Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway

P. Wegge[1] and T. Storaas[2]

[1] Department of Nature Conservation, Agr. Univ. of Norway, P.O. Box 39, N-1432 Ås-NLH, Norway
[2] Hedmark College, Department of Nature Management, N-2475 Opphus, Norway

Summary. The relationship between nest loss in boreal forest grouse and the fluctuations in small rodents was studied at Varaldskogen in southeast Norway during 1979–1986, covering two complete rodent cycles. Nest loss in capercaillie ($N=174$) and black grouse ($N=81$) was calculated according to Mayfield (1975) based on nests from radio-equipped hens ($N=77$) and nests found by other methods ($N=178$). Small rodent density was measured by snap trapping during spring and autumn. Losses varied as predicted by the classical alternative prey hypothesis (Hagen 1952 and Lack 1954, as elaborated by Angelstam et al. 1984): high losses during rodent crash years (85.5% capercaillie, 51% black grouse), and smaller losses during peak years (54.5% capercaillie, 32.5% black grouse). Losses were inversely related to autumn abundance of rodents in capercaillie ($P<0.05$), but the correlation was not significant for black grouse ($0.10<P<0.20$). In capercaillie, the only species with an adequate sample for analysis, no relationship was detected between spring density of rodents and nest loss. Losses during the prepeak years were nearly as high as during crash years, a result inconsistent with the model. We conclude that the numerical response of predators to their cyclic main prey (i.e. small rodents) probably play a main role during the low phase and prepeak year, whereas the dietary shift is most important during the peak and crash year of the cycle.

Key words: Nest loss – Nest predation – Boreal forest grouse – Tetraonids – Vole cycle

In the boreal forests of northern Fennoscandia the vertebrate communities consisting of small rodents (mainly *Clethrionomys glareolus*, *Microtus agrestis*, *Myopus schisticolor*, and *Apodemus sylvaticus*, medium-sized her-

bivores (mainly *Lepus timidus* and tetraonid birds) and predators preying upon these groups fluctuate in synchronous 3–4 year cycles (Hagen 1952, 1969; Lack 1954; Hørnfelt 1978). Angelstam et al. (1984) suggested two plausible mechanisms for the synchronous cycles: (1) Cycles in the vegetation produce cycles in the herbivores while predators track the vole populations; (2) "The alternative prey hypothesis": predation pressure upon grouse and hare varies with the abundance of voles. Predators track the vole populations, their primary prey, but shift to grouse and hares when voles become scarce. According to the alternative prey hypothesis the autumn short-term fluctuations in grouse may be caused by changing predation pressure on adults, eggs and/or chicks. Except for some preliminary data (Storaas et al. 1982) and Angelstam (1983), no study has yet looked critically into the tentative relationship between nest loss among tetraonids and the vole cycle in boreal forests. In this study we examine the alternative prey hypothesis by investigating how nest losses in capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* were related to the small-rodent cycle during an eight-year period in southeast Norway.

Study area

The study was carried out at Varaldskogen (60°10′N, 12°30′E) in Hedmark County, situated in the middle boreal zone (Abrahamsen et al. 1977). The forest associations are dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Birch *Betula verrucosa* is the most common deciduous tree, and bilberry *Vaccinium myrtillus* and heather *Calluna vulgaris* dominate the ground layer on undisturbed sites. The area is rather flat, elevated 200–400 m above sea level.

During the last 3–4 decades intensive logging and forest management have changed nearly half of the total forested area into 6–20 ha blocks of even-aged pine and spruce plantations. Other human disturbance is minimal.

Main small rodent species are field vole *Microtus agrestis*, bank vole *Clethrionomys glareolus*, wood lemming *Myopus schisticolor* and wood mouse *Apodemus sylvaticus*. Mountain hare *Lepus timidus* are common. Main egg predators are corvid birds, particularly jay *Garrulus glandarius*, red fox *Vulpes vulpes*, pine marten *Martes martes*, stoat *Mustela erminea*, and badger *Meles meles*.

The grouse populations, particularly capercaillie, were declining and numbered roughly 2 capercaillie and 6 black grouse per 100 ha during spring (Wegge 1983, and unpubl). Other ground-nesting birds are a few hazel grouse *Tetrasted bonasia*, passerines, and some species of water birds restricted to wetland habitats.

Material and methods

Nests

Nests were studied using radio-equipped females ($N=77$), and nests located using pointing dogs, reported to us by forestry planting crews or found by chance ($N=178$). Rates of nest loss did not vary between nests found by different methods (Storaas and Wegge 1985). Losses were calculated by Mayfield's (1975) method:

$$a=[1-(1-\tfrac{b}{c})^d] \times 100,$$

where a = estimated nest loss in percent, b = number of days with nest loss, c = total number of observed nest days, and d = incubation time, in days, of the species.

Data from radio-equipped females give the most precise estimate of nest loss, because they also provide information on losses during laying and relaying (Storaas and Wegge 1985). The conventional method, i.e. calculating nest loss as a percentage of nest loss of total number found, leads to underestimation but Mayfield's method partly corrects for this bias (Storaas and Wegge 1985). In this study nest loss is expressed according to Mayfield, using nests form both radio-equipped females and from nests found by other methods. To make data comparable, loss during the laying period and loss in relaid clutches (radiomarked birds) are omitted in the analysis.

Small rodents

Small rodents were caught in late August each year, and from 1981 also in late May, using snap traps baited with oil fat spaced 5 meters apart (Hørnfelt 1978). Trapping was done at fixed stations in all major habitats using a minimum of 600 trap-nights per season. Density is presented as the number of rodents caught per 100 trap nights (Christiansen 1983).

Results

Small rodents at Varaldskogen peaked during the autumns of 1980 and 1984 and crashed in the summers of 1981 and 1985 (Table 1). Whereas the autumn densities fluctuated widely, spring numbers were more constant, with similar indices in the peak year of 1984 and the two crash years. Lowest spring numbers (none caught) occurred two years after each peak year.

Nest losses in both capercaillie and black grouse followed the fluctuations in small rodents with lowest losses

Table 1. Abundance of small rodents, number of nests (N) and nest loss in percent (P) of capercaillie and black grouse at Varaldskogen 1979–1986

Year	Small rodents		Capercaillie		Black grouse	
	Spring	Autumn	N	P	N	P
1979	–	2	12	84	–	–
1980	–	27	47	48	26	7
1981	2	0	41	81	25	51
1982	0	1	17	67	6	80
1983	2	7	23	77	17	38
1984	2	32	19	61	7	29
1985	2	0	10	90	–	–
1986	0	6	5	60	–	–

Numbers caught by snap traps per 100 trap nights

Table 2. Rate of nest loss in capercaillie (in percent) during various phases of the small rodent cycle, Varaldskogen, Norway, 1979–1986

	Prepeak year	Peak year	Crash year	Low phase
1979–82	84	48	81	67
1983–86	77	61	90	60
Combined	80.5	54.5	85.5	63.5

during peak years and highest losses during crash years (Tables 1 and 2). For capercaillie losses increased from 48 and 61% (peaks) to 81 and 90% (crash years). Corresponding figures for black grouse were 7 and 29% (peaks) and 51% (crash year). There was a significant inverse relationship between autumn rodent density and nest loss in capercaillie ($r=0.827$, $P<0.05$, 6 df), but not for black grouse ($r=0.788$, $0.10<P<0.20$, 3 df) (Fig. 1), probably due to a smaller sample for this species. Further, there was no relationship between spring
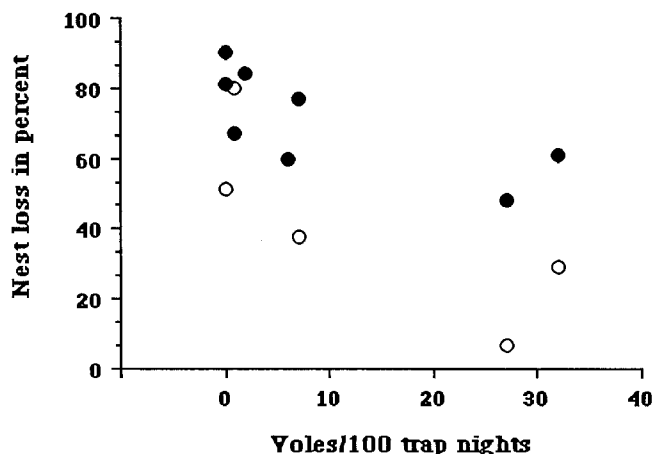

Fig. 1. Relationship between autumn abundance of small rodents and nest loss in capercaillie and black grouse, Varaldskogen, Norway, 1979–1986. ○ Black grouse; ● Capercaillie. Capercaillie: r = −0.827, P < 0.05, Black grouse: r = −0.788, n.s.

Table 3. Number of observed nests (N), nest days (ND), robbed nests (R) and nests robbed per nest day × 100 (I) during a rodent crash year (1981) and a rodent peak year (1984) at Varaldskogen, Norway

Year	May				June				
	N	ND	R	I	N	ND	R	I	
1981	14	112	3	2.7	12	114	11	9.7	$x^2 = 4.81, P < 0.05$
1984	21	250	10	4.0	16	141	5	3.6	$x^2 = 0.16$, n.s..

vole density and nest losses in capercaillie ($x^2 = 0.012$, ns), the only species with adequate data for analysis.

Losses were lower during rodent peak years than other years (Capercaillie: 54.5% vs 76.5%; black grouse: 32.5% vs 56.3%, respectively, Mann-Whitney U test, $P < 0.01$, both). For capercaillie a complete data set covering two vole cycles showed a consistant pattern of lowest nest loss during the peak year, followed by highest loss during the crash year, a more relaxed predation pressure during the low phase of the cycle and increased loss during the prepeak year (Table 2).

When the vole density crashed during spring and summer of 1981, the predation pressure on capercaillie nests increased significantly during the incubation period (Table 3). On the other hand, no decrease was observed in nest loss when the rodents built up to a peak during early summer of 1984 (Table 3).

Discussion

Capercaillie and black grouse at Varaldskiogen nest in all habitats and nest loss is unrelated to habitat type (Storaas and Wegge 1987). Losses varied considerably between years according to the general pattern predicted by the alternative prey hypothesis. Thus, our results confirm earlier reports on the relationship between the cyclic fluctuation in lemmings *Lemmus lemmus* and nest loss in the willow ptarmigan *Lagopus lagopus* (Myrberget 1970) and data on black grouse in Sweden (Angelstam 1983). However, our data indicate that losses are modified by the phenology of the vole cycle, i.e. the timing of irruption and crash in local populations of small rodents.

At Varaldskogen, predation on grouse nests is probably a random process because such nests constitute a very low food biomass for predators (Storaas and Wegge 1987). Nest losses are therefore expected to vary mainly with the numerical response of predators to their main prey, the small rodents. This pattern appeared to be confirmed by the data, except during the peak rodent year. Presumably, the predator density was then increasing, but with a superabundance of food predation on grouse nests was significantly relaxed.

Highest nest losses occurred during the crash years, in spite of a higher spring density of voles then than in the following low phase of the cycle. This was probably a combined effect of both the numerical increase in the predatory fauna following optimal breeding during the preceding peak rodent year *and* the sudden disappearance of their primary prey. This functional response was well illustrated during the crash year of 1981: in spring voles were still quite abundant and the decline did not occur before late in the incubation period. Nest loss was low during the first part an increased dramatically during late May and early June.

During the low phase and the prepeak year of the rodent cycle, nest loss is mainly determined by the resident number of predators and less by their behavioural response to the prey base. Following a rapid decline in voles, parts of a dense predator population may move out of the area and residents reduce their breeding investments (Hagen 1952, 1969; Craighead and Craighead 1956). The net effect is fewer predators, and since grouse nests only represent a low (and unpredictable) food source, no active search effort is initiated. Rates of nest predation are related to random search and total cruising distance of the remaining, low reproducing generalist predators.

An increased nest loss during the prepeak year was unexpected and not according to the alternative prey hypothesis as suggested by Angelstam et al. (1984). They argued that during the year just preceding the peak, predation would be lower than during the crash and low phase years. Our data show that the nest loss in capercaillie was nearly as high during the prepeak year as during the crash year. Since this result was repeated during two complete cycles, the pattern is probably real, although sample size was small some years. One possible explanation for this is that some predators may have immigrated to the area and started breeding attempts in response to the increasing rodent density detected the preceding autumn and early spring.

Angelstam (1983) related grouse reproductive success to the abundance of small rodents in spring, whereas other workers (Hagen 1952, Myrberget 1970; Storaas et al. 1982) referred to fluctuating numbers in the autumn. Our spring indices showed very small amplitudes compared to autumn, partly because traps were set in late May when nutritious plant food is readily available and voles are less vulnerable to trapping. Nevertheless, the lack of a statistical difference between nest loss between years of low and high spring rodent density further suggests that the dramatic and rapid increase in primary food in early summer during the peak year is a more important determinant of nest loss than spring numbers of rodents any given year.

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