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Weight-related renesting in capercaillie *Tetrao urogallus*

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In a population study during 1979-1988 at Varaldskogen in southeastern Norway, 234 capercaillie *Tetrao urogallus* nests and broods were classified as first nests or renests. Of the females that had their first nest depredated, 9-87% (mean 36%) renested. Over a 6-year period, autumn brood production increased from 30 to 38% due to renesting. Renesting is physically demanding for the females; the eggs in renests are fewer and smaller, and the females take more and longer recesses than when incubating first nests. All the females incubated their first nests till the eggs hatched or the nest was depredated. Two of the renesting females took more and longer recesses until they gave up their nests. The ability to renest seems to be weight-related, as yearling females, which weigh less than adult females, did not renest, and the weight of adult females on leks was highest in the two years when most renesting occurred. The female will renest if the nest is depredated during the first three days of incubation. Each of the following 19 days, all years combined, a mean of 26% of females who lost their nests renested. Capercaillie renesting was related to the vole cycle; it was highest in the year before the small rodents peaked and decreased through the vole crash and the year after.

Key words: incubation, nest predation, renesting, Tetrao urogallus

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Renesting may compensate for nest predation and has been shown to occur in most grouse species (e.g. Parker 1981) including capercaillie *Tetrao urogallus* (Spid-sø, Wegge & Storaas 1985). The renesting decision of female grouse should be based on the benefits and costs of the increased parental investment in laying a second clutch (Bergerud 1988). Bergerud & Gratson (1988) suggested that large grouse with long lives should renest less often than should species with short life expectancies. In capercaillie, natural mortality among adults

varies within means of 0.2-0.34 (Lindén 1981, Wegge, Larsen, Gjerde, Kastdalen, Rolstad & Storaas 1987, P. Kumpu, pers. comm.) which is a low mortality rate compared to 0.51, which was the average mortality rate of nine grouse and ptarmigan species (Bergerud 1988). A capercaillie clutch consisting of seven eggs weighs only about 14% of female body weight which is little compared to clutches weighing about 40% of female body weight in willow ptarmigan *Lagopus lagopus* and rock ptarmigan *L. mutus*; so the capercaillie female

should be able to renest every year. However, the probability of surviving for offspring (Storaas 1988, Wegge & Storaas 1990, Kastdalen & Wegge 1991) and mother (Wegge et al. 1987) vary within and between years, especially related to the small-rodent cycle (Storaas 1988, Wegge & Storaas 1990). Thus renesting could be a response to some proximate environmental cues such as vegetation, weather and abundance of insects, voles or predators, which could provide cues to the female of the survival chances of the second clutch. Renesting attempts could, however, solely depend on the physiological ability of the female to lay and incubate a second clutch.

In this paper, we show how the frequency of renesting in capercaillie changes between years and how large a fraction of broods that comes from renesting. We discuss if proximate environmental cues or the physical ability of the female determine if she will renest or not. We relate renesting to the time of nest loss, age, incubation patterns and the vole cycle.

Study area

The Varaldskogen study area (60°10'N, 12°30'E) comprising roughly 14,000 ha consists of moderately flat, undulating terrain, dominated by mixed coniferous forests of Scots pine *Pinus sylvestris* and spruce *Picea abies*, interspersed with bogs and lakes. Today, the semi-natural old forests are broken up into a mosaic of clearcuts and plantations, with about 1/5 of the remaining old forests distributed into patches mostly of <100 ha. A floristic description of the study area is given in Rolstad, Wegge & Larsen (1988), and the forest history is reviewed in Rolstad & Wegge (1988).

The fauna is typical of the west Palearctic boreal region; besides a medium-dense capercaillie population of 2-3 birds/km² in spring, black grouse *Tetrao tetrix* are common (5-7 birds/km²; Wegge 1983, P. Wegge, unpubl. data). Main predators are red fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, smaller mustelids *Mustela nivalis* and *M. erminea*, goshawk *Accipiter gentilis*, and the corvids raven *Corvus corax*, hooded crow *Corvus corone cornix* and jay *Garrulus glandarius*.

Methods

During 1980-1984, we captured, weighed and aged (Helminen 1963) 32 capercaillie females at the lek. During 1979-1984, we found 196 nests by monitoring 77 radio-

equipped females, by using pointing dogs and based on reports from foresters (see Storaas & Wegge 1987). We found 126 broods, using dogs during June and July 1979-1988, which were aged on the basis of the developmental stage of their wing feathers (Kastdalen 1986). Within years, the effort put into detecting nests and broods was distributed so that the probability of finding nests and broods was independent of hatching date. Thus, nest and brood samples were independent of the timing of hatching. Renests in the samples represent the proportion of re-layers among the robbed first nesting females in the same samples.

Based on information obtained from radio-equipped females, the number and size of eggs and distribution of hatching dates, we considered eggs hatching from day 1 to 14 as first nests and eggs hatching from day 15 and later as renests. Day one was the first day we observed that eggs had hatched in a given year. Using this method, 234 reproduction attempts could be classified as either first nests or renests. Incubation patterns were measured by putting a thermistor into the nests and recording the nest temperature on a Grant-recorder (Erikstad 1986, Storaas & Wegge 1997).

The number of potentially renesting females (depredated first nesters) in the sample was calculated each year using the following formula:

$$N_p = (N + B) * R,$$

where N_p = number of potential renesters which should be found, N = number of first nests found, B = number of first-layed broods found, and R = frequency of nest loss. Percent renesting was the percentage of the calculated number of potentially renesting females in the sample that actually renested. In 1981, the rate of nest predation was higher in June than in May (Storaas 1988). That year the number of potentially renesting females was calculated using the formula:

$$N_p = NR + BR (1-R_j) / (1-R),$$

where NR = the number of potential renesters based on the nest sample, BR = the number of additional potential renesters based on the brood sample and R_j = predation rate in June.

The probability that a female will renest after nest loss may decrease as the incubation period proceeds. However, if the predation rate is constant and the females must decide to renest immediately, the number of depredated nests, and thus potential renesters, will decrease with time. To investigate if renesting was related to the time of loss of the first clutch we compared the daily

distribution of possible renesters (females who lost their nest per day) with the daily occurrence of renests. If we assume that a constant time passes from when a nest is robbed until the female starts incubating the re-nest, the first renests in our sample will represent the re-laying fraction of the earliest depredated first nests in the sample. We used the combined distribution of first nests in all years and assumed a constant predation rate per day (R_c) based on 71% nest loss/year (Wegge & Storaas 1990). The number of potential renesters (P) on day t was the number of nests depredated that day and was calculated using the following formula:

$$P_t = N_t * R_c$$

where

$$N_t = NN_t + N_{t-1}(1 - R_c) - NN_{t-26}(1-R_c)^{26}$$

where N_t = number of nests on day t , NN_t = the number of new-laid nests on day t , $(1 - R_c)$ = daily survival, and 26 = the length of the capercaillie incubation period in days. Thus, the number of nests found one day is equal to the number of new nests laid that day plus the nests surviving from the day before minus the nests with eggs that hatched that day. The probability of re-nesting was calculated each day by dividing the number of actual renesters with the number of possible renesters. The calculations were done in LOTUS123. Statistics, MANOVA and t-tests were done in SYSTAT (Wilkinson 1990). Information on vole abundance was taken from Wegge & Storaas (1990).

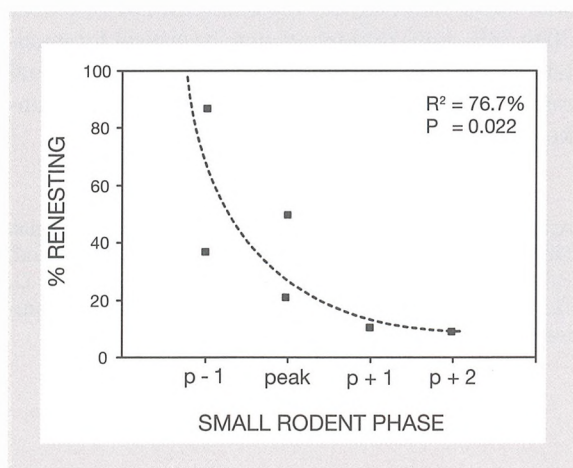


Figure 1. Percentage of potential renesters that re-nested in relation to the phase of the small rodent cycle.

Results

Time of nest loss and probability of re-nesting

The probability of re-nesting was very high for capercaillie females depredated during the first three days of the incubation period (>1 , probably because we classified a few early renests as first nests). For each of the following 19 days the probability approximated 0.26 ± 0.11 (SD).

Renesting in different years

We tested on a yearly basis if there was a difference between the proportion of first nests to renests and first broods to relaid broods using Fisher's exact test. Since no difference between the two independent samples was detected in any year, the samples were pooled. Between 8.8 and 87.3% of potential renesters re-nested in the different years (Fig. 1). The mean re-nesting rate through the 6-year period was 35.7%, increasing the mean hatching success from 30.4 to 37.9% during the six years of the study period.

The probability of re-nesting was highest the year before the small-rodent population peaked and it decreased through the vole crash to the year after ($r = 0.876$, $r^2 = 0.767$, $P = 0.022$; see Fig. 1). There was, however, a significant difference in re-nesting between the two small-rodent peak years 1980 and 1984 ($\chi^2 = 4.195$, $P < 0.05$), but no difference between the small-rodent peak year 1980 and the crash year 1981 (Fisher's exact test: $P = 0.274$).

Body weight

When caught at the lek, yearling females weighed less, $1,896 \text{ g} \pm 89$ (SD), than adult females ($2,095 \text{ g} \pm 106$; t-test: $P < 0.001$). After hatching, yearling females weighed $1,535 \text{ g} \pm 125$ (SD) and adult females weighed $1,706 \text{ g} \pm 125$ (SD), respectively. Both yearlings and adults lost 19% of their lek body weight (t-tests: $P < 0.001$). None of six radio-tagged yearlings re-nested, and none of nine females captured with relaid brood were yearlings. Seven adult females captured at the lek in 1983 and 1984, when re-nesting was frequent, tended to be heavier than the 13 females captured in 1980, 1981 and 1982, when re-nesting was rare (t-test: $P = 0.053$). In 1982 one re-nesting females weighed 2,200 g when captured at the lek, and thus was our heaviest radio-marked potential renester.

First-nesting adult females spent $55.4 \text{ minutes} \pm 12.6$ (SD) away from the nest during 1.9 recesses ± 0.3 (SD), re-nesting females spent $135.4 \text{ minutes} \pm 100.0$ (SD) away from the nest during 3.4 recesses ± 0.6 (SD) and yearling females spent $120.9 \text{ minutes} \pm 66.8$ (SD)

away from the nest during $3.3 \text{ recesses} \pm 0.5 \text{ (SD)}$ per day. The differences between the groups in the number of recesses and the time away from the nest were significant (MANOVA: $P = 0.033$ and $P = 0.001$, respectively). Two renesting and no first-nesting females abandoned their nest during incubation.

Discussion

All females had a first nest, but the extent of renesting attempts changed with one degree of magnitude between low and high years during the study period. This variation may be due to environmental cues related to the small-rodent cycle or summer insect abundance giving the female indications of egg and/or brood survival chances in a possible renest. Rodents as a cue, however, were unlikely, since renesting rates differed in two small-rodent peak years (1980 and 1984) and did not differ between a vole peak (1980) and crash year (1981). Cues related to insect abundance (Kastdalen & Wegge 1991, P. Wegge, unpubl. data) could explain the low rate of renesting in 1981 and 1982, but not the low rate of renesting in the *Lepidoptera*-larvae peak-abundance year of 1980. A high percentage of yearling females in the population could partly explain the low frequency of renesting in 1980 and 1981. However, in the spring of 1982 there were very few yearlings (Wegge 1983, P. Wegge, unpubl. data), and that year the renesting rate was the lowest measured during the study period. The high renesting rate in the small-rodent increase years and the decreasing rate till the year after the crash, indicates a relationship between grouse and vole reproduction through induced changes in the food quality (see Akcakaya 1992).

Small clutches in renests may be explained as a way to reduce the physical costs connected with renesting or to reduce the time until hatching. Moss, Watson, Rothery & Glennie (1981) found that late-starting captive red grouse *Lagopus l. scoticus* had smaller clutches even though food quality and availability were kept constant, indicating that calendar date is important. Capercaillie is the largest grouse species, and the young do not reach adult weight until their second autumn. We would therefore expect a correlation between the date of birth, autumn weight and survival of the chicks. However, we were surprised to find that the probability of renesting did not depend on the time of depredation (from day three to day 22 in the incubation period). In one season, the last eggs hatched five weeks later than the first eggs, and large clutches of six and seven eggs in two five-week delayed nests indicated that

the number of eggs in the renest depends on the body condition of the female, and that shortening the time until hatching is not crucial.

Smaller eggs in capercaillie renests were also described by Spidsø (1992), while willow ptarmigan have been reported to lay larger eggs in renests (Parker 1981, Erikstad 1986). Moss et al. (1981) found that red grouse chicks from large eggs grew and survived better than chicks from small eggs. Smaller eggs in capercaillie renests could be a result of reduced female body condition and weight, but the small eggs found in the two late large clutches indicate a lower need for yolk later in summer in our study area.

Capercaillie females were heavier in the years of high renesting frequency, but their body weight could not be related to the time of snow melt or the temperature in April. The females lost 19% of their body weight from mating till hatching. Yearling hens were lighter than adult females, took more recesses than the adult females, and did not renest. Renesters left the nest still more and for longer periods of time, probably to feed. Two of the renesters abandoned their nests after a period of more frequent and longer recesses. One of these females had a high lek weight of 2,200 g and still abandoned her renest. The females probably have to exceed some threshold weight or body condition in order to start a new breeding attempt, and still renesting may be too physically demanding to fulfil for an unsuccessful first breeder.

In 1979, 41% of the broods hatched from renests, but they comprised only 31% of the chicks hatched due to the smaller clutch sizes in renests. In 1981, 20 cm of snow fell seven days after the first hatching. In that year chicks from renests probably survived better than first broods. As a mean of all years, the proportion of females with successfully hatched broods increased by 26% from 30 to 38%. Such differences may be critical for maintaining capercaillie population densities. The survival rate of the chicks from relaid broods is, however, unknown.

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