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Nest site preferences of Capercaillie *Tetrao urogallus* and nest predation risk in relation to habitat fragmentation patterns were studied in an area of the Bavarian Alps, West Germany. Nest sites were located through radio-equipped females. Hens strongly preferred to nest in edge habitats, namely between mature forests and clearcuts. Nest predation risk was assessed by an experiment with artificial nests, considering effects of successional stage, patch size, and distance of nests from an edge. About two thirds of the nests were destroyed, mostly by mammal predators. Losses were lowest in stands of the youngest and the oldest successional stages. Predation was lower in edge habitats than inside forest stands. No difference in predation risk or in nest site preferences was found in relation to stand size. The results suggest that Capercaillie hens selected nest sites in order to minimize predation risk.

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Introduction

Capercaillie *Tetrao urogallus* are adapted to coniferous climax forests. Over most of their distribution range, however, remaining primary habitats have been fragmented by forestry into a patchwork of different successional stages. Under such conditions, Capercaillie concentrate in late stages of forest succession, but may also utilize younger age classes to some extent (Angelstam 1983, Wegge 1985, own unpubl. data).

Predation is an important factor influencing reproductive success in birds. Habitat fragmentation creates spatial variations in predation risk, with a tendency for higher losses near edges than inside homogeneous areas of habitat (Wilcove et al. 1986, Andrén and Angelstam 1988), and for increasing predation with decreasing patch size (Gates and Gysel 1978, Wilcove 1985, Andrén and Angelstam 1988, Møller 1988). The overall decline in Capercaillie numbers points to poor reproduction, and the question was raised whether nesting habitats might have become a limiting factor due to modern forestry practices (Klaus 1985, Storaas and Wegge 1987). From Central Europe, there is hardly any

information available about nesting habitat preferences of Capercaillie. One objective of this paper is to help to fill these gaps.

I evaluated predation risk in relation to fragmentation patterns of forests through an experiment with artificial nests, considering successional stage, stand size, and distance to edge. The results of the experiment should also help to explain the distribution of natural Capercaillie nests in the study area. I expected to find lowest predation rates on dummy nests in those habitat types preferred by nesting Capercaillie females.

This study was part of a continuing project into habitat relationships of alpine Capercaillie. In the course of the project, further data on nesting habitats will become available. Therefore, this paper should be considered preliminary.

Study area

The study was done in 1988–90 in the Teisenberg Capercaillie research area (50 km²) in the foothills of the

Fig. 1. Plot design used with artificial nests in the Teisenberg study area. Dots indicate nest positions.

Bavarian Alps, West Germany (47°48'N, 12°47'E). Elevations range from 700–1350 m. The climate is humid and temperate with an annual precipitation of 2000 mm. The area is snow-covered from December to April with snow depth exceeding 1 m. The area is covered by coniferous forests dominated by Norway spruce *Picea abies* mixed with fir *Abies alba* and beech *Fagus sylvatica*. The field layer is dominated by bilberry *Vaccinium myrtillus*. The study area is intensively managed by the Bavarian State Forest Service. Forest stands of various age classes form a mosaic with patches of 1–30 ha. The area holds a native Capercaillie population of 100–200 birds. According to game keepers, the numbers of these birds have been stable for at least 30 years. The population is not isolated, and exchange with Capercaillie of adjacent mountain ranges was regularly observed. Potential nest predators include red fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, beech marten *M. foina*, weasel *Mustela nivalis*, red squirrel *Sciurus vulgaris*, Raven *corax corax*, Carrion Crow *Corvus corone*, European Jay *Garrulus glandarius*, and Nutcracker *Nucifraga caryocatactes*.

Material and methods

Capercaillie females were caught with mist nets at leks in spring and in preferred habitats in autumn between spring 1988 and spring 1990, and were equipped with 28 g necklace transmitters. After mating, the birds were

located once or twice a day by triangulation from 50–500 m distance, and the start of incubation was determined. Nest sites ($N = 9$) were visited during the last week before the expected hatching date. Four additional nests were found by chance during habitat mappings. Because the time I spent in each habitat type was proportional to availability, I added these nests to the sample analyzed here.

Nest sites were characterized by successional stage, stand size (< 10 ha, 10–20 ha, > 20 ha), and by the distance of the nest from an edge (0–25 m, 25–75 m, > 75 m). Edge habitats included borders between forest stands of clearly distinct and different ages, and forest edges along roads or forest rides more than 10 m wide. Five successional stages were distinguished. These were clearcuts (covered by natural regeneration up to 2 m height), thicket stage (dense young forest before thinning), pole stage (young forest after first thinning), old forest (after second thinning and with sparse ground cover), mature forest (final felling stage, with dense ground vegetation). Habitat availability was estimated by a sample of 500 cross-points on a 250-m grid laid over the map.

Nest predation risk was assessed by an experiment with dummy nests. Simple ground nests were formed with material from the immediate surroundings such as twigs and leaves. Nests were placed underneath or close to trees, which were marked with coloured tape at about 1.5 m height. Each nest contained three brown eggs of domestic hens. To identify predators by bite or beak marks, one additional artificial egg made of gypsum covered with brown plasticine was fixed in each nest. A total of 135 dummy nests was put out on 15 May 1989. Nests were checked once a week and were considered robbed when eggs were destroyed or missing. The experiment was stopped after 35 days, which is the total laying and incubation period of Capercaillie.

Three forest stands, one small (5 ha), one medium (15 ha) and one large (25 ha) patch, were chosen as experimental plots for each of the five successional stages (see above). Nine nests were placed in each of these 15 experimental stands as illustrated in Fig. 1. All nests were 50 m apart. Three nests were placed at the edge, and three others at 50 m and 100 m distances inside the stand. The experimental stands bordered either clearcuts or old or mature forest.

Cover provided by ground vegetation within the experimental stands was assessed with the help of a 50 × 50 cm checkerboard with 25 black and white squares. The board was placed upright on the ground, and the proportion (%) of cover was estimated from a distance of 10 m at 5–15 random points in each stand. The mean of all measurements taken was used as an index of ground cover.

Data were analyzed by χ^2 standard methods, Bonferroni-Z-statistics (Neu et al. 1974, Marcum and Loftsgaarden 1980), and a loglinear multiway table analysis (Dixon 1988).

Fig 2. Distribution of Capercaillie nests ($N = 13$; filled bars) and habitat availability (open bars) in the Teisenberg study area, Bavarian Alps, FRG, in relation to (a) successional stage (I = clearcut, II = thicket, III = pole stage, IV = old forest, V = mature forest), (b) patch size, and (c) distance from an edge. Stars indicate values significantly different from random distribution (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Results

Capercaillie nests were not randomly distributed in relation to habitat fragmentation patterns (see Fig. 2). Nests were typically placed at the edge between mature forest and clearcuts. Females nested in clearcuts more frequently than expected ($P < 0.001$), while they avoided pole stage ($P < 0.001$) and old forest ($P < 0.001$) (Fig. 2a). Thickets and mature forests were used according to habitat availability. Nests were randomly distributed as regards forest patch size (Fig. 2b). With the exception of two nests placed 50 m from the nearest edge, all nests were found in edge habitats ($P < 0.001$). Females avoided nesting > 75 m from an edge (Fig. 2c).

Fig. 3. Cumulative rate of predation on dummy nests in the Teisenberg study area in 1989.

After 35 days, 87 (64%) of 135 dummy nests had been robbed. Most losses occurred during the second and third week, while very few nests (4.4%) were taken during the first week after the start of the experiment (Fig. 3). In 22 nests the type of predator could be identified by bite, claw, or beak marks on the dummy eggs. Twenty (91%) of these nests had been robbed by mammals, and two by birds. Only in a few cases could the species of predator be identified (4 fox, 6 marten). In 48 depredated nests no marks were left in the dummy eggs, and in 17 nests the dummy egg had been removed by the predator.

Losses of experimental nests were associated with successional stage ($P < 0.001$) and distance to edge ($P < 0.01$) but not with patch size (Fig. 4). In clearcuts, significantly fewer nests than expected were robbed ($P < 0.001$), whereas losses were higher in pole stage patches ($P < 0.05$). Nests placed at an edge were taken significantly less frequently than those inside a forest stand ($P < 0.001$). A loglinear multiway table analysis (Dixon 1988) did not reveal any significant interactions between the habitat factors tested. Predation rate on dummy nests was not significantly correlated with ground cover in the experimental plots (Spearman's rank correlation, $r_s = 0.40$).

Discussion

The nests of ground-nesting birds such as grouse are not easily found, and dummy nests are often used to study nest predation. However, previous studies showed that results from experiments with artificial nests concerning predator species composition and predation rates are not necessarily transferable to natural nests (Storaas 1988, Willebrand and Marcström 1988). Losses in dummy nests can only provide an index to differences in predation risk in relation to habitat features.

Fig. 4. Proportions (%) of dummy nests (N = 135) robbed in the Teisenberg study area in 1989, in relation to (a) successional stage (I = clearcut, II = thicket, III = pole stage, IV = old forest, V = mature forest), (b) patch size, and (c) distance to an edge. Broken lines indicate expected values, stars indicate values significantly different from random distribution (* P < 0.05, ** P < 0.01, *** P < 0.001).

With uncovered dummy nests, avian predation is usually more important, whereas natural nests camouflaged by the incubating female are mostly robbed by mammals (Storaas 1988, Willebrand and Marcström 1988). In this study, mammals were the major predators of artificial nests. Accordingly, losses of dummy nests were not significantly correlated with cover provided by ground vegetation. Also, the distribution of nest losses over time pointed to mammalian predators. They may initially have avoided the dummy nests because of human scent, which decreased with heavy rainfall during the first week.

Capercaillie hens exhibited pronounced preferences for nesting at the edge of clearcuts. From this, nesting habitat is rather increased than limited by forestry, and it is unlikely that availability of nesting habitat limited reproductive success. Capercaillie hens chose the habitat types that showed lowest predation rates of dummy nests. The results suggest that they selected nest sites in order to minimize predation risk. The predators involved were generalists and grouse nests usually occur at low densities. Therefore, it is unlikely that any predator hunted for grouse nests systematically. In the study area, grouse eggs were not important in the diet of either red fox (Storch and Kleine 1991) or marten (T. Ruck, pers. comm.).

In contrast to this study, Scandinavian Capercaillie were found to nest in a variety of habitat types. This was explained as a strategy to avoid predation by choosing unpredictable nest sites (Storaas and Wegge 1987). Which strategy a Capercaillie hen should apply in nest site selection may depend on the species composition, habitat preferences, and density of the predators present, and will also be affected by the density and distribution of nests and of alternative prey. Regional differences in nest site selection would be expected.

Increases in predation rates at forest edges in fragmented forest landscapes have been documented in several studies in North America (Gates and Gysel 1978,

Whitcomb et al. 1981, Ambuel and Temple 1983, Wilcove 1985) and Scandinavia (Andrén et al. 1985, Andrén and Angelstam 1988). Others, however, did not find increased predation rates at forest edges (Yahner and Wright 1985, Angelstam 1986, Ratti and Reese 1988). Angelstam (1986) argued that edge effects due to predators from outside a forest patch are most likely to occur if the productivity gradient between the patch and the surrounding matrix was steep. Hence, increased predation would be expected along farmland/forest edge but not necessarily between different successional stages in forest dominated landscapes. My results support this hypothesis. I only considered edges inside forests, and found neither increased predation in edge habitats nor an increase in predation with decreasing patch size. Furthermore, even the biggest patches of "productive" habitats such as clearcuts in my study area were far too small to support a population of predators. From all this, I expect predation at forest edges to be higher than inside forests only when the density of generalist predators in the area outside the forest is higher than in the forest itself.

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