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Ecology of the capercaillie (*Tetrao urogallus*) and forest management in relation to its protection in the West Carpathians

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ABSTRACT: Ecology of capercaillie (*Tetrao urogallus*) was studied in the mountains of Central Slovakia (West Carpathians) in 1981–2003. In the studied area, the capercaillie population inhabited especially old natural forests (100–250 years old) in the spruce-beech-fir (850–1,270 m a.s.l.) and spruce (1,250–1,530 m a.s.l.) vegetation zones. The overstorey stand age ranged between 80 and 250 years with the mean of 128 years. The understorey stand age ranged from 10 to 60 years. The overstorey tree density ranged between 200 and 1,050 stems per ha (mean 725). The understorey tree density ranged from 5 to 650 trees per ha (mean 290). Both males and females preferred old forests throughout the year. The results demonstrate a marked decrease (> 50%) in the numbers of cocks and hens on twelve monitored leks (28%) and a slight decrease (< 50%) on ten display grounds (24%). During the study period, capercaillie cocks became extinct on seven (16%) leks and in their surroundings. More or less constant numbers were found on twelve leks only (28%) and a slight increase occurred on two leks only (4%). A statistically highly significant correlation was found between the area of old-growth forest and the number of cocks attending a lek. In addition to forest deterioration predation appeared to be of major importance in limiting the numbers of capercaillies. Key points for forest management in relation to capercaillie protection are suggested.

Keywords: capercaillie; *Tetrao urogallus*; ecology; predator; forest; management

The capercaillie (*Tetrao urogallus* L.) is a large ground-nesting grouse species with precocial chicks inhabiting in small isolated populations also Central-European mixed spruce-beech-fir and mountain spruce forests in the West Carpathians (KLAUS et al. 1986; SANIGA 1996a,b,c). These forests underwent radical changes from natural regime to managed system especially in the course of the last century. Continuous multi-aged forests were transformed to a mosaic of even-aged stands.

In recent years, greater attention was paid to the effects of forest habitat changes on faunal diversity and performance of wildlife populations (e.g. HELLE 1985; VÄISANEN et al. 1986; LINDÉN 1989; STORAAS et al. 1999). In terms of landscape ecology this large-scale change in forest mosaic is expected to have profound effects on the space pattern and range use of wildlife species, especially those having home ranges and cruising radii within the critical area interval (ROLSTAD, WEGGE 1989a). Capercaillie belongs to this area-sensitive category, inhabiting old forests throughout the year, and having seasonal ranges between 10 and 1,000 hectares in size (WEGGE, LARSEN 1987).

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

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 West Carpathians (SANIGA 1996a,b,c, 1999, 2001).

This paper reports on the findings of a population study of twenty-three capercaillies in the mountains of Central Slovakia (West Carpathians). This study is aimed at evaluation of the ecological requirements of the capercaillie and suggestion of forest management in relation to this highly dimorphic tetraonid in the West Carpathians.

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MATERIALS AND METHODS

Study area

Field work took place in the mountains of Central Slovakia (Veľká Fatra Mts., Malá Fatra Mts., Kremnické vrchy Mts., Starohorské vrchy Mts., and Nízke Tatry Mts., West Carpathians, 18°50´–19°10´E; 48°47´–49°19´N) from 1981 to 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 the mean temperature of the warmest month (July) 14.5°C and of the coldest month (January) 5°C. 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 the above sea level and exposure).

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

The area is a mosaic of small patches of different groups of forest site types (classifications according to RANDUŠKA et al. 1986).

As for the age and spatial structure of forest stands, in the fir-beech and spruce-beech-fir vegetation zones, 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 clearcuts and plantations of various age and size. In the spruce vegetation zone, unmanaged natural forests around 150–180 years old predominate (80%).

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

Potential capercaillie egg and chick predators are corvid birds, particularly jay (*Garrulus glandarius*) and raven (*Corvus corax*), sparrow-hawk (*Accipiter nisus*), goshawk (*Accipiter gentilis*), golden eagle (*Aquila chrysaetos*), ural owl (*Strix uralensis*), tawny owl (*Strix aluco*). Among mammals there are red fox (*Vulpes vulpes*), pine marten (*Martes martes*), beech marten (*Martes foina*), small mustelids (*Mustela erminea, Mustela nivalis*), wild boar (*Sus scrofa*), brown bear (*Ursus arctos*), and lynx (*Lynx lynx*).

According to the latest census, the spring density of capercaillie is 0.1–0.7 males per km^2, roughly corresponding to 1/3 of female density (SANIGA 1999).

Field surveys

Capercaillies are difficult to count throughout the year, but it is practicable to count the number of cocks displaying on leks in spring (KLAUS et al. 1986). The accuracy of quantitative surveys depends on the exact timing of the census. In the initial phase of display activity (late March), the cocks do not visit leks regularly. The period between 20th April and 10th May is most suitable for capercaillie surveys in Central Europe (SANIGA 1998a). In this period, the hens also visit leks regularly.

In 1981–2003, a total of forty-three leks were monitored during the spring display season. The study was carried out by observing birds from the vicinity of the leks so that they were left undisturbed. Observation sites were usually occupied in the evening before the arrival of the males and were usually abandoned when the morning display ended. Capercaillies were counted at least twice during the spring display season on the lek. The census on the leks was carried out especially during the period between 20th April and 10th May (peak of lekking activity). A possible bias in the material is that data from some leks were not obtained during this peak period. The number of hens present on the leks is considered as underestimated in comparison with cocks as hens are much less conspicuous on the leks.

Leks were found during the spring display season by:

1. systematic search for potential areas during the morning and evening display and by snow tracking, respectively;
2. field checks of information obtained from local sources. Indirect evidence of capercaillie occurrence and activity was also collected (faeces, footprints in snow, shed feathers, scraps of unconsumed food such as broken twigs and absence of buds on seedlings, and findings of nests or egg-shells).

All these data helped to guide me to leks, roosting and feeding trees, and eventually, it made clear the seasonal distribution of the birds in the forests of the study area. Surveys of the capercaillie on leks were carried out with regard to the timidity of this shy tetraonid.

Differences in habitat preference were studied covering the four seasons: spring season (March–May), summer period (June–September), autumn season (October–November) and winter period (December–February). In all, 1,477 daytime locations (719 in spring, 165 in summer, 283 in autumn, and 310 in winter) were registered in the years 1981–2003. Although these observations did not provide absolute data on the number of individual birds in capercaillie populations, they were useful as relative data in relation to their seasonal preference of 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 the cases for which data were available, the number of activity trees was positively correlated with the number of present birds and the time of their stay. Intestinal faeces excreted regularly every 12–13 min (KLAUS et al. 1986) and caecal droppings excreted once or twice a day (MOSS, HANSSEN 1980) accumulate beneath the 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 melting snow show trees used during the preceding 5–6 months (GJERDE 1991).

Through the 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 spatial structure of the stands, influence of human activity).

Geobiocoenological nomenclature of the groups of forest site types was used according to RANDUŠKA et al. (1986). In the statistical analysis I used χ^2 test (ZAR 1996; HINTZE 1997).

RESULTS AND DISCUSSION

Habitat and distribution

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

In the study area, capercaillie population inhabited especially 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.) zones. Optimal conditions were met not only in mountain mixed forests with a canopy closure of the overstorey 60–l70%, composed of Norway spruce (*Picea abies*), fir (*Abies alba*), beech (*Fagus sylvatica*) and sycamore (*Acer pseudoplatanus*), but also in primeval spruce forests with interspersed beech (*Fagus sylvatica*), rowan (*Sorbus aucuparia*), and sycamore (*Acer pseudoplatanus*).

The presence of not too dense understorey composed of tree-species of the overstorey (for concealment, roosting and feeding), and of 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: $\chi^2 = 4.8$, $df = 1$, $P < 0.037$).

The capercaillie was not a permanent inhabitant in stands near the centres of human activities (frequented tourist paths, ski-slopes, mountain hotels) although these biocoenoses also fulfilled the capercaillie's habitat requirements in their species and spatial structure.

In the Alps (SCHRÖDER et al. 1982), the capercaillie population prefers especially mountain mixed forests composed of spruce, fir, beech and sycamore up to an altitude of 1,500 m. In higher alpine altitudes (1,500 to 1,900 m), birds occupy the larch-cedar-pine forests.

The capercaillie habitat in the Bavarian forest (SCHERZINGER 1976) does not differ from that of the West Carpathians (primeval spruce forests and mountain mixed stands up to 1,453 m a.s.l.).

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 zones. Occurrences in the fir-beech vegetation zone 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 the capercaillie study in the West Carpathians clearly demonstrate seasonal differences in habitat selection, conditioned by:

1. time and spatial food offer (in winter, the birds concentrated in stands with predominance of spruce – groups of forest site types *Sorbeto-Piceetum, Acereto-Piceetum, Fageto-Piceetum*; in summer, capercaillies preferred forest biocoenoses with abundance of bilberry bushes in the ground vegetation – *Sorbeto-Piceetum, Acereto-Piceetum* and *Fageto-Piceetum*; in spring, capercaillies occurred increasingly in the forests of the spruce-beech-fir vegetation zone;
2. climatic conditions and possibilities of concealment and roosting places (in winter, they were almost completely limited to the coniferous part of stands);
3. characteristic behaviour within the period of spring and autumn lek (visit to traditional display grounds).

Seasonal differences in habitat use in relation to forest age

Because the area of original forest in the study locality is smaller (20%) than that of plantation stands, part of the population had to use the latter. The birds preferred those man-made plantations that were very similar to natural forests by their species and spatial structure (80–120 years old, canopy closure of the overstorey 60–80%, developed understorey, rich vegetation cover). Overstorey stand age ranged between 80 and 250 years with the mean of 128 years. Understorey stand age ranged from 10 to 60 years. Overstorey tree-density ranged between 200 and 1,050 stems per ha (mean 725), which agrees with Finnish (VALKEAJÄRVI, IJÄS 1986) and Norwegian (ROLSTAD,

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

Season	Spring				Summer				Autumn				Winter			
Forest age	C		H		C		H		C		H		C		H	
	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
0–10 years	108	10	49	14	36	17	20	28	68	19	27	32	73	19	21	12
10–30 years	0	0	0	0	2	1	5	7	0	0	2	2	0	0	4	2
30–60 years	3	1	8	2	3	1	5	7	3	1	4	5	6	2	7	4
60–80 years	92	9	70	21	25	12	9	13	29	8	10	12	21	5	19	11
80 years	821	80	214	63	148	69	32	45	258	72	42	49	291	74	123	71
Sum	1,024	100	341	100	214	100	71	100	358	100	85	100	391	100	174	100

C – cocks, H – hens, N – number of locations

WEGGE 1987) findings. Understorey tree density ranged 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 for easy movement in and through the canopy. On the other hand, forests with overstorey stand density value under 200 stems per ha were too open and did not provide any suitable hiding places from predators. Understorey spruce was almost always present in habitats used by males but it often lacked in habitats used by hens, which agrees with GJERDE's (1991) findings.

Birds were also seen on clearings (Table 1) until the plantation closed and when they could move between the trees (7–12 years old). Managed stands at the age of 12(15)–30 years were avoided, which was understandable because the stands were too close to allow the movement of birds, and there was not light enough for food plants to grow. Females could select this habitat and also the forest at the age of 60–80 years especially during summer (7% and 13% frequency locations, respectively) and autumn (2% and 12% frequency locations, respectively) because it offered the best cover. Sexual differences in the utilisation of stands at the age of 10 to 30 and 60–80 years can be explained as a consequence of the pronounced sexual size dimorphism in this tetraonid. Females are only half the size of males, and manoeuvre easier in a dense habitat. However, the study of capercaillie population in southern Norway (GJERDE, WEGGE 1989) also revealed a clear age-dependent habitat selection among the 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 likely a result of the social organisation of the population. Thus the social organisation in the capercaillie population influences also habitat use especially during the winter.

Locations of males in old forests during the spring season (80%) were significantly higher than locations of 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. On the other hand, females preferred clearings (0–10 years) especially during the later part of summer and during the autumn seasons because there was an ample food supply (ants, early ripening raspberries and bilberries). At Varaldskogen (southern Norway), GJERDE et al. (1985) recorded 91% and 75% of male and female locations, respectively, in old forests during winter, which agrees with this study remarkably well.

Locations of males in old succession stages (forests > 80 years) during the summer period (69%) were also significantly higher than locations 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 succession stages increased gradually, particularly by males as well as by females. Presumably, it was due to an increasing proportion of bilberry (*Vaccinium myrtillus*) in the diet (KLAUS et al. 1986; SANIGA 1998b). Bilberry ripens in early August and this species has the highest coverage and productivity in the old, not too dense succession stages. This knowledge is in accordance with Finnish (RAJALA 1966) and Norway studies (ROLSTAD et al. 1988). During late August they recorded the highest capercaillie densities in old spruce forests – swamp and fresh heaths, i.e. bilberry-rich habitat types. Bilberry, which is the most important food plant for capercaillie in summer and autumn, has the greatest cover in forest stands > 80 years old. However, the association with bilberry is documented only indirectly, and future research should evaluate the availability and use of this important food species in greater 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. Ninety-two 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 Norwegian study of ROLSTAD et al. (1988).

My results of habitat selection in capercaillie during the winter season agree with earlier studies as the succession stages (> 80 years) of the forest were preferred (74% 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		Pine		Larch		Beech		Sycamore		C/D	Sum
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
Sum	370	77	47	10	23	5	15	3	17	3	10	2	92/8	482

N – number of locations, C – coniferous trees, D – deciduous trees

quency locations in males and 71% in females) (KLAUS et al. 1986; ROLSTAD, WEGGE 1989a).

Males used the 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, used edges of clearcuts in proportion to availability. Within clearcuts, males preferred edges of old forests. Within old forests, females avoided edges of clearcuts. Within old forests, females used edges of clearcuts 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 findings of KLAUS et al. (1986).

Positioning of daytime roosting sites in relation to tree species

Males preferred Norway spruce for daytime roosting all the year long, especially during the winter season (87% frequency locations, Table 2). Daytime roosting places at the bases of coniferous trees were preferred to deciduous ones (92% and 8% frequency locations, respectively). Coniferous trees were used as shelters almost dominantly especially during the winter season (96% frequency locations), which significantly corresponds with the preference of the forests of the spruce vegetation zone 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, pine) can substitute for spruce as cover when the birds roost on the ground, and the shrub layer can even be unimportant when the conditions for daytime snow roosting (drifts) are good (GJERDE 1991).

Positioning of daytime roosting sites in relation to tree height

In relation to tree height, capercaillie males roosted prevailingly near the trees higher than 10 m (72% frequency of observations). During the summer and autumn seasons, birds were also found to roost in thickets more frequently (19%, and 17% frequency of observations, respectively, Table 3), 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's et al. (2000) conclusions. According to these authors, it is possible that capercaillie males prefer a forest with well-developed understorey when roosting. I never found capercaillie males roosting at plantations, which was confirmed by LARSEN and WEGGE's (1985) conclusions that plantations are unsuitable habitats with respect to food and shelter against predators.

Population dynamics on leks

The results demonstrate a marked decrease (> 50%) in the numbers of cocks and hens on twelve monitored leks (28%) and a slight decrease (< 50%) on ten display grounds (24%). During the study period, capercaillie cocks became extinct on seven (16%) leks and in their

Table 3. Positioning of daytime roosting sites in capercaillie cocks in relation to tree height West Carpathians, Slovakia, 1981–2003, $n = 482$)

Season	Spring		Summer		Autumn		Winter		Sum	
Height class	N	(%)	N	(%)	N	(%)	N	(%)	N	(%)
1–5 m	25	10	14	20	17	20	13	16	69	14
5–10 m	28	11	13	19	14	17	11	13	66	14
<10 m	193	79	43	61	53	63	58	71	347	72
Sum	246	100	70	100	84	100	82	100	482	100

N – number of locations

Table 4. Relationship between the amount of old forests (over 80 years old) within 1 km radius of the lek centres and the maximum number of cocks attending a lek (West Carpathians, Slovakia, 1981–2003, $n = 43$ leks)

Old forest (%)	Number of cocks								Sum leks
	1	2	3	4	5	6	8	12	
21–30	3	1							4
31–40	2	2	1						5
41–50	2	2	1						5
51–60			3	1					4
61–70			3	2					5
71–80			4	8	1	1			14
81–90					1	3	1	1	6
Sum leks	7	5	12	11	2	4	1	1	43

surroundings. More or less constant numbers were found on twelve leks only (28%) and a slight increase occurred on two leks only (4%). The average number of birds per lek was 6.3 cocks and 6.0 hens when the monitoring started in 1981. It declined to 1.7 cocks ($r = 0.83$, $P = 0.001$, $y = –0.189x + 20.588$) and 2.6 hens ($r = 0.67$, $P = 0.001$, $y = –0.142x + 15.823$) per lek in 2003. The findings of this study concerning the numbers of cocks and hens visiting the leks during the display season agree roughly with KOIVISTO and PIRKOLA (1961), who monitored 185 leks in Finland. They found 2.3–5.2 cocks and 2.8–3.9 hens per lek.

Surrounding habitats are expected to influence the capercaillie population size on the lek (LARSEN, WEGGE 1985). Forest stands over 80 years old with suitable age and spatial structure covered 20–90% of the area within 1 km of the checked lek centres. On four leks surrounded by forest with only 20–30% old growth, 1–2 cocks displayed. On the contrary, on six leks with 80–90% old growth 5–12 cocks displayed (Table 4). Comparing the number of cocks on forty-three leks with the proportion of old-growth forest (over 80 years old with suitable spatial structure) within 1 km radius of the lek, a statistically highly significant correlation between the amount of old-growth forest and the number of cocks attending the lek was found (Pearson correlation coefficient $r = 0.725$, $P < 0.01$). It is supported by WEGGE and ROLSTAD's (1986) findings that leks surrounded by a high proportion of old-growth forest sustained more males than leks in fragmented areas. On five out of seven leks where capercaillies disappeared completely during the study period the surrounding habitat changed drastically. The presence of old-growth forests with suitable spatial structure within 1 km radius of the lek declined to less than 20%.

When old natural forests are fragmented by clearcuts, the landscape loses the qualities that are very important for this tetraonid. Transformation of the forest landscape from old-growth forests to clearcuts and younger stands augments the number of small rodents. It presumably favours higher densities of predators (especially marten and fox) that prey on capercaillie eggs and chicks (ROLSTAD, WEGGE 1989c). Furthermore, the fragmentation of continuous forest habitat and its replacement by young stands unsuitable for capercaillie disrupts the social organisation of capercaillie populations, particularly the formation of lek communities (KLAUS, BERGMANN 1994).

Moderate thinnings that leave > 500 overstorey trees/ha and small-scale clearcuts < 50 m in diameter are acceptable cutting operations within capercaillie leks (ROLSTAD 1989). However, important prerequisites probably are that lek populations should not be too small, e.g. > 5 displaying cocks, and that the surrounding areas should contain a high proportion of suitable habitats, e.g. > 50% old forest. According to ROLSTAD and WEGGE's (1989a) study, large clearcuts (> 20 ha) and heavy thinnings (leaving < 400–500 stems/ha) space out display activity areas and promote solitary display. Within a short time period (1–5 years), this need not affect the population size and reproductive performance significantly.

However, solitary display presumably restricts the female choice of mates, which in the long run can have profound evolutionary and ecological consequences. The overall population decline can be caused by the general fragmentation of natural old forest areas rather than by direct clearcutting of lekking grounds (ROLSTAD, WEGGE 1989b). Fennoscandian studies show that forest fragments isolated by more than 100–200 m must exceed 50 ha in order to support lekking males (ROLSTAD, WEGGE 1987). ROLSTAD and WEGGE (1989c) hypothesised that the fragmentation of climax coniferous forests increases the areas with grass and deciduous shrubs, which benefits early succession of grazing herbivores. It triggers a numerical response of small- and medium-sized predators, which, in turn, promotes a higher predaceous pressure on ground nesting birds such as capercaillie.

Hunt has been the main cause of regression in nine capercaillie lek populations. Reviews on shooting and compensatory survival after shooting in grouse were given by ELLISON (1991) and BAINES and LINDÉN (1991). Birds with low natural mortality rates like capercaillie can compensate for shooting to a limited extent only, in contrast to black grouse or hazel grouse (ELLISON 1991). If shooting occurs in autumn and mainly young birds are shot that are characterised by high winter mortality, the effect on the breeding population of adults can be negligible. In contrast, shooting in spring will almost always diminish the number of breeding birds because little time will be left for compensatory survival to occur (KLAUS, BERGMANN 1994).

Predators influencing the capercaillie populations

Predation appeared to be of major importance in limiting the numbers of birds including the capercaillie. Out of 75 capercaillie clutches 49 (65%) were destroyed. The main mammalian predators of capercaillie eggs were stone marten (*Martes martes*), pine marten (*Martes foina*), mustelids (*Mustela* sp.) and red fox (*Vulpes vulpes*) (altogether 18%), wild boar (*Sus scrofa*) (6%) and brown bear (*Ursus arctos*) (4%). According to KLAUS (1984), the participation of wild boar in capercaillie nest losses could locally reach 30%. The main avian predators of eggs were corvid birds, particularly jay (*Garrulus glandarius*) and raven (*Corvus corax*) (altogether 18%).

In the years with very cold weather during May (heavy snowfall), nests were destroyed by snow cover and abandoned (21%). Four clutches (8%) were found abandoned, their hens probably having been predated by goshawk (*Accipiter gentilis*), golden eagle (*Aquila chrysaetos*) and Ural owl (*Strix uralensis*), or by some of the mammalian predators – lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), martens (*Martes* sp.). The damage originator was not known in 12 destroyed and abandoned nests (25%).

The predaceous pressure on capercaillie nests decreased significantly during the incubation period (74% nest losses during the first half of May, *n* = 49; 54% in the second half of May, *n* = 35). Decreased nest losses during the incubation period were expected because no bird species except birds of prey and owls breeds at the time of capercaillie egg laying. Capercaillie nests quite early in spring prior to the onset of breeding of most sedentary and migratory birds. Thus the predaceous pressure on this forest-dwelling grouse is much higher in the first half of May than later when in the forest habitat inhabited by these tetraonid 53–59 bird species breed (SANIGA1994, 1995a,b). The second factor is that nests placed on the ground at the beginning of May can be exposed very much to predators until the vegetation has adequately developed (FULLER 1995). Thus the predaceous pressure on the early breeding birds is expected to be much higher than later as the breeding season progresses. Like the ANGELSTAM's study (1984) on black grouse, I recorded a more pronounced increase in capercaillie hen mortality during the nesting period (8%, *n* = 49) than in the other forest-dwelling tetraonids – hazel grouse hens (5%, *n* = 104). It was not surprising as the larger capercaillie females mate about 10–15 days earlier than the hazel grouse hens. Presumably, they are even more dependent on the access to limited snow-free patches and emerging new vegetation, thus putting themselves at a high risk of predation (WEGGE 1985). However, a larger sample can disclose that capercaillie hens are subjected to this pattern. STORAAS and WEGGE (1987) assume that the probability that a mammalian predator will detect a nest is not affected by forest fragmentation. On the contrary, the probability that a predator will find a brood can be assumed to be affected by forest fragmentation. There were fewer robbed nests inside the forest (37%, *n* = 31) than at the edge of the forest up to the distance of 20 m into its interior (60%, *n* = 44). This knowledge is in agreement with some studies conducted in Scandinavia (e.g. STORAAS, WEGGE 1987).

The main alternative prey species for typical forest-dwelling grouse predators are small rodents, which show multiannual cycles in the West Carpathians (SANIGA 1998b). Thus, the alternative prey can reduce forest grouse brood predation to some extent depending on the density of alternative prey species. However, when the loss of brood habitat is very high, brood density will be exceptionally high in the remaining brood habitat, and predators can benefit more from searching for broods in brood habitat than from searching for alternative prey (STORAAS et al. 1999).

When a continuous old forest is converted to a mosaic of different succession stages, the fauna changes (ADDICOT et al. 1987). A denser population of predators is expected to exert a higher pressure on the old-forest prey even though their search image is not fine-tuned to this prey category (BRITTINGHAM, TEMPLE 1983). As the forest becomes more fragmented, the distribution of old-forest species also becomes more clumped and predictable, thereby facilitating predators their search efforts. Conversely, a disruption of the continuous habitat means that the birds have to traverse unsuitably, open the habitat more frequently, thereby increasing their exposure to visual predators. Presumably, high predation on eggs and chicks is released by the increased carrying capacity for medium-sized predaceous mammals and corvid birds due to the creation of favourable habitats (clearcuts and young plantations) for microtine rodents and ungulates (STORAAS, WEGGE 1985). The effectiveness of predators on grouse species increases if the quality of the blueberry shrub layer is diminished by air pollution or by large herbivores (PORKERT 1978).

Fences, wires and disturbances

Out of 23 perished adult capercaillies, hitting fences was a common cause of death to 11 (48%) capercaillies. Fences used in mature forests where browsing by deer prevents the growth and development of natural regeneration pose a considerable hazard to capercaillie, especially when a fence runs through the forest. Two capercaillies were found to be killed on the cables of ski-lifts.

Enthusiastic gamekeepers and birdwatchers anxious to view a lek were harmful to capercaillie display. Similarly forest management during the display season caused continued disturbance and had a deleterious effect on lek capercaillie populations. Tourism is a significant limiting factor in most capercaillie habitats in Central Europe (KLAUS, BERGMANN 1994).

Several factors have contributed to the recent dramatic decline in capercaillie population in the mountains of the West Carpathians. Habitat deterioration has probably played the main role. The correlation between the amount of old forest and the number of cocks attending a lek has been significant. The presence of older trees has appeared to be important for capercaillie in the West Carpathians as elsewhere. Other factors have also contributed to the rapid decline. The recent decline in numbers has also been associated with an increase in rainfall and snowfall in early June. The number of rain- and snowdays in this crucial period when most of the chicks hatch has been inversely associated with capercaillie breeding success. Deteriorating climatic conditions for capercaillie could override any improvements in habitat quality (MOSS, PICOZZI 1994). Predation has appeared to be of major importance in limiting numbers of capercaillie populations. Fences have also been an important cause of capercaillie mortality. Continued disturbance caused by gamekeepers, enthusiastic birdwatchers and forest managers has had also a deleterious effect on lek capercaillie populations. The future of capercaillie populations in the West Carpathians will depend on the way in which the forest resources will be used and also on the effects of air pollution on forest health, ground vegetation and the abundance of insects available to chicks during the first weeks of their life (PORKERT 1991). Habitat improvement via forest management practices should be the most successful way to conserve the species.

Key points for capercaillie management

A recent decline in the numbers of capercaillies in Slovakia could be associated with several above-mentioned factors. We must now consider what actions can be taken to maintain and improve the present population.

1. Capercaillie is a big bird with large home range and it can disperse to long distances. Therefore forest management for this tetraonid needs to be strategically planned on a large scale rather than on a local forest or estate level (leks). The smallest subunit of the population that is to consider for management purposes is a lek (300–400 ha of suitable forest habitat). To be viable, the population should include several lekking units (3–4) to support a population of breeding capercaillie.
2. Forestry operations can also disturb a lek. A forest manager should plan to avoid forest operations within 1 km of the lek from March to June.
3. Patches of windthrow within forest ecosystems provide cover and feeding areas for adult capercaillie, so any small patches of windthrow should be retained in forest stands.
4. Deer fences sited through forests are an important cause of death and injury to woodland grouse. A forest manager should avoid siting fences to pass through woodland, especially in the neighbourhood of leks and remove any fences immediately after they have served their purpose.
5. Predators of capercaillie should legally be controlled by hunters.
6. Hunting negatively affects local capercaillie populations (continued disturbances have a deleterious effect on populations), so hunting of cocks should not be allowed.

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Ekológia tetrova hlucháňa (*Tetrao urogallus*) a management lesa vo vzťahu k jeho ochrane v Západných Karpatoch

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ABSTRAKT: V rokoch 1981–2003 bola skúmaná ekológia tetrova hlucháňa (*Tetrao urogallus*) v pohoriach stredného Slovenska (Západné Karpaty). V skúmanom území obývala populácia tetrova hlucháňa predovšetkým prírodné lesy vo veku 100–250 rokov smrekovo-bukovo-jedľového (850–1 270 m n. m.) a smrekového vegetačného stupňa (1 250–1 530 m n. m.). Vek hornej etáže porastov, v ktorých sa hlucháne vyskytovali, kolísal medzi 80–250 rokmi (priemer 128 rokov). Vek spodnej etáže sa pohyboval v intervale 10–60 rokov (priemer 25 rokov). Hustota hornej etáže sa pohybovala medzi 400 až 1 050 stromov na hektár (priemer 725 stromov). Hustota spodnej etáže dosahovala hodnoty medzi 5 až 650 stromov na hektár (priemer 290 stromov). Kohúty aj sliepky preferovali po celú časť roka sukcesne staršie štádiá lesa (nad 80 rokov). Výsledky demonštrujú značný pokles (> 50 %) v počte kohútov a sliepok na dvanástich tokaniskách (28 %) a mierny úbytok (< 50 %) na desiatich tokaniskách (24 %). Počas skúmaného obdobia lokálne populácie tetrova hlucháňa vyhynuli na siedmich tokaniskách (16 %). Viac-menej konštantné počty kohútov a sliepok boli zaznamenané len na dvanástich tokaniskách (28 %) a mierny prírastok hlucháňov bol zistený na dvoch tokaniskách (4 %). Medzi rozlohou vhodných porastov z hľadiska vekovo-priestorovej štruktúry a počtom tokajúcich kohútov na tokanisku bola zistená štatisticky významná závislosť. Predačný tlak bol popri strate optimálneho biotopu výrubom starých porastov druhým významným faktorom limitujúcim stavy v lokálnych populáciách tetrova hlucháňa. V závere autor navrhuje základné odporúčania pre manažovanie lesov z hľadiska ochrany tetrova hlucháňa.

Kľúčové slová: tetrov hlucháň; *Tetrao urogallus*; ekológia; predátor; les; management

V príspevku sú prezentované výsledky z ekologického výskumu tetrova hlucháňa (*Tetrao urogallus*), ktorý autor uskutočnil v pohoriach stredného Slovenska (Západné Karpaty) v rokoch 1981–2003.

V rokoch 1981–2003 autor sledoval populačné stavy tetrova hlucháňa na 43 tokaniskách v pohoriach Malej a Veľkej Fatry, Kremnických a Starohorských vrchov a Nízkych Tatier počas jarného obdobia toku (marec–máj). Skúmal rozdiely v preferencii biotopu počas štyroch ročných období: jarné obdobie (marec–máj), letné obdobie (jún–september), jesenné obdobie (október–november) a zimné obdobie (december–február). Celkovo autor získal 1 477 denných lokalizácií hlucháňov (719 v jarnom období, 165 v letnom období, 283 v jesennom období a 310 v zimnom období).

V skúmanom území obývala populácia tetrova hlucháňa predovšetkým prírodné lesy vo veku 100–250 rokov smrekovo-bukovo-jedľového (850–1 270 m n. m.) a smrekového vegetačného stupňa (1 250–1 530 m n. m.). Prítomnosť nie príliš hustého podrastu pod materským porastom (možnosti pre odpočinok, úkryt a kŕmenie) a pestrá druhová diverzita bylinnej etáže (potrava) tvorili dôležitú charakteristiku biotopu tetrova hlucháňa. Väčšina tokanísk (35) vykazovala viacvrstvovú porastovú štruktúru a len osem tokanísk tvorili jednovrstvové lesné porasty (štatisticky významný rozdiel: $\chi^2 = 4{,}8$, $df = 1$, $P < 0{,}037$).

Vek hornej etáže porastov, v ktorých sa hlucháne vyskytovali, kolísal medzi 80–250 rokmi (priemer 128 rokov). Vek spodnej etáže sa pohyboval v intervale 10–60 rokov (priemer 25 rokov). Hustota hornej etáže sa pohybovala medzi 400 až 1 050 stromov na hektár (priemer 725 stromov). Hustota spodnej etáže dosahovala hodnoty medzi 5 až 650 stromov na hektár (priemer 290 stromov).

Tak kohúty, ako aj sliepky preferovali po celú časť roka sukcesne staršie štádiá lesa (nad 80 rokov). Kohúty preferovali staršie sukcesné štádiá lesných porastov (nad 80 rokov) častejšie ako sliepky, zatiaľ čo u holín a zalesnených rúbanísk do 10 rokov tomu bolo naopak. V rámci starších sukcesných štádií porastov (nad 80 rokov) sliepky sa vyskytovali na okrajoch susediacich s rúbaniskami častejšie ako kohúty ($\chi^2 = 15,3$, $df = 1$, $P < 0,001$).

Počas celého roka kohúty najčastejšie odpočívali počas dňa pri báze kmeňov smreka obyčajného (*Picea abies*), obzvlášť však v zimnom období (87 % lokalizácií). Kohúty uprednostňovali denný odpočinok pri báze ihličnatých stromov počas celého roka (92 %).

Pokiaľ sa jednalo o výšku stromov, počas denného odpočinku kohúty uprednostňovali stromy vyššie ako 10 m (72 % lokalizácií). V jarnom a letnom období však vo zvýšenej miere (17–19 %) odpočívali počas dňa aj pri nižších stromoch (do 10 m).

Výsledky demonštrujú značný pokles (> 50 %) v počte kohútov a sliepok na dvanástich tokaniskách (28 %) a mierny úbytok (< 50 %) na desiatich tokaniskách (24 %). Počas skúmaného obdobia lokálne populácie tetrova hlucháňa vyhynuli na siedmich tokaniskách (16 %). Viac-menej konštantné počty kohútov a sliepok boli zaznamenané len na dvanástich tokaniskách (28 %) a mierny prírastok hlucháňov bol zistený na dvoch tokaniskách (4 %).

V roku 1981 pripadalo priemerne na jedno monitorované tokanisko 6,3 kohútov a 6,0 sliepok. Tieto hodnoty počas sledovaného dvadsaťtriročného obdobia výrazne poklesli: 1,7 kohútov ($r = 0,83$, $P = 0,001$, $y = –0,189x + 20,588$), resp. 2,6 sliepok ($r = 0,67$, $P = 0,001$, $y = –0,142x + 15,823$) na tokanisko v roku 2003.

Predpokladá sa, že lesné porasty v širšom okolí tokaniska ovplyvňujú populačný stav tetrova hlucháňa. Medzi rozlohou vhodných porastov z hľadiska vekovo-priestorovej štruktúry v širšom okolí tokaniska (s polomerom 1 km okolo tokaniska) a počtom tokajúcich kohútov na tokanisku bola zistená štatisticky významná závislosť (Pearsonov korelačný koeficient $r = 0,725$, $P < 0,01$). Keď sa rozloha starých porastov (nad 80 rokov) s vyhovujúcou vekovo-priestorovou štruktúrou zmenšuje a takéto lesné ekosystémy sa rozčleňujú pre tetrova hlucháňa nevyhovujúcimi porastmi (rúbaniská, mladiny, žŕďkoviny a žŕďoviny), lesné prostredie stráca dôležitú charakteristiku, ktorá je pre dlhodobé prežívanie populácií tohoto tetrovovitého vtáka nevyhnutná.

Predačný tlak bol popri strate biotopu výrubom starých porastov druhým významným faktorom limitujúcim stavy v lokálnych populáciách tetrova hlucháňa. V závere autor navrhuje základné odporúčania pre manažovanie lesov z hľadiska ochrany tetrova hlucháňa:

1. Tetrov hlucháň je vtáčí druh s veľkým teritóriom (desiatky až stovky hektárov), a tak manažment lesných porastov vo vzťahu k jeho ochrane musí byť strategicky plánovaný na dostatočne veľké územie (niekoľko stovák hektárov), nestačí uvažovať v dimenziách tokaniska (niekoľko hektárov). Najmenšiu populačnú jednotku prichádzajúcu do úvahy u tetrova hlucháňa predstavujú vtáky zúčastňujúce sa „spoločenského“ života počas toku v okolí jedného tokaniska. Takéto spoločenstvo hlucháňov obýva priestor 300–400 ha vhodného lesného biotopu. Populácia tetrova hlucháňa, pokiaľ má byť „životaschopná“, musí zahŕňať niekoľko takýchto tokaniskových populačných jednotiek (3–4), a preto pri návrhu lesopestovných opatrení vo vzťahu k tetrovovi hlucháňovi musíme uvažovať vo väčšom meradle (stovky hektárov).
2. Lesopestovné výkony narúšajú život populácií tetrova hlucháňa – obzvlášť citlivo počas obdobia toku. Preto by v tomto období (marec–máj) v okolí tokanísk mala byť vylúčená akákoľvek lesohospodárska činnosť.
3. Vývraty poskytujú hlucháňom vhodné úkrytové možnosti, a tak by mali byť v maximálnej miere ponechané v lesných ekosystémoch.
4. Ochranné pletivo proti zveri predstavuje pre tetrova hlucháňa veľké nebezpečenstvo, a tak by takýto spôsob ochrany založených kultúr mal byť citlivo zvažovaný a v tesnom susedstve tokanísk absolútne vylúčený.
5. Zvýšená pozornosť by sa mala venovať populačnej dynamike najvýznamnejších prirodzených predátorov tetrova hlucháňa a ich stavy by sa mali udržovať na „únosnej“ úrovni.
6. Odstrel kohútov tetrova hlucháňa negatívne ovplyvňuje lokálne populačné jednotky, a tak by sa nemalo uvažovať o povolení ich lovu.

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