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Change in the sex ratio of the Finnish capercaillie *Tetrao urogallus* population

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Earlier reports from Fennoscandia and Russia have shown that among adult capercaillies the proportion of females is 60-65%, mainly as a consequence of high mortality of male chicks during their first months of life. The Finnish August censuses of grouse (1964-1988) show that the percentage of female capercaillie has remained unchanged at about 60-65% in northern and eastern Finland. Over the same period the percentage of females in southern and central Finland has decreased significantly from 62 to 50%. The present geographical variation in the percentage of females seems to coincide with the amount of forest in the landscape; the proportion of females is lowest in the southern and western part of Finland where the proportion of agricultural land is highest. Data from 1989-1996 show that variation in August male density among game management districts in Finland (CV%: 21.9) is significantly smaller than that of females (CV%: 33.4). This suggests that the variation in female proportion is more dependent on variation in female than in male density. The most probable reasons for the change in sex ratio include predation on females by mammalian and avian predators and selective hunting (or closing of hunting seasons), but tests of these hypotheses are premature at present.

Key words: capercaillie, Finland, sex ratio, Tetrao urogallus

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The capercaillie *Tetrao urogallus* is a large sedentary tetraonid of the boreal taiga. It has a marked sexual size dimorphism with males weighing up to 5 kg and females weighing up to 2 kg. Females outnumber males in the adult capercaillie population. In most reports the proportion of females is 60-65% (Rajala 1974, Wegge & Grasaas 1977, Wegge 1980, Beshkarev, Blagovidov, Sokolski & Hjeljord 1995). The capercaillie is a lekking species, and the dominant

males of the leks do most of the copulations (Hjort 1970). Therefore, the female-biased sex ratio does not affect the possibility of females to copulate. The sex ratio at hatching is presumably 50:50 (see Lindén 1981a). High mortality of male chicks during their first months of life results in a female-biased sex ratio. Male chicks with higher energy requirements suffer increased mortality, especially in cold and rainy weather (Lindén 1981b). Male chicks learn to

fly at an older age than female chicks, which makes them more vulnerable to predation (Kalske & Lindén 1988). Small broods have unexpectedly high proportions of female chicks, at least in a declining capercaillie population (Wegge 1980, see also Lindén 1981b).

Based on their studies in Norway, Wegge, Rolstad & Gjerde (1992) hypothesised that old-forest fragmentation would increase the proportion of females in the adult capercaillie population. Natal dispersal of females is longer than that of males, which would promote female recruitment in forest fragments. In addition, they suggested that fragmentation of old forest would increase predation on males. On the other hand, there is evidence that forest fragmentation increases predation on nests of ground-nesting birds (Andrén 1989, Kurki & Lindén 1995). Moreover, it could be hypothesised that females are vulnerable to predation during the incubation and brood-rearing periods, which possibly could decrease the proportion of females in the adult population.

Finnish monitoring data on capercaillie (Rajala 1974, Lindén, Helle, Helle & Wikman 1996) show that the present adult sex ratio is male-biased in southern Finland, in contrast to a female-biased ratio a few decades ago; the female percentage of 60-65% has not changed in the northern and eastern parts of Finland. In this article we describe changes that have taken place in the sex ratio during the past decades and relate them to the recent population changes of the species. We also present plausible explanations for the temporal pattern observed.

Material and methods

August counts of grouse have been performed since 1964 in Finland (Rajala 1974, Lindén & Rajala 1981, Helle & Lindström 1991, Lindén et al. 1996). The counts are carried out by three observers who walk abreast 20 m apart from each other. The census belt covers 60 m. Field testing of the method has shown that in the main belt area adult males and females without broods are detected with 55% efficiency and females with broods with 90% efficiency (Brittas & Karlbom 1990). Males and females are easily distinguished in the field.

The so-called route censuses in 1964-1988 were located in the best brood habitats of grouse and they were not exactly the same in consecutive years (Rajala 1974). The yearly length of census routes was

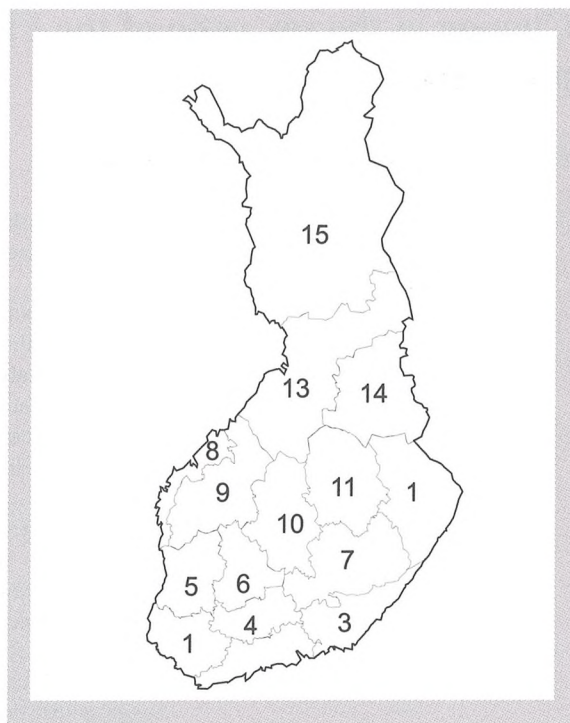


Figure 1. The 15 game management districts in Finland, in which sex ratios of capercaillie were monitored during 1964-1988 and 1989-1996.

about 25,000 km, with the length of a single route averaging about 25 km.

A new monitoring method was launched in 1988 with the same field procedure (the wildlife triangle scheme, Lindén et al. 1996). The basic unit is a triangular line with 4 km sides leading to a total length of 12 km. The lines are more randomly situated than the routes in the old monitoring system. They are also permanently marked in the field and remain the same. Because of their random location, they also cover less suitable grouse habitats. The yearly length of triangles studied is about 11,000 km.

We present the sex ratios separately for 1964-1988 and 1989-1996, because the results of the two monitoring methods are not fully comparable. The results are presented according to game management district (Fig. 1). To present temporal trends in sex ratios during 1964-1988, we applied different transformations to the data. Since the linear function in most cases fitted the data best, judged from the variances explained, we present the results as linear regression lines; since the variation in sample sizes was minor with respect to the massiveness of the data, logistic regression was not applied.

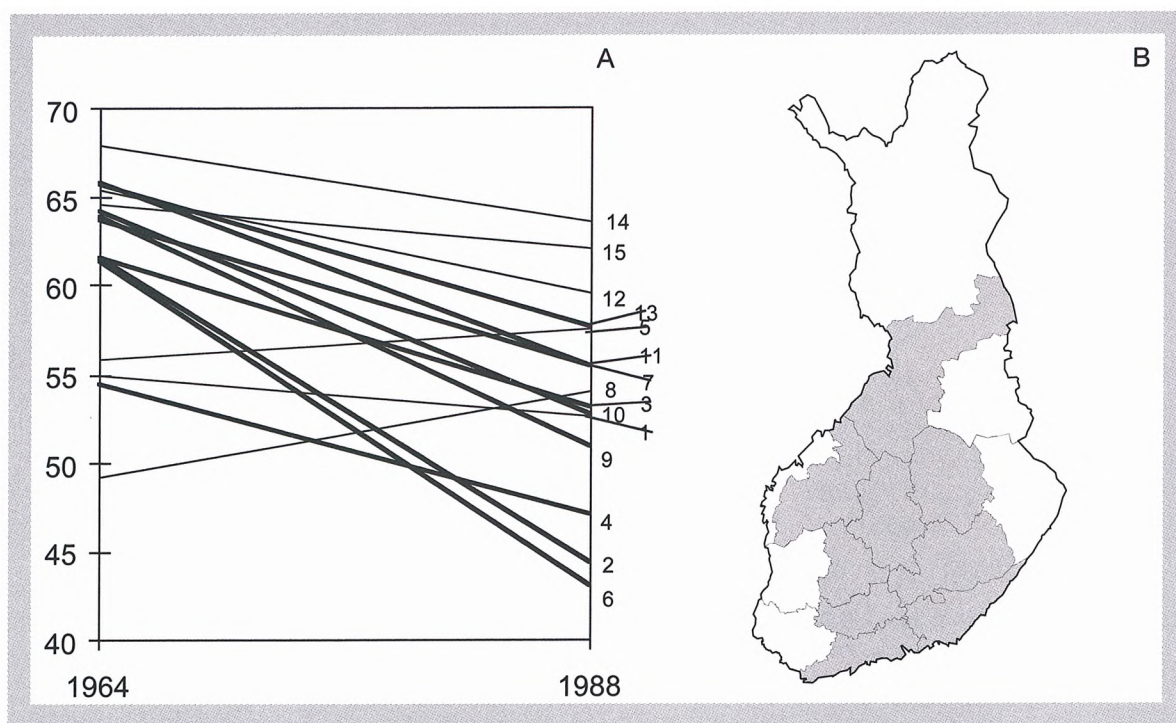


Figure 2. Changes in the sex ratio of capercaillie expressed by linear (A) regression lines of female percentages in 1964-1988 in Finland according to game management district (see district numbers in Fig. 1). Thick lines indicate statistically significant trends (A) and districts with significantly declining female proportions (FP) are shaded on the map (B).

Results

The mean female proportion (henceforth FP) for the whole of Finland decreased from 63% in the early 1960s to 53% in the late 1980s. There is, however, considerable variation between the game management districts. FP has remained unchanged or decreased only slightly in the northern and eastern parts of the country. The same pattern can be seen in the southwestern corner of Finland (districts 1 and 5, Fig. 2). In two game management districts in western Finland, FPs tended to increase over the time period, though not significantly. The remaining game management districts show decreasing trends. Nine of these declines are statistically significant. The area with a significant decrease in FP is uniform, covering most of southern Finland, except for districts 1, 5, 8 and 12 (see Fig. 2B).

There are no statistically significant trends in FP during 1989-1996 when analysed according to game management district. However, the geographic pattern in FP variation is clear (Fig. 3). FP is >50% in the northern and eastern parts of the country. To the south and west, the sex ratio is male-biased and in game management districts 4 and 6 FP is <40%.

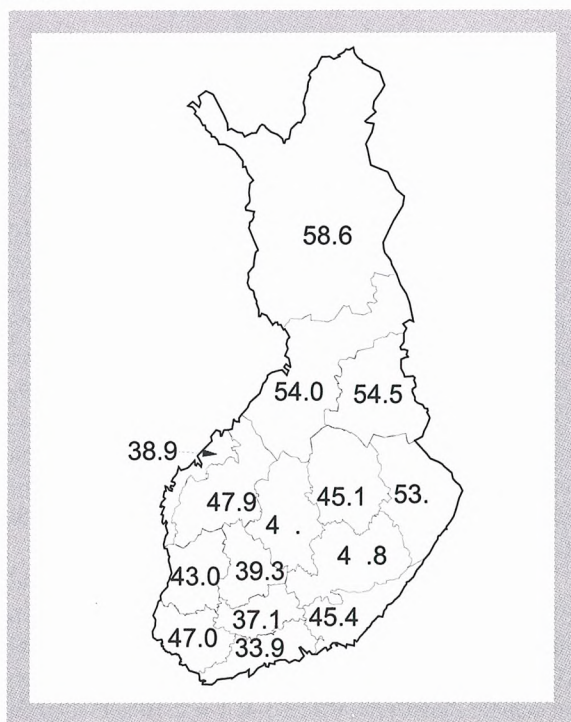


Figure 3. Mean percentages of females in the adult capercaillie population in the 15 game management districts in Finland during 1989-1996.

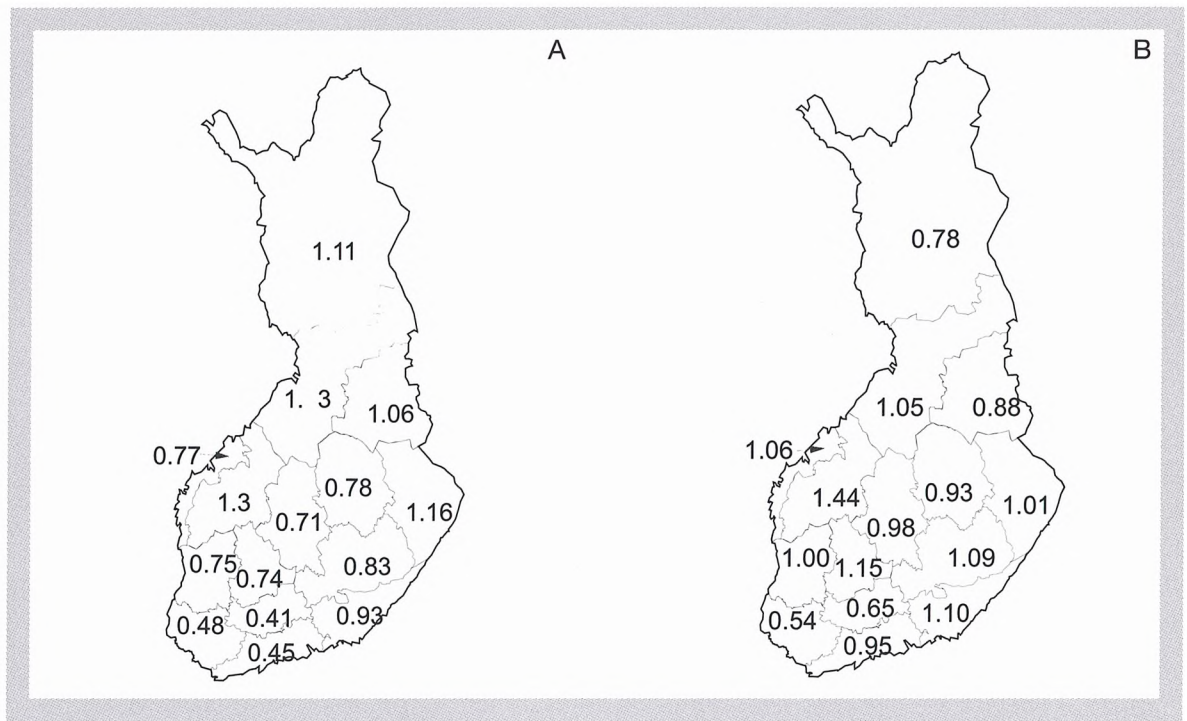


Figure 4. August densities (mean number of individuals per km² of forest land) of adult female (A) and adult male (B) capercaillie for the 15 game management districts in Finland during 1989-1996.

The results of the former route censuses and the later wildlife triangle censuses are not fully comparable. Both methods were used in eight game management districts in 1988 (Lindén, Wikman & Helle 1989), so some comparisons can be made. The route censuses yielded a mean FP of 58.8 and the wildlife triangle censuses a mean FP of 52.6%. The difference of 6.2 percent-units is significant ($P < 0.005$), but there is variation among the areas compared. To broaden the comparison, we compared the FPs of the 1986-1988 route counts with the FPs of the 1989-1991 triangle censuses according to game management district. A highly significant linear regression line fitted to the data predicts that the FP in route censuses is 6.4 percent-units higher than that in wildlife triangle censuses.

FP depends on the density of both females and males. In the August 1989-1996 data, variation in male density among game management districts (CV%: 21.9) was significantly smaller than variation in female density (CV%: 33.4; $t = 2.106$, $P < 0.05$; Fig. 4). This suggests that variation in FP is more dependent on the female than on the male component. In the 1989-1996 wildlife triangle data, the correlation

(r_s) between FP vs female density was +0.793 ($P < 0.01$) and vs male density -0.096 ($P > 0.1$).

We compared changes in FP in game management districts in 1964-1988 with relative density changes in the same period. A positive relationship would mean that a long-term population decline is associated with a decrease in female percentage. The relative density change was expressed using linear regression lines fitted to the data (see Lindén & Rajala 1981). There is a positive relationship between these two ($r_s = +0.174$), but it is not significant. A power-test of the statistic shows that the probability of finding a coefficient of 0.25, which would suggest a significant relationship, is low (0.15). Even if the relationship were real, it would be impossible to tell which came first; i.e. whether the changing FP is a consequence of the population decline, or whether the decreasing FP has resulted in a population decline.

We did a thorough methodological check to make sure that the change observed was not an artefact. The proportions of unidentified grouse species and unidentified sex in capercaillie, which are also recorded in the field, did not change during the study period (1964-1996) (statistics for the linear regres-

sions of these variables: $t = 0.875$ and 0.992 , respectively, $P > 0.1$ for both). There is no significant temporal change in the proportion of observations outside the main belt either ($t = 0.711$, $P > 0.1$). The black grouse *Tetrao tetrix* is also reported to have a female-biased sex ratio, e.g. in the 1960s in Finland (Rajala 1974). We analysed the black grouse data similarly according to game management district and found no significant changes in FP of black grouse. Our results suggest that the change in FP of the capercaillie is not an artefact, resulting from counting or recording procedures.

In good brood habitats, FP is about 6 percent-units higher than in random lines, according to the results of route and wildlife triangle censuses. The most probable reason for this is that, in good brood habitats, females are more often with broods and thus they are observed more efficiently than females without broods. Taking into account that the efficiency for these two groups is 90 and 50%, respectively (see Brittas & Karlbom 1990), and that the proportion of females with broods is 70% in good habitat and 30% in less good (average) habitat (see Lindén et al. 1989), we would expect a difference of 5% in FP in favour of good habitats. This difference is very close to that observed in comparisons of route and wildlife triangle censuses. The temporal change in FP could theoretically result from a change in habitat composition in August censuses. Although the routes would have been entirely in optimum habitats in the 1960s and in more random sites in the late 1980s, this would have decreased FP by 5 percent-units only, which is insufficient to explain the observed decrease in FP (average decrease in the southern part of Finland is 12%).

Discussion

The sex ratio in the adult capercaillie population has remained unchanged in northern and eastern Finland but the FP has declined dramatically in the southern part of the country. We were not able to perform strict tests to explain the change observed in FP. Here we discuss probable explanations for the phenomenon, which later studies should address.

Potential factors behind the temporal change in FP

The present variation of FP in Finland fits well with the proportion of cultivated and built-up areas in the

landscape. In northern and eastern Finland, still dominated by forests, the FP has remained unchanged during the past decades, whereas in the southern and central parts of Finland, where the impact of man on landscapes is heavier, FP has decreased. Interestingly, low FPs in the 1960s in western Finland (districts 5 and 8) are located in the oldest agricultural areas in Finland. There is no evidence, however, that changes in landscape structure *per se* have been the critical factor contributing to the temporal change in FP between 1964 and 1988 (see Kurki & Lindén 1995).

Based on the greater natal dispersal of females than of males (see e.g. Koivisto 1963), Wegge et al. (1992) predicted that FP should increase with increasing forest fragmentation. Agriculture has been fragmenting forest landscapes in southern Finland, but the FP has changed in the opposite direction of that predicted by Wegge et al. (1992).

The change in FP is a result of differences in mortality between males and females and the decreasing trend in the FP may have been caused by increased mortality of females associated with higher predation. Female capercaillies are optimum-sized prey for some predators, including goshawk *Accipiter gentilis*, eagle owl *Bubo bubo*, golden eagle *Aquila chrysaëtos*, red fox *Vulpes vulpes* and pine marten *Martes martes*, but males are too large for these predators. Furthermore, raccoon dog *Nyctereutes procyonoides*, badger *Meles meles* and American mink *Mustela vison* are more likely to predate on nests, which sometimes may lead to the killing of a female. These species, as a group, are more abundant in southern than in northern and eastern Finland (Hanski, Hansson & Henttonen 1991, Helle & Kauhala 1991, Helle, Lindén & Wikman 1996, Kurki, Nikula, Helle & Lindén 1998), and have increased in numbers in southern Finland in the past decades. Predation might therefore explain the temporal changes in FP. On the other hand, data from southern Norway (Wegge, Gjerde, Kastdalen, Rolstad & Storaas 1990) suggest that subadult males in fragmented forest areas are most vulnerable to predation by goshawk, red fox and pine marten in winter. Nest predation involving increased predation on females is probably not the key factor in our case, however, because we did not notice any temporal change in FP of black grouse which has a similar nesting behaviour.

The capercaillie is a game bird species which means that selective hunting could change the FP of the population. Unfortunately, we have no up-to-date

information on the number of males and females harvested. In the 1950s, the Finnish bag consisted of 45% females and 55% males (Helminen 1963). At that time, it was a tradition not to hunt females at all. Presumably, the ratio was the same in the early 1960s when the FP found in route censuses was ca 65%. Since the 1970s, the capercaillie hunting season has been closed in many southern game management areas; during periods with low population size in some areas and more or less continuously in other areas. It can be hypothesised that in the absence of capercaillie hunting, the number of males in the population should have increased, because the adult mortality of males is lower than that of females (Wegge et al. 1990).

The above-mentioned reasons are among the most likely ones to explain the increasing proportion of males in the capercaillie population in southern and central Finland. It is possible that the change is caused not by a single factor but by several interacting factors. We are able to test some of the hypotheses. Habitat and landscape characteristics of observation sites of female and male capercaillie in wildlife triangle censuses can be compared using GIS-based techniques (see Helle & Nikula 1996), which may throw new light on the effects of landscape structure on FP (including both direct and indirect effects). Effects of changing hunting practices and closing of hunting seasons on FP can be tested, too. To obtain a definitive explanation of the phenomenon, a detailed assessment of male and female mortality rates of capercaillie needs to be conducted in both northern Finland where a female-biased sex ratio exists and southwestern Finland where a male-biased sex ratio exists.

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