in the forest stand scale, where increased cover on the ground could promote the habitat quality.

Keywords capercaillie, forestry, landscape composition, wildlife triangle

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1 Introduction

Capercaillie densities have declined remarkably throughout its whole range (e.g. Hjorth 1970, Wegge 1979, Lindén and Rajala 1981, Beshkarev et al. 1995, Catt et al. 1998). In Finland, the density of capercaillie has decreased about 50% from the 1960s to the end of 1980s. However, in the 1990s this decreasing trend has stopped (Helle et al. 2003). Most commonly suggested reasons for the decline are forest management mediated unfavorable changes in forest structure (habitat loss, habitat degradation, forest fragmentation), increased predator populations, excessive hunting, and adverse changes in the climate (e.g. Helle and Helle 1991, Storaas et al. 1999, Kurki et al. 2000, Moss et al. 2001, Storch 2000, Ludwig et al. 2006).

Forest stand and landscape structure has changed considerably in Finland during the 20th century. 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 Scots pine (*Pinus sylvestris*) sowing, using large management units. Especially in northern Finland the clear-cut areas were large, even thousands of hectares (Leikola 1984, Valtanen 1994). Since then, the size of clear-cuts and their annual proportion has decreased to 0.85% of the forest land area. Due to the large regeneration areas the total growing stock volume of the forests first decreased but, since then, it started to increase due to the growth of young forests (see e.g. Finnish Statistical… 1992, 2005, Löfman and Kouki 2001). Also, the drainage of nearly five million hectares of peatland has converted large areas into growing forests. For example, the total growing stock in the 7th national forest inventory (1977–1984: 1.66 billion m^3) was higher than that in the 3rd inventory (1951–1953: 1.54 billion m^3). From the 7th to the 9th inventory (1996–2003) the growing stock volume increased further by 26%, from 1.66 to 2.09 billion m^3, and the overall forest cover (i.e. proportions of young thinning stand, advanced thinning stand and mature stand combined) increased from 34% to 46% of the total area (Finnish Statistical… 1992, 2005).

The importance of old or mature forests for capercaillie has been shown in many studies in Finland (e.g. Helle et al. 1994, Helle and Nikula 1996, Kurki et al. 2000, but see also Seiskari 1962) and elsewhere (e.g. Hjorth 1970, Wegge and Rolstad 1986, Rolstad and Wegge 1989, Picozzi et al. 1992, Swenson and Angelstam 1993, Hjorth 1994, Storch 1997), but relatively young stands have also been considered to be of adequate quality for capercaillie (Rolstad 1989, Rolstad and Wegge 1990, Storch 1993, Rolstad et al. 2007). In Finland, positive relationships between capercaillie and the proportion of thinning forests have been found in recent data, whereas the proportion of mature forests was not related to the number of males at leks (Miettinen et al. 2005) or was even negatively correlated with the capercaillie density (Miettinen et al. 2008). The positive relationship between capercaillie and thinning stands may indicate that the amount of potential suitable habitats for capercaillie is increasing due to growth of ‘the large age classes’ (forests regenerated in the 1950s and 1960s). However, the positive association between capercaillie and mature forests was still found in Northern Finland in data from the 1980s (Helle et al. 1994).

The main questions addressed in this study were: has the capercaillie habitat selection changed between these two periods and if so, how? We studied also, which landscape classes were abundant in capercaillie habitats during the two periods. We selected the years 1989–1992 and 2000–2003 for the study periods, and assessed capercaillie habitat selection in two scales (3 km and 800 m) using Finnish wildlife triangle count data (Lindén et al. 1996) and forest planning data. In the forest planning data areas are divided to relatively uniform stands. The size of a stand is commonly 0.5 to 100 ha, and e.g. soil features and tree layer characteristics are defined for each stand. We discuss the results taking into consideration the species habitat needs and the changes in the landscape structure between the study periods. Finally, we suggest methods for improving the capercaillie habitat quality in commercially managed forests in Finland.

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). The average cover of forest land (mean annual growth of trees >1 m^3 ha^{-1}) is 61.3% of the total area. The landscape is relatively flat, with an altitudinal range mainly between 170 and 400 m a.s.l. Most of the forests are in commercial use and the forest structure has changed considerably during the 20th century due to forest management and other human activities. Based on the statistics for 2003, Scots pine (*Pinus sylvestris*) is the dominant tree species (63.5% in the landscape data). Norway spruce (*Picea abies*) is dominant on 9.6%, and other tree species – mostly birches (*Betula* spp.) – on 2.6%. The rest 24.3% of the total area is treeless. Altogether 10.7% of the area consists of mature stands, 5.4% of advanced thinning stands, 29.7% of young thinning stands, 13.1% of seedling stands and 2.4% of clear-cuts and seed-tree stands. The proportion of scrubland is 15.4%, wasteland 16.8%, water 4.9% and human habitation 1.6% (class definitions in the section 2.3).

Fig. 1. Location of the study area and the studied wildlife triangles.

2.2 Capercaillie Data

The capercaillie data came from wildlife triangle summer censuses made in the years 1989–1992 and 2000–2003. The basic unit of this nation-wide monitoring program is a triangle-shaped transect on forest land, with a 4-km side length (total 12 km) (Helle and Lindström 1991, Linden et al. 1996). The triangles are counted twice a year. The summer counts are done 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 (used in the summer counts) the person in the middle walks along the line and the other two at a 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.

All the 24 wildlife triangles in the study area, which were counted at least twice during both study periods and included more than 80% of state-owned forest within 3 km around the triangle center point were selected to the study. For the capercaillie local population scale analyses (3-km scale) the total number of observed individuals per triangle was referred to as the local population density (ind/km^2), which is further divided to adult and juvenile densities. For the capercaillie home range scale (800-m scale) analyses we selected only the observations that included more than 90% of state-owned forests. The location of each observation was digitized to GIS database together with the information about census year, sex and age. In the 800-m scale 1989–1992 capercaillie data included 119 observations (46 males, 36 broods (female and brood) and 37 single females) and 2000–2003 data 108 observations (49, 24 and 35 observations, respectively). In the capercaillie home range analyses, one observation may include several individuals since broods and flocks were counted as only one observation in order to avoid pseudoreplication.

The detection probability of single adults is about 60% and for broods up to 100% (Brittas and Karlbom 1990), which increases the weight of broods in the pooled data. Adult capercaillie show site-fidelity and an individual may have been observed in consecutive years, which could violate the independency of the observations (Alldredge and Griswold 2006). Some individuals were probably observed during the following years, but their relative proportion in the data is low because in the capercaillie home range scale analyses (800 m) 15 of 119 and 10 of 108 observations located less than 1 km away from an observation of the same sex from previous year. The individuals may also move when the counters approach. This shift, however, is nearly always small (Brittas and Karlbom 1990) and should not affect the results. Even though the habitat selection pattern and density may be related (Fretwell and Lucas 1969, van Horne 1983), the comparison between the two time periods is justified because there was no difference in the density and reproductive success.

2.3 Landscape Data

The landscape data used in the study were forest planning data from Metsähallitus (an enterprise governing state-owned land in Finland), which included about 1 236 000 hectares in 173 800 forest stands, and covered 44% of the whole study area. In 3-km scale the average landscape data cover was 89.4%, whereas in 800-m landscapes surrounding the capercaillie observations it was 98.6%. The rest are private-owned areas, from which landscape data were not available. For those, we assumed a similar landscape composition as in the state-owned forests. Forest planning data field inventories 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 landscape data used in this study correspond to the situation in the beginning of the year 2003. Forests and other cover types were divided into 9 landscape classes (see Finnish Statistical… 2005): 1) mature stands, diameter at breast height (dbh) 24–40 cm), 2) advanced thinning stands (dbh 17–23 cm), 3) young thinning stands (dbh 8–16 cm), 4) seedling stands (young forests: dbh 0–7 cm), 5) clear-cuts (regeneration stage: clear-cuts and seed-tree stands), 6) water, 7) human habitation, 8) waste land and 9) scrubland. Waste land and scrubland are mostly sparsely-stocked mires. On waste land the potential annual increment is below 0.1 $m^3 ha^{-1}$ and on scrubland 0.1–1 $m^3 ha^{-1}$.

The landscape data were transformed to correspond to the time of each capercaillie observation. For the period 2000–2003, clear-cuts were transformed back into mature forest if the forest stand was cut after the capercaillie observation. For the analyses for the period 1989–1992, the growth was also taken into account on forest land if the stand was younger than 100 years. The following transformations were performed: 1) Clear-cuts and 0–6 years old seedling stands were transformed into mature stands, 2) 7–12 years old seedling stands into clear-cuts, 3) young thinning stands, diameter 11 cm or less, into seedling stands, 4) advanced thinning stands, diameter 19 cm or less, into young thinning stands, and 5) mature stands, diameter 23 cm or less, into advanced thinning stands. Metsähallitus forest planning data include the time (year) of all forest operations beginning from the year 2000. In Rovaniemi region (about one third of the study area) the time of forest operations was available already prior to 2000. This information was used to fit the clear-cut transformation for the first study period (1989–1992) as well as possible. In other transformations 3 cm diameter increment during the 11-year time period was assumed based on growth models included in the MOTTI forest growth simulator (Salminen et al. 2005), which is based on wide forest data.

2.4 Statistical Analyses

The capercaillie habitats were studied at two scales. First we studied the correlations between the capercaillie densities and landscape class proportion in the wildlife triangle scale, within 3-km buffer zones around the 24 wildlife triangle center points. We studied if there were differences between the average capercaillie densities between the study periods using paired samples T-test (2-tailed). The principal aim of this approach was to detect the possible changes in the capercaillie habitat selection. Within these landscapes 1) the capercaillie densities, and 2)

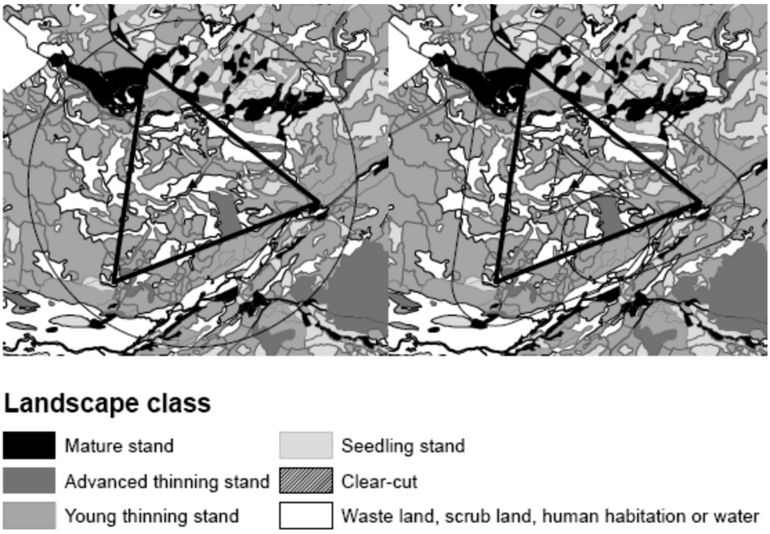

Fig. 2. On the left, wildlife triangle and 3-km radius landscape surrounding the wildlife triangle centre point. On the right, wildlife triangle, 800-meter buffer zone surrounding the wildlife triangle transect and 800 meter landscape surrounding a capercaillie observation. Each side of wildlife triangle is 4 km.

the changes in the mean capercaillie densities between the study periods, were compared with 1) the landscape class proportions in 1992 and 2003 and 2) their changes.

Second, we studied the habitat selection of capercaillie individuals more closely in smaller scale. We compared the landscape class proportions in 800-meter buffer zones around capercaillie wildlife triangle count observations to the available habitats. 800-meter buffer zones around the counted wildlife triangle transects represented the available habitats (Fig. 2). The 800-meter buffer zone (about 200 ha) approximately corresponds to the home range size of capercaillie (Rolstad 1988, Rolstad et al. 1988). One sample T-test (2-tailed) was carried out for the periods 1 and 2 on the pooled capercaillie data and for males, broods and single females separately.

Capercaillie habitat selection can, however, be associated with the large-scale spatial structure and changes in that (see e.g. Legendre 1993, Legendre et al. 2002). For example, within the 3-km scale mature stand proportion was negatively associated with young thinning stand ($r_{p\ 1992} = -0.69$, $p < 0.001$, $n = 24$, $r_{p\ 2003} = -0.61$, $p < 0.01$) and positively with clear-cut proportion ($r_{p\ 1992} = 0.43$, $p < 0.05$, $r_{p\ 2003} = 0.55$, $p < 0.01$) both in 1992 and 2003. Mature stand and seedling stand proportions showed signs of a positive correlation in 1992 ($r_{p\ 1992} = 0.38$, $p = 0.071$, $r_{p\ 2003} = 0.21$, n.s.). The proportion of young thinning stands had a negative relationship with that of clear-cut ($r_{p\ 1992} = -0.58$, $p < 0.01$, $r_{p\ 2003} = -0.65$, $p < 0.001$) and scrub land proportions ($r_{p\ 1992} = -0.42$, $p < 0.05$, $r_{p\ 2003} = -0.43$, $p < 0.05$) in both years, but with seedling stand proportion only in 2003 ($r_{p\ 1992} = -0.02$, n.s., $r_{p\ 2003} = -0.52$, $p < 0.01$). Due to this spatial pattern, we studied the capercaillie habitat selection in 800-m scale also by using compositional analysis (Aebischer et al. 1993) in Compos Analysis 6.2 (Smith 2005). The comparison between t-test results and compositional analysis results enables the evaluation, how the large-scale spatial pattern affects the results. In compositional analysis the significance levels were determined with randomization testing using 1000 iterations. In order to reduce the frequency of observations, where the landscape class proportions were 0, we reduced the amount of landscape classes from 9 to 5 by combining the smallest classes. Class 'Open' included water, human habitation and wasteland areas. 'Scrub' included scrublands, 'CcSeedl' clear-cuts and seedling stands, 'Yothinn' young thinning stands and 'AdMat' advanced thinning stands and mature stands.

3 Results

3.1 Local Population Scale

The mean capercaillie density (4.78 ind. km^{-2}, sd = 3.31 for the former period and 4.31 ind. km^{-2}, sd = 2.54 for the latter), adult density (2.74, sd = 1.78 and 2.49 ind. km^{-2} , sd = 1.75) or juvenile density (2.04, sd = 2.01 and 1.92 ind. km^{-2}, sd = 1.78) did not differ statistically between the study periods (Paired Samples T-test: $t < 0.676$ and $P > 0.505$ in all cases), although within the studied 24 wildlife triangles even large changes were detected (Fig. 3). There was no correlation between the period 1 and 2 densities ($r_p = 0.246$, $p = 0.246$) and the mean brood sizes, 2.73 and 3.26, respectively, did not differ either ($z = -0.822$, $P = 0.411$). The mean proportion of mature stand decreased from 15.9% in year 1992 to 10.6% in year 2003 (Paired Samples T-test: $t = -5.45$, $P < 0.001$). The proportion of advance thinning stands increased from 4.7% to 8.8% ($t = 4.23$, $P < 0.001$) and the proportion of young thinning stands from 31.5% to 34.6% ($t = 2.30$, $P < 0.05$). The mean proportion of seedling stands was 14.2% in 1992 and 12.2% in 2003, but this change was not statistically significant. The clear-cut (2.5%), water (2.5%), human habitation (0.9%), wasteland (11.2%) or scrubland (16.8%) proportions did not change.

The capercaillie local population density, adult density or juvenile density or the changes of those from period 1 to period 2 did not have any significant correlations with water, human habitation, waste land or scrubland proportions. The capercaillie local population density, adult density or juvenile density during period 1 was not significantly correlated with the proportions of landscape classes at year 1992 (Table 1). The capercaillie local population and juvenile densities during period 2 were positively correlated with the advanced thinning stand proportion at year 2003. Even though the correlations were not statistically significant in either study period, the coefficients between adult, juvenile and pooled capercaillie densities were all positive for the mature stand proportion in period 1 and reverse in period 2. For the young thinning stands, the opposite shift was found.

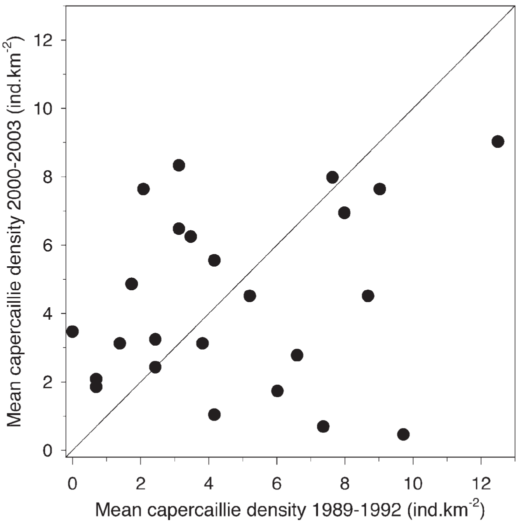

Fig. 3. Mean capercaillie density in each wildlife triangle during 1989–1992 (X-axis) and 2000–2003 (Y-axis). The straight line indicates unchanged mean density between the periods. Below the line density has reduced from 1989–1992 to 2000–2003 and above the line density has increased.

The change of adult density between the study periods was positively correlated with the young thinning stand proportion at year 2003 (Table 1, Fig. 4). The changes of local population density and adult density were negatively correlated with the mature stand proportions at year 1992 and at year 2003, as well as with the clear-cut proportion at year 1992. The changes in local population density ($r_{p\ 1992} = -0.437$, $p = 0.033$, $r_{p\ 2003} = -0.465$, $p = 0.022$) and adult density ($r_{p\ 1992} = -0.502$, $p = 0.012$, $r_{p\ 2003} = -0.592$, $p = 0.002$) were also negatively associated with the combined proportion of mature stands and advanced thinning stands at year 1992 and at year 2003 (Fig. 4). The change of landscape class proportions between 1992 and 2003 did not have any significant cor-

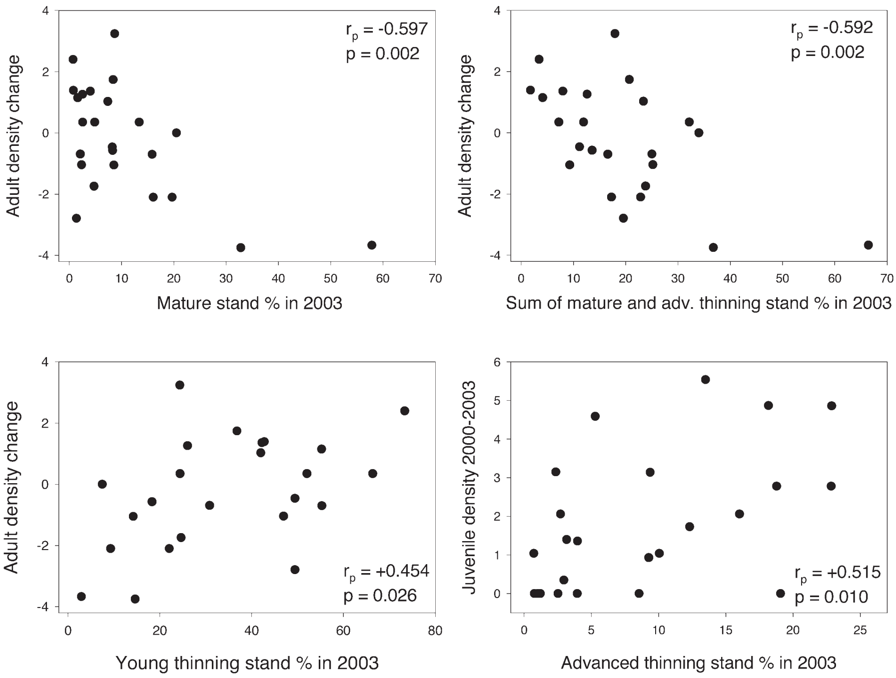

Fig. 4. Capercaillie adult density change or juvenile density in 2000–2003 (Y-axis) and landscape class proportions (X-axis) in 24 studied wildlife triangles. Note the different axis scales.

Table 1. Capercaillie density and density change correlations with the landscape class proportions in the 24 studied wildlife triangles during the two study periods. Statistical significance (Pearson corr.): ** p<0.01, * p<0.05.

		Mature stand	Advanced thinning stand	Young thinning stand	Seedling stand	Clear-cut
			Landscape class proportion at 1992			
Density 1989–1992	Pooled	0.32	0.26	–0.23	–0.12	0.24
	Adult	0.34	0.16	–0.20	–0.19	0.19
	Juvenile	0.23	0.28	–0.21	–0.03	0.22
Density change from 1989–1992 to 2000–2003	Pooled	–0.49*	0.05	0.37	0.25	–0.46*
	Adult	–0.54**	–0.04	0.38	0.36	–0.50*
	Juvenile	–0.30	0.10	0.26	0.09	–0.29
			Landscape class proportion at 2003			
Density 2000–2003	Pooled	–0.31	0.43*	0.23	–0.13	–0.05
	Adult	–0.38	0.14	0.37	–0.10	–0.13
	Juvenile	–0.18	0.52**	0.07	–0.12	0.03
Density change from 1989–1992 to 2000–2003	Pooled	–0.52**	0.03	0.39	–0.07	–0.12
	Adult	–0.60**	–0.08	0.45*	0.00	–0.14
	Juvenile	–0.31	0.10	0.23	–0.10	–0.07

Table 2. Average landscape class proportions (%) in the 800-meter wide belt around the wildlife triangle transects (Available) and in the surroundings of capercaillie observation sites (Used) during 1989–1992 and 2000–2003 in pooled capercaillie data and separately in male, single female and brood data sets. Statistical significance for the difference (one sample T-test): *** p<0.001, ** p<0.01, * p<0.05.

Landscape class	Available	Used				
		Pooled data		Males	Females	Broods
	%	%	p	%	%	%
1989–1992						
Mature stand	15.6	24.5***	<0.001	29.4***	19.8	23.1
Advanced thinning stand	4.9	3.9	0.125	4.9	1.6***	4.9
Young thinning stand	32.3	28.8	0.137	24.8	32.2	30.4
Seedling stand	14.0	12.3	0.162	10.0**	13.9	13.7
Clear-cut	2.2	2.6	0.365	2.4	2.7	2.7
Water	1.8	1.1***	<0.001	1.0**	0.7***	1.5
Human habitation	0.9	0.7***	<0.001	0.7	0.7*	0.5**
Wasteland	11.1	9.5	0.065	8.6	11.7	8.5
Scrubland	17.3	16.5	0.476	18.2	16.5	14.5
2000–2003						
Mature stand	10.3	7.6	0.081	8.6	7.1	6.6
Advanced thinning stand	9.8	10.2	0.768	8.7	7.7	17.0
Young thinning stand	36.6	42.3*	0.021	43.6	41.3	40.9
Seedling stand	11.6	9.9	0.110	9.1	13.9	5.6**
Clear-cut	1.5	0.9**	0.003	0.7**	1.1	1.1
Water	1.9	1.8	0.872	1.3**	2.1	2.6
Human habitation	0.9	0.8	0.806	0.5	1.2	0.9
Wasteland	10.9	9.4	0.119	9.1	10.1	8.8
Scrubland	16.5	16.9	0.782	18.3	15.3	16.3

relations with the changes in local population density, adult density or juvenile density between the study periods.

3.2 Home Range Scale

Mature stands were significantly more abundant in the male and pooled capercaillie habitats than in the available habitats during period 1 (1989–1992), but not during period 2 (2000–2003) (Table 2). However, also the availability of landscape classes changed between periods 1 and 2 following the same pattern as in the larger study scale. Advanced thinning stands were less abundant in relation to availability in single female habitats during period 1, but the proportion of advanced thinning stands was very high in brood habitats (17.0%) in period 2 in relation to available habitats (9.8%). However, this difference was not statistically significant. Young thinning stands were more abundant in pooled capercaillie habitats during period 2, but not during period 1. Seedling stands were less abundant in male habitats during period 1 and in brood habitats during period 2. Clear-cuts were less abundant in male and pooled capercaillie habitats during period 2 and human habitation areas during period 1. Water areas were less abundant in relation to availability in male, female and pooled capercaillie habitats during period 1, and in male habitats during period 2.

Based on compositional analysis (Table 3), classes Scrub (scrubland), AdMat (advanced thinning stands and mature stands) and Open (water, human habitation and wasteland) were statistically significantly preferred over the other landscape classes during period 1 in the pooled capercaillie habitats. During period 2 Yothinn (young thinning stand), Scrub and Open were the most preferred ones. Thus mature stands and

Table 3. Landscape class rank in the surroundings of capercaillie observation sites according to compositional analysis. Period 1 (1989–1992), males: n = 46, single females: n = 37, broods: n = 36 and period 2 (2000–2003), males: n = 49, single females: n = 35, broods n = 24). Sign '>>>' indicates statistically significant difference between classes ($p < 0.05$). AdMat = Advanced thinning stands and mature stands, Yothinn = Young thinning stands, CcSeedl = Clear-cuts and seedling stands, Scrub = Scrubland and Open = Water, wasteland and human habitation.

Type, period	1.	2.	3.	4.	5.
Pooled, 1989–1992	Scrub >	AdMat >	Open >>>	Yothinn >	CcSeedl
Pooled, 2000–2003	Yothinn >	Scrub >	Open >>>	Ccseedl >	AdMat
Male, 1989–1992	Scrub >	AdMat >	Open >>>	Yothinn >	CcSeedl
Male, 2000–2003	Scrub >	Yothinn >	Open >>>	AdMat >	CcSeedl
Female, 1989–1992	Scrub >	Open >	AdMat >	Yothinn >	CcSeedl
Female, 2000–2003	Yothinn >	CcSeedl >	Open >	Scrub >>>	AdMat
Brood, 1989–1992	AdMat >	Scrub >	Open >	CcSeedl >	Yothinn
Brood, 2000–2003	Yothinn >	AdMat >	Open >	Scrub >	CcSeedl

advanced thinning stands were more preferred than young thinning stands during the first period, whereas the opposite was true during the second period. The results of males, single females and broods were not identical, but in all categories the rank of class AdMat reduced and the rank of class Yothinn increased from period 1 to period 2. In the male habitats this change was statistically significant, but in the brood habitats the differences were not statistically significant. In the single female habitats the differences between these classes were not significant during period 1, but during period 2 young thinning stands were more abundant than advanced thinning stands and mature stands.

4 Discussion

4.1 Changes in Habitat Selection Pattern

The association between capercaillie adult density change from study period 1989–1992 to study period 2000–2003 and young thinning stand proportion in 2003 within 3-km buffer zones around wildlife triangle center points was positive. This indicates that the capercaillie summer habitat selection changed considerably between the study periods in northern Finland. Also the reverse associations between the changes of capercaillie adult and pooled densities between the study periods and the mature stand proportion in 1992 and 2003 suggests the same, although the reverse associations based largely on small number of wildlife triangles, where the proportion of mature forests was high. At the capercaillie home range scale (800 m) mature forests were more abundant in relation to their availability in the first study period. This is in agreement with the findings of many earlier studies (e.g. Rolstad 1989, Rolstad and Wegge 1989, Storch 1993, Helle et al. 1994, Kurki et al. 2000). During the second study period young thinning stands were more abundant in the capercaillie habitats than in the available habitats, but mature stands were not.

Also some earlier studies in Fennoscandia have indicated that forests may reach suitable structure for capercaillie already at relatively early successional stage (Winquist 1983, Valkeajärvi and Ijäs 1986, Miettinen et al. 2005, Miettinen et al. 2008). In the terms of forest management young thinning stands are middle-aged forests, and in the terms of forest succession those correspond to single-cohort stands in the stem exclusion stage (e.g. Oliver and Larson 1990). Recently Rolstad et al. (2007) reported about newly established capercaillie leks in young forests (26–46 yrs) in Southern Norway. They put forward two hypotheses to explain these observations. First, capercaillie leks are very traditional and they may persist for several decades in undisturbed areas. Therefore, today's leks in old forest may have been established when the forest was still young. Secondly, modern intensive forestry in Fennoscandia started during the 1950s and 1960s with large clear-cutting programs, and these environments have become suitable for capercaillie just recently. Our results support at least the latter hypothesis.

Scrubland, which is mostly peatland, had relatively high ranks in the results of compositional analysis. Peatland may provide late-summer resources for capercaillie that are not commonly present on heaths, e.g. berries such as cloudberries (*Rubus chamaemorus*) and cranberries (e.g. *Vaccinium microcarpum*). In scrubland the canopy cover is commonly low, but those have a more diverse canopy structure than managed stands due to variation in the soil characteristics (Hotanen et al. 2006). Scrubland stands are also temporally stable because they are not commonly logged. Consequently, scrublands can be beneficial e.g. for the capercaillie lek persistence. However, the proportion of scrubland did not differ between used and available habitats and was not related with the capercaillie density or density change either. Therefore they probably have only a complementary role for capercaillie as Seiskari (1962) has suggested.

4.2 Potential Factors behind the Changes

Mature stand proportion was positively correlated with the proportions of clear-cut and seedling stand, but young thinning stand proportion was in reverse association with the proportions of these classes. This could make mature stands and young thinning stands unequal in the frame of capercaillie habitat selection. At the beginning of modern forestry in the 1950s, vast areas were clear-cut (Leikola 1984, Finnish Statistical... 1992) in a very coarse-grained manner, up to clear-cut size of 18 000 hectares (Valtanen 1994), but later their total amount (Finnish Statistical… 1992, 2005) and size (see e.g. Löfman and Kouki 2001) decreased. At the beginning of 2000s these large clear-cut areas from 1950s were mostly young thinning stands. In a coarse-grained landscape the resources could be aggregated as suitable units for capercaillie also when their proportion is relatively low as the model of Rolstad and Wegge (1987) suggests, but because the remaining mature forest tracts have been cut to smaller units year by year in a fine-grained fashion, many suitable mature forest areas may have become too small for capercaillie (Mykrä et al. 2000).

Another explanation for the lowered rank could be that the mature forests have changed at the capercaillie microhabitat scale (i.e. forest stand scale) between the study periods because this method should filter the intercorrelation effects. The modern forestry started at the beginning of 1950s, and 40 or 50 years is only about half of the common rotation length in the study area. Therefore mature forests at the beginning of 1990s may have been less intensively managed than at the beginning of 2000s. In other words, a higher proportion of mature forests may have earlier had old-growth forest characteristics, i.e. resembled the natural boreal forests, which capercaillie is known to be adapted to (Hjorth 1970). The best mature forests for capercaillie may also have been clear-cut earlier because they were the oldest ones, included lots of merchantable wood and/or located on the most fertile soils.

It has been hypothesized that after certain threshold in forest succession the suitability of forest for capercaillie could be relatively constant e.g. in naturally developed or less intensively managed forests (Rolstad 1989, Rolstad and Wegge 1990). In managed north-boreal forests, however, the suitability of forests may also reduce over time due to management. The forest stand structural diversity is lower in mature managed forests than in near-natural boreal forests or in selectively cut forests in the past (Lilja and Kuuluvainen 2005). Therefore the degraded stand architecture, as suggested by Lindén et al. (2000), could reduce the quality in the capercaillie summer habitats. In the capercaillie winter habitats, in turn, the degraded tree-species composition may reduce the quality (Seiskari 1962). The old-growth boreal forest (i.e. multicohort forest) has been found suitable for capercaillie in the boreal region (e.g. Hjorth 1970, Swenson and Angelstam 1993). In southern Scandinavia and Central Europe thinning stands and multicohort stands are most likely too dense for capercaillie, and mature (single-cohort) forests could therefore provide the best available habitats for the species (Gjerde 1991, Klaus 1991, Storch 1993). In northern Finland mature managed forests could be too open for capercaillie on the ground (at the field layer height), and young thinning stands may have more suitable tree layer structure (canopy cover and cover on the ground) for the species.

4.3 Differences between Adults and Broods

Red fox (*Vulpes vulpes*), which is more abundant in open habitat dominated landscapes, is probably the most important factor limiting the reproductive output of grouse (Kurki et al. 2000). During the second study period seedling stands were less abundant in brood habitats than in available landscapes, which is in agreement with the findings of Kurki et al. (2000) and Wegge et al. (2007), where broods preferred more forested landscapes than females without a brood. But we detected also another difference between the adult birds and broods: the capercaillie juvenile density during period 2000–2003 showed a positive association with advanced thinning stand proportion in 2003, but adult density did not. In Finland both the reproductive output and adult survival of another tetraonid black grouse (*Tetrao tetrix*) have decreased during the latest decades, but recently the adult survival has started to increase (Ludwig 2007). Our finding may represent this pattern: the young thinning stands can provide new or recovering habitats for the adult capercaillie, but this stage of stand development is not (yet) necessarily suitable for the broods.

Bilberry (*Vaccinium myrtillus*) is an important field layer shrub species for capercaillie as a food source and cover for chicks (e.g. Sjöberg 1996). It also hosts several herbivorous invertebrate species that are an important food source for chicks (Storch 1993, Sjöberg 1996, Wegge et al. 2005). Capercaillie breeding success has been found to increase with increasing bilberry cover, but it did not increase further after the cover exceeded 15–20% (Baines et al. 2004). The mean proportional cover of bilberry in the field layer has reduced from 17.6% to 7.7% between 1950s and 1990s in Finland, although the frequency of bilberry has stayed nation-wide as >80% in 100 m^2 study plots (Hotanen et al. 2000). Managed middle-aged forests are commonly dense and their field layer is poor (Vanha-Majamaa and Reinikainen 2000). Thus there could be enough food and cover available for the adult birds in young thinning stands, but not necessarily enough food for the broods.

In the managed Finnish forests at least the oldest (or largest) of young thinning stands are typically ready for the first commercial thinning. In contrast, advanced thinning stands have been normally thinned. The available light in the field layer increases due to thinning, which benefits bilberry and thus leads to increased food availability for the chicks, but promoting the stand structural diversity may also be needed to provide also enough cover on the ground for the species. The understorey can provide places to hide from the predators for chicks and adult birds, but also places where also quite small chicks – with limited ability to fly – can reach to avoid e.g. the red fox. Selectively cut (i.e. multicohort) forests can also provide cover and food for the chicks (Kvasnes and Storaas 2007). Multicohort forest management would also lead to increased overall forest cover at the larger scales.

4.4 Conclusions

The capercaillie habitat selection changed considerably in northern Finland from the beginning of 1990s to beginning of 2000s. Also relatively young managed forests provide generally suitable habitats for the capercaillie, and managed forests can therefore have a high potential as capercaillie habitats. But the results showed also that the relative abundance of mature forests was low in the capercaillie habitats at the beginning of 2000s. Mature forests locate more commonly in unsuitable environment than e.g. young thinning stands, but based on the compositional analysis the habitat quality reduction would take place in the capercaillie microhabitat scale, i.e. within the forest stands. At the forest stand scale, thinnings were obviously the key point in the capercaillie habitat management. The modified thinning methods – aiming to increase tree layer diversity – could lead to millions of hectares of improved habitats for capercaillie and other forest-dwelling species in the boreal forests.

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