

Seasonal differences in habitat use in capercaillie (*Tetrao urogallus*) in the West Carpathians

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From 1981–2003, inter-seasonal differences in habitat use in the capercaillie (*Tetrao urogallus*.) were studied in the West Carpathians (Slovakia). In the study area, the capercaillie population mostly occupied forest biocoenoses within the spruce-beech-fir and spruce vegetation belts. During the spring season (March – May), capercaillies preferred stands of the spruce-beech-fir vegetation belt (54% frequency location in cocks and 52% in hens, respectively). Fewer records were obtained from the biocoenoses of the spruce vegetation belt (34% frequency locations in males and 40% in females, respectively). Forests of the spruce vegetation belt were favoured by males during the autumn (October – November) and winter (December – February) seasons (60% frequency locations and 52%, respectively). In contrast, hens preferred forests of the spruce-beech-fir vegetation belt also during the summer (June – September) and autumn seasons (44% frequency locations and 40%, respectively). Seasonal differences in habitat selection in relation to forest age were also found. Both males and females preferred forests older than 80 years throughout the whole year.

Key words: capercaillie, *Tetrao urogallus*, habitat use, West Carpathians.

Introduction

Capercaillie (*Tetrao urogallus* L., 1758) is a large ground-nesting grouse species with precocial chicks inhabiting C European mixed spruce-beech-fir and mountain spruce forest in the West Carpathians in small isolated populations (KLAUS et al., 1986; SANIGA, 1996a, b, c). These forests have been undergoing radical changes from a natural regime to a managed system in the course of the 20th century. Modern forestry is one of the most important landscape factors in forest ecosystems today. Especially during the last 50 years, the forestry practice of clear-felling has fragmented the forests into a mosaic of clear-cuts, plantations and remaining islands of old forest.

In recent years, more attention has been directed towards the effects of forest habitat changes on faunal diversity and performance of wildlife populations (e.g. HELLE, 1985; VÄISANEN et al., 1986; LINDÉN, 1981; STORAAS et al., 1999). The loss and insularization of forest habitat are accompanied by a loss of forest species diversity. In terms of landscape ecology this large-scale change in forest mosaic is expected to have profound effects on the spacing pattern and range use of wildlife species, especially those having home ranges and cruising radii within the critical area interval (ROLSTAD & WEGGE, 1989). The capercaillie belongs to this area-sensitive category, inhabiting old forest most of the year, and having seasonal ranges between 10 and 100 hectares in

size (WEGGE & LARSEN, 1987). Modern forestry modifies capercaillie habitats by fragmenting continuous forest, and by altering the internal structure and tree species composition of forest stands.

In recent decades, capercaillie populations throughout most of W Europe have declined markedly (e.g. NOVÁKOVÁ & ŠTASTNÝ, 1982; KLAUS et al., 1986; KLAUS & BERGMANN, 1994; SANIGA, 1999). A decline in capercaillie populations has also been observed during the last 20–30 years in Fennoscandia and Russia (e.g. RAJALA & LINDÉN, 1984; ROLSTAD & WEGGE, 1989).

Most Slovakian data concerning the population dynamics of the capercaillie come from hunting statistics (BANCÍK, 1969; FERIANC, 1977; RICHTER, 1983). Only a few serious ecological and ethological population studies have been made on this endangered grouse species in the W Carpathians (SANIGA, 1996a, b, c, 1999, 2001).

This paper is aimed at establishing seasonal differences in habitat use in relation to (i) vegetation belts, (ii) forest types and (iii) forest age in this highly dimorphic tetraonid in the mountains of the West Carpathians.

Study area

The field-work took place in the mountains of C Slovakia (Velká Fatra Mts, Malá Fatra Mts, Kremnické vrchy Mts, Starohorské vrchy Mts, and Nizke Tatry Mts, West Carpathians, 18°50′–19°10′ E; 48°47′–49°19′ N) from 1981–2003.

The topography of the study area rises from 600 m a.s.l. to 1,530 m a.s.l. The climate is moderately continental with a mean temperature of the warmest month (July) of 14.5°C and minus 5.5°C for the coldest (January). Annual mean precipitation is 1,000–1,400 mm, and the ground is usually covered with snow from mid-November to late March or April (depending on altitude and exposure).

In the area under study, mixed forest biocoenoses consisting of the spruce-beech-fir vegetation belt dominate (80%) (*Picea abies*, *Abies alba*, *Fagus sylvatica*, *Acer pseudoplatanus*). Coniferous forests of the spruce vegetation belt constitute around 10% of the study area (*Picea abies* dominated, sprinkled with *Acer pseudoplatanus*, *Fagus sylvatica*, and *Sorbus aucuparia*). Mixed forest ecosystems of the fir-beech vegetation belt constitute 8% of the study area (*Abies alba*, *Fagus sylvatica*, *Acer pseudoplatanus* and *Picea abies*) and ecosystems of the dwarf pine vegetation belt constitute 2% (*Pinus mugo*, *Sorbus aucuparia*, *Sorbus montisalpaie*, *Sorbus atrimontis*, and *Picea abies*).

The area is a mosaic of small patches of different groups of forest types (classifications to RANDUSKA et al., 1986). *Fageto-Aceretum*, *Abieto-Fagetum* and *Fageto-Abietum* cover about 80% of the forested area

under study, and *Sorbeto-Piceetum* with *Acereto-Piceetum* about 10%.

Regarding the age-space structure of forest stands, in the fir-beech and spruce-beech-fir vegetation belts, islands of old forests (over 80 years) very different in size (from 5 ha to maximally 50–75 ha) are broken up into a mosaic of clear-cuts and plantations of various ages and sizes. In the spruce vegetation belt, unmanaged natural forests around 150–180 years old predominate (80%).

Ground vegetation changes locally depending on the forest type. In the mixed forests (spruce-beech-fir vegetation belt), ferns (*Athyrium filix-femina*, *Dryopteris* sp.) are often common. In the biocoenoses of the spruce vegetation belt, dominant ground vegetation is bilberry (*Vaccinium myrtillus*), some species of graminoids (*Deschampsia flexuosa*, *Calamagrostis* sp.) and also ferns (*Dryopteris dilatata*).

According to the latest census work, the spring density of capercaillie is 0.1–0.7 males per km², roughly corresponding to 1/3 of female density (SANIGA, 1999).

Material and methods

Differences in habitat preference were studied covering four seasons: spring (March – May), summer (June – September), autumn (October – November), and winter (December – February). In all, 1181 nighttime roosting places (646 in spring, 120 in summer, 160 in autumn, and 255 in winter) and 1,477 daytime locations (719 in spring, 165 in summer, 283 in autumn, and 310 in winter) were recorded in the years 1981–2003. Although these observations did not provide absolute data about the number of individual birds in capercaillie populations, they were useful as relative data in relation to their seasonal preference to the forest ecosystems.

Because ground activities take place near to feeding and roosting trees, occurrence can be mapped by locating feeding and roosting trees (activity trees). An activity tree was a tree with a minimum of five droppings beneath it. A feeding tree was an activity tree beneath which I also found spilled needles with beak marks. I consider the number of activity trees to be a good measure of how much an area was used by capercaillie, because in cases for which data were available the number of activity trees was positively correlated with the number of birds present and the time of stay. Intestinal faeces excreted regularly every 12–13 min (KLAUS et al., 1986), and caecal droppings excreted once or twice a day (MOSS & HANSEN, 1980), accumulate beneath capercaillie feeding trees (identified by droppings and spilled needles) and roosting trees (droppings only) especially during winter. To ensure that the bird has stayed at the spot for some time, only heaps with three or more droppings were included. In early spring (March – early May), conspicuous yellowish-brown faecal remnants in the melting snow show trees used during the preceding 5–6 months (GJERDE, 1991a).

Censuses of capercaillies were carried out using the strip transect method (VERNER, 1985) at 15 study plots from 1989–2002 so that absolute values of density were established for certain groups of forest types and vegetation belts. All individuals seen up to a distance of 50 m to each side of the axis of the transect were counted. During the spring and summer season, the birds were usually counted twice a day (early in the morning from 03.00 to 09.00 CET and later in the evening from 17.00 to 20.00 CET). During the autumn and winter period, quantitative research was conducted in the morning after sunrise and in the afternoon before sunset. Data from the field checks from the transects under study were subsequently analysed and the density per 100 ha was calculated (ind./100 ha).

Eight study plots were selected in the spruce-beech-fir vegetation belt (altitude ranging from 850–1,270 m a.s.l.), three in the spruce vegetation belt (at an altitude of 1,250–1,530 m a.s.l.), two in the fir-beech vegetation belt (altitude ranging between 650–800 m a.s.l.) and two in the dwarf pine vegetation belt (1,350–1,480 m a.s.l.). In the forests of the fir-beech vegetation belt, a total length of transect of 35 km was investigated for each season. In the biocoenoses of the spruce-beech-fir vegetation belt, a total length of transect of 120 km was researched for each season. In the biocoenoses of the spruce vegetation belt, a total length of transect of 86 km was investigated for each season. In the biocoenoses of the dwarf pine vegetation belt a total length of transect of 40 km was investigated for each season.

Through observations of birds, evidence was collected to help define the ecological requirements of the capercaillie at various times of the year (number of individuals, sex, activity, intra- and interspecific interactions, weather conditions, age, tree composition and space-structure of the stands, influence of human activity).

The number of individuals present, and the lek and territorial behaviour description were studied at 43 display grounds within the spring (mid-March – mid-May) and autumn (October – mid-November) lek periods.

The geobiocoenological nomenclature of vegetation belts and groups of forest types was used according to RANDUŠKA et al. (1986). In the statistical analysis the χ^2 test (ZAR, 1996; HINTZE, 1997) was used.

Results and discussion

Habitat and distribution

As a typical inhabitant of the Palearctic boreal forests, in C Europe, the capercaillie is restricted to the climax stage of the forest from the lowlands up to the tree limit in the Alps, Pyrenees, and the Carpathians (KLAUS et al., 1986). Primeval forests in a stage of disintegration fit the ecological requirements of the capercaillie perfectly (EIBERLE, 1976).

In the study area, the capercaillie population inhabited old natural forests (100–250 years old) in the spruce-beech-fir (850–1,270 m a.s.l.) and spruce vegetation (1,250–1,530 m a.s.l.) belts in particular. Optimal conditions were met not only in mountain mixed forests with a canopy closure overstorey of 60–70%, composed of Norway spruce (*Picea abies*), fir (*Abies alba*), beech (*Fagus sylvatica*), and sycamore (*Acer pseudoplatanus*), but also in primeval spruce forests scattered with beech (*Fagus sylvatica*), rowan (*Sorbus aucuparia*), and sycamore (*Acer pseudoplatanus*).

The presence of a sparse understorey composed of tree-species of the overstorey (for concealment, roosting and feeding), and of a good species diversity of vegetation cover (for feeding) seemed to be very important features of the capercaillie habitat. Most leks (35) had a multilayered stand structure and only eight leks had a monolayered stand (statistically significant difference: $\chi^2 = 4.8$, $df = 1$, $P < 0.037$).

Seasonal differences in habitat use in relation to vegetation belts

The capercaillie's use of habitat in relation to the forest types and vegetation belts differed from season to season (Tab. 1). During the spring season (March – May), both males and females preferred forests of the spruce-beech-fir vegetation belt (54% and 52% frequency locations, respectively), but less so in the stands of the spruce vegetation belt (34% and 40% frequency locations, respectively). These two types of habitat were preferred to the remaining two habitats, which comprised 12% frequency locations in cocks and 8% in hens, respectively.

The frequency of observations during the display season corresponded with the distribution of the display grounds in the study area: most display grounds (15) were located in the *Fageto-Aceretum* forest type, eight leks in the *Fageto-Piceetum* forest type, five leks in the *Abieto-Fagetum* and *Fageto-Abietum*, and five leks in the *Sorbeto-Piceetum* and *Acereto-Piceetum* forest types (number of observations was insufficient for proof of statistical significance $\chi^2 = 6.2$, $k = 6$, $df = 5$, $\chi^2_{0.05} = 11.242$).

Regarding tree species composition, display grounds occurred in habitats ranging from a predominance of coniferous tree species (> 80%, 14 leks) to forests with predominance of deciduous trees (> 80%, 10 leks). Most leks (19) were made up of mixed forests. Neither absolutely pure coniferous nor deciduous forests were used for the leks (differences in preference of individual forest types

Table 1. Seasonal differences in habitat use in capercaillie in relation to vegetation belts and forest types (West Carpathians, Slovakia, 1981–2003, $n = 2,658$).

Vegetation belt	Season	Spring				Summer				Autumn				Winter			
		Forest		Type		C		H		C		H		C		H	
	Type	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
F-B	<i>Fageto-Abietum</i>	21	23	2	20	3	25	1	20	4	21	2	20	6	24	5	31
	<i>Abieto-Fagetum</i>	23	25	2	20	2	17	2	40	5	26	3	30	7	28	4	25
	<i>Fageto-Aceretum</i>	48	52	6	60	7	58	2	40	10	53	5	50	12	48	7	44
	Sum	92	9	10	3	12	6	5	7	19	5	10	12	25	7	16	9
S-B-F	<i>Fageto-Abietum</i>	47	9	19	11	8	10	3	10	19	19	3	9	13	8	8	11
	<i>Abieto-Fagetum</i>	59	11	22	12	9	12	2	6	12	12	4	12	9	6	6	8
	<i>Fageto-Aceretum</i>	192	34	69	39	25	32	13	42	30	29	15	44	52	35	17	24
	<i>Pracineto-Aceretum</i>	11	2	4	2	3	4	2	6	2	2	2	6	1	1	2	3
	<i>Fageto-Piceetum</i>	243	44	64	36	33	42	11	36	39	38	10	29	75	50	38	54
Sum	552	54	178	52	78	36	31	44	102	28	34	40	150	38	71	41	
S	<i>Sorbetto-Piceetum</i>	181	51	52	39	43	44	14	50	108	50	16	48	93	46	39	49
	<i>Acereto-Piceetum</i>	66	19	29	21	17	18	6	21	49	23	7	21	50	24	19	24
	<i>Fageto-Piceetum</i>	105	30	54	40	37	38	8	29	57	27	10	31	61	30	22	27
	Sum	352	34	135	40	97	45	28	39	214	60	33	39	204	52	80	46
DP	<i>Mughetum calcicolum</i>	28	3	18	5	27	13	7	10	23	7	8	9	12	3	7	4
Total		1024	100	341	100	214	100	71	100	358	100	85	100	391	100	174	100

Key: F-B – fir-beech vegetation belt; S-B-F – spruce-beech-fir vegetation belt; S – spruce vegetation belt; DP – dwarf pine vegetation belt; C – cocks; H – hens; N – number of observations.

by this number of observations were not statistically significant: $\chi^2 = 2.6$, $k = 3$, $df = 2$, $\chi_{0.05}^2 = 6.231$.

Norway spruce seemed to be an indispensable component of habitats used by capercaillie cocks and hens in the West Carpathians, as this tree species was present in all home ranges of the study birds. Spruce needles are a staple food of capercaillie populations in the West Carpathians during winter (SANIGA, 1998). In contrast, pine needles are a staple food of most other capercaillie populations (SEISKARI, 1962; GJERDE & WEGGE, 1989), thus their winter habitat contains there a preponderance of pine (GJERDE & WEGGE, 1989; WILKINSON et al., 2002).

At the end of spring, after the mating period, hens dispersed mostly into the stands of the spruce-beech-fir vegetation belt at a distance of 50–2,470 metres from the centre of the display grounds. After the display season, cocks appeared in the forests of all the vegetation belts under study, but with different frequency.

According to the strip transect censuses, the capercaillie population spring density fluctuated between 0.2 ind/100 ha (dwarf pine stands), 1.1 ind/100 ha (forests of the spruce vegetation belt), and 2.1 ind/100 ha (forests of the spruce-beech-fir vegetation belt). For the population occupying dwarf pine stands the density value was affected by the methodological bias derived from the disproportionately shorter length of the examined transect in comparison to the lengths of transects in the inferior vegetation belts.

During the summer season (June – September), males favoured forests of the spruce vegetation belt (45% frequency observations), whereas females preferred forest biocoenoses of the spruce-beech-fir vegetation belt (44% frequency locations) (Tab. 1).

Quantitative data obtained from summer transects also showed that the population reached its highest density value in the spruce vegetation belt (3.0 ind/100 ha). Fewer birds were found in natural forests of the spruce-beech-fir vegetation

belt (2.5 ind/100 ha), and in the dwarfed pine biocoenoses (0.5 ind/100 ha).

During the autumn (October – November), males preferred forests of the spruce vegetation belt more strongly (60% frequency locations), whereas females were evenly distributed in the forest ecosystems of the spruce-beech-fir and spruce vegetation belts (41% and 46% frequency observations, respectively). A similar distribution was also calculated from quantitative research on transects: the highest population density was found in the natural spruce forests (3.0 ind/100 ha), the population occupying forests of the spruce-beech-fir vegetation tier had a lower density (2.3 ind/100 ha).

The preference for the biocoenoses of the spruce vegetation belt during the summer and autumn seasons was conditioned by high food availability. Bilberry (*Vaccinium myrtillus*) forms an essential food component of capercaillie diet at this time of year (KLAUS et al., 1986; SANIGA, 1998), and plant communities with bilberry bushes are almost exclusively limited to the forests of the spruce vegetation belt in the study area (groups of forest types *Sorbeto-Piceetum*, *Fageto-Piceetum* and *Acereto-Piceetum*).

Habitat preference during the winter was very similar to the autumn. Within this period, capercaillies were mostly recorded in the coniferous parts of the stands.

Characteristic differences in habitat use during the autumn-winter period resulted both from the larger number of suitable hiding- and roosting-places and from the more favourable climatic conditions (higher average day-temperature, less wind) in coniferous stands, and from food availability during the autumn and winter. Spruce is the main food item in most of the European mountains during the winter (KLAUS et al., 1986; KRISTÍN, 1990; SANIGA, 1998).

During the autumn-winter period, hens often appeared in groups of 2–3(4) birds (107 out of 201 observations), whereas cocks were mainly observed as solitary individuals (350 out of 392 findings), with the exception of roosting-places, where 2–3 cocks sometimes spent the night a few metres (20–250 m) from each other especially in late winter. In S Norway, hens also often appeared in groups of 2–4 birds, whereas cocks lived mainly in solitary fashion (GJERDE et al., 1985). During the autumn display season (October–mid-November), some of the cocks would visit display grounds and spend part of the day there (sometimes the whole night, sometimes they arrived in the early morning and flew away about an hour after dawn). Partic-

ipation of hens in the autumn lek seemed to be occasional.

In S Norway, contrary to my observations, the most obvious cue in habitat selection during the winter period for both sexes was the presence of pine trees, which were used for feeding and arboreal roosting (GJERDE, 1991a) and spruce-dominated forests and younger plantations were avoided by all sex/age capercaillie groups (GJERDE & WEGGE, 1989).

The results of this study on seasonal differences in habitat selection showed that the permanent occurrence of capercaillie in the West Carpathians was restricted to the area of both natural and managed forests of the spruce-beech-fir, spruce and dwarfed pine vegetation belts. Occurrences in the fir-beech vegetation belt below the altitude of 700 m were considered temporary, since there were no suitable coniferous stands for birds to spend the winter permanently.

The results of a 23 year study of the capercaillie grouse in the West Carpathians clearly demonstrate seasonal differences in habitat selection, affected by (i) time-space food availability (in winter, the birds concentrated in stands with a predominance of spruce-groups of forest types *Sorbeto-Piceetum*, *Acereto-Piceetum*, *Fageto-Piceetum*; in summer, capercaillies preferred forest biocoenoses with an abundance of bilberry bushes in ground vegetation – *Sorbeto-Piceetum*, *Acereto-Piceetum*, and *Fageto-Piceetum*; in spring, capercaillies occurred increasingly in the forests of the spruce-beech-fir vegetation belt; (ii) climatic conditions, and the possibilities of concealment and roosting places (in winter, they were almost completely limited to coniferous part of the stands); (iii) characteristic behaviour within the period of the spring and autumn lek (visit of the traditional display grounds).

These differences in observations were statistically significant between all seasons (in males: spring-summer $\chi^2 = 32.2$, $df = 4$, $P < 0.05$; spring-autumn $\chi^2 = 42.2$, $df = 4$, $P < 0.05$; spring-winter $\chi^2 = 38.7$, $df = 4$, $P < 0.05$; summer-autumn $\chi^2 = 51.3$, $df = 4$, $P < 0.05$; summer-winter $\chi^2 = 29.0$, $df = 4$, $P < 0.05$). Similar seasonal differences in habitat selection by capercaillie have been described in other areas of C and N Europe (SCHERZINGER, 1976; PULLI-AINEN, 1982; GJERDE, 1991a, b).

Males preferred Norway spruce for daytime roosting all year round, especially during the winter (87% frequency locations, Tab. 2). Daytime roosting places at the base of the coniferous trees were favoured to deciduous (92% and 8% fre-

Table 2. Positioning of daytime roosting sites in capercaillie cocks in relation to tree species (West Carpathians, Slovakia, 1981–2003, $n = 482$).

Tree species	Spruce		Fir-tree		Pine		Larch		Beech		Sycamore		C/D	Total
Season	N	%	N	%	N	%	N	%	N	%	N	%	%	N
Spring	189	77	30	12	8	3	5	2	10	4	4	2	92/8	246
Summer	41	59	7	10	9	13	7	10	3	4	3	4	82/18	70
Autumn	69	82	6	7	3	4	2	3	2	2	2	2	93/7	84
Winter	71	87	4	5	3	4	1	1	2	2	1	1	96/4	82
Total	370	77	47	10	23	5	15	3	17	3	10	2	92/8	482

Key: C – coniferous trees; D – deciduous trees.

Table 3. Positioning of night-time roosting places in capercaillie cocks (West Carpathians, Slovakia, 1981–2003, $n = 1,049$).

Tree species	Spruce		Fir-tree		Pine		Larch		Beech		Sycamore		Rowan	Snow burrow	Snag	C/D	Total			
Season	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N			
Spring	135	23	37	6	75	13	42	7	229	39	51	8	4	1	0	0	21	3	42/58	594
Summer	19	20	9	9	14	14	10	10	26	27	12	12	3	3	0	0	5	5	43/57	98
Autumn	57	39	17	12	24	17	9	6	20	14	9	6	0	0	6	4	3	2	68/28	145
Winter	82	39	30	14	29	13	20	9	16	8	6	3	0	0	27	13	2	1	66/21	212
Total	293	28	93	9	142	13	81	8	291	28	78	7	7	1	33	3	31	3	50/47	1049

For C and D see Table 2.

quency locations, respectively). Coniferous trees were used as shelter almost exclusively, especially during the winter season (96% frequency locations), which significantly corresponds with the preference for the forests of the spruce vegetation belt during this period. The proportion of daytime roosting places near the trunk of deciduous tree species rose in the spring and summer season (8% and 18% frequency locations, respectively). Other coniferous tree species (fir-tree, pine) may substitute for spruce as cover when the birds roost on the ground, and a shrub layer may be unimportant when conditions for snow-daytime roosting (drifts) are good (GJERDE, 1991a).

During the display season, males preferred to roost in deciduous trees at night (58% frequency locations, Tab. 3), whereas at other times of the year birds roosted more often in coniferous trees (43% in summer, 68% in autumn, and 66% frequency locations in winter, respectively). Seasonal differences in selection of tree species for night-time roosting were affected by (i) climatic conditions (better in canopies of coniferous species); (ii) protection against potential aerial and ground predators (better cover in conifers especially dur-

ing the winter season); (iii) display activity of the cocks (better visibility of displaying males in deciduous trees).

Seasonal differences in habitat use in relation to forest age

Because the area of original forest in the study region is smaller (20%) than that of plantation stands, part of the population had to use the latter. The birds' preferences were largely for those human plantations very similar to the species-space structure of natural forests (80–120 years old, canopy closure of the overstorey of 60–80%, developed understorey, rich vegetation cover). Overstorey stand age varied between 80–250 years with a mean of 128 years. Understorey stand age ranged from 10 to 60 years. Overstorey tree-density varied between 400–1,050 stems per ha (mean 725), which corresponds with Finnish (VALKEAJÄRVI & IJÄS, 1986), and Norwegian (ROLSTAD & WEGGE, 1987) findings. Understorey tree density varied from 5 to 650 trees per ha (mean 290). Stands with higher overstorey and understorey density values were too dense to give the birds an opportunity to move in and

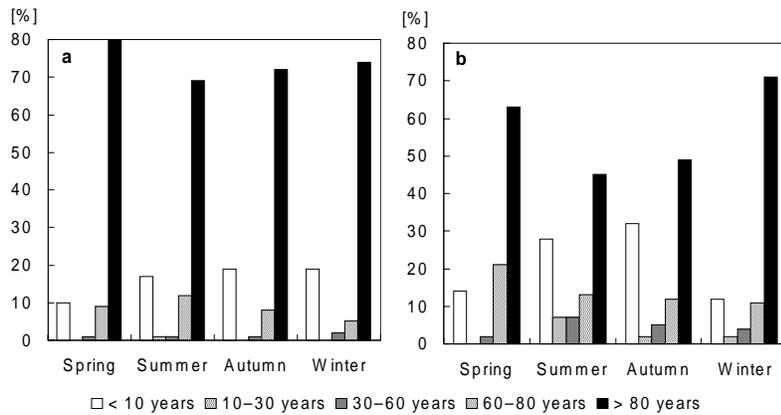


Fig. 1. Seasonal differences in habitat use in capercaillie in relation to forest age (West Carpathians, Slovakia, 1981–2003, $n = 2,658$): a – cocks, b – hens.

through the canopy fairly easily. However, forests with an overstorey stand density of 400 stems per ha were too open and did not provide suitable hiding places from predators. Understorey spruce were almost always present in habitats used by males, but were often lacking in habitats used by hens, which agrees with GJERDE's (1991 a) findings.

Birds were also seen on clearings (Fig. 1) until the plantation closed and they could move among the trees (7–12 years old). Managed stands of the age of 12(15)–30 years were avoided, which was understandable because the stands were too close to permit movement of birds, and there was not enough light to allow food plants to grow. Females may have selected this habitat and also forest of 60–80 years old especially during summer (7% and 13% frequency locations, respectively) and autumn (2% and 12% frequency locations, respectively) because it offered the best cover. Sexual difference in utilization of stands in the age of 10–30 and 60–80 years may be explained as a consequence of the pronounced sexual size dimorphism in this tetraonid. Females are only half the size of males, and manoeuvre more easily in dense habitat. However, the study of a capercaillie population in southern Norway (GJERDE & WEGGE, 1989) also revealed a clear age-dependent habitat selection among males: old males were only occasionally located outside the old natural forest, whereas subadult males used middle-aged pine plantations almost to the same extent as females. The minor difference in body size between adult and subadult males is not likely to lead to differences in habitat preference. According to these authors the discrepancy is a most likely a result of the social organization of the population. Thus the social organization in capercaillie populations espe-

cially during the winter also influences habitat use.

The sightings of males in old forests during the spring season (80%) was significantly higher than females in this habitat (63%, $\chi^2 = 25.8$, $df = 1$, $P < 0.001$). Males preferred old forest (> 80 years) and avoided young plantations (0–30 years) especially during the spring and winter seasons. In contrast, females preferred clearings (0–10 years) especially during the latter part of the summer and during the autumn, because there was an ample food supply (ants, an early ripening of raspberries and bilberries) (Fig. 1). At Varaldskogen (S Norway), GJERDE et al. (1985) recorded 91% and 75% of male and female sightings, respectively, in old forests during winter, which agrees remarkably well with this study.

Recordings of males in old successional stages (forests > 80 years) during the summer (69%) was also significantly higher than that of females in this habitat (45% frequency locations, $\chi^2 = 30.1$, $df = 1$, $P < 0.001$). Throughout the summer and autumn seasons, the use of old successional stages increased gradually, particularly for males but also for females. Presumably, this was due to an increasing proportion of bilberry (*Vaccinium myrtillus*) in the diet (KLAUS et al., 1986; SANIGA, 1998). Bilberry ripens in early August and this species reaches highest coverage and fertility within the old, not too dense successional stages. This knowledge is in accordance with the Finnish (RAJALA, 1966) and Norway studies (ROLSTAD et al., 1988). During late August they recorded the highest densities of capercaillie in old spruce forest-swamp and fresh heaths, i.e., bilberry-rich habitat types. Bilberry, which is the most important food plant for capercaillie in summer and autumn, reaches greatest cover in forest stands > 80 years old. However, the association

with bilberry is only indirectly documented, and future research should evaluate the availability and use of this important food species in more detail (ROLSTAD et al., 1988).

Both males and females preferred old forests throughout the autumn season. Males used old forests more often and clearcuts less often than females (Fig. 1) Ninety-two of the frequency locations of males throughout the autumn were in old forests and in old-forest-clearcut edges. Eighty-one percent of the locations of females were in these habitats, which was less than for males ($\chi^2 = 22.9$, $df = 1$, $P < 0.001$). This is in accordance with the Norway study of ROLSTAD & WEGGE (1987).

The results on habitat selection in capercaillie during the winter season agree with earlier studies, as the successional stages (> 80 years) of the forest were preferred (74% frequency locations in males and 71% in females, respectively) (KLAUS et al., 1986; ROLSTAD & WEGGE, 1989).

Males used habitat edge in proportion to availability, and no specific preference or avoidance was found with respect to tree and shrub coverage or tree and stand layering in all seasons. Within old forests, males preferred forest interiors, using edges of clear-cuts in proportion to availability. Within clear-cuts, males preferred the edges of old forests. Within old forests, females avoided the edges of clear-cuts. Within old forests, females used edges of clear-cuts more often than males ($\chi^2 = 15.3$, $df = 1$, $P < 0.001$). The importance of edges in capercaillie habitat was stressed by STEIN (1974), and supported by the study of KLAUS et al. (1986).

In relation to height of trees, capercaillie males roosted predominantly near trees higher than 10 m (72% frequency observations). During the summer and autumn, birds were found to roost to a larger extent in thickets (19%, and 17% frequency observations, respectively, Fig. 2), which corresponds with habitat use in relation to forest age. Vegetation types with well-developed understorey were preferred whereas forests which were thinned by reducing the amount of understorey spruce (single-layered stands) were avoided, which is in accordance with FINNE et al. (2000). According to these authors, it is possible that capercaillie males prefer forest with a well-developed understorey when roosting. Capercaillie males were never found roosting in plantations, which confirms LARSEN & WEGGE (1985) conclusions that plantations are unsatisfactory habitats for food and shelter against predators.

Several studies, including this one, have documented the importance of spruce and forest un-

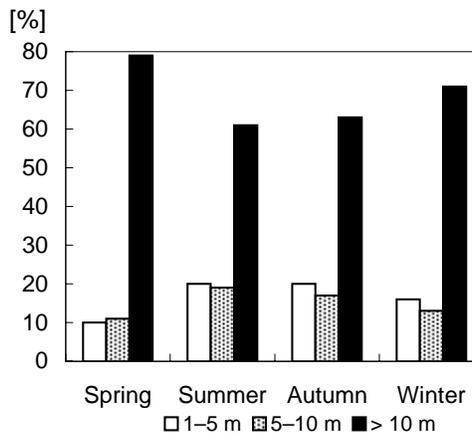


Fig. 2. Positioning of daytime roosting sites in capercaillie cocks in relation to tree height (West Carpathians, Slovakia, 1981–2003, $n = 482$).

derstorey for capercaillie males. SEISKARI (1962) stated that the dependence on spruce seemed to be the essential feature in the habitat requirements of capercaillie during the snow-free season. In a large uncut reserve in the northern Russian taiga, BESHKAREV et al. (1995) reported an extensive use of clumps of spruce within the open pine-dominated forest during daytime in spring. The importance of understorey cover for capercaillie males in winter was documented empirically and demonstrated experimentally by removing spruce trees in intensively used areas (GJERDE, 1991a, b). According to FINNE et al. (2000), to create a forest suitable for both roosting and foraging 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.

Because dense cover reduces the probability that the cocks 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. FINNES's et al. (2000) 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. The forest structures preferred by

capercaillie in winter may be optimal when hiding from predators, or those preferences may simply reflect the forest types that support the best food (GJERDE, 1991a, b). 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 understorey (such as middle-aged plantations and spruce-dominated old forest) when roosting (FINNE et al., 2000).

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