Nest loss and chick mortality in capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) in West Carpathians

Miroslav SANIGA

Institute of Forest Ecology, Slovak Academy of Sciences, Research Station, SK-976 02 Staré Hory, Slovakia; e-mail: uelsav@bb.sanet.sk

A b s t r a c t . From 1983–2001, nest and chick losses in capercaillie and hazel grouse were studied in the mountains of Central Slovakia (Veľká Fatra Mts, Malá Fatra Mts, Kremnické vrchy Mts, Starohorské vrchy Mts, and Nízke Tatry Mts, 18°50'–19°10'E; 48°47'–49°19'N). Out of 75 capercaillie clutches 49 (65%) were destroyed. Out of 159 hazel grouse clutches 104 (65%) were destroyed. The main mammalian egg predators were stone marten (*Martes foina*), pine marten (*Martes martes*), mustelids (*Mustela* sp.), and red fox (*Vulpes vulpes*) (altogether 22%), wild boar (*Sus scrofa*) (9%), and brown bear (*Ursus arctos*) (3%). The predation pressure on capercaillie and hazel grouse nests decreased significantly during the incubation period (74% nest losses during the first half of May, 54% in the second half of May). Nest losses in both capercaillie and hazel grouse followed the fluctuation in small rodents, with lowest losses during peak year (57%) and highest losses during crash year (82%) and prepeak year (80%). Average number of capercaillie chicks accompanying a hen in June significantly decreased during the study period (5.0 in 1983, 2.6 in 2001). In contrast, in hazel grouse, no significant decrease in number of chicks per hen in June was recorded during the study period.

Key words: capercaillie, hazel grouse, predation pressure, West Carpathians

Introduction

Capercaillie (*Tetrao urogallus* L.) and hazel grouse (*Bonasa bonasia* L.) are largely confined to the Palearctic boreal coniferous forest, but isolated populations occur also in Central-European mountainous forests (B e r g m a n n et al. 1982, K l a u s et al. 1986).

Long-term counts in Central Europe show, especially in capercaillie and in some regions also in hazel grouse, a persistent downward trend of numbers especially in the second half of this century (B e r g m a n n et al. 1982, K l a u s et al. 1986). A decline in capercaillie populations has also been observed during the last 20–30 years in Fennoscandia and Russia (e.g. R a j a l a & L i n d é n 1984, R o l s t a d & W e g g e 1989a). Due to high nest and chick predation, areas heavily harvested by clearcutting and replanting practices during the last three decades in Norway have become capercaillie sinks, and chick losses are higher in the fragmented forest matrix than in larger, intact blocks of old forest (W e g g e et al. 1992). Many local capercaillie populations have even disappeared during the last few decades in Central Europe (e.g. N o v á k o v á & S ť a s t n ý 1982, K l a u s & B e r g m a n n 1994, S a n i g a 1999).

Although various aspects of these tetraonids have received much study in Europe (e.g. H j o r t h 1970, S c h e r z i n g e r 1976, R o l s t a d & W e g g e 1989a, G j e r d e 1991a,b), populations in the West Carpathians have received little attention. Most Slovakian data concerning the population dynamics of capercaillie and hazel grouse come from hunting statistics (B a n c í k 1969, F e r i a n c 1977, R i c h t e r 1983). Some data on the

population density of these tetraonids are available from the mountains in the West Carpathians (S a n i g a 1996a,b, 1999).

This paper reports on the findings of a nineteen-year capercaillie and a thirteen-year hazel grouse study in the mountains of Central Slovakia. This study is aimed at nest and chick losses of these forest-dwelling tetraonids. I examine the relationship between nest and chick losses and predation factors.

Study Area

The 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, 18°50'–19°10'E; 48°47'–49°19'N, area about 1000 km^2) from 1983–2001.

The topography 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 precipation 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 see-level and exposure).

In the area under study, mixed forest biocoenoses consisting of the spruce-beech-fir vegetation tier dominate (90%) (*Picea abies, Abies alba, Fagus sylvatica, Acer pseudoplatanus*). Coniferous forests of the spruce vegetation tier constitute around 10% of the study area (*Picea abies* dominated, sprinkled with *Acer pseudoplatanus, Fagus sylvatica,* and *Sorbus aucuparia*).

The area is a mosaic of small patches of different groups of forest types (classifications according to R a n d u š k a 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%.

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

Main small rodent species are bank vole (*Clethrionomys glareolus*), common vole (*Microtus arvalis*), and wood mouse (*Apodemus sylvaticus*). Potential capercaillie and hazel grouse egg and chick predators are corvid birds, particularly jay (*Garrulus glandarius*) and raven (*Corvus corax*), sparrowhawk (*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*), stone marten (*Martes foina*), small mustelids (*Mustela erminea, Mustela nivalis*), wild boar (*Sus scrofa*), brown bear (*Ursus arctos*), and lynx (*Lynx lynx*).

The grouse populations, particularly capercaillie, were declining and numbered between 0.5 and 2.7 capercaillie (S a n i g a 1999) and between 5.0 and 11.0 hazel grouse per 100 ha during spring (S a n i g a 1995a). Other ground-nesting birds are a few woodcocks (*Scolopax rusticola*) and passerines.

Material and Methods

In 1983–2001, nest and chick losses in capercaillie and in 1989–2001 in hazel grouse were studied. Altogether, 75 capercaillie clutches, 98 hens with chicks in June and 96 in the period

between 1 August and 15 September were checked. Altogether, 159 hazel grouse clutches, 165 hens with chicks in June and 159 in the period between 1 August and 15 September were examined. As the conventional method, i.e. calculating nest loss as a percentage of nest loss of total number found, leads to underestimation, in this study nest loss is expressed according to M a y f i e l d ' s (1975) method.

Nests predators were identified from indirect evidence based on tracks, bite marks on egg-shells and also from location and handling of eggs. Raven and jay predation was easily distinguished from that of mammalian predators. Among the latter, pine and stone martens, stoat, fox, and lynx were difficult to separate and were lumped together except in those cases when clear evidence was available (tracks on snow, hair).

Results and Discussion

N e s t   l o s s e s   a n d   t h e   v o l e   c y c l e

Predation appears to be of major importance in limiting the numbers of birds, including capercaillie and hazel grouse. Out of 75 capercaillie clutches, 49 (65%) were destroyed. Out of 159 hazel grouse clutches, 104 (65%) were damaged. The main mammalian egg predators of capercaillie and hazel grouse were pine marten, stone marten, mustelids, and red fox (altogether 22%), wild boar (9%), and brown bear (3%). According to K l a u s (1984), the proportion of nest loss by wild boar on capercaillie can locally reach 30%. The main avian egg predators were corvid birds, particularly jay and raven (altogether 18%).

In the years with very cold weather during May (heavy snowfall), nests were destroyed by snow cover and abandoned (20%). Nine clutches (6%) were found abandoned, their hens probably having been predated by goshawk, golden eagle, or ural owl, or by some of the mammalian predators – lynx, red fox, marten. The damage agent was not known in 34 destroyed and abandoned nests (22%).

Predation pressure on capercaillie and hazel grouse nests decreased significantly during the incubation period (74% nest loss during the first half of May, n = 129; 54% in the second half of May, n = 105). A decrease in nest losses during the incubation period was expected as, at the time of egg-laying, there only birds of prey and owls are breeding. Capercaillie and hazel grouse nest quite early in the spring prior to the onset of breeding of other resident and migratory birds. Thus the predation pressure on the two forest-dwelling grouse species is much higher in the first half of May than later when the forest habitat is inhabited by 53–59 breeding bird species (S a n i g a 1994, 1995a,b). A second factor is that nests placed on the ground at the beginning of May may be exposed to predators until the vegetation has adequately developed (F u l l e r 1995). Like the study of A n g e l s t a m (1984) on black grouse, I recorded a pronounced increase in capercaillie hen mortality during the nesting period (8%, n = 49) than hazel grouse hens (5%, n = 104). This was not surprising, as the larger capercaillie females mate about 10–15 days earlier than the hazel grouse hens. Presumably, they are therefore even more dependent on access to the limited snow-free patches and emerging new vegetation, thus putting themselves at a high risk of predation (W e g g e 1985). However, a larger sample may disclose that capercaillie hens are subjected to this pattern. S t o r a a s & W e g g e (1987) assume that the probability that a mammalian predator will detect a nest is not affected by forest fragmentation, but the probability that a predator will find a brood may be assumed to be affected by forest fragmentation. Fewer nests were robbed inside the forest (38%, n = 91) than at the edge of

the forest up to the distance 20 m into its interior (61%, n = 143). This result is in contrast to some findings in Bavaria, where predation on dummy nests was lower near forest edges than inside forest stands (S t o r c h 1991) but in agreement with some studies in Scandinavia (S t o r a a s & W e g g e 1987).

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

When continuous old forest is converted to a mosaic of different successional stages, the fauna changes (A d d i c o t t et al. 1987). A denser population of predators is expected to exert a higher pressure on the old-forest prey, even if their search image is not fine-tuned to this prey category (B r i t t i n g h a m & T e m p l e 1983). As the forest becomes more fragmented, the distribution of old-forest species also becomes more clumped and predictable, thereby facilitating predators in their search efforts. Conversely, disruption of the continuous habitat means that birds have to traverse unsuitable, open habitat more frequently, thereby increasing their exposure to visual predators. Presumably, high predation on eggs and chicks is released by increased carrying capacity for medium-sized predation mammals and corvid birds due to the creation of favourable habitats (clearcuts and young plantations) for microtine rodents and ungulates (S t o r a a s & W e g g e 1985).

B e r g m a n n et al. (1982) mention goshawk, sparrowhawk, hobby, golden eagle, ural owl, tengmalm's owl, jay, and raven as the main avian predators of hazel grouse. Pine marten, stone marten, red fox, wild boar, and stoat are mentioned to be the main mammalian predators.

Nest losses in relation to the vole cycle

Small rodents in the study area peaked in number during the late spring and in summer 1996 and crashed in late autumn and during winter. Lowest spring vole density occurred during the year preceding the peak year (1995) and during the year after the peak year (1997).

Nest losses in both capercaillie and hazel grouse followed the fluctuation in small rodents with lowest losses during peak year (57%) and highest losses during crash year (82%) and prepeak year (80%). Losses were lower during vole peak year than other years (Table 1, Mann-Whitney U-test, $p < 0.01$). Data showed a consistent pattern of lowest nest loss during the peak year, followed by the highest losses during the crash year, a more relaxed predation pressure during the low phase of the cycle and increased loss during the prepeak year. There was a significant inverse relationship between spring rodent density and nest losses in both grouse species ($r = 0.720$, $p < 0.05$, 8 df). When the rodent density crashed during winter, the predation pressure on capercaillie and hazel grouse nests

Table 1. Number of nests (N) and nest loss in percent (P) of capercaillie and hazel grouse (West Carpathians, Slovakia, 1993–2001).

Year	1993	1994	1995	1996	1997	1998	1999	2000
N	16	23	17	21	18	20	23	21
P	76	72	80	57	82	69	61	69

increased significantly during the incubation period of the following year. W e g g e & S t o r a a s (1990) on the contrary, did not find a relationship between spring vole density and nest losses in capercaillie at Varaldskogen (Norway).

W e g g e & S t o r a a s (1990) found that when the vole density crashed during spring and summer, the predation pressure on capercaillie nests increased significantly during the incubation period. On the other hand, they observed no decrease in nest losses when the rodents built up a peak during early summer.

Capercaillie and hazel grouse in the West Carpathians breed in various forest habitats (S a n i g a 1994, 1995a,b, 1996a,b). There was no significant relationship between habitat type and nest losses in either forest grouses, probably due to a smaller sample size. Losses varied considerably between years according to the general pattern predicted by the alternative prey hypothesis that predaceous pressure upon forest grouses varies with the density of rodents. Thus, results of this study confirm earlier reports on the relationship between the cyclic fluctuation in the lemmings (*Lemmus lemmus*) and nest losses in black grouse (*Tetrao tetrix*) (A n g e l s t a m 1984), and also data on willow ptarmigan (*Lagopus lagopus*) in northern Europe (M y r b e r g e t 1970). W e g g e & S t o r a a s 1990, who studied the relationship between vole density and nest losses in capercaillie and black grouse in Norway, found that losses were modified by the phenology of the vole cycle, i.e. the timing of irruption and crash in local populations of small rodents.

In the West Carpathians, predation on forest-dwelling grouse nests is probably a random process because such nests constitute a very low food biomass for mammalian and avian predators. Nest losses are therefore expected to vary mainly with the numerical response of predators to their main prey, the small rodents (W e g g e & S t o r a a s 1990). This pattern appears to be confirmed by the data of this study.

Highest nest losses were found in the crash year, in spite of a higher spring density of small rodents than in the following low phase of the cycle. This was probably a combined effect of both the numerical increase in the predation fauna following optimal breeding during the preceding peak rodent year and the sudden disappearance of their primary prey (W e g g e & S t o r a a s 1990). According to these authors, during the low phase and during the prepeak year of the vole cycle, nest loss is mainly determined by the resident number of predators and less by their behavioural response to the prey phase. Following a rapid decline in small rodents, parts of a dense predator population may move out of the area and residents reduce their breeding investments (H a g e n 1969).

An increased nest loss during the prepeak year was unexpected and not according to the alternative prey hypothesis as suggested by A n g e l s t a m et al. (1984), that cycles in the vegetation produce cycles in the herbivores while predators track the vole populations. They argue that during the year preceding the peak, predation will be lower than during the crash and low phase years. Results of this study show that the nest losses in capercaillie and hazel grouse were nearly as high during the prepeak year as during the crash year. One possible explanation for this is that some predators may have migrated into the area and started breeding attempts in response to the increasing vole density detected in the preceding autumn and early spring (W e g g e & S t o r a a s 1990).

A n g e l s t a m (1984) relate grouse reproductive success to the abundance of small rodents in spring, whereas other authors (M y r b e r g e t 1970, S t o r a a s et al. 1982) refer to fluctuating numbers in the autumn. According to W e g g e & S t o r a a s (1990), dramatic and rapid increase in primary food in early summer during the peak year is a more important determinant of grouse nest loss than spring numbers of rodents in any given year.

According to R o l s t a d & W e g g e (1989b), by removing climax coniferous forest in Fennoscandia modern forestry indirectly affects the recruitment negatively by promoting predaceous pressure on capercaillie eggs and chicks. They hypothesize that fragmentation of climax coniferous forests increases the areas with grass and deciduous shrubs, which benefits early successional grazing herbivores. This triggers a numerical response in small- and medium-sized predators, which promotes a higher predation pressure on ground nesting birds such as capercaillie and hazel grouse.

Chick losses and the vole cycle

Altogether 65 out of 98 capercaillie hens were observed leading chicks in June (Table 2). The mean number of chicks per hen in June was 2.9 over the whole study period 1983–2001. However, the average number of chicks accompanying a hen in June significantly decreased during the study period ($r = 0.88$, $p = 0.0003$, $y = -0.421x + 42.396$). It was remarkable that there was a lower mean number of chicks per hen in June in peak year of voles (1996) than in either the previous prepeak year or the following crash year. Similarly, the number of juveniles per hen in the period between 1 August and 15 September was lower in the peak year of small rodents than in prepeak year, yet the differences were not significant due to a small sample size.

Altogether 136 out of 165 hazel grouse hens were observed leading chicks during June (Table 3). The mean number of chiks accompanying a hen was 4.2 over the whole study 1989–2001. There was not significant decrease in number of chicks per hen in June during the study period.

Between 1 August and 15 September, 65 out of 96 capercaillie hens led chicks (Table 4). The mean number of juveniles per hen was 2.2 over the whole study. As in June the average number of chicks accompanying a hen significantly decreased during the study period ($r = 0.77$, $p = 0.0003$, $y = -0.409x + 41.155$).

Altogether 124 out of 159 hazel grouse hens were observed leading chicks in the period between 1 August and 15 September (Table 5). The mean number of chicks accompanying

Table 2. Observations of capercaillie hens with chicks in June (West Carpathians, Slovakia, 1983–2001, $n = 98$).

Year	Number of chicks						Total	Average per hen
	0	3	4	5	6	7		
1983				2			2	5
1984	1						1	0
1986					2	1	3	6.3
1987					1		1	6
1989			2	3	1		6	4.8
1990	3			3	1	1	8	3.5
1991	3		2	2	1		8	3
1992	4		1	1	2		8	2.6
1993	2				1		3	2
1994			1				1	4
1995	2	1	1	2			6	2.8
1996	3	1	1	1			6	2
1997	3	1	1	2			7	2.4
1998	3	3	3	1			10	2.6
1999	3	3	3				9	2.3
2000	3	3	3				9	2.3
2001	3	3	3	1			10	2.6
Total	33	15	21	18	9	2	98	2.9

Table 3. Observations of hazel grouse hens with chicks in June (West Carpathians, Slovakia, 1989–2001, n = 165).

Year	Number of chicks								Total	Average per hen
	0	2	3	4	5	6	7	8		
1989	1		2	6	4	5			18	4.4
1990	3	1	2	4	1		4	3	18	4.5
1991	2		2	4	3	4	2		17	4.4
1992	3	2			1	3		1	10	3.5
1993	2			3	2		2	2	11	4.7
1994				3		2			5	4.8
1995	3		4	5	2		3		17	3.7
1996	2	3				2	3		10	3.9
1997	5		2	2	2	2			13	2.8
1998	2			4			5		11	4.6
1999	3	2		5	4				14	3.1
2000	3		1	3	4	1			12	3.4
2001	2			3	2	2			9	3.8
Total	31	8	13	42	25	21	19	6	165	4.2

Table 4. Observations of capercaillie hens with chicks between 1 August and 15 September (West Carpathians, Slovakia, 1983–2001, n = 96).

Year	Number of chicks						Total	Average per hen
	0	2	3	4	5	6		
1983			1	1	1		3	4
1984		1		1		1	3	4
1986			1	2	1		4	4
1987		1	1		1		3	3.3
1989			2	3			5	3.6
1990		2	2	2			6	2.7
1991	2	3	3				8	1.9
1992	3		2	2			7	2
1993	2	1	2				5	1.6
1994			1	1			2	3.5
1995	3		2	2			7	2
1996	3		2	2			7	2
1997	4	2	2	1			9	1.6
1998	3		1	2			6	1.8
1999	4		1	2			7	1.6
2000	2	3	2				7	1.7
2001	3		2	2			7	2
Total	29	13	27	23	3	1	96	2.2

a hen was 3.3 over the whole study and there was not significant decrease during the study period. In contrast to capercaillie, the mean number of hazel grouse chicks per hen in June and also in the period between 1 August and 15 September in the peak year of small rodents 1996 was significantly higher than in the following crash year.

A higher predation pressure on the capercaillie and hazel grouse chicks was expected in the prepeak and crash years than during peak year. Nonsignificant differences between years with high vole population density and years preceding and following rodent outbreak were probably due to the fact that during the time when hens were leading chicks (June and period between 1 August and 15 September, respectively) the food offer for the main predation fauna was substantially higher than in May when hens incubated clutches. Thus, in spite of the low vole

population density mammalian and avian predators had in June and in the early autumn period between 1 August and 15 September more food offer in the form constituting of eggs and juveniles of other forest-dwelling birds and small mammals. Unsuitable weather conditions (abrupt heavy rains and snowfalls in late spring) caused lower average number of capercaillie chicks per hen during the peak year of small rodents in 1996. On the contrary, in the prepeak and in the crash years of small rodents there were more suitable weather conditions which compensated a higher predation pressure on the capercaillie and hazel grouse chicks.

Predation pressure on chicks was high in spite of the fact that as breeding season progressed food offer for predators was continually increasing. Mean clutch size in capercaillie was 6.8 eggs (n = 75). In nests which were not destroyed or abandoned (n = 26), an average of 5.8 chicks hatched. Hens led an average of only 2.9 chicks (n = 98) in June and only 2.2 chiks (n = 96) in the period between 1 August and 15 September (Tables 2,4).

Mean clutch size in hazel grouse was 7.6 eggs (n = 159). In nests that were not damaged or abandoned (n = 35), on average 6.7 chicks hatched. Hens led on average of 4.2 chicks (n = 165) in June and only 3.3 chicks (n = 159) in the period between 1 August and 15 September. The proportion of hens without chicks in June was higher in capercaillie (34%, n = 98) than in hazel grouse (19% , n = 165). According to W e g g e et al. (1990), capercaillie broods seem to have higher mortality during the first four weeks after hatching, especially in intensively logged forests.

L i n d é n (1981) reported 33.6% capercaillie nest losses in Finland in 1966–1977. In Russia losses (43%) were much higher (S e m e n o v - T y a n - S c h a n s k i 1960). In Norway, capercaillie nest losses fluctuated between 25–41% in the years 1953–1962 and 1967–1976 (W e g g e & G r a s a a s 1977, St o r a s & W e g g e 1985, 1987, W e g g e & S t o r a a s 1990). According to K l a u s (1984), in Thuringia (Germany) nest losses fluctuated between 35–67% in 1971–1975 and was 67% in 1976–1983. Nest losses in capercaillie depend on many factors, such as habitat type, vegetation cover, timing of the egg-laying, egg colour, nest locality, weather condions (M ü l l e r 1984). Predation pressure on capercaillie chicks is modified by regional differences, but also depends on season and other factors (K l a u s et al. 1986). Uncamouflaged nests are more easily detected and

Table 5. Observations of hazel grouse hens with chicks between 1 August and 15 September (West Carpathians, Slovakia, 1989–2001, n = 159).

Year	Number of chicks						Total	Average per hen
	0	2	3	4	5	6		
1989	2		3	6	5		16	16
1990	2		2	4	6		14	3.7
1991	4		1	5	5	2	17	3.5
1992	4			3	5		12	3.1
1993	1			5	4		10	4
1994	2				1	4	7	4.1
1995	4		1		5	2	12	3.3
1996	4		1		5	2	12	3.3
1997	4	2	7	1			14	2.1
1998	4			1	3	5	13	3.8
1999	4		3	4	2		13	2.7
2000	3			3	3		9	3
2001	4			1	3	2	10	3.1
Total	42	2	18	33	47	17	159	3.3

robbed by corvid birds (raven, jay). In contrast, mammalian predators use much scent, thus nest camouflage does not play a significant role.

Very similar nest losses in hazel grouse were found by other authors (S e m e n o v - T y a n - S c h a n s k i i 1960, G a v r i n 1969, B e r g m a n n et al. 1982). Nest losses are much higher in years when the weather conditions during May and June are unsuitable – heavy rains or snowfalls (G a v r i n 1969). According to S e m e n o v - T y a n - S c h a n s k i i (1960), parasites may cause 40–94% of capercaillie chicks of fledging age to perish. Nest losses in hazel grouse caused by mammalian and avian predators reached 10–12% in central part of Russia. Monthly mortality of the hazel grouse chicks was 10–12% in the Ural region (B e r g m a n n et al. 1982) and was correlated with the weather conditions during late spring and early summer. Mean numbers of hazel grouse chicks per hen were very similar to the data in this study (7.4 in June and 4.9 in August, n = 45).

L I T E R A T U R E

ADDICOTT, J.F., AHO, J.M., ANTOLIN, M.F., PADILLA, D.K., RICHARDSON, J.S. & SOULK, D.A., 1987: Ecological neighbourhoods: scaling environmental patterns. *Oikos, 49: 340–349.*

ANGELSTAM, P., 1984: Sexual and seasonal differences in mortality in the Black Grouse *Tetrao tetrix* in boreal Sweden. *Orn. Scand., 15(2): 123–134.*

ANGELSTAM, P., LINDSTROM, E. & WIDEN, P., 1984: Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia, 62: 199–208.*

BANCÍK, L., 1969: Lesníctvo a problematika ochrany a rozšírenia hlucháňa na Slovensku [Forestry and problematic of the protection and distribution of the capercaillie in Slovakia]. *Čs. ochrana prírody, 8:251–262 (in Slovak).*

BERGMANN, H.H., KLAUS, S., MÜLLER, F. & WIESNER, J., 1982: Das Haselhuhn. *Ziemsen Verlag, Wittenberg-Lutherstadt, 196 pp.*

BRITTINGHAM, M.C. & TEMPLE, S.A., 1983: Have cowbirds caused forest songbirds to decline? *BioScience, 33: 31–35.*

FERIANC, O., 1977: Vtáky Slovenska 1 (Birds of Slovakia 1). *Veda, Bratislava, 682 pp.(in Slovak, with summaries in Russian and German).*

FULLER, R.J., 1995: Bird life of woodland and forest. *Cambridge University Press, 244 pp.*

GAVRIN, V.F., 1969: [Ecology of the Hasel grouses in the primeval forest Bialovieza]. *Ochotn. Choz. Belovežskaja Pušča Minsak, 3: 146–172 (in Russian).*

GJERDE, I., 1991a: Cues in winter habitat selection by capercaillie. I. Habitat characteristics. *Orn. Scand., 22: 197–204.*

GJERDE, I., 1991b: Cues in winter habitat selection by capercaillie. II. Environmental evidence. *Orn. Scand., 22: 205–212.*

HAGEN, Y., 1969: Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent fluctuations. *Fauna, 22: 73–126.*

HJORTH, I., 1970: Reproductive behaviour in Tetraonidae. *Viltrevy, 7: 181–596.*

KLAUS, S., 1984: Predation among capercaillie in a reserve in Thuringia. In: Lovel, T. & Hudson, P. (eds), *Proc. Int. Grouse Symp., 3: 334–346.*

KLAUS, S. & BERGMANN, H.H., 1994: Distribution, status and limiting factors of capercaillie (*Tetrao urogallus*) in central Europe, particularly in Germany, including an evaluation of reintroductions. *Gibier Faune Sauvage, Game Wildl., 11: 57–80.*

KLAUS, S., BERGMANN, H.H., ANDREEV, A.V., MÜLLER, F., PORKERT, J. & WIESNER, J., 1986: Die Auerhühner. *Ziemsen Verlag, Wittenberg-Lutherstadt, 276 pp.*

LINDÉN, H.,1981: Changes in Finnish tetraonid populations and some factors influencing mortality. *Finn. Game Res., 39: 3–11.*

MAYFIELD, H.F., 1975: Suggestions for calculating nest success. *Wilson Bull, 87: 456–466.*

MYRBERGET, S., 1970: On the part played by predation in short-term variations in the population of willow grouse in Norway. *Int. Congr. Game Biol., IX: 458–464.*

MÜLLER, F., 1984: The loss of capercaillie clutches – an evaluation of a ten year study on simulated nests in the western Rhön mountains. In: Lovel, T. & Hudson, P. (eds), *Proc. Int. Grouse Symp., 3: 347–353.*

NOVÁKOVÁ, E. & ŠŤASTNÝ, K., 1982: Bestand und Bestandsentwicklung des Auerhuhns in Böhmen und Mähren. In: Kempf, C. (ed.), *Actes Coll. Int. Grand Tetras: 35–42.*

RAJALA, P. & LINDÉN, H., 1984: Finnish tetraonid populations in 1982–83 according to the August route-censuses. *Suomen Riista, 31: 92–99.*

RANDUŚKA, D., VOREL, J. & PLÍVA, K., 1986: Fytocenológia a lesnícka typológia [Fytocoenology and forestry typology]. *Príroda, Bratislava, 339 pp. (in Slovak).*

RICHTER, V., 1983: Početnosť hlucháňa na Slovensku [Number of capercaillies in Slovakia]. *Poľovníctvo a rybárstvo, 10: 10–11 (in Slovak).*

ROLSTAD, J. & WEGGE, P., 1989a: Effects of logging on capercaillie *Tetrao urogallus* leks. II. Cutting experiments in south-eastern Norway. *Scand. J. For. Res., 4: 111–127.*

ROLSTAD, J. & WEGGE, P., 1989b: Capercaillie *Tetrao urogallus* populations and modern forestry – a case for landscape ecological studies. *Finn. Game Res., 46: 43–52.*

SANIGA, M., 1994: Bird community of the forests of the spruce-beech-fir vegetation tier in the Veľká and Malá Fatra mountains. *Biologia, Bratislava, 49/5: 787–794.*

SANIGA, M., 1995a: Breeding bird communities of the fir-beech to the dwarfed-pine vegetation tiers in the Veľká and Malá Fatra mountains. *Biologia, Bratislava, 50/2: 185–193.*

SANIGA, M., 1995b: Seasonal dynamics of the bird assemblages in the natural forests of the spruce vegetation tier. *Folia Zool., 44(2): 103–110.*

SANIGA, M., 1996a: Habitat characteristics of Capercaillie (*Tetrao urogallus*) leks in central Slovakia. *Biologia, Bratislava, 51/2: 191–199.*

SANIGA, M., 1996b: Distribution, habitat preferences and breeding biology of the Capercaillie (*Tetrao urogallus*) population in the Veľká Fatra mountains (West Carpathians). *Biologia, Bratislava, 51/2: 201–211.*

SANIGA, M., 1998: Quantitative-qualitative damage of the woody plants by the mammals and birds in the plantings and natural seedings. *Forest. Jour., 44(1–2): 101–109 (in Slovak, with a summary in English).*

SANIGA, M., 1999: Population dynamics of Capercaillie *Tetrao urogallus* on leks in Central Slovakia in the period 1981–1997. *Vogelwelt, 120, Suppl.: 235–240.*

SEMENOV-TYAN-SCHANSKII, O.I., 1960: [Oecology of the Tetraonids]. *Trudy Laplands. Zapov., 5: 1–318 (in Russian).*

SCHERZINGER, W., 1976: Rauhfusshühner. *Scr.-Reihe Nationalpark Bayer. Wald, Heft 2, 71 pp.*

STORAAS, T., WEGGE, P. & SONERUD, G., 1982: Destruction des nids de grand tetras et cycle des petits rongeurs dans l'est de la Norvege. *Actes du Colloque International sur le Grand Tetras (Tetrao urogallus major). Colmar 1981, p. 166–178.*

STORAAS, T. & WEGGE, P., 1985: High nest losses in capercaillie and black grouse in Norway. In: Lovel, T. & Hudson, P. (eds), *Proc. Int. Grouse Symp., 3: 481–498.*

STORAAS, T. & WEGGE, P., 1987: Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. *J. Wild. Manage, 51: 167–172.*

STORAAS, T., KASTDALEN, L. & WEGGE, P., 1999: Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes. *Wildlife Biol., 5: 187–192.*

STORCH, I., 1991: Habitat fragmentation, nest site selection, and nest predation risk in Capercaillie. *Orn. Scand., 22: 213–217.*

WEGGE, P., 1985: Spacing pattern and habitat use of Capercaillie hens in spring. In: Lovel, T. & Hudson, P. (eds), *Proc. Int. Grouse Symp., 3: 261–277.*

WEGGE, P. & GRASAAS, 1977: Population studies of capercaillie (*Tetrao urogallus*) in South Norway. *Viltrapport, 5: 22–39 (in Norwegian, with a summary in English).*

WEGGE, P. & STORAAS, T., 1990: Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. *Oecologia, 82: 527–530.*

WEGGE, P., ROLSTAD, J. & GJERDE, I., 1992: Effects of boreal fragmentation on capercaillie grouse: empirical evidence and management implications. In: McCullough, D.R. & Barret, R.H. (eds), Wildlife 2001: Populations. *Elsevier Sci. Publ.: 738–749.*