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# Daytime roosting and habitat preference of capercaillie *Tetrao urogallus* males in spring - the importance of forest structure in relation to anti-predator behaviour

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Radio-equipped adult capercaillie *Tetrao urogallus* males (N = 10) were tracked during April and May 1996-1997 in a coniferous forest in southeastern Norway, which has been subjected to clear-felling and replanting during the last five decades. With the use of radio-telemetry daytime habitat preference was investigated at two levels of scale: within home range and within forest stands inside home ranges. In addition, roosting habitat preference within stands was investigated by locating heaps of intestinal faeces, henceforth called roosting sites. Within forest stands, forest structure and visibility were measured at roosting sites (N = 94) and at random plots (N = 188). Within home ranges the birds used plantations and old naturally regenerated forest according to availability, and open bogs were avoided. Of the roosting sites, 90% were located underneath the low branches of Norway spruce *Picea abies* trees. For roosting within old naturally regenerated stands (> 70 years old) males preferred sites with higher tree density, higher vertical and horizontal cover and lower visibility than in the surrounding forest. In young and middle-aged plantations, on the contrary, roosting sites tended to have lower tree density (P = 0.118), but still seemed to have better cover than the surrounding forest (P = 0.117). The forest structure preference of roosting sites was reflected in the use of vegetation types within the old naturally regenerated forest. Because dense cover reduces the probability that the birds are detected by a predator, but at the same time increases the risk of being killed once detected, capercaillie males have to compromise between shelter and outlook. Our data indicate that males prefer good cover at the expense of good overview of the surroundings when selecting roosting sites, and that tree density is usually too dense in younger plantations, probably because outlook is reduced and flying obstructed.

*Key words:* anti-predator behaviour, capercaillie, forest structure, habitat, roosting, spring

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The large capercaillie *Tetrao urogallus* is a forest-dwelling, polygynous (Wiley 1974) grouse which mates at traditional lekking grounds (Hjorth 1970). During the lekking period adult males occupy more or less exclusive daytime territories of approximately 30–50 ha, at most extending radially 1 km from the lek centre (Wegge & Larsen 1987, Storch 1997). Larsen & Wegge (1985) revealed a preference for old mixed coniferous forest during daytime, and found that the size of daytime territories was inversely related to the proportion of old forest within them. During the last 50 years, the forestry practice of clear-felling has fragmented the forest into a mosaic of clear-cuts, plantations and remaining islands of old forest. Logging experiments have shown that reduction and fragmentation of the old forest surrounding a lek strongly affect the lek population (Lindén & Pasanen 1987, Rolstad & Wegge 1989a, Wegge, Rolstad & Gjerde 1992). However, little is known about the structural requirements of the capercaillie habitat during spring.

Templov (1947, cited in Seiskari 1962) stressed the importance of separating habitat preferences of different behaviour. Wegge & Larsen (1987) suggested that daytime territories may serve for rest and energy conservation. During most of the spring period nutritious plants are either absent or patchily distributed, and males predominantly feed on food plants which are readily accessible but less digestible (Storch, Schwarzmüller & von den Stemmen 1992, Borchtchevski 1995). Lindén (1984) reported that males in captivity had a low energy intake and a pronounced weight loss during the mating season. On this basis, we hypothesise that males partly satisfy their energy demands by weight loss, and that resting and digesting are important activities during daytime in spring. Because predation pressure in late winter and spring is substantial (Wegge, Gjerde, Larsen, Kastdalen, Rolstad & Storaas 1989), we consider avoidance of predators to be the main objective when choosing roosting sites.

Males roost on the ground (Gjerde 1991a, M. H. Finne, pers. obs.), and are preyed upon by both avian and ground predators (Wegge et al. 1989). To avoid predation both the probability of being detected and the probability of being killed once detected must be kept low. These are partly incompatible requirements. By comparing the forest structure at roosting sites with control plots in the surrounding forest we investigated the roosting habitat preference at the spatial level of forest stands. With the use of radio-telemetry, we investigated habitat selection at higher spatial levels, and we discuss habitat selection in relation to forest structure

and predator avoidance. Today, the pristine boreal forests are being replaced with even-aged plantations all over Scandinavia. By choosing a study area heavily influenced by the modern forestry practice of clear-felling and replanting, we could assess how a bird originally adapted to the later successional stages of the forest responded to the changed forest composition.

## Study area

The study was conducted at Varald State Forest, 60°10'N, 12°30'E, in southeast Norway. The study area belongs to the middle boreal coniferous zone (Abrahamsen, Jakobsen, Dahl, Kalliola, Wilborg & Pålsson 1977), and covers 40 km<sup>2</sup>, ranging in altitude within 200–400 m a.s.l. Mean temperatures are 16.2°C in the warmest month (July) and -7.3°C in the coldest month (January). Snow usually covers the ground from November to April. The forest is dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, sprinkled with birch *Betula* spp. and aspen *Populus tremula*. The most common vegetation type is mixed coniferous forest, *Vaccinio - Pinetum boreale* (Hesjedal 1973, Kielland-Lund 1981), constituting ca 40% of the study area. If left undisturbed, the mature forest of this type is dominated by pine in the tree layer and spruce in the lower strata. At poorer and/or drier sites pine is the only tree species, while spruce replaces pine at richer sites. Because of varying soil conditions, the old mature forest is a mosaic of mixed stands and pure pine and spruce stands, spread out in a fine-grained pattern (in relation to the capercaillie's cruising radius). Ground cover consists mainly of *Vaccinium* spp. and heather *Calluna vulgaris*.

Until the 1950s, the area was only subjected to selection cutting and small-scale clear-cutting. During the last 50 years, 75% of the area has been converted to clear-cuts and plantations of varying age. The size of the new stands averages about 4 ha, with the largest being almost 50 ha. Plantations are often monocultures of either pine or spruce, and a large proportion of the remaining old forest has been thinned by reducing the understory of spruce and pine. Except for logging, human activity is minimal, and the wild fauna is typical of the middle boreal zone. The main predators of adult capercaillie are red fox *Vulpes vulpes*, pine marten *Martes martes* and goshawk *Accipiter gentilis* (Wegge et al. 1989). According to the latest census work, the spring density of capercaillie males is 0.5–0.7 males/km<sup>2</sup>, roughly corresponding to 1/3 of female density. The den-



sity of black grouse *Tetrao tetrix* is about twice that of capercaillie, whereas the hazel grouse *Bonasa bonasia* is scarce (P. Wegge, unpubl. data).

## Material and methods

### Capturing of birds and radio-telemetry

During the springs of 1996 and 1997, 10 males were captured on six different leks and equipped with backpack or necklace radio-transmitters. All were aged adults, i.e. >2 years old, based on beak measurements (Wegge & Larsen 1987). Except for one bird, all males were triangulated more than 25 times, which is regarded as the minimum number of locations to get a reliable estimate of spring home range of capercaillie males (Wegge & Larsen 1987). One bird was located 19 times, but was included because estimate of the size of home range was not an objective of our study. Four of the males were radio-tracked both years. To avoid pseudo-replication, only the home range estimate from the year with the highest number of radio locations was used in the data analysis. To investigate habitat use, the birds were located by radio triangulation during daytime (when off the lek) between 1 April and 31 May. For home range estimations ( $N = 10$ ), we only used triangulations in which the longest side of the triangle was shorter than 150 m ( $N = 344$ ); for investigation of the use of successional stages we used triangulations in which the longest side was shorter than 100 m ( $N = 325$ ), and for the investigation of the use of vegetation types we used triangulations in which the longest side was shorter than 50 m ( $N = 272$ ).

### Investigation of habitat use

We investigated habitat preference at two levels of scale: within home range and within forest stands inside the home range. Within the home range, habitat use was investigated with reference to successional stage. Within stands of old forest (>70 years) we investigated preference for vegetation types, and within plantations (11–70 years old) we investigated preference for dominant tree species.

The use of forest successional stages was extrapolated from a forest company map from 1994 (revised in 1999). We distinguished four successional stages: 1) clear-cuts and plantations  $\leq 10$  years old, 2) plantations 11–70 years old, 3) naturally regenerated forest >70 years old and 4) open peat bogs. To investigate preference for vegetation types we used a detailed vegetation map (smallest entity 0.05 ha). In accordance with Hes-

jedal (1973) and Kielland-Lund (1981), we distinguished between six vegetation types: 1) lichen-pine forest (A2 - *Cladonio-Pinetum boreale*), 2) mixed coniferous forest (A3 - *Vaccinio-Pinetum boreale*), 3) *Vaccinium*-spruce forest (B2 - *Eu-Piceetum abietis*), 4) *Calluna*-rich pine-bog forest (G1 - *Oxycocco-Pinetum cladonietosum*), 5) wet *Vaccinium*-rich pine forest (G2 - *Oxycocco-Pinetum vaccinietosum*) and 6) spruce swamp forest (G3 - *Chamaemoro - Piceetum abietis*).

All maps were digitised, and ArcView 3.1 was used for analysis. We used Ranges V to perform the minimum convex polygon method (Mohr 1947) for delineating home ranges.

### Investigation of roosting sites

At the scale of forest stand, we also investigated selection of forest structure at roosting sites. Roosting sites were located by searching for small heaps of intestinal faeces (droppings) at spots where the birds had been triangulated precisely, or a bird had just been flushed. We also checked if the faeces were fresh either by investigating the colour and texture, or by using a trained dog. Hence the location of roosting sites was absolutely precise. For radio-tagged individuals, only roosting sites from different days were used. To ensure that the bird had stayed at the spot for some time, only heaps with three or more droppings were included. We made measurements on forest structure and visibility at the roosting sites ( $N = 94$ ) and on two control plots in the vicinity of each roosting site ( $N = 188$ ). The control plots were situated 30 m from the roosting sites in random directions and in the same vegetation type and successional stage as the roosting site. All but 10 roosting sites were situated underneath the low branches of spruce trees. The control plots of these roosting sites were placed next to a spruce tree of the same height class as the roost tree.

Inside circular plots of a 4-m radius (50 m<sup>2</sup>) we counted the number of spruce, pine and deciduous trees in the height classes 1–4, 4–8 and >8 m and estimated the total canopy closure and the canopy closure of trees 1–4 m high, henceforth called shrub coverage. In addition we estimated the forest density by measuring the total basal area of all visible trees in m<sup>2</sup>/ha using a relascope (Bitterlich 1984). We described the cover in a direct way by estimating the visibility along the ground and aslant upwards. The upward gradient was 20%. Visibility was estimated in 20 different directions spread out in a systematic manner. The two visibility measurements were done in different ways. In the aslant upwards measurement we focused on the visi-



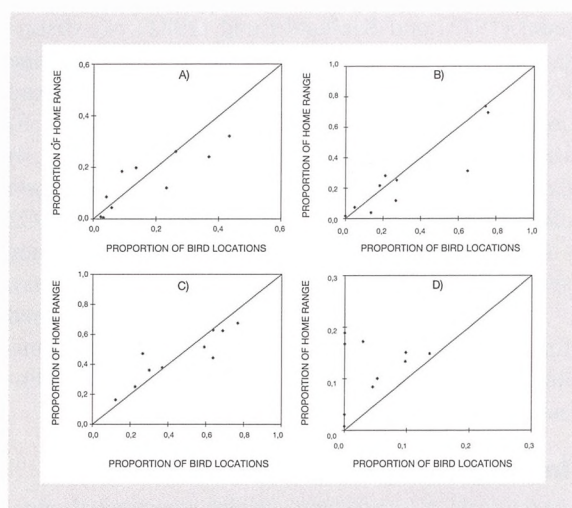


Figure 1. Relationship between the proportion of locations of capercaillie males within each of the successional forest stages and the percentage of this stage within the males' home ranges (forest <10 years old (A); 11-70 years old (B); >70 years old (C); and open bogs (D)). Each plot represent one male. Plots on the 45° median line indicate that males made no active selection of this particular successional stage.

bility towards the spot. We asked ourselves how close a raptor must be sitting in this direction in order to detect a capercaillie male? Along the ground we asked ourselves how far away a capercaillie can detect an approaching fox or pine marten in this direction? In directions with no cover the visibility was set at 70 m. The measurements were done holding our heads 30 cm above the ground.

### Investigation of forest types

We described the structure of different forest types available to the birds. Estimations were done in the same way as for roosting sites with the exception of basal area, which was excluded. Stands were picked out randomly from the vegetation map, and depending on the size of the stand, 3-15 plots were spread out systematically with

Table 2. Distribution of capercaillie roosting sites in different successional forest stages and types (see details on forest types in the text).

Forest stage	Number of sites	Percent	Forest type	Number of sites
>70 years old	78	83	A2	1
			A3	54
			B2	7
			G1	2
			G2	6
11-70 years old	15	16	G3	8
			Pine	4
			Spruce	11
0-11 years old	1	1		
In total	94	100		

a 30 × 30 m grid system. A total of 39 stands were investigated this way.

### Statistics

For data analysis we used the Wilcoxon Signed-Rank tests and standard linear regression analysis. For the analysis of habitat selection, individuals were used as sample units and the level of significance was corrected when more than one parameter was estimated simultaneously. For the analysis of roosting sites with reference to forest structure, roosting sites were used as sample units. Because of skewed distributions, we often used the trimmed mean (observations below the first quartile and above the third quartile removed before averaging) to describe central tendency.

## Results

### Habitat use

Within home ranges the birds used plantations and old naturally regenerated forest according to availability, and avoided open peat bogs ( $W_s = 55.0$ ,  $P = 0.006$ ; Fig. 1). Among plantations 11-70 years old, the more open pine-dominated stands (Table 1) were

Table 1. Some selected forest structure characteristics of different forest types at Varald State Forest, southeast Norway. The figures are mean values of 2-5 stands.

Forest type <sup>1</sup>	Total canopy closure (%) <sup>2</sup>	Total tree density (stems/ha) <sup>2</sup>	Visibility along the ground (m) <sup>2</sup>	Visibility aslant upwards (m) <sup>2</sup>
A2 >70 years (2)	49.5 (4.5)	774 (254)	8.4 (1.1)	21.1 (4.8)
A3 >70 years (3)	51.4 (1.9)	948 (70)	7.4 (0.3)	10.9 (1.6)
B2 >70 years (4)	65.0 (6.7)	1942 (224)	7.3 (0.5)	8.4 (1.2)
G1 >70 years (3)	20.7 (0.9)	980 (148)	20.9 (3.4)	23.8 (1.2)
G2 >70 years (3)	49.4 (5.6)	1498 (286)	7.5 (1.3)	9.5 (1.8)
G3 >70 years (4)	56.6 (7.6)	1814 (290)	8.3 (1.2)	7.6 (1.3)
Pine 11-70 years (9)	44.6 (9.1)	2040 (1000)	8.1 (3.7)	14.3 (8.5)
Spruce 11-70 years (8)	55.7 (13.4)	2180 (900)	5.5 (1.7)	7.0 (2.5)

<sup>1</sup> Numbers of stands investigated in each forest type are given in parentheses.

<sup>2</sup> Standard errors are given in parentheses.



Table 3. Positioning of capercaillie roosting sites in relation to tree basis and height. Height class refers to the height of the roosting trees.

Position	Number of sites	Percent	Height class	Number of sites	Percent
At the base of a spruce tree	84	89	1-4 m	29	35
			4-8 m	23	27
			> 8 m	32	38
Not at the base of a tree	10	11			
In total	94	100			

preferred ( $W_s = 35.0$ ,  $P = 0.010$ ), and among old forest stands the three densest vegetation types, *Vaccinium*-spruce forest (B2), wet *Vaccinium*-rich pine forest (G2) and spruce swamp forest (G3; see Table 1), tended to be preferred ( $W_s = 41.0$ ,  $P = 0.093$ ). Old forest stands were avoided after thinnings ( $W_s = 38.0$ ,  $P = 0.038$ ).

### Roosting sites

Most roosting sites were located underneath the lower branches of spruce trees in mixed coniferous forest (A3) >70 years old (Tables 2 and 3).

#### Old forest >70 years old

Both total canopy closure and shrub coverage were higher at roosting sites than on control plots in the old forest (total canopy closure:  $W_s = 2484.5$ ,  $P < 0.001$ ; shrub coverage:  $W_s = 1964.5$ ,  $P = 0.004$ ; Fig. 2A). This resulted in shorter visibility at roosting sites than on control plots both along the ground ( $W_s = 985.0$ ,  $P = 0.006$ ) and aslant upwards ( $W_s = 451.0$ ,  $P < 0.001$ ; Fig. 2B). A higher density of spruce 1-4 m high ( $W_s = 1438.0$ ,  $P = 0.034$ ) and 4-8 m high ( $W_s = 1438$ ,  $P = 0.020$ ) made the proportion of spruce ( $W_s = 1861.5$ ,  $P = 0.021$ ) and the total density of trees higher at roosting sites than on control plots ( $W_s = 1730.0$ ,  $P = 0.037$ ). Basal area was higher at roosting sites than on control plots in mixed coniferous forest ( $W_s = 1038.0$ ,  $P = 0.002$ ), whereas there was no difference in the denser spruce-dominated vegetation types (see Table 1). In summary, in the old forest the density of spruce trees and total density of trees were higher at roosting sites than on control plots. This resulted in higher total canopy closure, higher shrub coverage and lower visibility both along the ground and aslant upwards.

#### Plantations 11-70 years old

Of a total of 15 roosting sites in plantations, 11 were situated in stands dominated by spruce trees (see Table 2). As found in the old forest, roosting sites in plantations seemed to have higher total canopy closure than control plots ( $W_s = 74.6$ ,  $P = 0.177$ ; Fig. 3A). At roosting sites situated in spruce-dominated plantations (SDP), visibility upwards was significantly shorter

than on the control plots ( $W_s = 12.5$ ,  $P = 0.075$ ; Fig. 3B). In contrast to the pattern in old forest, tree density at roosting sites tended to be lower than on control plots in plantations ( $W_s = 32.0$ ,  $P = 0.118$ ). In SDP, the basal area at roosting sites was lower than on control plots ( $W_s = 14.0$ ,  $P = 0.10$ ). The apparent dominance of spruce trees at roosting sites in old forest was not found at roosting sites in plantations.

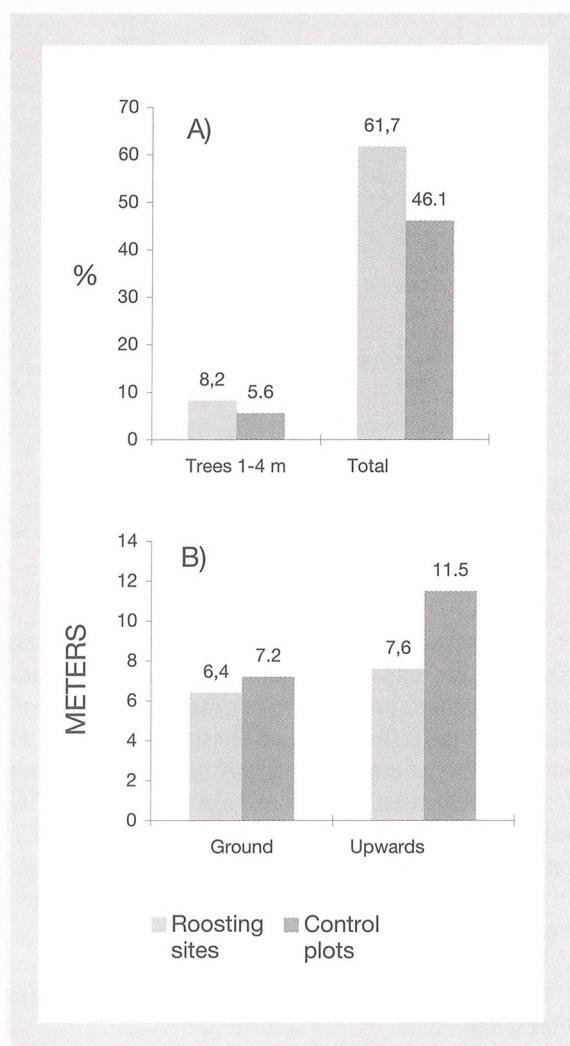


Figure 2. Canopy closure of trees 1-4 m high and in total (A), and visibility (B) along the ground and aslant upwards at roosting sites and on control plots in old forest (successional stage 4).



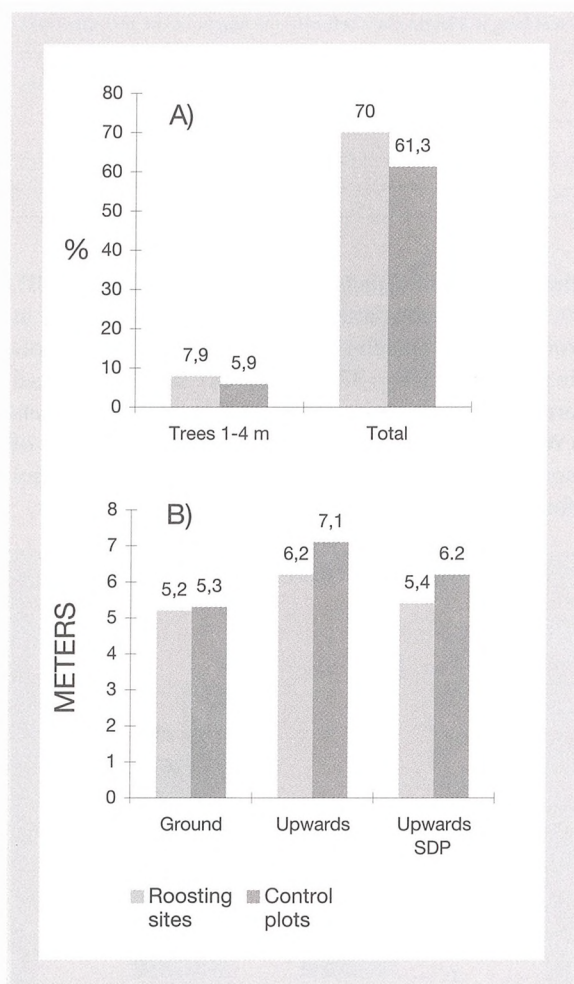


Figure 3. Canopy closure of trees 1-4 m high and in total (A), and visibility (B) at the ground and aslant upwards at roosting sites and on control plots in plantations 11-70 years old. SDP = spruce-dominated plantations.

We compared differences in tree density between roosting sites and control plots in the different successional stages using linear regression analysis, and found that the difference (tree density at roosting site - tree density at control plot) was negative for young forest, and increased with forest age to intersect the x-axis at approximately 85 years (Fig. 4). In the study area, plantations are below the age of 85, and most naturally regenerated stands are above that age. The straight-line fit was:

$$\Delta \text{Tree density (roosting site - control plot)} = 0.06 \text{ Forest age} - 5.18$$

Both the constant ( $t = -2.55$ ,  $P = 0.017$ ) and the slope ( $t = 2.58$ ,  $P = 0.016$ ) were significant.

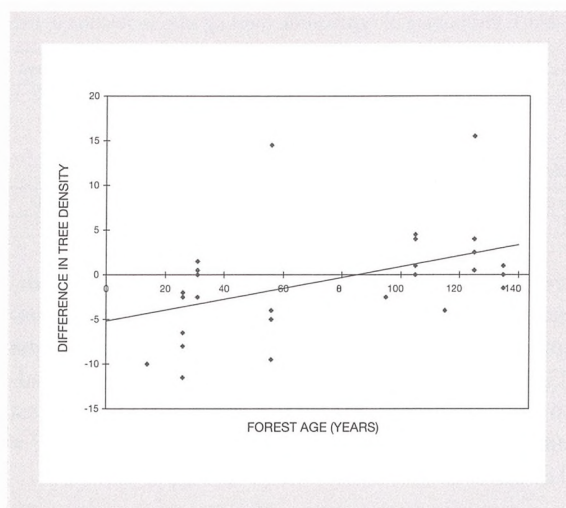


Figure 4. Straight-line fit relating difference in tree density between roosting sites and control plots (roosting site - control plots) to forest age.

## Discussion

Within home ranges successional stages were used according to availability, and within the old forest birds roosted in forest with a higher density of trees than in the surrounding forest, especially spruce in the lower strata (multi-layered forest). Spruce trees retain lower canopies than pine trees when they mature, and therefore contribute more to the vertical cover close to the ground. This gave the roosting sites better cover than the control plots both horizontally and vertically. There was less difference in forest density between roosting sites and control plots in the spruce-dominated forest than in the mixed coniferous forest, indicating that the forest structure of the average spruce-dominated forest is closer to the optimal roosting habitat than mixed coniferous forest. When investigating habitat use the same pattern emerged: vegetation types with well developed understory were preferred, and stands which had been thinned by reducing the amount of understory spruce and pine (single-layered forest) were avoided.

Contrary to the roosting sites in the old forest, the roosting sites in plantations tended to have lower total tree density than the control plots, even though the cover seemed to be better and the visibility shorter at the roosting sites. The difference in tree density was larger (and significant) in spruce-dominated plantations, probably because they generally offer better cover than pine-dominated stands, and that shelter therefore is sufficient, also when tree density is moderate. The reason for the better cover at lower tree density at roosting sites in plantations may be that young trees develop larger and deeper crowns when the inter-tree



distance is larger, and that the birds select spots where this compensates for the lower stem density. A preference for spruce at roosting sites was not found in plantations, probably because the difference between pine and spruce with respect to deepness of the crown is smaller among young trees than among old trees. As a result young pine stands offer sufficient cover in the lower strata.

As hypothesised earlier, when trying to avoid predation the birds have to compromise between shelter and outlook. Old forest is in general too open to fulfil the demand for shelter. In plantations, cover is more appropriate, but tree density is sometimes too high, probably because flying is obstructed and outlook reduced.

The general impression in the literature is that capercaillie males prefer open-spaced old forests (Rolstad & Wegge 1989b, Storch 1995). The preference for this kind of forest has been explained as a result of anti-predator behaviour; the capercaillie male is said to have adopted a 'detect predator / escape' or 'detect predator / self defence' strategy (Rolstad, Wegge & Larsen 1988, Storch 1993). Therefore it is advantageous to detect the predator early to assess if defence or escape is the appropriate strategy. A short inter-tree distance may interfere with predator escape (Gjerde, Wegge, Pedersen & Solberg 1985, Rolstad & Wegge 1989b). Another explanation for the preference for open stands, which is emphasised especially by researchers in Central Europe (Klaus, Andreev, Bergman, Müller, Porkert & Wiesner 1986, Storch 1993) and Scotland (Picozzi, Catt & Moss 1992), is the richer ground vegetation in stands where more sun is let through the canopy. This is considered to be important both for food and shelter. What these authors have not discussed, is the possibility that habitats with different structure may be preferred for different activities. It is possible that capercaillie males prefer forest with an open stand structure and a rich ground vegetation (such as old mixed coniferous forest) when foraging, and dense forest with a well-developed understory (such as middle-aged plantations and spruce-dominated old forest) when roosting.

At Varaldskogen, an all-season avoidance of plantations by adult capercaillie males has been reported (Gjerde & Wegge 1989, Larsen & Wegge 1985, Rolstad 1988, Rolstad et al. 1988). We found a frequent use of plantations within the home ranges (two of the males were located in plantations in 75% of the triangulations). A reason for the sparse use of plantations reported in earlier investigations at Varaldskogen may be that the forestry practice of clear-cutting is fairly new. The time which has elapsed between the field work of earlier studies at Varaldskogen and our study is about 15

years, which is a long time period for a growing stand. Larsen & Wegge (1985) studied the general habitat preference of capercaillie males in spring at Varaldskogen during 1979-1982 and found that plantations were unsatisfactory habitats for food and shelter. They further said that plantations may after some time provide sufficient cover to improve the quality of the daytime territories and after 15 years this appears to have happened in this area.

When reviewing habitat preference of capercaillie, Storch (1995) refers to the original habitat of the capercaillie as forest with an open-spaced stand structure and rich ground vegetation. The primeval boreal forests were probably denser than the old forests we experience today. In most forest areas in Norway, felling of trees for firewood and selection-cutting has been common for centuries, and has reduced the tree density and the density of the understory. In addition, commercial forestry has further reduced the quality of the forest as roosting habitat by exploiting multi-layered spruce-dominated forests and thinning of pine-dominated forests by removing understory spruce and pine. Several studies, including our study, have documented the importance of spruce and forest understory for capercaillie. Seiskari (1962) stated that the dependence on spruce seems to be the essential feature in the habitat requirements of capercaillie during the snow-free season. In a large uncut forest reserve in the northern Russian taiga, Beshkarev, Blagovidov, Teplov & Hjeljord (1995) reported an extensive use of clumps of spruce within the open pine-dominated forest during daytime in spring. The importance of understory cover for capercaillie males in winter has been documented empirically and demonstrated experimentally by removing spruce trees in intensively used areas (Toverud 1984, Gjerde 1991a, b). A lack of suitable habitat for roosting within the old stands i.e. forest with a well developed understory, may be part of the reason for the somewhat surprisingly high use of plantations which was found in our study.

To be suitable as male habitat, areas surrounding capercaillie leks should contain forest with a high vertical cover close to the ground. The basis of such forest is formed in the early successional stages. By thinning the young even-aged plantations at an early stage, trees develop low canopies. In this way flying is less obstructed and the future old forest will obtain high cover in the lower strata. To create forest suitable for both roosting and foraging, we believe that a varying forest structure and density is advantageous, and thinnings in middle-aged plantations should be executed in a way that increase the heterogeneity of the stand in relation to type of tree species and stem density. High vertical



cover close to the ground can also be obtained by rejuvenating the forest on the basis of selection-cutting and natural regeneration instead of clear-cutting and planting. Where old trees have been felled, young trees rejuvenate in the openings, creating a multi-layered forest with a high cover close to the ground. When thinning old mixed forest stands of the lower and medium site productivity classes it is important that the natural mixture of spruce and pine is retained.

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