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Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes

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We used hunting dogs and man to simulate the searching for nests and broods of forest grouse, i.e. capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix*, by mammalian predators. Our aim was to find out if and how forest fragmentation affects the searching efficiency of predators. In total, we found 73 capercaillie and 35 black grouse nests and 20 young capercaillie broods. We calculated that a mammalian predator will detect a capercaillie nest if closer than 1.6 m (95% C.I.: 0.7 - 2.2), a black grouse nest if closer than 1.1 m (95% C.I.: 0.8 - 1.6), and a capercaillie brood if closer than 39 m (95% C.I.: 17 - 89). Nests were distributed in all habitat types, whereas broods were restricted to specific brood habitats. Due to this and the difference in the detection radius between nests and broods, we estimated that the predator gain of searching for broods in brood habitat is about 80 times higher than the gain of searching for nests which are situated in all habitat types in our study area. As young broods concentrate in highly restricted habitats, the predator gain of searching for broods increases exponentially with the loss of brood habitat, whereas it decreases linearly with increasing nest predation. We discuss this mechanism as a possible process explaining the observed decline in capercaillie populations in fragmented forests and consider its implications for grouse management.

Key words: detection function, forest fragmentation, grouse, predation, *Tetrao tetrix*, *Tetrao urogallus*

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Capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix* are large ground-nesting grouse species with precocial chicks inhabiting Fennoscandian boreal forests. These forests have changed from a natural regime consisting of fires with intervals of 30-200 years to a managed system of selective cutting and natural regeneration for the last 150-350 years, and today they appear as fragmented mosaics of clearcuts, even-aged younger stands and remnants of the older naturally regenerated forest (Essen, Ehnström, Ericson & Sjöberg 1997). In Fennoscandia, capercaillie have decreased during the last decades (e.g. Lindén 1989), presumably as a result of loss and fragmentation of the old natural forest to which the species is adapted (e.g. Rolstad & Wegge 1989a, Wegge, Rolstad & Gjerde 1992). For instance, in the Finnish forest landscape the probability that an observed capercaillie or black grouse hen will have a brood has been shown to be positively associated with the proportion of closed canopy cover (Kurki, Helle, Lindén & Nikula 1997). Due to high nest (Storaas & Wegge 1985) and chick predation (Kastdalen & Wegge 1990), areas heavily harvested by clearcutting and replanting practices during the last three decades have become capercaillie sinks (Wegge et al. 1992), and chick losses are higher in the fragmented forest matrix than in larger, intact blocks of old forest (Wegge, Gjerde, Kastdalen, Rolstad & Storaas 1990).

Capercaillie and black grouse may nest in both natural and managed habitats (Storaas & Wegge 1987). Young broods, however, prefer insect-rich forest types in late seral stages (Rodem, Wegge, Spidsø, Bøkseth & Barikmo 1984, Kastdalen & Wegge 1985). Hunting dogs searching for forest grouse detect nests and broods differently: when a dog approaches an incubating hen, she will sooner or later flush and reveal her eggs, usually before the dog catches her scent, whereas when approaching a brood the dog almost always catches the scent and starts to follow the scent-track to the location of the brood before this flushes.

Forest fragmentation may have lead to increased predation on grouse nests or broods either by increasing predator density or by increasing the efficiency with which predators find grouse broods (Wegge et al. 1990, Kurki, Nikula, Helle & Lindén 1998). Due to differences in the detection distance and habitat use between nests and broods, forest fragmentation may affect predation on nests and broods differently. Using hunting dogs and man to simulate mammalian

predators, we investigate, in this paper, by which mechanisms forest fragmentation may have lead to lower grouse reproduction.

Study area

The study was conducted at Varaldskogen (60°10'N, 12°30'E) which consists of roughly 14,000 ha moderately flat, undulating terrain, dominated by mixed coniferous forests of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, interspersed with bogs and lakes. Today, the semi-natural old forests are fragmented into a mosaic of clearcuts and plantations, with the remaining old forest (about 1/3) distributed into patches mostly smaller than 100 ha. A floristic description of the area is given in Rolstad, Wegge & Larsen (1988), and the forest history is reviewed by Rolstad & Wegge (1989a).

The fauna is typical of the west Palearctic boreal region with a medium-density capercaillie population (2-3 birds/km² in spring) and a somewhat denser black grouse population (5-7 birds/km²) (Wegge 1983, and P. Wegge, unpubl. data). Potential predators of grouse are red fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, smaller mustelids *Mustela nivalis* and *M. erminea*, goshawk *Accipiter gentilis*, and three species of corvids. Red fox, pine marten and smaller mustelids are probably the most important predators on grouse nests (Storaas & Wegge 1997) and on broods up to five weeks of age (Kastdalen & Wegge 1990).

Material and methods

During 1979-1998 we conducted various grouse studies at Varaldskogen. During 1979-1981 we searched for nests using pointing dogs. The dogs detected few nests and caused the hen to react the same way as when a man approaches the nest; when a dog or a man came too close to the nest, the female flushed and the nest was found. The flushing distances from capercaillie nests to a dog (N = 8) and a man (N = 65) was 3.7 and 3.8 m respectively, and from black grouse nests to both a dog (N = 7) and a man (N = 29) the distance was 2.0 m. We therefore used man and dogs as representatives of mammalian predators.

During June 1996-1998, the distance from where the dog first detected the scent to the location of the

capercaillie brood was measured on 20 occasions. The age of the broods varied from newly hatched to three weeks. The young chicks were sitting hard or had moved only a few metres during the time from when the hunting dog detected the scent till it spotted the chicks.

We only measured the distance from the nest or brood to the detector (dog or man). We did not measure the angle from the walking line to the detected nest or brood, so we calculated the effective detection radius (EDR) around the nests and broods using the program DISTANCE (Buckland, Anderson, Burnham & Laake 1993). In general, we calculate the EDR around a person observing some species from one point, and the EDR is the radius of the sampled area which should be divided by the number of all observed objects when calculating the density. In our study, we calculated the detection function around nests and broods. Hence, we assume that the number of nests that a mammalian predator will detect equals all the nests it will come closer to than the EDR. With this approach, a predator searching the forest will detect all nests and broods within 2 EDR, the estimated search width, from its path. These distances are dependent on wind, humidity and temperature, however, as the estimates are based on real, measured distances, the detection functions are realistic. The functions will probably change to some extent between predator species and individuals, but this should not affect the comparability of the EDRs of nests and broods. In our calculations we assumed that no detection differences between capercaillie and black grouse broods exist.

We used the EDR-estimates to model the gain that predators will obtain by searching for grouse nests or broods at various levels of forest fragmentation. As capercaillie and black grouse nest in all habitat types, and as the predation rate on grouse nests does not differ between habitats (Storaas & Wegge 1987), we may assume that the probability that a mammalian predator will detect a nest is not affected by forest fragmentation. However, as young broods concentrate in specific habitats (Wegge, Storaas, Larsen, Bø & Kolstad 1982, Rodem et al. 1984) the probability that a predator will find a brood may be assumed to be affected by forest fragmentation. As the biomass of chicks/km² brood habitat equals the biomass of chicks borne/km² divided by the proportion of remaining brood habitat, a change from 100% to 90% brood habitat increases the biomass in the remaining brood habitat by 11% while a change from 20 to 10%

brood habitat increases the biomass in the remaining brood habitat by 100%. The gain of a predator from searching for grouse depends on the biomass of eggs or chicks, the EDR, the proportion of the area in which the nests and broods are distributed and the probability of finding an egg or capturing a chick when a nest or brood is detected. Thus, the predator gain per kilometre moved will be $2 \text{ EDR} \times 1 \text{ km} \times \text{gram eggs or chicks/km}^2 \text{ nesting or brooding area}$. However, the total biomass of eggs will change with predation and renesting, and biomass of chicks will change with individual chick growth and with predation. To estimate the predator gain we used the weight of the eggs laid in the first nesting attempt. Furthermore, we calculated the number of hatched broods from the spring density of females minus the measured nest loss (Wegge & Storaas 1990), and used the weight of a 5-chick brood approximately two weeks old (one capercaillie chick = 100 g, one black grouse chick = 50 g).

Results

Information on nests/km², estimated search width, areas used for nesting and brooding and calculated predator gain are summarised in Table 1.

The estimated search width (2 EDR) was 3.2 m (95% C.I.: 1.4 - 4.4) and 2.2 m (95% C. I.: 1.6 - 3.2) for capercaillie and black grouse nests, respectively (DISTANCE, point-transects). The search width for nests in naturally regenerated and man made forests did not differ between capercaillie (*t*-Stat = 0.04, *P* = 0.48) or black grouse (*t*-Stat = 1.36, *P* = 0.09). With nests (containing eggs weighing 1,700 g/km², see Table 1) distributed in all habitat types (Storaas & Wegge 1987), the total gain for predators moving one kilometre with the measured searching width was 4.4 g grouse eggs (see Table 1).

Effective search width for capercaillie broods was 78 m (95% C.I.: 34 - 178). If all clutches hatch, a predator will find 156 g chicks/km moved if all area irrespective of habitat type was used by broods. However, if only 10% of the habitat is used by broods, the predator will gain 1,560 g/km moved if searching only this habitat type. With 70% nest predation, which is recorded in the study area (Wegge & Storaas 1990), the gain will increase from 70 g when all area is used, to 702 g when only 10% of the area is used by broods. Hence, in our study area, where young broods only use 20% of the area

Table 1. Data from the Varaldskogen study area including density of females, percent of the area used by nesting females (nesting area) and broods (brood area), estimated search width (2 EDR) for nests and broods, egg and chick weights/km², estimated predator gain/km moved and survival rates of nests and broods.

	Capercaillie	Black grouse	Total	Reference
Females/km ²	2	4	6	Wegge (1983)
Nesting area (%)	100	100	100	Storaas & Wegge (1987)
Brood area (%)	20	20	20	Kastdalen & Wegge (1990)
2 EDR, nests (m)	3.2	2.2		
2 EDR, broods (m)	78	78		
Egg weight/km ² (before predation)	700	1000	1700	
Chick weight/km ² brood habitat (÷ egg predation)	1000	1000	2000	
Chick weight/km ² brood habitat (egg predation as in study area)	300	600	900	
Egg gain (g)/predator/km moved in the study area	2.2	2.2	4.4	
Chick gain (g)/predator/km moved in the brood habitat	117	234	351	
Daily survival of nests	0.9535	0.9773		Wegge & Storaas (1990)
Daily survival of broods	0.9573			Kastdalen & Wegge (1990)

(Kastdalen & Wegge 1990; see Table 1) the predator gain is about 80 times higher when searching for broods in the remaining brood habitats than when searching for nests in all habitat types.

As nest are located in all habitat types, the predator gain of searching for nests is independent of forest fragmentation (Fig. 1). However, the gain of searching for broods increases rapidly when suitable brood habitat is reduced to 20-30% of the area and the search is limited to this habitat type. When the loss of brood habitat is higher than ca 70%, the brood density and predator gain increase exponentially (see Fig. 1). The main alternative prey species for typical

grouse predators are small rodents, which in Fennoscandia show multiannual population cycles (Wegge & Storaas 1990). Alternative prey may reduce grouse brood predation to some extent depending on the density of alternative prey species. However, when loss of brood habitat is very high, brood density will be exceptionally high in the remaining brood habitat, and predators may benefit more from searching for broods in brood habitat than from searching for alternative prey (see Fig. 1).

Discussion

The predator gain of searching for nests is low due to both the distribution of nests in all habitat types (Storaas & Wegge 1987) and the narrow effective detection width, which does not change between naturally regenerated and man made habitats. Increased predation on nests of capercaillie and black grouse (Storaas & Wegge 1985) is best explained by the numerical response of predators to forest fragmentation, as also suggested by Kurki et al. (1997).

However, in our study we have shown that increased predation on broods may be explained by forest fragmentation alone without increased predator density. In areas where brood habitats have become limited as a result of loss and fragmentation of old, insect-rich habitats, searching for broods in remaining brood habitats may become an advantageous predator foraging strategy. In our study area, young capercaillie broods showed a strong preference for old, moist *Vaccinium*-rich forests selectively cut and naturally regenerated, and avoided clearcuts

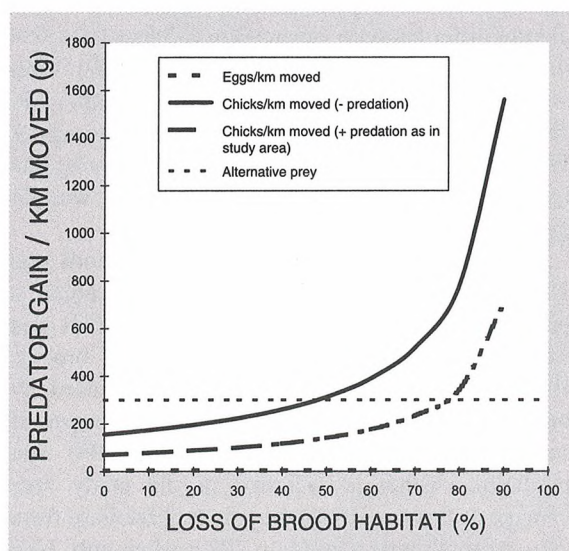


Figure 1. Estimated predator gain of searching for forest grouse eggs and broods in relation to loss of brood habitat.

(Rodem et al. 1984), and capercaillie chick losses are higher in the fragmented forest matrix than in larger, intact blocks of old forest (Wegge et al. 1990).

Only 20% of our study area was used by capercaillie broods. Hence, we would expect a higher predation rate on broods than on nests, as predators would gain more from searching for broods in the remaining brood habitat. However, the survival rates of capercaillie nests and broods during the incubation period (lasting 26 days) is 29% (Wegge & Storaas 1990) and 32% (Kastdalen & Wegge 1990), respectively, indicating a biologically similar predation rate. The predators do not compare the gain of searching for broods with that of searching for nests as nests and broods are available at different times. The gain of searching for grouse broods will rather be compared with the gain of searching for voles or other prey species in areas not used by broods. If the brood habitat is diminished further, we will expect an exponential increase in brood mortality.

Our results have implications for the understanding of the process underlying the patterns observed in relation to habitat fragmentation. Rolstad & Wegge (1989b) and Andrén (1994) predicted that at a certain threshold of fragmentation, populations will decline more than could be expected from habitat loss alone. We have suggested a mechanism, i.e. increased predation on young broods, which may explain how loss of capercaillie and black grouse habitat may affect grouse populations in such a way that the decrease in population size will be higher than could be expected from habitat loss alone.

Marcström, Kenward & Engren (1988) conducted a fox and pine marten removal experiment on two non-fragmented boreal forested islands. Both the frequency of females with broods and chicks per brood in August increased following predator removal, indicating lower predation rates on both nests and broods. To test our results, predator removal experiments in areas with a gradient of available brood habitat are required. We also stress the importance of long-time studies to quantify nest and brood survival in relation to changes in forest fragmentation.

Our results may also have implications for the conservation of woodland grouse. Many threatened species may be conserved through protection of smaller patches of certain 'key' habitats. As a means of safeguarding biological diversity, Scandinavian forestry and nature conservation organisations have focused on the need of protecting such key habitats comprising < 5% of forest area in Sweden (Sjöberg

& Lennartsson 1995). But to protect the vulnerable reproduction stage of capercaillie and black grouse, it is not sufficient with minor 'cosmetic' patches and corridors in which the broods may move. Piccozzi, Moss & Kortland (1999) lost all their radio-equipped capercaillie broods due to predation in an area where the available brood habitats were fire-breaks between plantations. In order to sustain a sufficient capercaillie and black grouse production, at least half the forest area (see Fig. 1) should be maintained and managed to be prime brood habitat, which probably is possible by selective cutting in old, natural forests and early thinning in plantations, particularly on moist sites.

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