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Seasonal mortality of black grouse *Tetra tetrix* during a year with little snow

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The seasonal mortality of black grouse *Tetrao tetrix* was studied in south-eastern Norway (60°26'N, 10°54'E), in a study area dominated by up to 80% Norway spruce *Picea abies*. Modern forestry with clear-cuttings has been practised, and 50% of the forest was younger than 30 years. Fourteen males and seven females were captured on a lek in spring 1991 and equipped with radio transmitters. During the following 12 months, 72% of the birds were killed, mostly by predators. No birds died from capture through July. In autumn, predation was higher, with four black grouse being killed. Mortality was highest during winter, with 58% of the birds dying. The goshawk *Accipiter gentilis* was the most important predator during winter. High predation by goshawks in winter 1991-92 may have been the result of black grouse being more vulnerable to predation because limited snowfall precluded snow roosting, or of an invasion by goshawks. Therefore, snow roosting may be an important antipredator behaviour in black grouse. The effect of increased adult mortality is discussed in relation to chick production.

Key words: antipredator behaviour, black grouse, Norway, seasonal mortality, snow roosting, Tetrao tetrix

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Many grouse species roost in the snow during winter when snow conditions are suitable. This may be an important way of conserving energy during cold weather (Andreev 1977, Marjakangas, Rintamäki & Hissa 1984). The snow roosting behaviour may also be an effective way of avoiding predators (Bergerud & Gratson 1988, Marjakangas 1990). If this is an important feature of snow roosting, predation would be expected to increase during winters with little snow.

Recent studies in Scandinavia have shown that black grouse *Tetrao tetrix* suffer high mortality during the breeding season (Angelstam 1984, Willebrand 1988). Angelstam (1984) also recorded a peak in mortality of males in November, but assumed that no mortality took place during the winter from February to April (Angelstam 1984). The annual mortality rate was estimated at 44%. In another study on black grouse, annual mortality rates for males varied between 48 and 72% and for females between 43 and 52%, with a peak in mortality during the breeding season and another for males during February-March (Willebrand 1988).

In this study we investigate timing of predation on black grouse and which predators are involved. Mortality rates are then related to snow conditions during the winter, and mortality in relation to chick production is discussed.

Study area

The study area was situated on both sides of the lake Skrukkelisjøen in southeastern Norway (60°26'N, 10°54'E). The lake is situated at 330 m a.s.l. with surrounding hills reaching to approximately 600 m. The forest is dominated by Norway spruce *Picea abies*.

Modern forestry with clear-cuts has been practised since World War II and 50% of the forest was less than 30 years old. The average size of plantations and forest stands was about 30 ha. On the southern side of the lake, glyphosate has been used to inhibit deciduous brush growth, and here vegetation was mostly even-aged monocultures of spruce. At the other side of the lake, the forest was more varied, with more birch *Betula* spp., and with scattered Scots pine *Pinus sylvestris*.

Between 15 and 20 males visited the display ground where black grouse were captured. The winters differed between the two years of study with maximum snow depth of 120 cm in 1990-91 and only a few days with 10-20 cm of snow in 1991-92.

Methods

Black grouse were captured on the display ground during the last week of April and the first week of May in 1990 and 1991. Ten males were equipped with necklace radio transmitters in 1990, and 14 males and seven females were instrumented in 1991.

The radio-collared birds were located 1-3 times each month throughout the year. Cause of death and predator species involved were identified when possible, and mortality rates were calculated by season. Spring is defined as April-June, summer as July-August, autumn as September-December and winter as January-March. Percent mortality in each of the four seasons was calculated from the number of birds alive at the start of each season. Seasonal mortality rate thus was the proportion of birds killed to birds alive at the start of the season in question. Annual mortality rate was calculated from all birds except for three grouse with which contact was lost. Because we did not know whether these three birds were dead or alive, they were excluded from the calculations of mortality rates and were omitted from the season in which contact was lost.

Results

Owing to transmitter failures, we can not calculate predation rates of birds caught in 1990. Of the 21 birds captured in 1991, nine were killed by predators and four died of unknown causes. Furthermore, we lost contact with one bird in August and two in October. Their fate is unknown and they were excluded from mortality calculations.

High mortality of black grouse was recorded from May 1991 through April 1992. The annual mortality rate was 72%. About half of the birds were killed by goshawks *Accipiter gentilis* (46%), 23% were killed by pine martens *Martes martes* and about one third (31%) were killed by unknown predators. None of the black grouse captured and instrumented at the lek died during the first weeks after handling. Neither did any birds die during May-July. The first mortalities among the 21 radio-collared black grouse occurred in August, when one female was killed by a pine marten and a male was killed either by a pine marten or a red fox *Vulpes vulpes*.

Two black grouse died in the summer, compared to four in the autumn (Fig. 1), but this difference was not statistically significant. In autumn, a female was taken by a goshawk, and the other three birds died of unknown causes, i.e. no remains other than the transmitter were found. However, one male may have been shot during the hunting season.

The highest mortality was found in winter with

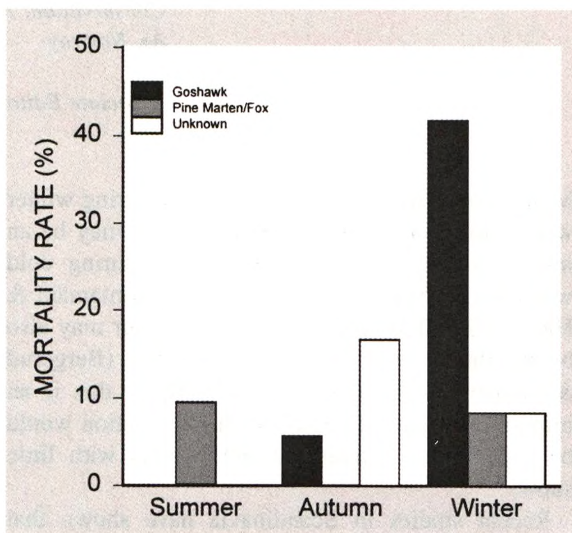

Figure 1. Seasonal mortality rates of black grouse according to predator species involved in the study area at Skrukkelisjøen, southeastern Norway, during 1991-1992.

seven of the 12 remaining birds dying, giving a mortality rate of 58%. The most important predator during this period was the goshawk (see Fig. 1). Only one bird was taken by pine marten, and one was killed by an unidentified predator. The predation peaked in March.

Discussion

Capturing, handling and instrumenting grouse is likely to be a situation of stress for the birds. The stress along with the initial discomfort of the transmitter and possible internal injuries, may directly provoke death or increase vulnerability to predators. A change in behaviour and food intake after radio instrumenting red grouse *Lagopus l. scoticus* was noted by Boag (1972), and he suggested that this may lead to a higher vulnerability to predation, especially during the first week following instrumentation. Furthermore, among black grouse instrumented in Sweden, mortality within the first week after capturing was probably a result of handling and/or the transmitter (Angelstam 1984, Willebrand 1988). In fact, Angelstam (1983) reported that within the first four days after capture, 10.2% of the instrumented birds died, suggesting that the handling strongly affected survival. However, in our study none of the birds died during the first three months after being instrumented. Thus handling and instrumenting do not necessarily increase mortality immediately.

The transmitter may in general increase the mortality compared to unmarked birds. However, evidence that collar transmitters cause increased mortality of galliformes is inconclusive (Hines & Zwickel 1985). In black grouse use of transmitters was suggested not to have affected survival of the birds still alive 1-2 weeks after capture (Angelstam 1983, Willebrand 1988). No measurable effect of transmitters on survival was found in hazel grouse *Bonasa bonasia* (Swenson 1991). Radio-equipped red grouse survived as well as birds without transmitters (Lance & Watson 1977), and use of necklace transmitters had no measurable effect on survival of red grouse (Thirgood, Redpath, Hudson, Hurley & Aebischer 1995). Furthermore, recovery rates of pheasants *Phasianus colchicus* were similar for birds with and without transmitters (Marcström, Kenward & Karlbom 1989). It is, however, important that the ratio of transmitter to body weight is low. A high ratio had a detrimental effect on survival of pheasants (e.g. Warner & Etter 1983). We have no data to evaluate the effect of transmitters on survival of black grouse in our study. However, ratio of transmitter to body weight was below 3% for females and 2% for males. This is well below the recommended limit of 4% (Cochran 1980). Thus, we suggest that the mortality of black grouse in our study was not affected by the transmitters.

More than 70% of the radio-tagged black grouse in our study area died during the year 1991-92. In a 3-year study in Sweden, black grouse suffered high predation one year, with 72% of the males being killed, but with less than 50% of the females being killed (Willebrand 1988). During the other years of the above-mentioned study, predation was around 50% for both sexes. The increased mortality of males in that particular winter was attributed to raptor predation (Willebrand 1988). In our study, close to half of the birds were killed by goshawks, most of them during winter, suggesting that raptor predation is an important mortality factor in some years.

Mortality of black grouse is not evenly distributed throughout the year. High mortality of females has been found during egg laying and incubation (Angelstam 1984, Willebrand 1988). In our study no birds were killed during the breeding period, and all survived until August. Neither did instrumented black grouse from other areas studied in southeastern Norway suffer mortality from May to July (Spidsø & Hjeljord, unpubl. data), contradicting the results of Angelstam (1984) and Willebrand (1988). Most of

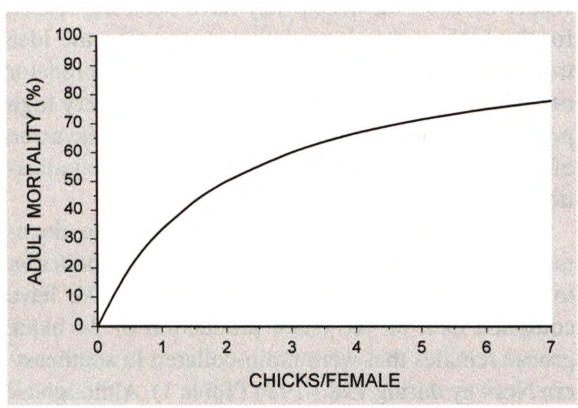

Figure 2. Relationship between annual adult mortality and chick production required to maintain a stable black grouse population. The curve is based on the equation: P = Nm/N(1-m)F, or P = m/(1-m)F; N = the current population, m = adult annual mortality, F = proportion of females in the population and P = number of chicks per female. The curve is based on a male/female ratio of 1/1. A different ratio would move the curve higher up or lower down.

Table 1. Chick production of 34 female black grouse radio-instrumented at four locations in Norway since 1980. Data from Kolstad, Bø & Wegge (1985) and Hjeljord & Spidsø (unpubl. data).

Location	Varald	Varald	Bjørke	Hurda	Hobøl	Hobøl	Total
Year	1980*	1981**	1985**	1991*	1993	1994*	
Females instrumented	6	14	4	7	2	1	34
Broods in August	3	0	0	0	0	0	3

* small rodent peak year
** small rodent crash year

our birds were killed between January and March, with peak mortality in March. The goshawk was the most important predator, and only a few birds were taken by mammalian predators. Willebrand (1988) also found an increase in predation on males in February-March, apparently because of an invasion of goshawks. On the other hand, Angelstam (1984) reported that mortality in males was highest in November. This suggests that mortality may differ in time and space according to different conditions and predators.

Snow roosting is suggested to be an important antipredator option for black grouse in winter (Marjakangas 1992). By roosting in snow, birds will be less vulnerable to predation by raptors. However, blue grouse *Dendragapus obscurus* preferentially used subalpine fir *Abies lasiocarpa* as nocturnal roost sites (Pekins, Lindzay & Gessaman 1991), and Pekins et al. (1991) suggested that energy conservation and not predator avoidance was the primary determinant of nocturnal roost site selection. In our study area, snow roosting was not possible during the winter of 1991-92 which may have been the reason for the high goshawk predation, supporting the idea that snow roosting is an important antipredator behaviour in northern areas. However, this very high predation could also have been caused by an invasion of goshawks that winter, although we have no indication of such an invasion.

The high mortality of adult black grouse documented in our study requires a high chick production to maintain the population level (Fig. 2). We have compiled data on the chick production of 34 black grouse females that were radio-collared in southeastern Norway during 1980-1994 (Table 1). Although all females survived the nesting and brooding period, most lost their eggs or chicks. Thus, 17 females lost their eggs. Many of the remaining females lost their chicks for unknown reasons, but predation was suspected to be the main cause of death (Kastdalen & Wegge 1991). The number of chicks in the three surviving broods was not known, but assuming 4 chicks/brood, the estimated number of chicks/female would be 0.35. Reproduction data from 18 of the 34 females was collected during small rodent crash years (see Table 1), when brood loss is generally high (Wegge & Storaas 1990). Our figures therefore may represent years with medium to poor reproduction.

An increase in adult mortality requires a relatively larger increase in chick production to balance the population. If the annual adult mortality rate of black grouse is 50%, 2 chicks/female are necessary to maintain a stable population (see Fig. 2). With a 20% increase in adult mortality giving a mortality rate of 70%, a net chick production of 5 chicks/female is required to maintain the population. Assuming a male/female ratio of 40/60, the chick requirement is reduced to 4 chicks/female.

A combination of 70% annual adult mortality and a chick production of 0.35/female will lead to a population reduction of 55% in one year and 83% in two years. This may explain the very rapid decrease in the Scandinavian black grouse populations during some periods (Hjeljord 1980). With a weak density dependent influence on mortality and reproduction (Myrberget 1988), stochastic events like changes in winter weather condition and rodent numbers may be important in the population dynamics of Scandinavian grouse. In general our data support the findings of Storaas & Wegge (1985) that predation is the main proximate factor in the regulation of Norwegian grouse numbers.

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