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Autumn population size of capercaillie *Tetrao urogallus* in relation to bilberry *Vaccinium myrtillus* production and weather: an analysis of Norwegian game reports

Vidar Selås

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From a study area in Aust-Agder, southern Norway, game reports from 1920-1978, supplemented with autumn counts carried out during 1968-1984, were used to determine whether the autumn population size of capercaillie *Tetrao urogallus* showed no increase, a slight increase or a strong increase compared to the population size the previous year. Based on the mast depression hypothesis, it was predicted that adverse weather conditions should have less influence on the reproduction and thus also on the autumn population size in post-mast years of bilberry *Vaccinium myrtillus* than in other years, because of a higher food quality and therefore also a higher body condition of the birds. In a logistic regression model, only the bilberry index and the June-September temperature of the previous year contributed significantly to explain the status of the capercaillie population. A negative effect of high summer temperatures in the previous year was highly significant when analysing post-mast years separately, possibly because bilberry plants were less depressed after a high seed crop if summer temperatures and thus primary production were high. Only when years with high bilberry production were analysed separately, did I find effects of weather conditions which could be assumed to have direct impacts on breeding success, such as snow conditions in spring and precipitation in early summer.

Key words: bilberry masting, mast depression hypothesis, plant quality, population fluctuation, *Tetrao urogallus*, weather

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In Norway and Sweden, autumn population sizes of capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, willow grouse *Lagopus lagopus* and hazel grouse *Bonasa bonasia* fluctuate in synchrony with voles *Clethrionomys* spp., with peak intervals of 3-5 years (Hagen 1952, Angelstam, Lindström & Widén 1985, Hörnfeldt, Löfgren & Carlson 1986). There are at least two possible explanations for this pattern:

1) Prey switching by generalist predators with voles as

main prey results in reduced survival of grouse eggs and chicks when voles become scarce (Hagen 1952, Angelstam, Lindström & Widén 1984, Lindström, Angelstam, Widén & Andrén 1987, Marcström, Kenward & Engren 1988);

2) Fluctuating quality of some common food plants influences survival and reproduction of both grouse and voles (Widén, Andrén, Angelstam & Lindström 1987, Selås 1997, 2000a).

This paper focuses on the latter hypothesis, but it

should be noted that the two hypotheses are not mutually exclusive.

Bilberry *Vaccinium myrtillus* is a food plant of great importance to both voles and grouse. In winter, bilberry shoots form the basic food for *Clethrionomys*-voles (Hansson & Larsson 1978, Hansson 1985). During summer, grouse hens and chicks feed on bilberry shoots and leaves as well as flowers and berries (Spidsø & Stuen 1988, Pulliainen & Tunkkari 1991). In addition, caterpillars feeding on bilberry leaves are crucial as food for newly hatched grouse chicks (Atlegrem 1991, Kastdalen & Wegge 1991). The number of such caterpillars should be expected to fluctuate in synchrony with vole and grouse populations if food quality is of importance (see Selås & Steel 1998). Further support for the hypothesis of a fluctuating food quality is that the mean body weight of moose *Alces alces* calves, which feed on bilberry in autumn, is positively correlated with the number of bank voles *Clethrionomys glareolus* in the succeeding year (Selås, Sonerud, Histøl & Hjeljord 2001).

The bilberry usually produces high seed crops, termed masts, with intervals of 3–4 years (Myrberget 1982, Selås 2000b), and vole and grouse populations are known to peak in bilberry post-mast years (Nordhagen 1928, Laine & Henttonen 1983, Selås 1997). A possible reason for this plant-herbivore relationship is that masts are produced at the expense of the chemical defence against herbivores as expressed in the mast depression hypothesis (Selås 1997, 1998a). Resource allocation to chemical defence should, however, depend not on the amount of reserves used for seed production, but rather on the amount available afterwards. This amount may in turn depend partly on the photosynthetic activity in the mast year, which again should depend on summer temperatures. If so, there should be a negative relationship between the peak population level of herbivores and the summer temperatures in the preceding (mast) year. Such a relationship has actually been found for both bank vole and capercaillie, as well as for the green oak leaf roller moth *Tortrix viridana*, in southern Norway (Selås 2000c, V. Selås, unpubl. data).

Weather may influence not only the bilberry, but also the breeding success and thus the population levels of grouse. Heavy rain has been assumed to be critical for the survival of chicks (Marcström 1960, Slagsvold & Grasaas 1979, Marcström & Höglund 1980, Erikstad & Spidsø 1982, Steen, Steen, Stenseth, Myrberget & Marcström 1988), while snow cover in spring affects food availability and thus possibly the body condition of hens prior to egg laying (Siivonen 1957, Moss, Watson & Parr 1975, Slagsvold & Grasaas 1979, Pulliainen & Tunkkari 1991, Swenson, Saari & Bonczar

1994). However, if food quality fluctuates, the effects of weather on grouse reproduction may also vary between years. This is due to the fact that the birds are likely to be more vulnerable to the unfavourable weather conditions mentioned above if the availability of high-quality food is low.

When analysing grouse population fluctuations in relation to the mast depression hypothesis, four categories of years should be distinguished:

- 1) Years with low bilberry production both in the preceding and the current year. The prediction is that in such years, plant resistance to herbivory is high, and the reproductive success of grouse low;
- 2) Years with low bilberry production in the preceding year but a high production in the current year. Grouse reproduction may be high enough to give some population increase because of improved food quality in late summer. Good grouse reproduction may, however, require favourable weather conditions in spring and early summer, when food conditions are still poor;
- 3) Years with high bilberry production both in the preceding and the current year. Grouse reproductive success may depend on whether the current high seed crop was produced because the level of stored resources in bilberry plants was still relatively high after the first mast year, or because individual plants were not synchronised with regard to seed production;
- 4) Years with high bilberry production in the preceding year but low production in the current year. If plants are so depressed after the high seed crop that they are not able to rebuild their chemical defence until autumn, then the reproductive success of grouse should be high and a marked population increase should be expected.

In this paper I use game reports supplemented with hunting statistics and autumn count results from southern Norway to analyse the autumn population size of capercaillie in relation to bilberry production and weather during 1920–1984. For years with a low bilberry production but a high bilberry production in the preceding year, a negative correlation between capercaillie autumn population sizes and summer temperatures in the preceding year has already been reported (Selås 2000c). For these years, spring and summer weather of the current year appeared to be of less importance, though there was a tendency for a negative effect of much rain in June–July. So far, however, no analyses of the impacts of weather for the other three categories of bilberry years have been reported.

Material and methods

The study area, which is situated in the boreo-nemoral zone, lies in the southeastern part of the county of Aust-Agder in southern Norway, and includes the municipalities of Vegårshei, Tvedestrand, Åmli, Froland, Moland, Risør and Gjerstad (see the map in Selås 2000b). The climate is sub-oceanic, and snow usually covers the ground from December through March or April. Climatic data used in the study were taken from a meteorological station situated within the study area (Selås 2000a). The study area is dominated by forests (80%), mostly of poor and intermediate productivity, with scattered lakes (10%), bogs (5%) and agricultural land (<2%). The forests are characterised by a fine-grained mosaic of young, medium and old-aged coniferous, mixed and deciduous stands. Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, European oak *Quercus petraea*, aspen *Populus tremula* and birch *Betula* spp. are the dominant tree species, whereas bilberry is a common and often dominant plant species in the field layer.

For the period 1932-1978, annual indices of bilberry production (value 0-2) were calculated from game reports as described by Selås (1997, 2000a,b; Fig. 1). For the period 1925-1931, a bilberry production index was calculated from reports on bilberry export (Selås

2000b; see Fig. 1). During 1907-1924, the annual production of wild berries (bilberries, cowberries *Vaccinium vitis-idaea* and cloudberry *Rubus chamaemorus* pooled) in Aust-Agder in general was estimated as percent of a normal year (Valseth, Gullen & Lunner 1976). Bilberry and cowberry will often flower in synchrony, whereas the flowering of cloudberry usually is not synchronised with the two former species (Myrberget 1982). For the years 1919-1924, which are of interest in the present study, information given in local newspapers and by Anonymous (1919) and Grasaas (1977) confirmed, however, that the indices given by Valseth et al. (1976) reflected the production of bilberries. The values given by Valseth et al. (1976) were transformed by setting the lowest and highest values equal to the lowest and highest values calculated from game reports (see Fig. 1). For the period 1979-1985, I used the annual amount of bilberries picked by one family living within the study area to calculate indices for bilberry production (see Fig. 1).

During 1920-1945, members of the Norwegian Hunter and Fisher Union completed game reports for each county, and the results regarding the autumn population level of capercaillie and other game species were published annually in the union's journal. From these articles it was not possible to calculate indices for population levels, but it could be assessed whether there was no increase, a slight increase or a strong increase in the autumn population of capercaillie compared to the previous year. In the study area, annual fluctuations in autumn population levels have been much higher than in spring population levels (Grasaas 1963, Wegge & Grasaas 1977, Selås 2000a). I therefore assumed that variations in the autumn population size compared to that of the previous year mainly reflected variations in chick production, and that variations in adult population size in spring was of less importance.

In public game reports from 1932-1978, the autumn population size of capercaillie was designated as lower than (value 0), equal to (value 1) or higher than (value 2) that of the preceding autumn. Few reports from before 1945 existed, and there was only one report from Aust-Agder for 1978, but for the period 1945-1977 annual indices could be calculated using the mean values from all reports from the selected municipalities (for 1975, reports from two neighbouring municipalities had to be used). Forester T. Grasaas, who filled in game reports from Vegårshei during 1940-1956, gave annual reports on the capercaillie population size to the journal of the Norwegian Hunter and Fisher Union during 1968-1978 (see references in Selås 2000a). Because the number of game reports was low in this period (only three years with reports from Vegårshei), I included all

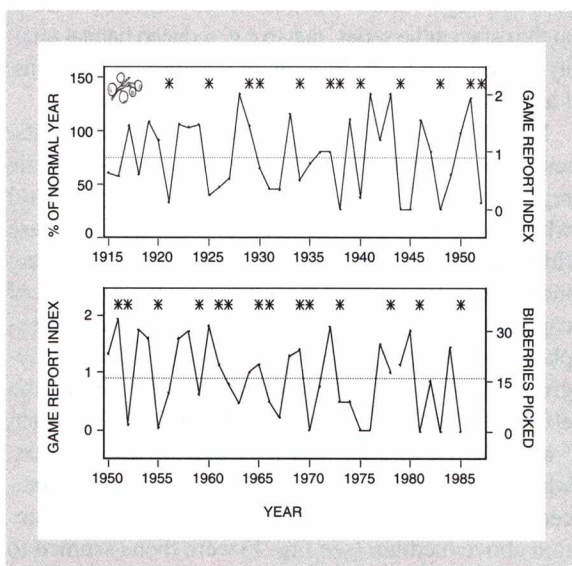


Figure 1. Annual variation in bilberry production in a study area in Aust-Agder, southern Norway. For most years the indices were calculated from game reports (see text). The horizontal dotted line corresponds to the mean value. Years with high vole populations are marked with an asterisk. Information on vole numbers was taken from game reports and the following articles: Wildhagen (1952), Grasaas (1963, 1971), Myrberget (1965), Christiansen (1981, 1983), Spidsø & Selås (1988).

evaluations given by Grasaas when calculating game report indices.

Grasaas (1963) used the number of capercaillie hunted in Vegårshei as an index for the autumn population size during 1953-1962 (Fig. 2). The first difference (= annual change) of this ln-transformed hunting index was significantly correlated with the index calculated from game reports ($r = 0.88$, $P = 0.012$, $N = 9$; see Fig. 2). During 1968-1983, capercaillie were counted each autumn along line transects in Vegårshei (Wegge & Grasaas 1977, Wegge 1979, 1980, Grasaas 1980, Krafft 1980, 1981, 1982, 1983, 1984; see Fig. 2). Based on these counts a slight increase in the autumn population could only be assumed in three years, viz. 1972, 1978 and 1980. Grasaas (1973, 1980) reported that there was an increase in 1978, but not in 1972. According to the game reports, there was rather a decrease in 1972, and therefore I assumed that there was no increase that year. Capercaillie was not counted in Vegårshei in 1984, but according to counts in nearby areas, there was a slight increase also this year (Krafft 1985).

When the capercaillie index from 1945-1977 was ln-transformed, it did not differ from a normal distribution (Shapiro-Wilks test: $W = 0.94$, $P = 0.09$), and the only significant autocorrelation was at time lag one ($r = 0.56$, $P < 0.001$). The ln-transformed capercaillie

index was compared with the bilberry index of the previous year and three weather indices. Because of the autocorrelation, a linear model was fitted to the data using the method of Generalised Least Squares, where the errors are allowed to be correlated. In this model the errors were assumed to follow an autoregressive AR (1) process, i.e. a simple linear regression model with first-order autoregressive errors. Calculations were performed in the R software environment (Ihaka & Gentleman 1996). A stepwise procedure (backward elimination) was used. If the significance probability attributed to an explanatory variable was higher than 0.10, it was removed from the model.

As a measure of snow cover in spring, I used two categories, i.e. early and late snow melt (Grasaas 1977, Selås 2000a). As an index of weather conditions in early summer, I used the total amount of precipitation in June and July, which is assumed to be important for chick survival. As an index of summer temperatures in the last year, I used the mean temperature for the four months June-September, which by forest scientists has been assumed to be of vital importance to both growth and seed production of forest trees in Norway. None of the explanatory variables were significantly correlated. Neither was there a significant autocorrelation in any of the series. The bilberry index was the only independent variable that differed from a normal distribution ($W = 0.91$, $P < 0.001$) due to a high proportion of low and high values. Because there might be a trend in the capercaillie series, due to e.g. reduced habitat quality caused by forestry or increased predator populations, I also used year as an explanatory variable.

For the period 1920-1984, I conducted likelihood ratio tests (corrected for overdispersion) in ordinal logistic regression models (backward elimination procedure) where each year was regarded as having no increase (index ≤ 1.0), a slight increase (index > 1.0) or a strong increase (index > 1.5) in the autumn population size of capercaillie, compared to the preceding year. The explanatory variables were the same as in the stepwise regression model, but I also included the interaction effects of bilberry production and weather. Thereafter, I analysed separately the four categories of years, which were based on the bilberry production in the preceding and current year. Years with a bilberry production above medium (see Fig. 1) were then assumed to have a high bilberry production. Thus, in these analyses, only weather indices and year were used as independent variables.

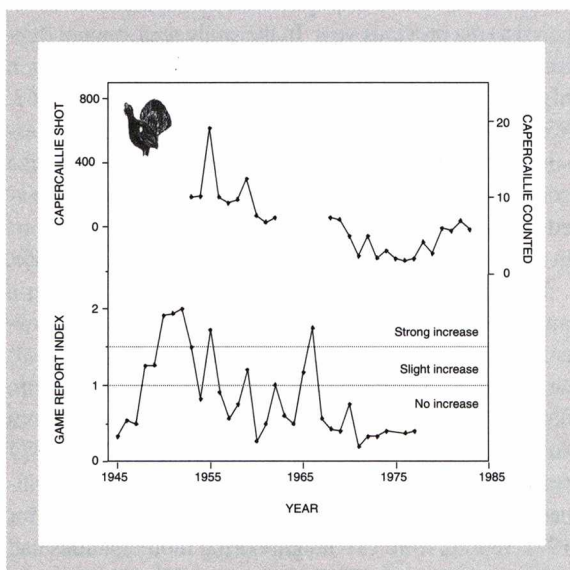


Figure 2. Number of capercaillie hunted (Grasaas 1963) or counted (Wegge & Grasaas 1977, Wegge 1979, 1980, Grasaas 1980, Krafft 1980, 1981, 1982, 1983, 1984) in the municipality of Vegårshei, southern Norway, and game report indices for the autumn population size of capercaillie in Vegårshei and neighbouring municipalities. In game reports, the autumn population size was termed as lower than (value 0), equal to (value 1) or higher than (value 2) that of the previous year. The calculated index gives the mean value for all reports from the study area.

Table 1. Autumn population size of capercaillie for the four categories of bilberry production years described below. The table gives the number of years with no increase, a slight increase and a strong increase, respectively, compared to the autumn population size of capercaillie of the previous year. N = total number of years. 0/0-year: bilberry production < average both in preceding and current year; 0/1-year: bilberry production < average in preceding year and > average in current year; 1/1-year: bilberry production > average both in preceding and current year; 1/0-year: bilberry production > average in preceding year and < average in current year.

| Autumn population size | 0/0 years (N = 16) | 0/1-years (N = 16) | 1/1-years (N = 17) | 1/0-years (N = 16) | All years (N = 65) |
|------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| No increase | 15 | 10 | 8 | 4 | 37 |
| Slight increase | 1 | 5 | 6 | 5 | 17 |
| Strong increase | 0 | 1 | 3 | 7 | 11 |

Results

During 1919-1984, high seed crops of bilberry were usually produced at intervals of 2-4 years (see Fig. 1). Most increases in the autumn population of capercaillie were observed in or after years of high bilberry production (Table 1), but there were also several mast years in which the capercaillie populations did not increase. For the period 1945-1977 (N = 33), the only explanatory variable which was not removed from the model was the bilberry production index of the preceding year, which had an almost significant effect ($R^2 = 0.10$, $P = 0.058$; see Fig. 2).

In the logistic regression model, all interaction terms and the variables year, early/late spring and rain in June-July were removed from the model. Thus, the only variables that contributed to explain whether there was no increase, a slight increase or a strong increase in the capercaillie autumn population during 1920-1984 (N = 65) was the bilberry index of the preceding year ($\chi^2 = 8.00$, $P = 0.005$) and the mean temperature in June-September in the preceding year ($\chi^2 = 5.95$, $P = 0.015$). For most years with a strong increase in the capercaillie autumn population, the preceding year had both a high bilberry production and a low mean temperature in June-September.

When considering only years with low bilberry production but a high bilberry production in the previous year, there was a significant negative effect of both the mean temperature in the preceding summer ($\chi^2 = 12.49$, $P < 0.001$) and of the year ($\chi^2 = 5.64$, $P = 0.018$; Fig. 3). For years with a strong increase in the autumn population of capercaillie, the mean summer temperature of the preceding (mast) year ranged within 12.2-13.1°C (mean: 12.7), whereas for the years with no or a slight increase it ranged within 13.1-15.1°C (mean: 14.1).

For all but one of the 16 years which had a bilberry production index below medium both in the preceding and current year, there was no increase in the capercaillie autumn population (see Table 1). As there was only one year with a slight increase (1949), it was not possible

to run a logistic regression analysis for this category. In 1949, a promising bilberry production was reported to be destroyed by drought relatively late in the summer, so that the berries became too small to be utilised by man. Thus, despite of the low bilberry index, the bilberry production may have been sufficient to explain the slight increase in the autumn population of capercaillie that year. In addition, the amount of precipitation in June-July that year (see below) was lower than for any of the other years in this category.

Of the 16 years with few bilberries in the preceding but many in the current year, five had increasing and one (1950) had a strongly increasing autumn population of capercaillie (see Table 1). In the logistic regression analysis, two variables were not removed from the model, i.e. late or early snow melt ($\chi^2 = 3.45$, $P = 0.063$) and the total amount of precipitation in June-July ($\chi^2 = 6.34$, $P = 0.012$; Fig. 4), but the effect was significant

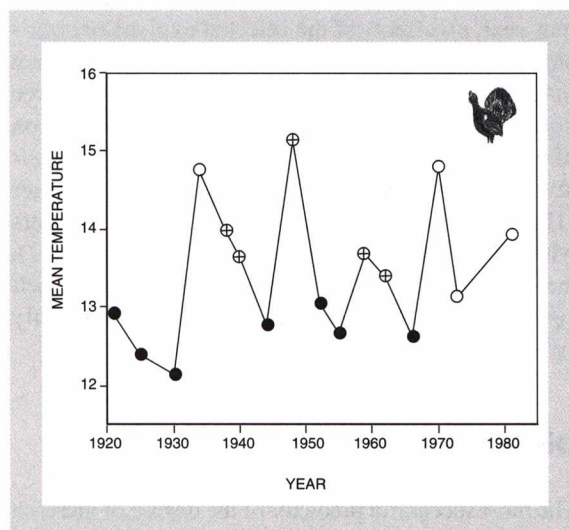


Figure 3. Mean temperature in June-September of the previous year for years with a bilberry production below average, but a production above average in the previous year (1/0 years). The years were further categorised based on the autumn population size of capercaillie, compared to the size in the previous year. ● symbolises years with a strong increase, ⊕ years with a slight increase, and ○ years with no increase in the capercaillie autumn population.

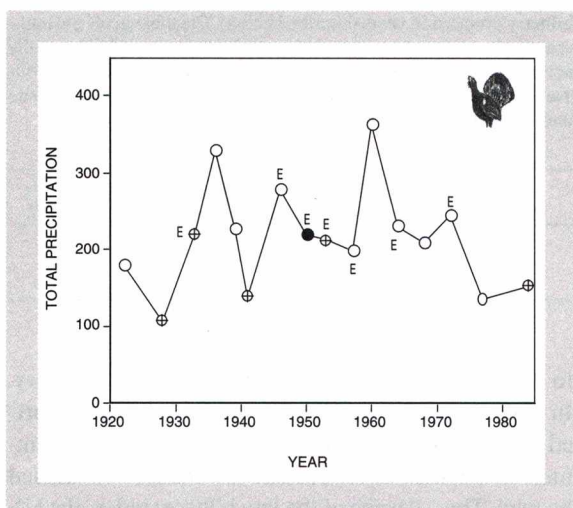


Figure 4. Total amount of precipitation in June-July for years with a bilberry production above average, but a production below average in the previous year (0/1 years). E indicates years with an early snow melt. The years were categorised based on the autumn population size of capercaillie compared to the size in the previous year. ● symbolises years with a strong increase, ⊗ years with a slight increase, and ○ years with no increase in the capercaillie autumn population.

only for the latter. However, if there actually was a slight increase in the capercaillie autumn population size in 1972, as indicated by the autumn counts (see Fig. 2), there was a significant positive effect of both early snow melt ($\chi^2 = 4.49$, $P = 0.034$) and a low amount of precipitation during June-July ($\chi^2 = 5.45$, $P = 0.020$).

For the last category of years, i.e. the 17 years with a high bilberry production both in the preceding and current year, no effects of the selected explanatory variables were found when correcting for overdispersion in the data. It should be noted, however, that the three years with a strong increase in the autumn population of capercaillie, viz. 1929, 1943 and 1951, all had relatively low temperatures in the preceding summer (11.2, 12.4 and 12.6°C, respectively). When all years with a high bilberry production were pooled ($N = 33$), there was an almost significant effect of both snow melt ($\chi^2 = 3.77$, $P = 0.052$) and precipitation in June-July ($\chi^2 = 3.29$, $P = 0.070$).

Discussion

The most successful predictor of the degree of increase in the autumn population size of capercaillie in southern Norway during 1920-1984 was the bilberry production of the previous year, but also the summer temperature of mast years was of importance. When summer temperatures were high in a bilberry mast year, the succeeding post-mast year usually had no or only a slight

increase in the capercaillie population, despite large vole population sizes. Since bilberry is an important food source for capercaillie chicks in late summer, an early rise in the content of chemical defence compounds in post-mast years may be more critical for this species than for *Clethrionomys*-voles, which are most dependent on bilberry as a source of food in winter. While capercaillie chicks may suffer from increased mortality due to low food quality in August-September, vole populations may not be seriously affected until winter, when they are forced to concentrate on bilberry as their main source of food. Only after cold mast years, bank vole populations in the study area have remained high until spring or summer two years after the mast year (V. Selås, unpubl. data).

Early snow melt and a low amount of precipitation in early summer were associated with increasing autumn populations of capercaillie only in years with a high bilberry production. If the bilberry production was low both in the current and the previous year, there was usually no increase in the autumn population of capercaillie, regardless of weather conditions. Thus, for years other than post-mast years, both favourable weather conditions and a high bilberry production appeared to be necessary for a good chick production. The significance of the bilberry production may be ascribed to the nutrients provided by the flowers or the berries themselves (e.g. Spidsø & Stuen 1988) and/or the increased quality of bilberry leaves in late summer. The importance of bilberry masting may be one reason why there are contradicting opinions with regard to the impact of weather for grouse breeding success in Scandinavia (see e.g. Steen et al. 1988), because in previous studies bilberry mast and post-mast years have not been analysed separately from other years.

Since voles were more or less abundant in all post-mast years, also in those with no increase in the capercaillie population, it could be concluded that high vole populations, which are commonly believed to serve as a buffer against egg and chick predation, are no guarantee of a good chick production in Aust-Agder. However, the impact of predators should not be ignored, because the body condition of grouse will probably affect their vulnerability to predation (Widén et al. 1987). In addition, high food quality combined with high numbers of caterpillars on bilberry leaves (Kastdalen & Wegge 1991, Selås & Steel 1998) in post-mast years may reduce the time needed for foraging, which again should reduce the predation risk for both grouse hens and chicks.

Even parasites may contribute to enhance the difference in breeding success between post-mast years

and other years, by influencing the body condition of the grouse. In a study area in Buskerud, eastern Norway, Brinkmann (1926) found that a higher proportion of grouse were infected by coccidiosis *Eimeri brinkmanni* in 1925 than in 1926. The chick production was highest in 1926, presumably due to the high production of wild berries in eastern Norway in general in 1925 (Nordhagen 1928). In Aust-Agder, where the bilberry production was high in 1924 and low in 1925, the proportion of infected birds was lower and the autumn population size higher in 1925 than in 1926 (Brinkmann 1926).

I also found a negative effect of year in the analysis of post-mast years during 1920-1984. It has commonly been argued that increased populations of generalist predators are responsible for the general negative trend in Fennoscandian grouse populations from the 1960s onwards. Especially the red fox *Vulpes vulpes* seems to have a negative effect on grouse populations (Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994, Selås 1998b, Smedshaug, Selås, Lund & Sonerud 1999). However, there has always been years of very low grouse populations, even early in the 20th century when the numbers of generalist predators, such as red fox and pine marten *Martes martes*, were much lower than in recent years (Hjeljord 1980). High populations of generalist predators may prevent grouse populations from reaching as high peak levels as they occasionally did in Norway in the 1920s, 1940s and 1950s (Hjeljord 1980), but this remains to be tested experimentally.

In multiple correlation analyses there is always a possibility that some explanatory variables give significant test results by chance alone. Besides, the analyses had to be based on capercaillie and bilberry indices obtained from a variety of sources (the best available), and they may not always have given correct estimates of the real numbers. Because of possible biases in the data, the results of this study should be considered mainly as suggestive for further research. The main conclusion, however, is that the effect of weather should not be ignored, even if it probably is of less importance than the factors which are responsible for the larger, and often regular, fluctuations in grouse populations. This is because weather conditions may be important for the degree of population increases and decreases, as indicated by this analysis of game reports from southern Norway.

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