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Distribution and structure of Capercaillie (*Tetrao urogallus*) leks in a Scandinavian mountain range area

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Photo by Kjell Sjöberg

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Abstract
The Capercaillie (*Tetrao urogallus*) is distributed along the whole Scandinavian mountain range, but so far few studies exist about habitat selection, reproductive success, survival rate, lek structure and distribution, etc. of Capercaillie in this region. In this study, I searched for Capercaillie leks during the years 2003-2007 in valleys of the Scandinavian Mountain Range near the village of Tärnaby, Västerbotten County. In total, 20 lek sites were discovered, their locations in the landscape described, and the numbers of territorial males at each lek counted. Within the study area, the influence by forestry so far is small, compared to the situation on lower elevations and in more central part of the boreal forest region where most capercaillie studies have been performed. Observation of Capercaillie males in the study area suggests that the distribution of leks and the number of attending Capercaillie males is different than in other parts of Fennnoscandia. The lek sites were typically found in the upper parts of the coniferous forest, in the edge between the spruce and birch vegetation belts, or in forests mixed with Norway spruce (*Picea abies*) and birch (*Betula pubescens* ssp. *Czerepanovii*). The height of the forest varied from 0 to 25 m, but tree height of 10 to 18 m was preferred in areas of the leks. In lower parts of the valley, leks were also found in broader belts of coniferous forest.

Keywords: capercaillie, *Tetrao urogallus*, Scandinavia, mountain range, leks, solitary display, edge zone, juniper

Introduction

The Capercaillie (*Tetrao urogallus*) is a large, dimorphic grouse that is distributed from Scotland to central Siberia and Altai in the east, from 70°N in the north to 40° N in the south. It is not equally distributed within this distribution range. In southern Europe, for example, it is mainly found in mountain regions (Johnsgard 1983, Ahlén and Tjernberg 1996). This big woodland grouse has been characterized as a bird preferring old coniferous forests (Hjort 1994). The species seem to have undergone a general decrease in Sweden during the last decades (Svensson et al. 1999). The most accepted explanation for this is fragmentation of habitats due to modern forestry and management (Storch 2001). For example, clear-cuts become impoverished for several years for this woodland grouse (Gjerde and Wegge 1989).

Spacing is necessary for the survival of a species, but also for fitness and reproductive success (Begon et al. 1999). In birds, males often spread out shorter distances than females, while the opposite is common among mammals, where the females more often stay near the place they are born (natal philopatry, Greenwood 1980). Capercaillie cocks often establish near their natal site (< 4 km), while females often disperse up to 30 km (Koivisto 1963 in Storch 2001). After establishing at a lek at the age of two or three years, territoriality and site fidelity remain strong in adult males (Wegge and Larsen 1987). They are thought to stick to their home range most of the year for the rest of their life. Therefore it is evident that the habitat has to provide at least such fundamental requirements as food and protection even during the harsh period of the year with snow covering the ground and subsequently during a period when some of the food is not available to the birds (Gjerde and Wegge 1989).

A number of mating systems are found in grouse species. Indeed the tetronidae is the group of birds that shows the widest range in mating systems (Höglund and Alatalo 1995). However, it is suggested that other mating systems has evolved from non-lekking arrangements. Many grouse species have both lek mating and non-lek mating populations. The Capercaillie is a polygynous species where males and females only meet at certain sites, display grounds, lek sites or leks, for mating. After establishing at a lek, the males stay within their home range most of the year. In February the male may start their display activity and it normally culminates in the late April or beginning of May. During the entire displaying period, site fidelity is strengthened and the male is seldom far away from the lek site, which normally is situated at the edge of his home range (Hjort 1994, Gjerde and Wegge 1989, Storch 1995a). This lek site is by definition shared by more than one male, and each male has his own home range in connection to the lek (Hjort 1994, Wegge and Larsen 1987).

From studies of very large leks (>25 males), it could be concluded that Capercaillie males have individual territories on the lek, but in their home ranges they demonstrate a social system with a hierarchical organization in such a way that adult males are territorial, regardless of breeding status, when they attend the lek. Off the lek, it is only high ranked males that demonstrate their higher status (Wegge et al. 2005). Leks or display sites are typically consecutive from year to year (Wegge and Larsen 1987).

In winter and spring, including the lekking period, males tend to stay within a 1 km radius of the lek, but outside the lekking period they disperse within a 3 – 4 km radius, sometimes more, during summer. At the end of the winter the Capercaillie often shows a strong preference for small parts (0.1-0.5 ha) of the home range (Gjerde 1990a).

Studies of Capercaillie lek arrangement and spacing have been conducted for example in Russia (Beshkarev et al.1995), Estonia (Viht 1997), Northern Europe (Wegge and Larsen 1987), Central Europe (Storch 1997), Slovakia (Saniga 1996a), the French Pyrenees (Catusse 1993) and Scotland (Picozzi et al. 1992). A more or less even distribution of Capercaillie leks is found in areas with coniferous forests. However, in the highest parts, close to the timberline in the Alps, a different pattern is observed. There the Capercaillie leks are distributed like a string of pearls along the timberline (Hjort 1994). Apparently it is the territorial demands of the male Capercaillie which affects the distance between leks (Gjerde et al. 2000) and consequently leads to an even distribution of leks. Most of the Scandinavian studies of Capercaillie so far are done in the southern boreal forest (Wegge and Larsen 1987). In southern Europe, surveys have focused on capercaillie living in mountain habitat (Catusse 1993, Menoni 1997).

In this thesis I present results from a study of Capercaillie lekking sites in an area almost undisturbed by forestry. Clear-cut felling in recent years has influenced only a few percent of the total area. Most other studies of Capercaillie in Fennoscandia are conducted in areas heavily influences by forestry. In my study area the Capercaillie are thus able to select lekking sites in forests with minor influence by forestry. The forested areas along the Scandinavian Mountain range, with typical vegetation zones dominated by either Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*) in the conifer vegetation belt and birch forests further up along the mountain slopes have not previously been examined with respect to Capercaillie lekking grounds.

Based on the observational knowledge about the structure and distribution of Capercaillie leks in the region (for example that there seem to exist several small leks with only one or two displaying males), one main question in my study has been to find out whether males display solitarily or at communal display grounds. In addition, it is also interesting to document if solitary males choose other display sites than collectively-displaying cocks. Further, the study also includes some documentation of two of the fundamental requirements for survival of Capercaillie in the Scandinavian Mountain Range, i.e. food and shelter.

My hypothesis or prediction is that in the forested valleys of the Scandinavian Mountain Range, the distribution and composition of the Capercaillie leks are more similar to the situation in the European Mountain Ranges like the Alps and Pyrenees Mountains than the situation in the areas in northern Sweden at lower elevations.

Study area

The study was conducted at Boksjödalen (65 40´ N, 15 50` E) situated in the mountain region in the northern part of Sweden, during winters of 2002–2007. The terrain is composed of an elongated valley with relatively moderate slopes. The altitude of the study area is 460 m a.s.l. at the bottom of the valley and the mountains reach altitudes of 800–1400 m a.s.l. The total study area exceeds 7000 ha.

Coniferous forests of Norway spruce dominate ca. 50 % (ca. 3800 ha) of the study area while the remaining ca. 50% is covered with Downy birch (*Betula pubescens* ssp. *Czerepanovii*). The hillsides of the valleys are typically wooded with spruce in the lower parts and birch in the upper parts. Norway spruce reaches 650-700 m a.s.l.. The coniferous

forest limit strongly sinks from the eastern part of the mountain to the western parts and this can be about 200 m (Rune 1974, Sjörs 1956). The birch forest in the mountains may reach 850 m a.s.l.. In the middle part of the study area there is mainly deciduous forest, but with a few larger forest patches (>100 ha) with spruce forest. In the area around Jukksjaure Lake both flat areas and steep hillsides exist. Spruce forests dominate the valley south and west of this lake, but patches of Scots pine are also present. The area north and northwest of Lake Jokksjaure is dominated by birch. In a larger context the study area is situated in the northern boreal zone and the climate is slightly oceanic because of some influence from the Norwegian coast (Ahti et al. 1968).

Figure 1. The habitat at one of the Capercaillie leks (lek no. 19) at the valley of Boksjön, with a multilayer structure of mixed coniferous/deciduous forest. This display site is situated at the edge zone between birch and spruce forest at an altitude of 587 m a.s.l..

Within the birch forests, patches (1-5 ha) of spruce forests are scattered, especially at the lower parts of the valley. However, in some parts of the valley, the birch forest has not yet been invaded by spruce (Sjörs 1956). In the coniferous (spruce) forest, birch is sprinkled and pine also exists sparsely. The deciduous species, Goat willow (*Salix caprea L. ssp. caprea*), Rowan *(Sorbus aucuparia),* Grey alder (*Alnus incana* (L.) Moench var. *borealis)* and willows *(Salix sp.)* are sprinkled over the whole study area. Juniper (*Juniperus communis* ssp. *alpina*) is a common bush-species up in the upper hillsides and in the birch forest. This species seldom reaches 2 m above the ground because the snow will press down the arch-like-growing juniper when the snow depth reaches ca. 1m., and just a few branches will be visible above the snow (Sjörs 1956).

The settlement is alongside the watercourses. There are nine small villages each consisting of one to nine farms. The roads are also situated in the lower parts of the valleys.

In the county of Västerbotten, the coniferous part of the mountain forest is dominated by spruce (Ekman 1987). The spruce forest has been logged for non-commercial purposes to a limited extent before the middle of the 20th century. In the 1940s the possibility to transport

timber to the coastal area was improved when rocks and other obstacles were cleared from watercourses and the timber could be floated in the rivers. This led to increased logging in the conifer forests within the study area (S:son-Wigren and Sandström 2001, Linder 1984). Most logging has been selective, but a few areas were clear-cut and regenerated with pine and spruce. In 1950's about 120 ha were clear-cut and regenerated with coniferous trees, mostly spruce. Today this area is a 50-year old conifer forest, which is situated in the eastern part of my study area, near the village Storskog. Spruce covers 7/10 and pine trees about 2/10 of the regenerated area. Some Larch (*Larix europaea)* was also planted. In the last 25 year, 110 ha of the coniferous forest were clear-cut and approximately the same area was selectively logged.

The acreage of selectively logged areas from the middle of the 20th century is difficult to measure, but such areas are thought to be of minor importance and have been assumed to little affect of Capercaillie distribution since gaps are filled up with new trees (cf. Begon et al. 1999). Later on, selective logging from 1980's and 1990's constitutes ca. 25 ha. In addition there are a few small plantations of pine (>2 ha). The birch-dominated forest is almost only primeval forest.

Most of the Capercaillie leks are situated in private coniferous forests where the hunting pressure is supposed to be quite low, while the areas which were opened for hunting in 1994 is crown land (including the regenerated area of 120 ha mentioned above). The hunting pressure on the crown land is probably higher.

In the mountain-near region as elsewhere in northern Sweden it was a common habit among people to hunt Capercaillie with snares during the first half of the 20th century. Snaring under Capercaillie roosting trees for food was common among the local people. This method was legal for catching all species of grouse in Sweden until the end of 1967 in certain areas (Johansson 2005). One of the many tales about hunting success in older times tells that one young hunter had to use a sledge to transport a catch of Capercaillie home to the house far into the mountain birch forest (Andersson 2003). This story may only be a single event, but might indicate further poaching for food on leks in the deciduous forest in the mountain near forest and at least suggests that considerable harvest of the Capercaillie population was common in the Tärna-district in the early 20th century (Larsson 2003). Overall, at these stories suggest that Capercaillie were at least fairly common in the area at the beginning of the former century (1920-1950).

The most important wintertime predators in Scandinavia are ground predators such as Red fox (*Vulpes vulpes*) and Pine marten (*Martes martes*), and the avian predator Goshawk (*Accipiter gentilis*). Female Capercaillie are in most cases killed by goshawk (Gjerde 1991). Raven *(Corvus corax)* and the Hooded crow *(Corvus corone cornix)* take the young of several woodland grouse.

Methods

Distributions of leks

All behaviour and other signals between individuals of the same species used to show territorial manners and sexual stimulus are called display. Generally there should be at least two males displaying at a traditional site in order to be designated as a lek (Höglund and Alatalo 1995). A display site with only one displaying Capercaillie male should therefore be ignored if using this strict definition. However, not including all displaying males may

risk underestimating the numbers of males at leks and numbers of leks, so all registered lekking grounds were considered as potential active leks in my study (cf. Andreasen 2001). In my study, I have recorded seven solitary displaying Capercaillie males in addition to thirteen display grounds where more than one male attended. These observations of solitary displaying males which night after night visited the same place, strongly suggests that these places ought to be considered leks. The solitary males maintained their display activity during a period of almost three weeks and it was concluded that females visited most of the sites. Thus, for simplicity I use the term lek for both display grounds with solitary, site-tenacious males and display grounds with two or more collectively displaying males with an inter-male distance of less than 100 m (cf. Rolstad and Wegge 1987, Andreasen 2001).

Grouse droppings are of two kinds: caecal droppings and woody (intestinal) droppings. The former are fluid and excreted once or twice a day. The latter are sausage-like with high dry matter content during the winter season (Gjerde 1990b). Trees with caecal droppings from cocks on the snow (Fig. 10) in the late winter and spring are the most markers to find Capercaillie display sites. The sex of the bird that had used a certain tree or walked on the snow was determined from size of the droppings. Gjerde (1990b) found that male droppings had a mean diameter of 11.0 mm and those of females 8.7 mm and stated that droppings larger than 9.8 mm should be classified as males.

Display sites were identified in three ways:
(a) Conifer (spruce) and deciduous (birch) forests were searched for tracks of Capercaillie, mainly during March and April. Tracks and other supplementary information, like roosting trees with droppings, feathers from Capercaillie or flushing birds were marked on a GPS

Figure 2. A Capercaillie lek site at the valley of Boksjön dominated by 50-year old birch forest with some scattered spruce trees. The display site is situated at the edge between the birch and the spruce forest.

(Global Position System). These positions were transferred to a map. Aggregations of the plots may indicate where display activity can be expected.

(b) Potential areas were systematically searched during the time for morning displays. Places where leks were thought to be possible were visited and checked by listening for sounds from Capercaillie cocks. Several of the potential sites were visited more than ten times in the search for display activities. At a few leks I heard one displaying male but afterwards I have flushed 2 and 3 males.

(c) Field-checking information from local sources. The villagers in my study area and nearby regions were asked for information about presence of Capercaillie lek sites. The information given was later checked in the field.

Lekking habitat and altitudes

After a lek site was found, (i) the type of environment in the locality, (ii) the arrangement of tree species, (iii) age composition of the stand within a circle of 100 m of the display site were determined. Age composition of the lek environment has been divided into (i) multi-layered forests or (ii) trees of the same age (mono-layered or plantations either with one tree species or overgrown stand).

Classifications of forests were made in four types; 1) coniferous, 2) deciduous, 3) mixed forest with both coniferous and deciduous trees and 4) the edge zone between coniferous and deciduous forest. Great parts of coniferous forest contain deciduous trees and conversely the birch forests partly hold some spruce trees at lower elevations. An edge zone can be either the transition from coniferous forest to deciduous forest (this is almost always the case at higher altitudes) or at coniferous patches surrounded by deciduous forest.

Altitudes were determined with a GPS. Slopes, plain ground, ridges or depressions for the lekking ground were visibly observed.

Numbers of Capercaillie males at leks

As I have not had possibility to investigate all lekking sites by myself at the best time of the lekking season the same year, I have included other observations, mainly tracks and other signs in the snow pointing out in one direction from the lek site (Hjort 1994). This revealed that several of the lek sites were attended by just one male.

All observations in vicinity of leks, i.e. (a) numbers of singing males, (b) flushed cocks and (c) tracks in sectors radial out from leks (Hjort 1994, Wegge and Larsen 1987), were considered to estimate numbers of males. Lek number 8, situated in a plantation, was just counted by the methods (a) and (b), since it is seldom possible to see more than one or two males due to the dense vegetation.

There is some uncertainty about the numbers of males at some of the Capercaillie leks studied. Several of the records are estimated from other sources than direct observations of birds on the leks. There is also some uncertainty about what period the leks were visited by males, i.e. if the counting of the number of males was carried out during the peak of the lek or not (c.f. Andreassen 2001). For that reason, in this study I regard the margin of error to be plus or minus one male; in the leks with 4-6 males it could be plus or minus two males.

Numbers of Capercaillie females at leks

Numbers of females at Capercaillie leks vary even more than males. They often sit in trees and are hard to count at the lek, but in such situations they sometimes cackle and thereby reveal their presence (Fig. 3). Normally, however, the presence of females was established by visible observations or by listening, observing tracks or by observing specific tracks the males show when females are present, e.g. tracks when the male has been circling many rounds on the same spot but or tracks from “fluttering jumps” of the male (Dahl 2005).

Figure 3. A Capercaillie female visiting a capercaillie lek in a mountain birch forest. *Photo by Kjell Sjöberg*

Winter foraging and roosting behavior

In the birch forest or the mixed deciduous/coniferous area, the Capercaillie is obliged to use food from trees and scrubs accessible above the snow surface in his home range. The preferred species during winter are, pine, spruce, juniper and birch. The birch forest and the upper parts of the spruce forest round two of the leks sites (leks. no. 4, 14) were searched for tracks and signs from Capercaillie during midwinter. When tracks were found I followed them to find out what activities there had been performed there. Feeding and roosting behavior was examined.

Feeding activity is detected by tracks close to either trees or shrubs. The tips of the branches reveal cutting marks on the needles. Straight bite marks often in > 45° angles to the branch are found in spruce and juniper. Often there are dropped needles with bite marks and droppings present on the snow surface.

Length of the tracks were measured, what kind of foods, and piles of droppings were recorded. Sex of the bird was determined by size of the droppings (see above). If there were found burrows in the snow, they were examined if they contained caecal droppings or just

woody droppings from the Capercaillie. If just woody droppings where found I considered as the roosting place were used this for daytime-roosting; if caecal droppings also were found I considered as a night roosting place. Trees around the landing place were examined as regards to fresh droppings from Capercaillie to see if there had been night roost. If snow-burrows were found the temperature for the present period was obtained from the local SMHI measuring station.

Foraging on birch buds and catkins is only possible to detect when such foraging is done from the ground and snow conditions reveal Capercaillie tracks (Fig. 9), dropped needles or bite marks on tips of birch branches. This type of feeding activity presupposes that the branches can be reached by the bird and this normally only occurs when birches have been bent or broken down.

Results

During the main mating period in the years 2003, 2004, 2005, 2006 and 2007, I found Capercaillie leks at 15 different places, which together with 5 earlier known lek sites, in total makes 20 leks. All lekking sites were treated as leks since all visited leks showed 1) wing draw marks in the snow from Capercaillie at several times and /or 2) Capercaillie song were heard at sites that showed several tracks from male night roosting in sites adjacent to the lek the days before the lekking period culminates.

Distributions of leks

The display sites were evenly distributed in the study area (Fig. 4). The display sites were the same in consecutive years. When agriculture and other unsuitable areas are excluded (for example deciduous forests with few or no junipers, or steep slopes), the Capercaillie leks were regularly spaced and the distance between the display sites varied from 1.0 km to 4.2 km (Table 1).

An example of an attempt of a male Capercaillie to settle in a vacant area (ca. 20 ha) between two display sites in order to colonize a patch with sparse spruce forest was observed in 2003. I found a numbers of tracks where one male had been. However, I was not able to find out if this male were displaying on this patch or not (I had not developed the listening technique at that time), and the next year no males were found in this area.

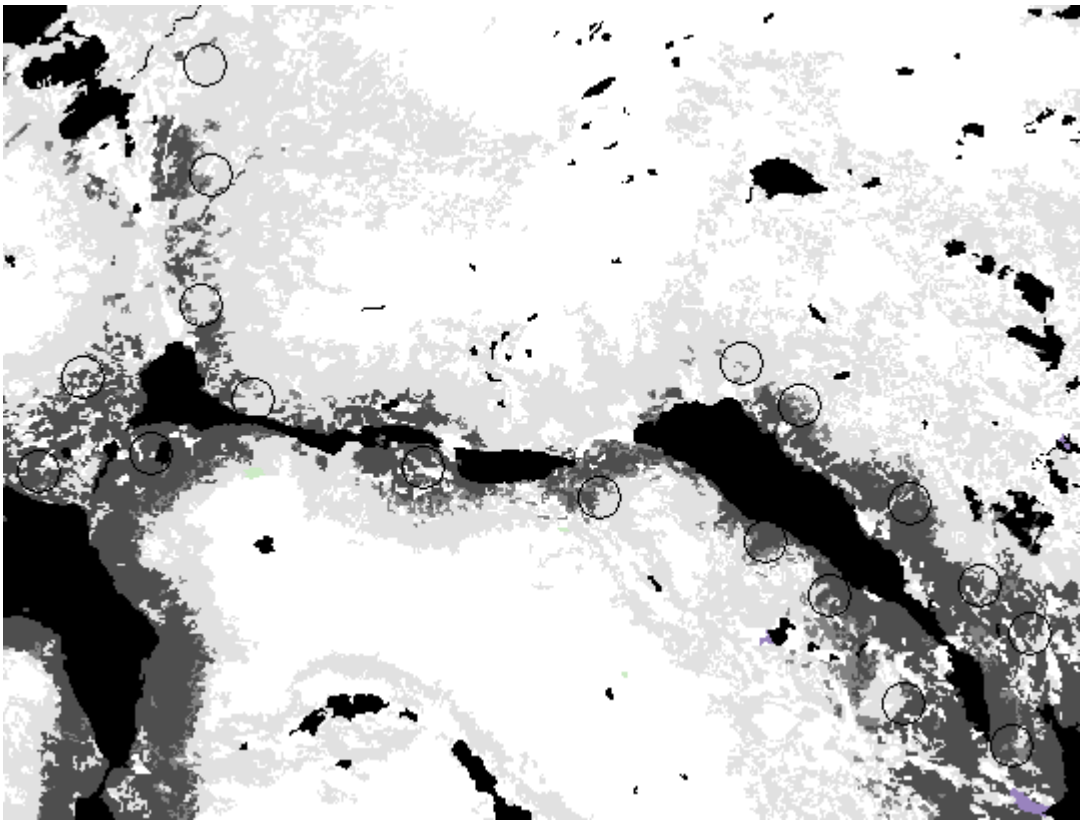

Figure 4. Map of Capercaillie display sites in the valley of Boksjön –Jukksjaure –Björkbacken. Black= water; dark gray= coniferous forest; middle gray= mixed forest; light gray= deciduous forest; white areas–treeless areas.

Table 1. Minimum distance in km between adjacent Capercaillie leks in the mountain forest in Björkbackenvalley of Boksjön in northern Sweden. *Distance between two leks across a lake.

1																				
2																				
3		2,3																		
4																				
5																				
6			2,6		2,1															
7			4,2																	
8																				
9								1,4												
10									1,0											
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12	2,5	2,6																		
13		3,3			2,2	2,6														
14				1,8							3,3									
15							3,7													
16															3,7					
17											2,7*					1,8				
18																	2,9			
19									2,4									2,5		
20																		2,9	2,3	
Lek no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

Lekking habitats and lekking site altitudes

Eighteen Capercaillie leks were situated in old forest and two in two different 50-year old coniferous plantations (Table 2). Fourteen of the leks were in the edge zone between spruce and birch forest; four of these was located in spruce patches in the birch forest (Table 2, leks no. 1–4). Seven leks were situated in the coniferous forest (Table 2, leks no. 5-11). Of these, two were placed next to narrow parts of bogs (Table 2, leks no. 6-7), three next to roads (Table 2, leks no. 5, 9 and 10) and one lek in a dense, 50-year old, pine plantation (Table 2, lek no. 8). The last lek was situated in a forest dominated by coniferous trees, in an edge zone between spruce forest and an approximately 50-year old rejuvenation of spruce, which not yet had been cleared.

Table 2. Capercaillie lek habitat in mountain forest in Björkbacken valley of Boksjön, in northern Sweden. Main tree species, estimated age, edge-zone at the centre of the display site are shown. Displays adjacent to roads are marked with *.

Lek no. and Name	Altitude	Main Forest	Multi-layered	Age	Edge-zone between deciduous/coniferous
Birch forest					
1 Björkbacken	600	Birch	X	>80	X
2 Videgård	590	Birch	X	>80	X
3 Leksnäs*	520	Birch	X	>80	X
4 Granlund	600	Birch	X	≈50	X
Mixed coniferous forest					
5 Forsbäck*	520	Mixed Conifer	X	>80	
6 Jokksjaure	500	Mixed Conifer	X	>80	
7 Mellansjö	520	Mixed Conifer	X	>80	
8 Laukabäcken	580	Spruce/Pine		≈50	
9 Storskog södra*	560	Spruce	X	>80	
10 Storskog östra*	540	Spruce	X	>80	
11 Oltokkskiftet	580	Spruce	X	>80	X
Mixed Decidious/Coniferous forest					
12 Fansen	600	Spruce/Birch	X	>80	X
13 Västervik	600	Spruce/Birch	X	>80	X
14 Nils-Eriksberget	620	Spruce/Birch	X	>80	X
15 Raukshobben	580	Spruce/Birch	X	>80	X
16 Lasses hobben	560	Spruce/Birch	X	>80	X
17 Tj-länning	580	Spruce/Birch	X	>80	X
18 Lovovardo	620	Spruce/Birch	X	>80	X
19 Måratshobben	580	Spruce/Birch	X	>80	X
20 Granhobben	580	Spruce/Birch	X	>80	X

The leks in the deciduous forest (Fig. 2, Table 2, leks no. 1-4), were situated in groves (>2ha) of spruce trees. Sixty percent of the leks were situated in the upper parts of the hillsides (Fig. 8). A combination of smooth terrain and old forest is frequently chosen (Fig. 5, 6, 7 and Table 2). The spruce trees could be 15–20 m tall at maximum and deciduous trees could reach 10-12 m. The general height of the canopy is approx. 10-12 m (Fig. 5, 6, 7). The forest at the lek sites is generally old, multilayered and relatively open, so visibility in some directions may exceed 70 m. The tree density (trees > 3 m tall) in the core areas of the lek sites is between 500 and 800 trees/ha (Fig. 5, 6 and 7). All Capercaillie leks but two were situated in old forest (Table 2, > 80 year) and most of them were situated in or in connection with spruce forest. Most of their territories (arenas or display areas) are situated in the coniferous forest.

One of the leks (Table 2, lek no. 8) was situated in a plantation (≈ 50-year-old) of Scots pine with small open areas. The plantation is not yet cleared, and thus the distance visible at the ground

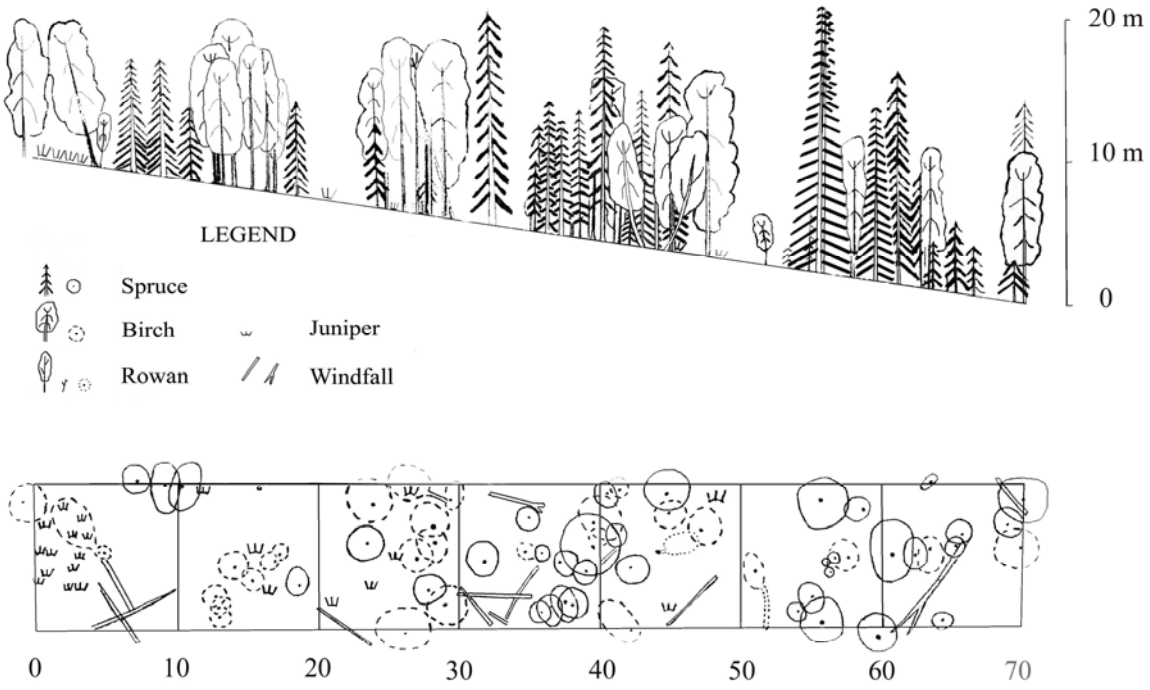

Figure 5. Forest stand structure in a Capercaillie display site (lek no. 14) in mixed deciduous and coniferous forest 620 m a.s.l.. The lek was situated at a relatively high altitude with rather thin spruce stand in a south-west location.

level was normally less than 30 m. With exception of this lek in the plantation, most of the solitary males sang in zones with mixed stands of birch and spruce.

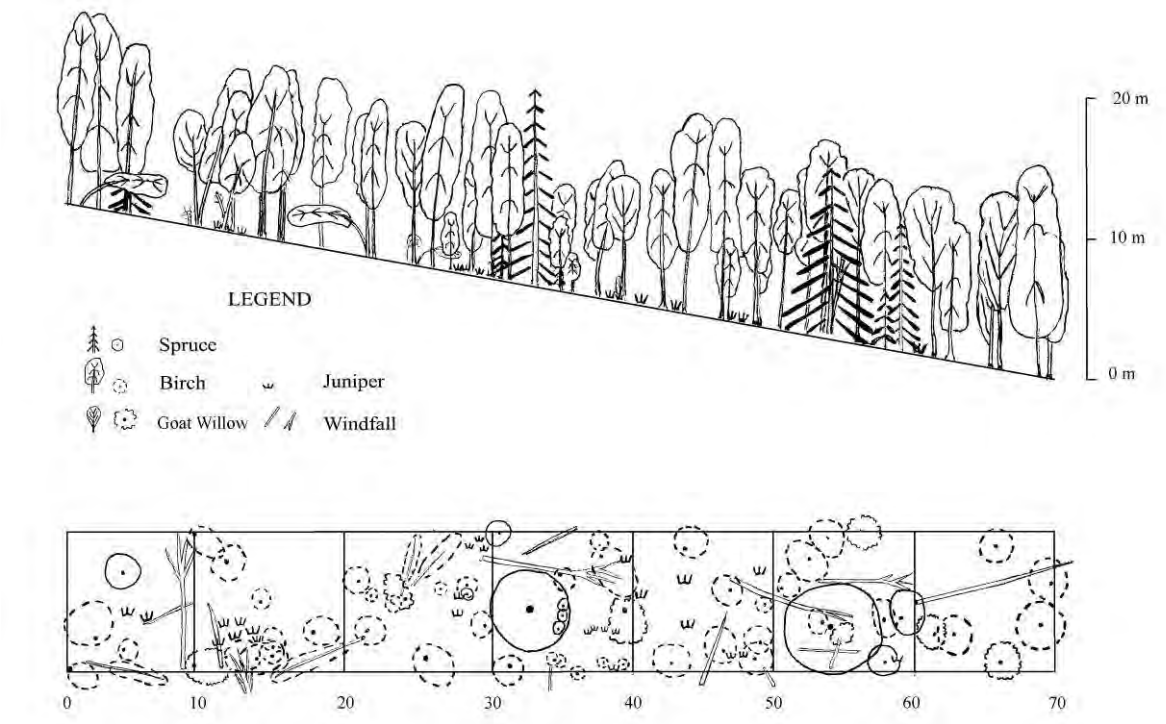

Figure 6. Forest stand structure in Capercaillie display site (lek no. 2) situated in a mixed deciduous and coniferous forest at 590 m a.s.l.. The lek was completely surrounded by birch forest in a south-west location.

The snow depth at the time of the mating period (2003) reached 60 cm at leks at higher elevations, while it is more moderate, ca. 30 cm, at the lower parts of the valleys. Two of the sites are located in the low terrain.

In the spring 2003 there were two display sites at Tängvattnet situated in pure birch forest (these leks, situated ca. 50 km westward of my study area), are not included in Table 3 with displaying males. I visited one of these display sites and found caecal droppings from one Capercaillie male below the trees. At the other site, one cock showed aggressiveness towards people. This male was for one or another reason killed in the next year and was found dead near a snowmobile track (Stabbfors 2004).

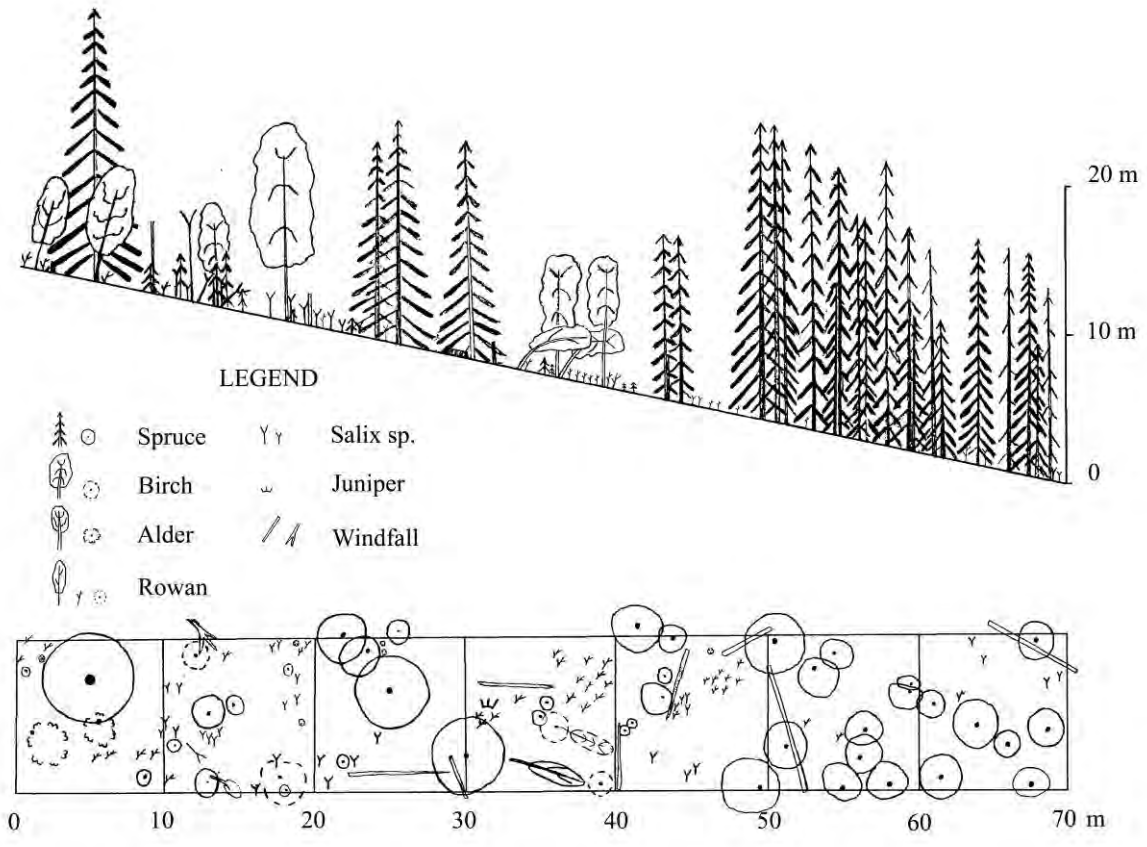

Figure 7. Forest stand structure at a Capercaillie display site situated in mixed deciduous and coniferous forest at 570 m a.s.l. (lek no. 17). In the lower parts of the capercaillie home range the spruce forest was comparatively denser.

Numbers of male Capercaillies at the display sites

The average number of territorial Capercaillie cocks is approximately 2 cocks per lek (Table 3). However, the number of males at a lek varies from year to year. At lek no. 8 with 5-6 males in 2005, I could only hear 3 males the next year. Ten of the leks had 2-3 males and seven of these lekking sites were just visited by one male, or showed tracks from just one displaying male (Table 3).

One morning during the lekking period in 2004 there were two displaying males and two other, obviously very young males (as indicated by their immature plumage). The latter tried to display but were chased away by the older males.

In total, there are approximately 30-35 territorial males in the study area (Table 1), which consists of >70 km^2. This gives a density of 1 male per square kilometre coniferous forest.

Table 3. The number of Capercaillie males at display sites in the study area along the valley of Boksjön and at Björkbacken, close to the valley. * indicates that the lek was not yet found or not visited during a particular year.

Lek no. and Name	Numbers of males			
	2003	2004	2005	2006
1 Björkbacken	1	1	0	*
2 Videgård	*	*	1	*
3 Leksnäs	1-2	2	1	1
4 Granlund	2	3	3	2
5 Forsbäck	2	*	2	*
6 Jokksjaure	3	*	3	*
7 Mellansjö	2-3	*	3	>1
8 Laukabäcken	*	*	5-6	>3
9 Storskog södra	2	2	1	1
10 Storskog östra	*	*	*	1
11 Oltokkskiftet	2-3	*	1-2	*
12 Fansen	3	*	*	*
13 Västervik	1	*	1	*
14 Nils-Eriksberget	1-2	2	1	*
15 Raukshobben	1-2	*	*	2
16 Lasses hobben	1	*	1	*
17 Björkbacka-skiftet	2-3	*	2	*
18 Lovovardo	1	*	1	1
19 Måratshobben	*	*	*	>1
20 Granhobben	*	*	*	2

Numbers of female Capercaillies at display sites.

Most of the lek sites I have visited were also visited by one or more Capercaillie females (Table 4). At one lek site (lek no. 9), I have twice (2003 and 2005) seen one single cock displaying with 11 and 13 hens present.

Winter foraging

In my study juniper and spruce were important food sources. Areas with natural and plantations of pine tree may be more attractive, but spruce is the most abundant green food for Capercaillie in the winter. Several males associated with the mountain forest leks used home ranges in birch forest during midwinter, when juniper needles are available as food due to appropriate snow conditions, i.e. at moderate snow depth, < 60 – 80 cm. Heavy snowfall did not prevent birds from visiting areas with juniper as long as the food was available above the snow surface. I have flushed males foraging from juniper bushes in 25 cm fresh snow. The most frequent activities when male Capercaillie are visiting birch forests seems to be foraging in patches with juniper bushes and sparse spruce, combined with roosting under spruce trees or in snow burrows. The cocks regularly walk distances of 40 to 80 meters on the snow surface; sometimes the tracks on the snow could trips may exceed 150 m. In the birch forest, there were almost always one or several spruce trees visible from the place where the Capercaillie has landed on the snow. From late autumn (November) I observed tracks from a male Capercaillie in a section of the birch forest about 650-750 m from one of the lek sites (lek no. 4). I have been visiting this spot of 5-6 ha during the winter seasons 2003/2004, 2004/2005, 2005/2006 and 2006/2007. The pattern of using habitats with juniper bushes culminates in midwinter if this source of food is still available above the snow surface at that time. During the first winter, 2003/2004 only tracks from one male (at the time) were found. The same was the case during the next

winter. I found males visiting such habitats 5 or 6 times during periods when snow covers the grounds (October–April 2003/2004, 2004/2005), which corresponds to in average 1.5 times per month.

Table 4. The number of Capercaillie females at display sites in the study area along the valley of Boksjön and at Björkbacken (close to the valley) a particular year. V=visible, T=tracks of females, L=listening, mti= male tracks indicate females has been present, f= Numbers of females Date of observation: e.g. 8/5= May 8.
* indicates that the lek was not yet found or not visited during the actual year.

Lek no. and Name	2003	2004	2005	2006
1 Björkbacken	V, 2 f, date 8/5	*	*	*
2 Videgård	*	*	V	V, 2 f, 7/5
3 Leksnäs	V	V, 4 f, 3/5	V	V, >2 f
4 Granlund	V	L	L	L, 2 f
5 Forsbäck	*	*	*	*
6 Jokksjaure	*	*	V, 3 f. 5/5	*
7 Mellansjö	V	*	L, 28/4	*
8 Laukabäcken	*	*	V, >10, f. 8/5	*
9 Storskog södra	V, 10 f, 8/5	V	V, 13 f, 8/5	V, 4/5
10 Storskog östra	*	V, 5/5	V	V
11 Oltokkskiftet	*	*	V	*
12 Fansen	*	*	*	*
13 Västervik	*	*	*	*
14 Nils-Eriksberget	T, 1 f, 2/5	V	*	*
15 Raukshobben	*	*	*	
16 Lasses hobben	mti	*	L, 24/4	*
17 Björkbacka-skiftet	*	*	L, 25/4	*
18 Lovovardo	mti	*	*	*
19 Måratshobben	*	*	*	V, 1 f, 18/4
20 Granhobben	*	*	*	*

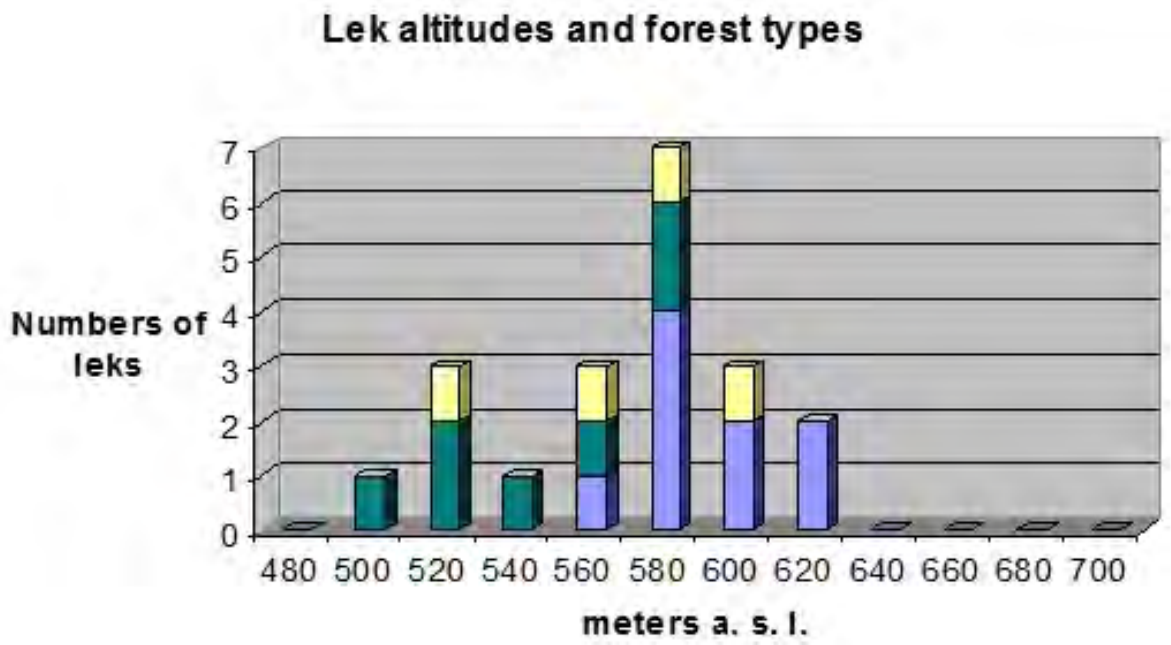

Figure 8. Distribution of Capercaillie lek site altitudes in Boksjödalen-Jukksjaur. Dark green= conifer dominated forest; yellow=deciduous (birch) dominated forest; blue/grey= mixed deciduous/conifer forest.

Figure 9. Tracks of a Capercaillie male that has been foraging from birch branches.

In the third winter (2005/2006), at least two males used this habitat. Near lek no. 4, the specific grove (ca 20 x 25 m) with juniper bushes mentioned above, was visited 6 times in a period of three weeks. In general the localities used always had one or several spruce trees in sight. These records were made on fresh snow on 4 occasions. In the fourth year the visits by the males disappeared when access to juniper needles in the area ceased due to deep snow cover in the early part that winter. In the lower part of this area there are more spruce trees and I estimate that more than half of the food is spruce needles and the rest is juniper. However, at the specific juniper groove in the upper part of the area, juniper constituted 100% of the food.

Birch trees have plenty of buds and are also rich in catkins, but the flexible branches of the trees do not allow the heavy males to forage in the canopy of the trees. However, when treetops of birch are bent down due to snow and ice or split by storms the buds do become available. During the winter 2006-2007, birch tops were torn down at some spots and thus available for foraging males (Fig. 9).

Roosting

In the mountain region daytime roosting of Capercaillie is done either on the ground or in trees. When snow conditions permits, roosting in snow burrows occur during nighttime. Piles of droppings under spruce trees, near the base of the tree or close to it, reveal the most common type of roost during daytime. In one case the male had roosted outside lower branches, possibly because the lower branches were too dense to creep under the big spruce. He had continued to walk 1 meter along the lower branches and then turned back, finally roosting on the snow outside the branches. If snow conditions are suitable for the capercaillie to dig burrows, males seem to use this behavior for roosting on the ground. This is often done in connection with feeding by walking on the snow cover. Most of these snow roosting (n=9) were noticed close to juniper shrubs or a few meters away from the

feeding place. In one of these burrows I found caecal droppings and concluded that the male had stayed there for the night. During January and February daytime roosting in snow burrows were assumed to take place between 10.15 AM and 14.15 PM with regard to day roost (the snow burrows did not contain caecal droppings). I have also observed that males after eating needles from the upper branches in a spruce tree had landed in the snow close to the feeding tree. Thereafter they dug a burrow in the snow. In these latter cases I did not find caecal droppings in the snow-burrows so I classify them as daytime roosting. In one case of roost in snow-burrows the temperature was approximately -29 C°, in all other observations of digging snow-burrows the temperature were in between -3 and -12°C.

If the birds are feeding in deciduous forest with large distances between spruce trees, heaps of droppings can be found under deciduous trees bent down into an arch. Birch trees (3 cm-12 cm thick) which are bent down by snow and ice to create an arch, are sometimes used as roosting sites both during daytime (one observation) and during night (3 observations). This behavior is also found sometimes in the spruce forest when deciduous trees are bent down into an arch and heaps of droppings is found under the arch.

Figure 10. Capercaillie droppings under a birch tree used as “night tree” near a display site in the valley of Boksjön.

Four times (during 2005/2006) I found that a male had used a night roost site in at birch tree, staying in this area for the night. At one occasion of these stay overnight, two males were flushed at the same juniper stand. In one case the cock had landed 3 m from its night roost site and started to walk on the snow. After walking 190 m it passed many juniper shrubs without stopping. Finally he started to eat juniper needles about 50 m from a frequently used juniper stand. Here I flushed the male no. 2. Male no.1 was flushed about 85 m from male no. 2. Male no. 1 had at first landed 6 m from the track of male no. 2 and immediately lifted 25 m for a new landing and starting walking on snow for about 80 m. This was observed about 1 hour after dawn with fresh snowfall.

Discussion

Distributions of leks

In an undisturbed forest with large continuous patches of old forests, the distribution of Capercaillie leks is expected to be even (Beshkarev et al.1995, Viht 1997, Wegge and Rolstad 1986, Storch 1997, Saniga 1996a, Catusse 1993 and Picozzi et al. 1992). In agreement with this, I found an even distribution of lek sites in my study area. The distance between the leks (1.0-4.2 km) is similar to that reported by other authors. The even distribution may also be ascribed to the almost untouched forest (cf. Wegge et al. 1992). An increased population size generally results in more leks and more males per lek site (Wiley 1991).

Lekking habitats and altitudes

In the valley I studied, most of the leks were situated at higher elevations in the coniferous forest, but where the valley is broader leks were also found at lower altitudes (500-520 meters a.s.l, see Fig. 8). In the Alps Capercaillie leks are situated in the upper half of the slopes (Hjort 1994, Saniga 1996b, Saniga 2002, Menoni 1997), which often coincide with edge zones. In my study area the leks are situated in the edge zone between spruce and birch vegetation belts. Hjort (1970, 1994) found that the sites of larger leks were situated in areas with more open space. This suggests that when a lek holds an increasing number of males, the display site may move to a location with more open space, while the solitary males stay in more concealed sites. In my study area the forest is in general more open in the upper regions (Fig. 1, 5, 6, 7 and 10), especially in the edge zone between spruce and birch forests, compared to the lower part of the spruce forest. The displaying males, which are adapted to execute display activities in a forest environment (Hjort 1994), could be more exposed to avian predators in the zone between spruce and birch forests, while a solitary male is not as visible to avian predators in a denser surrounding than in a more open area.

The areas near villages are avoided by lekking Capercaillie, and this decreasing pattern is observed in areas with open water too (Helle et al. 1994). However, if there are just a few houses or residents in a village, males could appear just some hundred meters from, for example, a farm.

One of the studied leks is situated in a 50-year-old plantation of pine trees. The plantation has no large open area. This habitat is obviously suitable for the Capercaillie, which apparently can use even relatively young and commercial forests when branches are strong

enough for perching and winter foraging (Storch 1995b), and apparently such forests can be used also as lekking sites (Rolstad and Wegge 1987, Gjerde 1991).

Number of males at leks

The number of Capercaillie males is expected to be high in primeval forest with large continuous patches of old forest around the leks (e.g. Wegge et al. 1992). Lekking grounds with one or two males constitute two thirds of the leks in my study area. One likely explanation is that the quality of the habitat is rather low, resulting in low number of males at each lek (c.f. Hjort 1994). Another possible reason for the low number of males (compared to the number of females) is the stress male chicks suffer because they grow up twice as fast the first summer as their sisters, which exposes them more to predators and of course higher death rate among male chicks during years with bad food resources (Lindén in Hjort 1994, Wegge 1980). The pure deciduous forest, which often is adjacent to these leks provide poorer Capercaillie food during the entire winter. Hunting is also one possible explanation, although it is not too extensive due to the low density of Capercaillie. Most likely, however, there are several reasons for low number of males.

Capercaillie leks with solitary males?

Solitary display sites are described in the literature by several authors and the reason for development of solitary display sites might be explained in different ways, for examples: 1) New leks are created either due to succession in habitat or changes in landscape (Gjerde et al. 2000). When there is enough space between existing leks (Wegge and Larsen 1987), such new leks are created by subadult males (Wegge and Larsen 1987) or by males that are forced to move to new areas due to forest management activities, if those males are able to attract females to stay in such areas between existing leks. 2) A stable but dynamic lek. This dynamic could both concern space, plasticity (Catusse 1993) and number of males. 3) A lek of a population at the edge of becoming extinct (Pollo et al. 2005, Quevedo et al. 2006). 4) In fragmented boreal forest when old forest patches are reduced to less than 100 ha only solitary display ensue (Rolstad and Wegge 1987).

Old males belonging to a lekking ground, whether communal or solitary, might have an advantage and a higher rank *per se* than sub adult males. They are established at the lek, while sub adult males are just visiting the lek site or the area, or they are settling as neighbours at the same lek site or lekking ground nearby. The old males can demonstrate their superiority over the sub-adults by being more skilled in the display activities (Hjort 1994, Storch 1997, Eliassen 2000, Wegge et al. 2005). They do not risk that other adult males are showing up, since the intrinsic site fidelity is strong in this species. The adult males seldom change home range, not even outside the lekking period, for most time of the year (Wegge and Larsen 1987, Wegge et al. 1992, Storch 1995a, Wegge et al. 2003). Strong site fidelity is found also in other grouse species, for example Sage grouse *Centrocercus urohasianus* (Schroeder and Robb 2003) and Black grouse, *Tetrao tetrix* (Rintamäki et al. 1995). Site fidelity is also shown for Capercaillie hens (Wegge 1985, Menoni 1997).

There might also be advantages for a male to display at a lek of his own, for example the movement in and out to daytime area will be shorter. The initial point for this discussion is that the distribution of males is even over the region, for example, like in my study area. If the Capercaillie males only displayed at communal leks (which my results do not indicate) I consider the males should gather at big leks and this would result in greater distances

between leks. Supporting this, Wegge et al. (2003) found that bigger leks (>25 males) had a longer inter-lek distance (4 km). This is the only paper that I have found that reports a longer distance than 2 km. A longer inter-lek distance might decrease a Capercaillie male's knowledge about the area, which may have importance to survival (Hjort 1994).

All lek sites will normally be visited by females (Rolstad and Wegge 1987). Apparently, females actively assess several males before mating (Hjort 1970) and there seems to be a tendency for females to visit several leks if the leks are small (Storch 1997). This may involve more mating at least in a short term. Usually mating is reserved for the highest ranked male at the lek site; typically one single male mates with all hens on a lek (Wegge and Larsen 1987), provided that the females stays long enough for mating (Clutton-Brock et al. 1992). In the longer term, perhaps fewer females will visit the lek when the number of males is low (Menoni 1997) and hence fewer occasions for mating. One advantage of bigger leks could be that there are more males to choose between for females, and there are also more eyes to detect predators (Hjort 1994).

The large proportion of leks with just one or two males in my study area contradicts the prevailing opinion that Capercaillie should prefer a communal display (cf. Hagen et al. 2005). Rather, it rather seems to be the fact that some males choose to display at their own lekking ground while other individuals prefer communal displays (Höglund and Alatalo 1995). In a very sparse population there may not be enough males to display communally.

In another lekking species, Black grouse, examples of solitary displaying males are found, although only in low-density populations (Höglund and Stöhr 1996). Solitary birds often display from trees and such unusual behavior may have been overlooked in many lekking species (Höglund and Alatalo 1995). Many species have both lek mating and non-lek mating populations. Perhaps solitary displaying males have been overlooked when it has been concluded that a species has a lek mating system (Höglund and Alatalo 1995). Communal display is perhaps not necessary for successful reproduction for Capercaillie.

I found that that the larger Capercaillie leks (> 4 males) have greater variations in numbers of males, while the leks with one or two males remain more constant. Andreasen (2001) discovered small leks to fluctuate or decline less than bigger leks, but he noticed that this decrease was only found in one part of his study area. However, he did not report that the small leks disappeared. I interpret Andreasen (2001) as a decline in density of the population in the area that had decreased. A decline in my study area was reflected by a decrease in numbers of males at the bigger leks, not in the extinction of leks. The small leks have a good ability to remain as a lek. As long as density of the Capercaillie males is relatively good I speculate that the numbers of leks will be more stable than numbers of males at the bigger leks.

In the study area leks occur in a regular pattern. Small leks should be vulnerable to stochastic events that can result in extinction of these leks, but the regular pattern with relatively great portion of leks with very few males might indicate that sub adult males prefer to start new leks when there are vacant areas (if females are present there) and the habitat is adequate. Perhaps gaps will be taken into account first and then males will fill up already established leks.

Gjerde et al. (2000) describes how new leks could occur if males visiting females in the inter-lek zones are successful in keeping them there until mating. Gjerde et al. (2000) and

Gjerde and Wegge (1989) also documented cases where sub adult cocks courted females in order to mate outside the lek site.

Adult Capercaillie males are in general tolerant against juvenile males (Hjort 1994). At the time when the solitary displaying male is about to disappear there may already have been one or more sub adult males joining this lek, or at least visiting his lek. When succession takes place, the old male disappears and a younger male replaces him, possibly one of those that have been allowed to share the lek. If the older male had been completely alone when he passes away, the lek might go extinct at least for a while but the area will sooner or later be reoccupied. The ability and potential for dispersal might be more apparent for Capercaillie males at low population density due to independence to select among more areas with fewer interactions with other males. This ought to be easier than competing with several other males. Therefore gaps will sooner or later be filled up as there are subadult males ready to establish leks (cf. Wolff 1997, Matthysen 2005).

Winter foraging

Some adult Capercaillie males seem to stay in their home ranges throughout the winter. Those males that live in the border between coniferous and deciduous forests make more or less, regular visits to the birch forest. Although they are forced to have a low-energy strategy to handle the demands of the winter, the birds move between of preferred spots with in their home range (Gjerde 1990a). Male Capercaillie has been observed feeding among juniper shrubs (Seiskari 1962, Edström 2005, this study). Smaller and bigger areas with juniper in the birch forest seem to be attractive to the males during when snow covers the ground. I have also made one observation where a male has landed on the snow surface 5 m from a 50-year old pine plantation, walked on the snow and started to eat from juniper shrubs. In areas with a few spruce trees or juniper shrubs, these trees/shrubs will serve both as a food resource and shelter during roosting (Andersson 2002, Olofsson 2004, this study), but when juniper is not available any longer due to snow conditions the visits also cease. Even though juniper is perhaps the most preferred winter food for the males, needles of spruce is more abundant and must be seen as the basic food for males living in or in connection to the conifer (spruce) forest. The Capercaillie has also been recorded feeding on birch catkins (Fig. 9) in the mountain near areas where no juniper was available (Andersson 2003). These observations are also in agreement with studies in the Cantabrian Mountains (Rodrigues and Obeso 2000), where remnants of birch buds have been found in Capercaillie droppings.

There are several examples presented by local people where it has been concluded that both male and female Capercaillie have their home ranges, including the display sites, in pure birch forest, e.g. Björkbakken (Andersson 2003), Norra Fjällnäs (Eriksson 2003), Boitikken (Israelsson 2003), Överuman (Burman 2003), Rönäs (Larsson 2003). All these examples are from areas close to my study area. Males having their lek site in the birch/spruce forest may leave their normal home range when food supplies cease. However, there also exist observations of Capercaillie which stay in deciduous forests during the whole year (Andersson 2003, 2007, Rodrigues and Obeso 2000). Other males leave their home ranges when food has decreased due to snow conditions (Israelsson 2003, Söderström 2005).

Regardless of the adaptation to the local situation, males may switch or partially migrate (Schroeder and Braun 1993) from their autumn/winter home range (only small clumps of spruce or other coniferous trees < 0.1 %) when winter conditions are too harsh and they will return next spring to attend the lek (Israelsson, 2003). This behavior is also observed in

the spruce forest in the eastern edge (Storskog) of the study area and another male 30 km south the study area at Sundsberget (Sjöberg 2004).

Roosting in winter

Most of the Capercaillie males in my study area have access to coniferous forest in their home range (Table 2, leks no. 5-20). Some of the males seem to prefer to be at the edge zone between coniferous forest and deciduous forest (Table 2, leks no. 12-20), but some of the males have their lek on islands (0-4 ha) of coniferous forest enclosed by birch forest (Table 2, leks no. 1-4). These latter males are not confined to their lek and the coniferous trees around it; they often made trips (< 1 km) in to the birch forest. If there are small patches with coniferous trees or bushes available. I consider the reason for these excursions as both for foraging and for maintaining their home range. According to Gjerde (1990a) there exist certain microhabitat conditions in such patches, but I also think that this behaviour is an anti-predator strategy, since a male almost never stays in a spot for a longer time (>12 h). An exception from visiting a patch just for one day occurred several times during the winter 2006. This winter the juniper was accessible for the whole winter season at the especially popular juniper groove mentioned above and several other places. One interesting observation in the winter 2005/2006 was partly the first winter that I found two maybe three males, in this area with lots of juniper (750 m away from lek no. 4), it was the only time I observed that males had night roosting in the same area.

If the snow conditions allow, roosting also occur in snow burrows during the night and then the male sometimes stayed until the next day. When feeding at daytime on the ground the Capercaillie usually chose a place for roosting on the ground. The lower branches of the spruce trees are often used as cover during daytime roosting (c.f. Haneborg et al. 2000). When the snow conditions are right, snow burrows are preferred as roosting sites. Such conditions occur when the snow depth is about 50 cm and the snow has a fine-grained structure (c.f. Seiskari 1962). Snow burrows for roosting could also be dug directly after feeding needles of juniper or spruce from the ground. Spidsö et al. (1997) concluded that the Black grouse were more vulnerable to predation when they could not dig roosting burrows in the snow. Gjerde (1991) and Haneborg et al. (2000) came to the conclusion that the large and conspicuous cocks depend on ground roosting sites and cover by spruce trees when hiding from avian predators. In addition to feeding, this is also a likely explanation to why cocks, with a home range in birch forests, often visit areas with juniper and spruce trees. All the visits by the males seemed to be at irregular interval, and often at certain parts of the birch forest with junipers, possibly as a general strategy to avoid predators. If this is the case, this potential anti-predator strategy would be somewhat at odds to the case when males stay overnight, perhaps to supervise the home range from intruding capercaillie males.

Conclusion

Today the occurrence of Capercaillie, particularly males, is sparse and patchy in the deciduous (i.e. birch forest) in my study area, while in coniferous forests the Capercaillie has a more even distribution, although the population is still rather sparse. The habitat in the deciduous forest is to a large extent unaffected by logging and fragmentation, but in my study area few male Capercaillie settle in the poorer and harsher environment of this type of forest. The poor habitat is the likely explanation for the low population level. However, in a long-term point of view, predators like the Red fox, Marten, Raven and the Hooded crow may have increased. The even distribution of lekking grounds and the few territorial males

at most of the leks indicates that not all males are dependent on communal display. Less dense parts of the spruce forest, at higher altitudes are the most typical lekking ground.

Future studies, and aspects of capercaillie management

My study raises some questions. More importantly, it suggests further investigations to find out why there are so few Capercaillie males in the region. At what stages (e.g. juvenile) do the losses of males occur? I suggest studying hunting pressure, as well as the climate's effect on the juvenile stage. Can the population in this area tolerate an increased fragmentation? Can forest management be done, and if so, to what extent? It would also be interesting to follow the dynamics of the population. Will the leks grow or decrease, and will the established display sites remain when the population fluctuates? Other interesting aspects are the dispersal patterns. For example, how far do juvenile males disperse from their natal sites, and do all adult Capercaillie stay in their home valley? Finally, do they choose a vacant lek area if there is enough space or do they attend and join a lek with several males? In other areas, clear-cutting has had a great impact on Capercaillie populations. The question is if the mountain range capercaillie population can withstand great impacts on the coniferous forest. The male Capercaillies may be particularly sensitive to hunting pressure, so it would be interesting to follow the effects of the hunt.

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Literature cited

Ahti, T., Hämet-Ahti, L. and Jalas, J. 1968. Vegetaion zones and their sections in nothern Europe. Ann. Bot. Fenn. 5:169-211.

Ahlén, I. and Tjernberg, M. 1996. Rödlistade ryggradsdjur i Sverige – Artfakta. Artdatabanken, SLU, Uppsala.

Andersson, T. 2002, 2003, 2007. pers. comm. Tjäderprojektet SLU. Umeå.

Andreassen, Ø. 2001. Spatial distribution and size of capercaillie leks in Pinega Natur Reserve, Russia, 1986-2000. –MSc thesis, Agricultural University of Norway, Norway, 35p.

Begon, M., Harper, J.L. and Townsend, C.R. 1999. Ecology, Populations and Communities, 3rd Edition. Boston, USA, 1098 pp.

Beshkarev, B., Blagovidov, A., Teplov, V., and Hjeljord, O. 1995. Spatial distribution of male Capercaillie in the Pechora-Illych Nature Reserve in 1991-92. – In: Jenkins, D. (Ed.): Proceedings International Symposium Grouse 6, World Pheasant Association, Reading, UK and Institutio Nazionale per la Fauna Selvetica, Ozzana dell Èmilia, Italy, pp. 48-53.

Burman, S. 2003. Pers comm.

Catusse, M. 1993. Spatial and temporal plasticity of Capercaillie (*Tetrao urogallus*) Arena in the French Pyrenees. Ecology and Evolution 2: 145-156.

Clutton-Brock, T. H., Price, O. and MacColl, A. 1992. Mate retention, harassment and the evolution of ungulate leks. Behavioral Ecology 3: 234-242.

Dahl, E. 2005. Pers. comm.

Edström, K. O. 2005. Pers. comm.

Ekman, H. 1987. Fjällskog. SNF Förlag. Stockholm

Eliassen, S. 2000. Daytime space use and social interactions in male capercaillie during spring. – MSc thesis, University of Bergen, Norway, 66 p.
Eriksson, I. 2003. Pers. comm.
Gjerde, I. and Wegge, P. 1989. Spacing patterns, habitat use and survival of capercaillie in a fragmented winter habitat. - Ornis Scand. 22:219-225.
Gjerde, I. 1990a. Winter ecology of a dimorphic herbivore: Temporal and spatial relationships and habitat selection of male and female Capercaillie *Tetrao urogallus* L. – Dr. scient. Thesis, Zoological Museum, Department of Animal Ecology, University of Bergen, Norway.
Gjerde I. 1990b. Determination of sex in capercaillie *Tetrao urogallus* by means of dropping size. Cinclus. 13: 91–92.
Gjerde, I. 1991. Cues in winter habitat selection by Capercaillie. I. Habitat characteristics. – Ornis Scand. 22: 197-204.
Gjerde, I., Wegge, P. and Rolstad, J. 2000. Lost hotspots and passive female preference: the dynamic process of lek formation in capercaillie *Tetrao urogallus* grouse. - Wildlife Biology 6: 291-298.
Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140-1162.
Hagen, C. A., Pitman, J. C., Sanderock, B. K., Robel, R. J. and Applegate, R. D. 2005. Age-specific variation in apparent survival rates of male lesser prairie-chickens. The Condor 107: 78-86.
Haneborg Finne, M., Wegge, P., Eliassen, S. and Odden, M. 2000. Daytime roosting and habitat of Capercaillie, *Tetrao urugallus*, males in spring – the importance of forest structure in relation to anti-predator behaviour. Wild-Life Biology 6: 241-249.
Helle, P., Helle, T. and Lindén, H. 1994. Capercaillie (*Tetrao urogallus*) Lekking Sites in Fragmented Finnish forest landshape. Scandinavian Journal of Forest Research 9: 386-396.
Hjort, I. 1970. Reproductive Behaviour in Tetraonidae. Viltrevy Volume 7: 183-596.
Hjort, I. 1994. Tjädern en skogsfågel. Skogsstyrelsens förlag, Jönköping, Sweden. 182 p.
Höglund, J. and Alatalo, R. V. 1995. Leks Princeton University Press - Princeton, New Jersey. 245 p.
Höglund, J. and Stöhr, S. 1996. A Non-Lekking Population of Black Grouse *Tetrao tetrix*. Journal of Avian Biology 28 (2): 184-187.
Israelsson, G. 2003. Pers. comm.
Johansson, S. 2005. Pers. comm. (Svenska Jägarförbundet)
Johnsgard, P. 1983. The Grouse of the World. Lincoln, NE: Univeristy of Nebraska Press.
Koivisto 1963. Über den Ortswechsel der Geschlechter beim Auerhuhn nach Markierungsergebnissen. Vogelwarte 22: 75-9. - In Storch 2001
Larsson, H. 2003. Pers. comm.
Lindén, H., Milanoff, M., and Wikman, M. 1984. Sexual differences in growth strategies of capercaillie. Finnish Game Res. 42: 29-35.
Linder, P. 1984. Kirjesålandet. En skogsbiologisk inventering av ett fjällnära urskogsområde i Västerbottens län. Sveriges lantbruksuniversitet, Institutionen för skoglig ståndortslära. Umeå, Sweden. 103 pp.
Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28: 403-416.
Ménoni, E. 1997. Locations and size of capercaillie *Tetrao urogallus* leks in relations to territories of hens. Wildlife Biology 3: 137-147.
Olofsson, T. 2004. Pers. comm.

Picozzi, N., Catt, D. C. and Moss, R. 1992. Evaluation of capercaillie habitat. Journal of Applied Ecology 29: 751-762.
Pollo, C. J., Robles L., Seijas, J. M., García-Miranda, Á. and Otero, R. 2005. Trends in the abundance of Cantabrian Capercaillie *Tetrao urogallus* cantabricus at leks on the southern slope of the Cantabrian Mountains, north-west Spain. Bird Conservation International 15: 397-409.
Quevedo, M., Bañuelos, M. J., Sáez, O. and Obeso, J. R. 2006. Habitat selection by Cantabrian capercaillie *Tetrao urogallus cantabricus* at the edge of the species' distribution. Wildl. Biol. 12: 267-276.
Rintamäki, P. T., Alatalo, R. V., Höglund, J. and Lundberg, A. 1995. Male territoriality and female choice on blackgrouse leks. Animal Behav. 49: 759-767
Rodrigues, A. E. and Obeso, J. R. 2000. Diet of the Cantabrian Capercaillie: geographic variation and energetic content. Ardeola 47: 77-83.
Rolstad, J. and Wegge, P. 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. Oecologia 72: 389-394.
Rune, O. 1974. Fjälltrakterna. In: In Brink et al. (eds.) Ekologi och landskap. Praktisk miljökunskap. Natur och Kultur, pp. 135-146.
Saniga, M., 1996a. Distribution, habitat preferences and breeding biology of the Capercaillie (*Tetrao urogallus*) population in the Velká Fatra mountains (West Carpathians). Biológia, Bratislava, 51 (2): 201-211.
Saniga, M., 1996b. Habitat characteristics of Capercaillie (*Tetrao urogallus*) leks in central Slovakia. Biológia, Bratislava, 51 (2): 191-199.
Saniga, M. 2002. Habitat features of the capercaillie (*Tetrao urogallus*) leks in the West Carpathians. Journal Of Forest Science 48 (9): 415–424.
Schroeder, M. A. and Braun, C. E. 1993. Partial migration of greater prairie-chicken in northeastern Colorado. The Auk 110 (1): 21-28
Schroeder, M. A., and Robb, L.A. 2003. Fidelity of greater sage-grouse, *Centrocercus urophasianus* to breeding areas in a fragmented landscape. Wildl. Biol. 9: 291-299.
Seiskari, P. 1962. On the winter ecology of Capercaillie, *Tetrao urogallus*, and the Black grouse, *Lyrurux tetrix*, in Finland. Finn Pap. Game Res. 22:1-119.
Sjöberg, K. 2004. Unpublished.
Sjörs, H. 1956. Nordisk växtgeografi. Svenska bokförlaget. Stockholm, Sweden, 240p.
Spidsö, T. K., Hjeljord, O. and Dokk, J. G. 1997. Seasonal mortality of black grouse *Tetra tetrix* during a year with little snow. Wildlife Biology 3: 205-209.
S:son-Wigren, C. and Sandström, H. 2001. Skogsbruk i fjällkanten. Ord & visor förlag, Skellefteå, Sweden, 223 p.
Stabbfors, B. 2003, 2004. Pers. comm.
Storch, I. 1995a. Annual home ranges and spacing patterns of capercaillie in Central Europe. J. Wildl. Manage. 59 (2): 392-400.
Storch, I. 1995b. Habitat requirements of capercaillie. - In: Jenkins, D. (Ed.); Proceedings of the 6th International Symposium on Grouse. World Pheasant Association, Reading Great Britain, pp. 151-154.
Storch, I. 1997. Male territoriality, female range use, and spatial organization of capercaillie leks. Wildlife Biology 3: 149-161.
Storch, I. 2001. *Tetrao urogallus* capercaillie. BWP Update, 3, 1 – 24.
Svensson, S., Svensson, M. & Tjernberg, M. 1999. Svensk fågelatlas. Vår Fågelvärd, supplement 31, Stockholm.
Söderström, M. 2005. Pers. comm.
Viht, E. 1997. Forest characteristics of capercaillie *Tetrao urogallus* display grounds and their surroundings in Estonia. Wildlife Biology 3: 291.

Wegge, P. 1980. Distorted sex ratio among small broods in a declining capercaillie population. Ornis Scand. 11:106-109.
Wegge, P. 1985. Spacing pattern and habitat use of capercaillie hens in spring. 3rd Internat. Symp. Grouse. pp. 261- 277.
Wegge, P. and J. Rolstad. 1986. Size and spacing of capercaillie leks in relation to social behavior and habitat. Behavioral Ecology and Sociobiology 19: 401-408.
Wegge, P. and Larsen, B. B. 1987. Spacing of adult and subadult male common capercaillie during the breeding season. The AUK 104: 481-490.
Wegge. P., Rolstad, J. and Gjerde, I. 1992. Effects of boreal forest fragmentation on capercaillie grouse: Empirical evidence and management implications. In Wildlife 2001: Populations, D.R. Mc Cullough and R.H. Barret (eds.) Elsevier Sci. Publ. 738-749.
Wegge, P., Kvålsgard, T., Hjeljord, O. and Sivkov, A. 2003. Spring spacing behaviour of capercaillie males does not limit numbers at leks. - Wildlife Biology 9: 283-290.
Wegge, P., Eliassen, S., Haneborg Finne, M., Odden, M. 2005. Social interactions among Capercaillie *Tetrao urogallus* males outside the lek during spring. Ornis Fennica 82: 147-154.
Wiley, R. H. 1991. Lekking in birds and mammals: Behavioral and evolutionary Issues. Advances in the study of behavior 20: 201-291.
Wolff, J. O. 1997. Population regulation in mammals: an evolutionary perspective. J. Anim. Ecol. 66: 1-13.