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Relationships between patterns of incubation and predation in sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix*

Torstein Storaas & Per Wegge

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To investigate the effect of timing, frequency and duration of incubation recesses of female grouse on predation, thermistors were placed in 29 nests of capercaillie *Tetrao urogallus* and 10 nests of black grouse *Tetrao tetrix* in southeast Norway during 1983-84. Two female capercaillie were killed by goshawks *Accipiter gentilis* during recesses and 15 capercaillie and three black grouse nests were depredated. The incubation patterns of 20 capercaillie and nine black grouse were measured during 165 and 75 days, respectively. There was no difference between species in how long females stayed away from the nest each day, but black grouse took more and shorter recesses than capercaillie. The recess activity of both species peaked before and after a period of low activity during the night. Although black grouse took the first recess earlier and the last recess later than capercaillie, they also took few recesses in dim light. Nest losses were not associated with the time or frequency of departures from the nest. The data presented suggest that factors other than predation risk may be responsible for the patterns of incubation recesses observed in grouse.

Key words: black grouse, capercaillie, incubation, predation, recess, Tetrao tetrix, Tetrao urogallus

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Skutch (1962) pointed out the bewildering diversity of avian incubation patterns. These patterns have probably evolved in relation to at least three major factors: 1) physical requirements of the embryos for development, 2) metabolic requirements of the parent(s), and 3) predation on eggs and the parent(s) (Afton 1980). Because grouse commonly lose 50% of their nest clutches due to predation, there should be intense selection on the behaviour of females during incubation to minimise the probability of nest failure (Bergerud & Gratson 1988:504). Sympatric capercaillie and black grouse at Varaldskogen in southeast Norway where this study was carried out, lost 71 and 41% of nests, respectively (Wegge & Storaas 1990). However, Storaas & Wegge (1987) did not find that the nest loss for either species was associated with the amount of cover at the nest site, or the type of habitat in which the nest was located.

In grouse, the probability that a clutch will be depredated may be affected by the time of day (Angelstam 1984, Erikstad 1986, Bergerud & Gratson 1988: 517), the frequency (Erikstad 1986) and the duration of the female's recesses. The duration of incubation recesses may be important as eggs are visually much more conspicuous when the female is absent (pers. obs., Bergerud & Gratson 1988:517). However, covering the eggs does not necessarily ensure their safety because mammalian predators (Bower & Simon 1990) and pointing dogs (pers. obs.) are able to detect nests while the female is incubating.

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Anecdotal studies of the incubation pattern in capercaillie (Semenov-Tyan-Shanskii 1960, Lennerstedt 1966, Pulliainen 1971), and in black grouse (Semenov-Tyan-Shanskii 1960, Robel 1969, Angelstam 1984) have not reported any cases of nest loss.

In this study we measured when, how often and for how long females of sympatric capercaillie and black grouse left their nests, and recorded when females were killed and nests were depredated to determine possible relationships between incubation behaviour and predation.

Study area and methods

Our study was conducted in the boreal forest at Varaldskogen field station (60°10'N, 12°30'E), Hedmark County, southeast Norway. Norway spruce *Picea abies* and Scots pine *Pinus silvestris* were the dominant tree species, while *Vaccinium* spp. and heather *Calluna vulgaris* dominated the ground layer. Potential egg-predators were the red fox *Vulpes vulpes*, pine marten *Martes martes*, badger *Meles meles*, stoat *Mustela erminea*, weasel *Mustela nivalis*, hooded crow *Corvus corone cornix*, common raven *Corvus corax* and Eurasian jay *Garrulus glandarius*. The northern goshawk *Accipiter gentilis* was the only avian predator large enough to kill breeding females. For more details of the area see Storaas & Wegge (1987).

Most nests were discovered by locating incubating radio-equipped females, a few were found by chance at different stages of incubation. During 1983 and 1984, we placed a thermistor vertically in the centre of the nest cups of 29 capercaillie and 10 black grouse, with the top of the thermistor just below the upper surface of the eggs to record when the female was sitting on the nest. The thermistor was connected to a Grant Temperature Recorder (Erikstad 1986) placed out of sight about 50 m from the incubating female and the wire to the thermistor was buried to make it invisible. One nest which we suspected was depredated as a result of our activity was omitted from the sample.

We got information on predation from all nests, but 24-hour recordings were only obtained from 20 capercaillie and nine black grouse females for a total of 165 and 75 days, respectively. Our measurements started on 10 May and ended on 28 June. We recorded when females were killed and nests depredated to determine possible relationships between incubation behaviour and predation. To take into account within-individual variation we compared the two species with individual nested in species as a random factor in proc MIXED (SAS, version 6.12). The three responses of recess time were log transformed to fulfill the criteria of normal distribution. The significance of the three measures of recess time were revealed by performing a backwards selection procedure in logistic models (loglinear regression) including all three measures of recess time. In the logistic models we used the average of the three recess time variables per individual as predictors. Over time, the duration of recesses varies within individuals (Storaas, unpubl. data). However, within-individual variation is very small compared to between-individual variation in recess time. The average recess time per individual should therefore be a sufficient measurement to reveal any effect of recess time on the risk of nest predation.

Results

Incubation

The total time away from the nest during a day was highly variable especially for capercaillie (Table 1). For all capercaillie nests combined, the median time away from the nest per day was 66.3 minutes for a median of 2.4 recesses. In black grouse the median time away from the nest was 84.1 minutes for 4.0 recesses. Black grouse took more ($F_{1,27}$ = 11.18, P =

Table 1. Time spent away from nests and the number of recesses per day for incubating capercaillie and black grouse in Norway. Successful nests include all nests that were not depredated.

Species	Nest fate	N	Recesses (no/day) Median (min. - max.)	Time away (min/recess) Median (min. - max.)	Time away (min/day) Median (min. - max.)
Capercaillie	All	20	2.4 (1.0 - 4.2)	27 (2 - 266)	66 (30 - 373)
	Successful	10	2.1 (1.0 - 4.2)	26 (2 - 266)	64 (30 - 373)
	Depredated	10	2.7 (1.5 - 4.0)	27 (3 - 99)	67 (42 - 204)
Black grouse	All	9	4.0 (2.3 - 5.0)	20 (1 - 51)	84 (57 - 115)
	Successful	6	4.0 (2.3 - 5.0)	20 (1 - 51)	84 (61 - 115)
	Depredated	3	4.0 (2.9 - 4.6)	19 (6 - 41)	84 (57 - 94)

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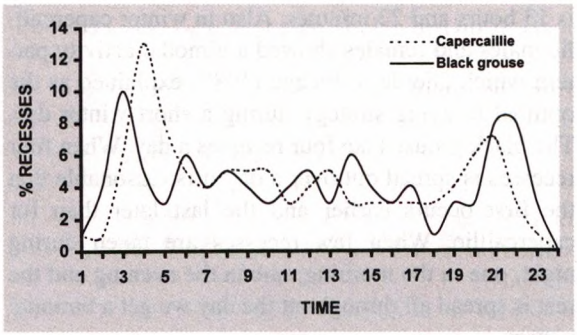


Figure 1. Distribution throughout the day of the time when capercaillie and black grouse left their nests for incubation recesses. All observations from all 24-hour observation periods were used.

0.002) and shorter recesses ($F_{1,27}$ = 6.31, P = 0.018) than capercaillie, but total time away from the nest per day did not differ between the species ($F_{1,27}$ = 0.36, P = 0.556).

Both capercaillie and black grouse showed a bimodal activity pattern; few recesses during the night and most after sunrise and before sunset with the highest peak in the morning (Fig. 1). Mean time for the black grouse females to take the first recess in the morning was 04:14 (95% Confidence Interval (C.I.) [02:54-05:34]) while capercaillie waited till 05:55 (95% C.I. [05:01-06:48]). The capercaillie females left their nests for their last recess in the evening at 19:18 (95% C.I. [18:32 - 20:03]) and black grouse at 21:12 (95% C.I. [20:04-22:20]). Black grouse took the first recess earlier ($F_{1,27}$ = 6.15, P = 0.020) and the last recess of the day later ($F_{1,27}$ = 4.22, P = 0.049) than capercaillie. The sun rose between 04:53 and 03:54, and set between 21:35 and 22:44 during the study period. The summer night at 60°N is light, and also the black grouse took a few recesses in dim light (see Fig. 1).

Predation

We found two female capercaillie that had been killed by goshawks, and 15 capercaillie and three black grouse nests that had been robbed during 624 observed grouse days. The probability per day of losing a nest was higher than the probability of being killed (pooled sample, χ^2 = 13.067, df = 1, P < 0.001). In 1,595 capercaillie and black grouse recesses (pooled sample) two females were killed giving a probability of being killed per recess of 0.0013. The probability of nest loss was not statistically different between species (χ^2 = 0.25, df = 1, P = 0.651).

Table 1 shows large variation in the incubation pattern of females of both successful and depredated nests. However, there was no difference in the amount of time away from the nest, number of recesses per day or total amount of time away from the nest per day in successful and unsuccessful capercaillie ($\chi^2_{1,27}$ < 0.08, P > 0.783) nor in black grouse ($\chi^2_{1,27}$ < 0.11, P > 0.735).

The timing of departures for the first and last recess of the day did not differ between successful and robbed capercaillie females ($\chi^2_{1,27}$ < 0.73, P = 0.394). This pattern was similar for black grouse females ($\chi^2_{1,27}$ < 0.980, P = 0.516).

We recorded the time when two female capercaillie were killed and 13 capercaillie nests were robbed. One female was killed with full crop on her way back from her morning recess (04:19) and one 200 m from the nest during daytime (15:37). Nest losses occurred throughout the day. We divided the day into two periods: 1) morning and evening when most recesses occurred (hours 03-06, 20-21), and 2) the rest of the day. Only one capercaillie nest was robbed during 180 recesses in period 1 while 12 nests were robbed during 204 recesses in period 2. Fewer nests were robbed in period 1 than should be expected if there was an association between the number of recesses and nest losses (χ^2 = 6.28, df =1, P = 0.012).

Of the 13 depredated capercaillie nests, three were detected by predators while the female was incubating at night. Comparing the time of loss to the recess pattern of the previous days, makes it probable that seven more nests were detected when the female was on the nest. The remaining three nests may have been detected during a recess or during incubation.

Discussion

The incubation patterns in grouse may have evolved in response to predation on females or eggs. Angelstam (1984) suggested that female black grouse left the nest early in the morning and late at night when it was too dark for goshawks to hunt. In our study most females took their first recess after sunrise and their last recess before sunset when it was light and the probability of being killed during a recess was still low. Furthermore, only two out of 76 radio-marked capercaillie and 36 black grouse were killed during a recess by a raptor during 1980-1986 in our study area (unpubl. data). It is therefore unlikely that the observed pattern has evolved to avoid predation on females.

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The risk of predation on eggs was substantial, however, and the incubation pattern may have evolved to avoid nest predation. Female capercaillie and black grouse usually fly directly from and to the nest when taking recesses (Pulliainen 1971, pers. obs.). Erikstad (1986) suggested that corvids may detect nests of willow ptarmigan *Lagopus lagopus* by observing such activity. If so, there should be a correlation between the number of recesses per day and nest losses. If many nests are depredated by visually oriented predators such as corvids, there should also be a correlation between the amount of time away from the nest and nest losses. However, few nests were destroyed in the period when the females took most recesses per hour indicating that nests were not found by detecting eggs or by observing female activity. There was also no difference in the timing, frequency and duration of incubation recesses between successful and unsuccessful females. In fact, the nests of black grouse, with more recesses than capercaillie, survived best in our study, and in a larger sample (Storaas & Wegge 1987). Corvids which hunt by vision are probably not important predators on the eggs of forest-dwelling grouse. This agrees well with observations by Willebrand & Marcström (1988) of predation on black grouse nests.

The majority, if not all, nests in our study were detected by predators while the female was incubating the eggs. Since the losses were independent of nesting cover (Storaas & Wegge 1987) it is probable that the predators detected the nests by olfactory cues or by flushing the female by chance. The low rate of nest loss in the morning and evening periods could be a consequence of the high recess activity then; interestingly, our dogs did not find clutches when the female was absent and nests of greater prairie chickens *Tympanuchus cupido* were only depredated while a female was sitting on the eggs (Bowen & Simon 1990). On warm sunny summer days it is usually too dry for pointing dogs to find grouse from eight o'clock in the morning until after five in the afternoon (pers. obs.). Perhaps grouse could leave the nest before eight and after five to make the nest more difficult to find for mammalian predators. However, the females did stay at the nest also during most of that period.

Capercaillie usually left the nest twice a day. Since they seldom left the nest when it was dark, it is reasonable that they would take one recess in the morning and one in the evening. The time between the mean first morning and the mean last evening recess is 13 hours and 23 minutes. Also in winter capercaillie males and females showed a bimodal activity pattern which Gjerde & Wegge (1987) explained as the optimal foraging strategy during a short winter day. The black grouse take four recesses a day. When four recesses is spread out over a day it is reasonable that the first occurs earlier and the last later than for capercaillie. When few recesses are taken during night, one in the morning, one in the evening and the rest is spread all throughout the day we get a bimodal pattern.

Erikstad (1986) found that lower-weight willow ptarmigan females left the nest at any time throughout the day and more often than heavier females. For capercaillie and black grouse there is no reason to believe that eventually more recesses of light females will give higher nest predation. Our results suggest that the incubation pattern shown by capercaillie and black grouse was not related to nest losses. However, the overall risk of nest loss is high, so females should try to reduce the total length of the incubation period by incubating for as constant a time as possible. Predation may act to reduce the overall recess time in grouse, and may make body reserves during incubation quite critical.

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