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ORIGINAL ARTICLES

Population dynamics of capercaillie *Tetrao urogallus* in relation to bilberry *Vaccinium myrtillus* production in southern Norway

Vidar Selås

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Forester T. Grasaas' data on numbers of capercaillie *Tetrao urogallus* cocks and hens observed at leks and clutch sizes in Vegårshei, southern Norway, during 1953-1962 (high population level) and 1969-1978 (low population level) were analysed with regard to bilberry *Vaccinium myrtillus* production, autumn population indices and snow conditions in spring. From the mast depression hypothesis, it was predicted that the number of capercaillies counted at leks and the mean clutch size should be high after high seed crops (masts) of bilberry, usually produced at intervals of 3-5 years. In stepwise regression models, both the bilberry index of the preceding year and the autumn population index one (hens) or two (cocks) years earlier contributed to explain the mean number of capercaillies counted at leks during 1970-1978. Capercaillie clutch sizes were highest in years with early thaw, but the effect was significant only for the period 1969-1978. For this period, there also was a positive effect of the bilberry index and a negative effect of the autumn population index of the previous year. It is concluded that the synchronous population fluctuation of grouse and voles in Norway and Sweden cannot be explained by the alternative prey hypothesis alone, and that food quality should also be considered as a possible contributing factor when analysing population fluctuations of grouse and other herbivorous species.

Key words: bilberry masting, clutch size, mast depression hypothesis, plant quality, population cycles, population dynamics, Tetrao urogallus

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In the boreal zone of Fennoscandia, capercaillie *Tetrao urogallus*, black grouse *T. tetrix*, willow grouse *Lagopus lagopus* and hazel grouse *Bonasa bonasia* fluctuate synchronously (Moksnes 1972, Myrberget 1977, Sørensen 1977, Hörnfeldt 1978, Hjeljord 1980, Hörnfeldt, Löfgren & Carlson 1986, Ranta, Lindström & Lindén 1995). The breeding success of these species is usually higher when voles are abundant than when

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they are scarce (Myrberget 1970, 1974, Angelstam 1983, Angelstam, Lindström & Widén 1984, Wegge & Storaas 1990), resulting in the well-known synchronous 3-5 year population fluctuations of voles and grouse in Norway and Sweden (Hagen 1952, Hörnfeldt 1978, Angelstam, Lindström & Widén 1985, Hörnfeldt et al. 1986).

Reduced predation pressure on eggs and chicks from generalist predators mainly preying on voles has been assumed to be the main reason for the increased breeding success of grouse in peak vole years (Hagen 1952, Angelstam et al. 1984). This idea has later been supported by both experimental and observational studies (Lindström, Angelstam, Widén & Andrén 1987, Marcström, Kenward & Engren 1988, Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Jäderberg, Lemnell, Martinsson, Sköld & Swenson 1994, Smedhaug, Selås, Lund & Sonerud 1999). Outside Norway and Sweden, however, the grouse cycle does not always follow the vole cycle (Lindén 1989, Hudson 1992, Ranta et al. 1995), and therefore the alternative prey hypothesis cannot explain all grouse population cycles. Other factors which have been suggested as possible causes for grouse population cycles are parasites, food quality and intrinsic regulatory processes (Watson & Moss 1979, Lindström 1994). Based on a study of grouse hens' vulnerability to predation during the vole cycle, Widén, Andrén, Angelstam & Lindström (1987) suggested that food quality may be at least a contributing factor in the synchronised vole and grouse fluctuations in Sweden and Norway.

A possible link between voles and grouse in Fennoscandia is the bilberry *Vaccinium myrtillus*, which is an important food plant for *Clethrionomys*-voles in winter (Hansson & Larsson 1978, Hansson 1985), and for all forest-living grouse species in spring, summer and autumn (Kaasa 1959, Ahnlund & Helander 1975, Brittas 1988, Pulliainen & Tunkkari 1991). According to the mast depression hypothesis, cyclic population fluctuations of herbivores are caused by mast seeding of their food plants, because mast is suggested to be produced at the expense of chemical defence against herbivores (Selås 1997, 1998a). Bilberry usually produces high seed crops at intervals of 3-5 years (Myrberget 1982a, Selås 1997), and peak populations of voles or grouse have been reported from post-mast years of bilberry (Nordhagen 1928, Tast & Kalela 1971, Laine & Henttonen 1983, Selås 1997).

Both voles and grouse are known to be negatively influenced by high levels of chemical defence compounds in their food plants (see Seldal, Andersen & Högstedt 1994, Guglielmo, Karasov & Jakubas 1996, Hewitt & Kirkpatrick 1997). Currently, our knowledge of chemical defence in plants is, however, limited, and in several studies no relationship between the secondary plant compounds selected for analysis and vole or grouse numbers have been found (Jonasson, Bryant, Chapin & Andersson 1986, Lindroth & Batzli 1986, Laine & Henttonen 1987, Oksanen, Oksanen, Lukkari & Sirén 1987, Sinclair, Krebs, Smith & Boutin 1988, Hanssen, Pedersen & Lundh 1991). As long as we do not know whether mast seeding influence the digestibility or nutrient value of the plants, the causal relationship between bilberry masting and vole or grouse numbers remains unknown. Due to the complexity of the production of chemical defence compounds in plants (e.g. Karban & Baldwin 1997), studies on annual variations in grouse body condition, survival and reproduction may still be the best way to test for correlations with any fluctuations in food quality.

If spring densities of grouse depend on the autumn densities in the previous year (e.g. Myrberget 1984, Wegge 1984, Angelstam et al. 1985, Lindström, Ranta, Lindén & Lindén 1997), spring populations should be at their highest *after* peak vole years, because the reproduction and thus the autumn density, is usually high when voles are abundant. If, on the other hand, spring densities also depend on food quality, e.g. because high food quality improves winter survival, then it could be predicted from the mast depression hypothesis that spring populations should be high also in post-mast years of bilberry, i.e. *in* peak vole years. This is because the mast depression hypothesis predicts that the chemical defence of bilberry plants should be lowest, and thus food quality for grouse highest, in autumn, winter and spring after the mast production.

Both the alternative prey hypothesis and the mast depression hypothesis predict that the reproduction and thus the autumn density of grouse should be highest in peak vole years, i.e. one year after bilberry mast years. Unlike the alternative prey hypothesis, however, the mast depression hypothesis predicts that this should be caused partly by a better body condition of the hens due to higher food quality in spring. Hence, according to this hypothesis, we should expect not only higher egg and chick survival, but also larger clutch sizes, in peak vole years. Clutch sizes may, however, also be influenced (inversely) by the reproduction in the previous year, because a lower mean clutch size should be expected if there is a high number of juvenile hens in the breeding population (Lindén 1983).

In this paper, I analyse forester T. Grasaas' data on

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spring population indices and mean clutch sizes of capercaillie from southern Norway in relation to autumn population indices and reports on bilberry production. The study of Grasaas was conducted during two separate 10-year periods, one with generally high population levels of capercaillie, and one with lower population levels. Slagsvold & Grasaas (1979) found that an early snow melt was one variable which coincided with high autumn densities of capercaillie in the study area. Since snow depth obviously influences the availability of bilberry plants to capercaillies in spring, I also included information on snow conditions in the analyses.

Even though the focus of this paper is on possible effects of food quality, it should be remembered that the mast depression and the alternative prey hypotheses are not mutually exclusive. Thus, support for one of these hypotheses does not automatically lead to rejection of the other.

Material and methods

In Vegårshei and the northern parts of the neighbouring municipality of Tvedestrand, in the county of Aust-Agder, southern Norway (58°48'N, 8°57'E), forester T. Grasaas studied different aspects of capercaillie population dynamics during 1953-1962 and 1969-1979 (Grasaas 1955, 1956, 1957, 1958, 1960, 1961, 1962, 1963, 1971, 1972, 1973, 1977, 1978, 1980 and T. Grasaas, unpubl. data, see also Wegge & Grasaas 1977). The study area covers approximately 350 km^2, and is situated 100-300 m a.s.l., 20-25 km inland from the coast, in the boreo-nemoral zone. The climate is suboceanic, and snow usually covers the ground from December through March or April. For more detailed descriptions of the study area, see Wegge (1980) and Spidsø & Stuen (1988).

As an index of snow conditions in spring, I used the 'date of snow melt', i.e. the date when the ground at the meteorological station in Vegårshei (58°45'N, 8°52'E) was finally free of snow (Table 1). However, the date of snow melt did not reflect the availability of bilberry plants prior to egg laying perfectly. For instance, in 1972 Grasaas characterised both the winter and spring as favourable despite the relatively late date of snow melt, because there was almost no snow until March, and almost snow free ground on 15 April. Therefore, I also used Grasaas' two categories 'early' and 'late' thaw, based on the occurrence of snow-free spots in the study area in late April, when analysing the data (see Table 1).

Spring population indices and clutch sizes of the capercaillie were compared with a bilberry production index of the previous year. Indices of bilberry produc-

Table 1. Information on the date of snow melt, bilberry production and number of capercaillie eggs and nests for all and first clutches in Vegårshei, southern Norway. Data from Grasaas (1955, 1957, 1958, 1962, 1963, 1971, 1972, 1973, 1977, 1978, T. Grasaas, unpubl. data), except for the bilberry index, which was calculated from game reports (numbers are given in parentheses). * = years in which the thaw was considered to have been early by Grasaas. In the category 'first clutches', both second and undated clutches were omitted.

Year	Date of snow melt	Bilberry index	All clutches		First clutches	
			Eggs	Nests	Eggs	Nests
1952		0.10 (10)				
1953	27. March*	1.75 (12)	278	38	267	36
1954	05. May	1.59 (27)	228	32		
1955	16. April*	0.03 (29)	231	31	227	30
1956	26. April	0.64 (25)	244	35	244	35
1957	04. April*	1.59 (22)	280	38	253	34
1958	02. May	1.71 (14)	267	37		
1959	21. March*	0.62 (13)	146	21	130	18
1960	22. April	1.82 (11)	186	27		
1961	16. March*	1.14 (14)	202	26		
1962	26. April		101	14		
1968		1.29 (7)				
1969	02. May	1.40 (5)	114	18	109	17
1970	10. May	0.00 (6)	122	18	101	15
1971	10. April*	0.75 (4)	63	9	43	6
1972	24. April*	1.80 (5)	81	11	76	10
1973	22. March*	0.50 (2)	84	11	78	10
1974	03. April*	0.50 (2)	66	9	66	9
1975	15. April*	0.00 (2)	42	6	42	6
1976	02. April*	0.00 (6)	43	6	37	5
1977	05. May	1.50 (4)	47	7	40	6
1978	10. May		39	5	39	5

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tion were calculated from game reports from Vegårshei, Tvedestrand and their neighbouring municipalities (see Selås 1997). It was not possible to calculate a bilberry index for 1978, and therefore available data on capercaillie from 1979 were not used. In each game report the bilberry production, which was assumed to be of importance for grouse and other game species, was evaluated as either lower than medium (0), medium (1) or higher than medium (2). The annual bilberry index is then the mean of all reports from that year (see Table 1). For 1975 there were no game reports available from the selected municipalities. This year, however, two representatives of the forest authorities in Aust-Agder, both living in Vegårshei, reported to different local newspapers, and independently of each other, that the bilberry production was lower than medium because of a summer drought. I therefore used their statements as 'game reports' for 1975. Also two game reports from other parts of Aust-Agder evaluated the bilberry production to be lower than medium.

For most years the bilberry production was mentioned by local newspapers, and these statements were all in accordance with the berry indices, even for years when the number of game reports was low, such as 1971, 1973, 1974 and 1977. The annual berry production was evaluated also by the Agricultural Price Reporting Office, from which I have received reports for 1953, 1955-1961 and 1968-1970. The bilberry production was termed as high in 1953, 1957, 1958, 1960, 1961 and 1969, and low in 1955, 1956, 1959 and 1970. In 1968, with an intermediate berry production, the Agricultural Price Reporting Office claimed that the summer was too dry in southern Norway to give high seed crops. From 1971-1973 Myrberget (1982a) obtained information on berry production from the forest authorities in each county. The reports from Aust-Agder confirmed that the berry production was high in 1972. Hence, game reports seem to give reliable indices of the bilberry production.

Grasaas also mentioned the rich production of bilberries in 1953, 1954, 1957, 1958, 1969, 1972 and 1977, and the low production in 1955. According to information given by Grasaas, vole populations peaked in post-mast years of bilberry in the study area (Selås 1997). Most of these peak years were apparently common for large areas of the southern part of Norway (Myrberget 1982b, Christiansen 1983).

Spring population indices and clutch sizes were also compared with the population indices of the previous autumn. As indices of autumn densities, Grasaas used the total number of cocks and hens killed by hunters in Vegårshei during 1953-1962. During 1968-1977, when the capercaillie was not hunted due to the general lower population level, estimates from counts along line transects were available (Wegge & Grasaas 1977, Wegge 1979, 1980). Because of differences in indices of autumn population densities, the data from the two periods had to be analysed separately. When analysing spring population indices and clutch sizes from the first period, only the years 1954-1962 (1955-1962 for capercaillie cocks, see below) could be used, since there were no indices for autumn densities prior to 1953.

Grasaas used the mean number of capercaillie cocks and hens observed from permanent blinds at leks as indices of spring population sizes. In 1953 and 1954, 45 and 27 leks were investigated, respectively. During 1955-1962, the annual number of leks varied from three to 10 (mean 5.8), and during 1970-1978 from eight to 15 (mean 9.1). In 1969 only one lek was visited. Counts at leks were conducted by members of the local hunter organisation, under the supervision of Grasaas, in the last week of April, when the hens visit the leks for copulation. Each lek was usually visited only once, and by the same person(s) each year. The number of capercaillies observed at a lek is thus a minimum estimate of the true number, but as the same method was used each year, this approach should be expected to reveal annual fluctuations in spring densities. The number of capercaillies observed in spring was tested against the autumn population indices in the previous year. For capercaillie cocks, I also used the autumn index obtained two years earlier, because the cocks will usually not get access to leks until they are two years old (Wegge, Rolstad & Gjerde 1991).

One aim of Grasaas' study was to investigate the impact of weather on newly hatched chicks, and Grasaas therefore tried to determine the mean hatching date each year. Grasaas received reports on capercaillie nests found by chance by forest workers and members of the hunter and fisher union, and most nests were controlled several times until hatching. Annual mean clutch sizes were calculated from nests known to be completed (see Table 1). This also included second clutches, i.e. clutches laid by hens that had lost their first clutch (see e.g. Spidsø, Wegge & Storaas 1984).

Because the number of second clutches, which tend to be smaller than first clutches, may vary during the vole cycle due to variations in the predation pressure or variations in the hens' body condition, they should be excluded from the present analysis. This was done for the second period (1969-1978) from which I had access to original data, but not for period one (1953-

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1962) because Grasaas did not always distinguish between first and second clutches in his articles. For those years from period one where information on second clutches are given (see Table 1), their annual proportion varied within 0-14%. For period two (when some undated clutches were omitted from the analysis), the annual proportion of second clutches varied within 0-9%.

The effect of bilberry production, snow cover and autumn population indices on spring population indices and clutch sizes during 1954(55)-1962 and 1969(70)-1978 was tested by backward elimination in a stepwise regression model. If the significance probability attributed to an explanatory variable was higher than 0.10, it was removed from the model. A backward procedure was used because I wanted to find the best combination of the selected variables. The only variables that differed from a normal distribution were the autumn population indices (Shapiro-Wilk tests; cocks 1953-1962: W = 0.81, P = 0.018; hens 1953-1962: W = 0.79, P = 0.010; 1969-1978: W = 0.82, P = 0.027). In multiple tests, dependence between explanatory variables can lead to confounding results. There was, however, no correlation between the date of snow melt and the bilberry index of the preceding year (r = 0.02, P = 0.95, N = 20) or autumn population indices (cocks 1953-1962: r = 0.24, P = 0.51; hens 1953-1962: r = 0.23, P = 0.52; 1969-1978: r = 0.17, P = 0.64). Neither was there any significant correlation between the autumn population indices and the bilberry index (cocks 1953-1962: r = -0.55, P = 0.10; hens 1953-1962: r = -0.56, P = 0.10; 1969-1978: r = 0.49, P = 0.15).

Also convergent autocovariance within different series may lead to spurious relationships in time series analyses. Therefore, I conducted an autoregressive analysis for all time series used for each period. Because of the multiplicative nature of population growth, all capercaillie population indices were ln-transformed in these analyses. For the period 1953-1962, there was a significant negative autocorrelation for the number of cocks observed at leks (r = -0.88, P = 0.021) and a positive autocorrelation for the number shot (r = 0.85,

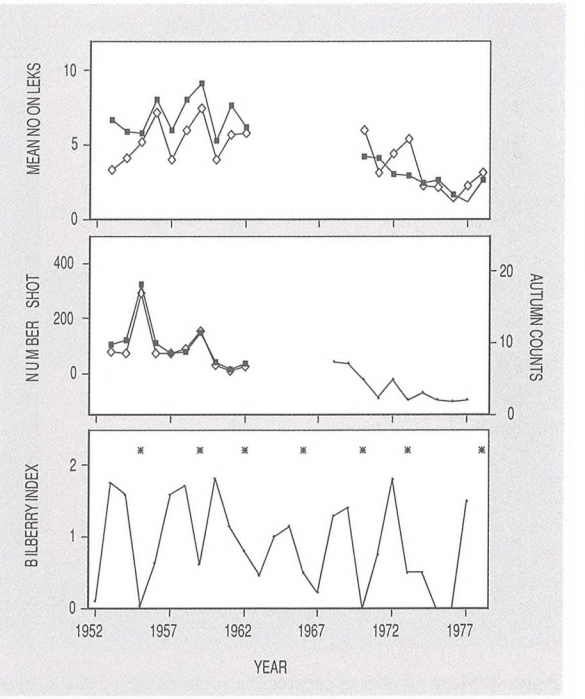


Figure 1. Spring and autumn indices of capercaillie cocks (■) and hens (◊) and bilberry production index from Vegårshei, southern Norway. Spring indices give the mean number of capercaillies observed on leks, autumn indices during 1953-1962 the total number hunted in Vegårshei, and autumn indices from the period 1969-1977, when the capercailie was not hunted, give the number (cocks and hens pooled) per km² estimated from counts along line transects (Wegge & Grasaas 1977, Wegge, 1979, 1980). The indices for bilberry production are calculated from game reports (see Table 1). Peak vole years are indicated with asterisks in the bilberry production figure.

Table 2. Results from stepwise regression models using backward elimination, with the mean number of capercaillie cocks and hens observed at leks (year t) as response. The order of variable elimination is given in parentheses after the P-values. N = number of years. Data originate from Figure 1 and Table 1.

	1954-1962				1970-1978			
	Cocks (N = 8)		Hens (N = 9)		Cocks (N = 9)		Hens (N = 9)	
Explanatory variables	R^2	P	R^2	P	R^2	P	R^2	P
Bilberry index (t-1)	-	0.457 (5)	-	0.973 (2)	0.20	0.045	0.23	0.032
Date of snow melt	-	0.420 (3)	-	0.532 (3)	-	0.879 (1)	-	0.637 (2)
Early/late thaw	-	0.803 (2)	-	0.869 (1)	-	0.574 (2)	-	0.960 (1)
Autumn index (t-1)	-	0.859 (4)	-	0.460 (4)	-	0.354 (3)	0.59	0.029
Autumn index (t-2)	-	0.668 (1)	-	-	0.61	0.004	-	-
Selected model	-	-	-	-	0.81	0.007	0.82	0.006
Adjusted R^2	-	-	-	-	0.75	-	0.76	-

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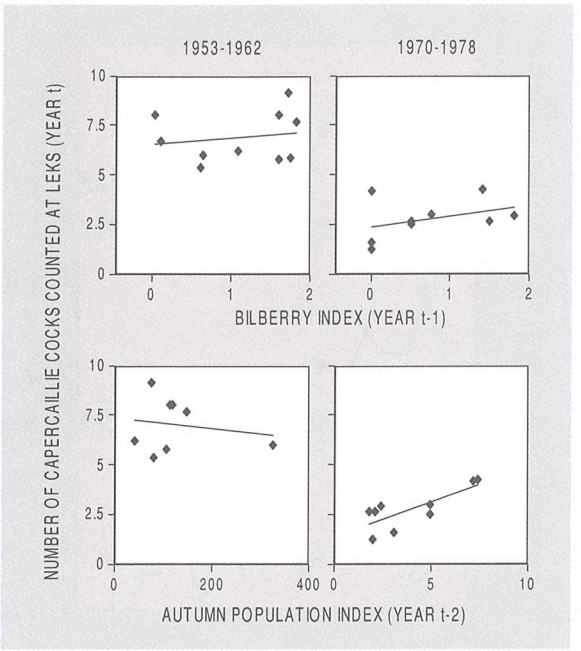


Figure 2. Mean number of capercaillie cocks observed at leks in or near Vegårshei, southern Norway, related to bilberry production in the previous year (upper figures) and autumn population indices two years earlier (lower figures), during a period with high population levels (1953-1962; left figures) and a period with lower population levels (1970-1978; right figures). Data originate from Figure 1 and Table 1.

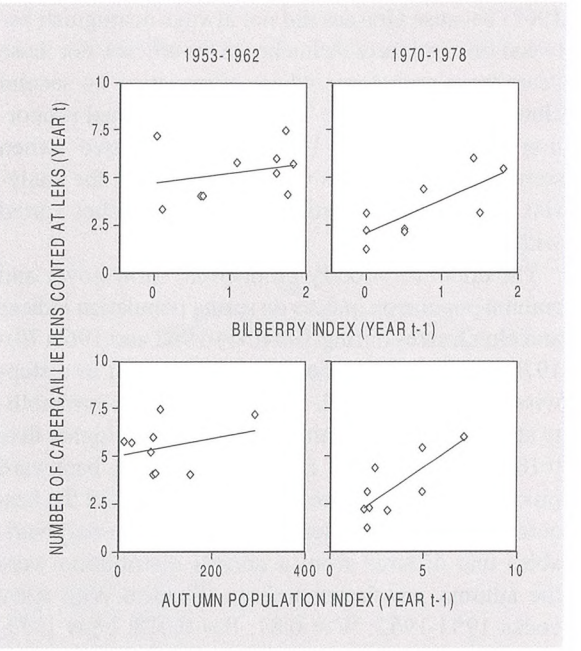


Figure 3. Mean number of capercaillie hens observed at leks in or near Vegårshei, southern Norway, related to bilberry production in the previous year (upper figures) and autumn population indices one year earlier (lower figures), during a period with high population levels (1953-1962; left figures) and a period with lower population levels (1970-1978; right figures). Data originate from Figure 1 and Table 1.

P = 0.032) at a time lag of four years. The date of snow melt was significantly positively autocorrelated at a time lag of two years (r = 0.77, P = 0.025), and negatively correlated at time lags of three (r = -0.77, P = 0.043) and five (r = -0.91, P = 0.032) years during 1953-1962. For the period 1969-1978, there was a significant negative autocorrelation for the date of snow melt at a time lag of four years (r = -0.88, P = 0.021).

Results

There was a significant positive correlation between the mean number of cocks and hens observed at leks (1953-1962: r = 0.80, P = 0.006, N = 10; 1970-1978: r = 0.69, P = 0.039, N = 9; Fig. 1). Between the total number of cocks and hens hunted in autumn during 1953-1962 there was also a significant positive correlation (r = 0.98, P < 0.001, N = 10; see Fig. 1).

Table 3. Results from stepwise regression models using backward elimination, with the mean clutch size (year t) of capercaillie as response. The order of variable elimination is given in parentheses after the P-values. For the period 1954-1962, all clutches were used, whereas for the period 1969-1978, second clutches and undated clutches were omitted. N = number of years. Data originate from Figure 1 and Table 1.

	1954-1962 (N = 9)		1969-1978 (N = 10)	
Explanatory variables	R^2	P	R^2	P
Bilberry index (t-1)	-	0.431 (1)	0.18	0.014
Date of snow melt (t)	-	0.639 (2)	-	0.964 (1)
Early/late thaw (t)	0.35	0.093	0.26	0.033
Autumn index (t-1)	-	0.227 (3)	0.35	0.018
Whole model	0.35	0.093	0.80	0.017
Adjusted R^2	0.26		0.69	

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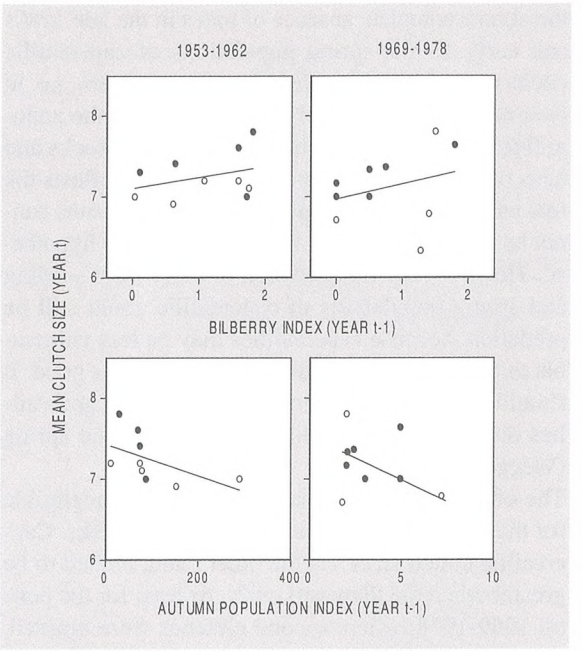


Figure 4. Mean clutch size of capercaillie in relation to bilberry production (upper figures) and autumn population size of the previous year (lower figures) in Vegårshei, southern Norway, during 1953-1962 (left figures) and 1969-1978 (right figures). For the first period all clutches were used; for the latter period second clutches and undated clutches were omitted (see Table 1). ● = years with early snow melt; ○ = years with late snow melt. Data originate from Table 1 and Figure 1.

For the period 1954(55)-1962, neither the bilberry index of the previous year, the date of snow melt, the dummy variable early-late thaw nor the autumn population index one or two years earlier had a significant effect on the mean number of cocks or hens observed at leks (Table 2, Figs. 2 and 3). The high numbers observed in spring 1956 may, however, have been caused by the high autumn density in 1955 (see Fig. 1). When 1956 was omitted from the analysis, there was a significant positive effect of the bilberry index on the mean number of hens at leks ($R^2 = 0.47$, $P = 0.040$, $N = 9$; see Fig. 3). For the period 1970-1978, when the capercaillie population was lower than during 1953-1962, the bilberry index of the previous year had a significant positive effect on the mean number of both cocks and hens at leks (see Table 2 and Figs. 2 and 3). There was also a significant positive effect of the autumn population index one (hens) or two (cocks) years earlier (see Table 2 and Figs. 2 and 3).

In stepwise regression models with the mean clutch size as response, the dummy variable early-late thaw was selected as explanatory variable for both periods, i.e. 1954-1962 and 1969-1978, but the effect was significant only for the second period (Table 3). Clutch sizes were largest when the thaw set in early (Fig. 4). For the latter period, in which second clutches had been omitted, there was also a significant positive effect of the bilberry index and a significant negative effect of the autumn population index of the previous year (see Table 3 and Fig. 4). Of the years in period one from which information on second clutches exists (see Table 1), the proportion of these (and thus the increase in mean clutch size after removal of second clutches) was highest in 1959. When the analysis was conducted without this year, there was a significant positive effect of both an early thaw (Partial $R^2 = 0.73$, $P = 0.004$) and a high bilberry index of the previous year (Partial $R^2 = 0.17$, $P = 0.034$; see Fig. 4).

Discussion

For the period 1970-1978, when the general population level was low, the mean number of capercaillies observed at leks was positively related to the bilberry index of the previous year and the autumn population index one (hens) or two (cocks) years earlier. Thus, for this analysis, the positive effect of bilberry masting on winter survival, as predicted by the mast depression hypothesis, was supported. The findings were also in agreement with the general assumption that spring densities of capercaillie hens depend on autumn densities in the previous year, whereas the number of cocks at leks depends on autumn population levels two years earlier. During 1969-1978, clutch sizes also correlated with the bilberry index (positively), as predicted by the mast depression hypothesis, and with the autumn population index (negatively), as predicted from the assumed relationship between autumn and spring densities and the general rule of smaller clutch sizes in first-year breeders.

For the period 1954-1962, both the autumn population index and the bilberry index seemed to be of less importance for the number of capercaillies observed at leks, as well as for the mean clutch sizes. One possible explanation is that the relative importance of some unknown factor(s) was larger during the 1950s, when the general population size was high. However, the time series analysed were short and may thus have been sensible to any biases in the data. A possible source of error is that the indices of bilberry production and the number of capercaillies at leks were not obtained from exactly the same sites each

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year. The number of game reports, from which bilberry indices were calculated, was highest for the period 1954-1962, whereas the number of leks investigated was highest for the period 1970-1978. The bilberry index was verified by obtaining information from other sources, but this was not possible for the capercaillie indices.

Unfortunately, I could not distinguish between first and second clutches for all years during 1953-1962. In addition, estimates of autumn population levels based on hunting bags may be more biased than counts along line transects, e.g. because of a numerical or functional response by hunters. Thus, the possibility exists that the difference between the two periods was an artificial one, caused by less reliable capercaillie indices (spring and autumn population indices and clutch sizes) for the former than for the latter period. It should be mentioned, however, that counts might also be biased due to annual variations in weather conditions and thus flushing distances. For instance, Wegge & Grasaas (1977) claimed that in 1973 the autumn population was the same as in 1972, and that the low number counted in 1973 was caused by unfavourable weather conditions during the censuses.

Despite the possible errors mentioned, the results from 1970-1978 suggest that there is some relationship between bilberry production and the number of capercaillies observed at leks in the following year. Unless the capercaillies for some reasons are more active at leks in post-mast years, and thus are more easily detected by the investigators, the most likely explanation is that winter survival is improved when bilberry production is high. This result is thus in accordance with the mast depression hypothesis, because the predicted increase in food quality in autumn due to bilberry masting is likely to increase winter survival. It is, however, possible that any increase in winter survival is caused solely by the energy-rich food provided by the berries. Increasing vole populations should be of less importance because the main predator on adult capercaillie hens in winter and spring, the goshawk *Accipiter gentilis* (Wegge, Larsen, Gjerde, Kastdalen, Rolstad & Storaas 1987), do not switch to vole hunting in peak vole years (Höglund 1964, Sulkava 1964, Widén 1987).

Also the red fox *Vulpes vulpes* is an important predator on adult capercaillie cocks (Wegge et al. 1987). In Aust-Agder a positive trend in the mean number of capercaillie cocks observed on leks during the 1980s coincided with a decrease in fox populations caused by sarcoptic mange (Selås 1998b). However, even with the almost complete absence of foxes in the late 1980s and early 1990s, spring populations of capercaillie cocks peaked in peak vole years (Selås 1998b), i.e. in post-mast years of bilberry (Selås 1997). If the annual fluctuation in the number of capercaillie cocks and hens observed at leks from 1970 onwards reflects the real annual variation in spring density, the results cannot be fully explained by the alternative prey hypothesis. However, the link between bilberry mast seeding and spring populations of capercaillie could still be predation, because capercaillies may be less vulnerable to predation when their body condition is good. It should be noted that the mortality of adult capercaillies due to predation is highest in winter and spring (Wegge et al. 1987).

The effect of an early thaw seemed to be negligible for the number of capercaillies observed at leks. Capercaillie clutch sizes, on the other hand, tended to be greater when the thaw was early. At least for the period 1969-1978, where second clutches were omitted, the mean clutch sizes were also influenced by the bilberry index (positively) and the autumn population index (negatively) of the previous year. For the willow grouse, clutch sizes have been highest in peak vole years and in years with an early snow melt (Myrberget 1986, see also Erikstad, Pedersen & Steen 1985, Hanssen & Utne 1985). Hens of both species visit snowless spots to feed on ground plants such as bilberry in early spring, but they also eat wintered berries of *Vaccinium* and *Empetrum hermaphroditum* (Pulliainen & Tunkkari 1991). In the study of Pulliainen & Tunkkari (1991), berries constituted 25% and bilberry stems 9.5% dry weight of crop contents from 13 capercaillie hens shot in spring. However, since protein, and not energy, is thought to be the limiting nutrient for egg production (Moss 1972), berries are probably of less importance to clutch sizes.

Also other studies indicate that there is a link between the body condition of grouse and the bilberry production or vole number. In central Sweden, Brittas (1988), found that both the body condition and the *in vitro* digestibility of *Vaccinium* and *Eriophorum* plants from crops of willow grouse hunted in spring was lowest in years when microtine populations crashed, and highest in a peak microtine year. The *Eriophorum*-species in question have a cyclic seed production quite similar to those of bilberry and other *Vaccinium*-species (Myrberget 1982a, Laine & Henttonen 1983). In both Sweden and Norway the vulnerability of grouse hens to goshawk predation has been negatively correlated with vole numbers (Widén et al. 1987,

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V. Selås unpubl. data). Because grouse hens are probably most vulnerable when foraging on the ground (cf. Widén et al. 1987, Lima & Dill 1990), this pattern has been interpreted as a result of reduced need for foraging caused by high food quality in post-mast years, when voles are abundant (Widén et al. 1987).

The best support for the idea of higher food quality in post-mast years is perhaps the correlation between the reproduction of grouse or the number of voles on one hand and the number of fledglings produced by the pied flycatcher *Ficedula hypoleuca* on the other (Thingstad 1997, Selås & Steel 1998). This small passerine frequently feeds on caterpillars on bilberry leaves (Atlegrim 1991), which should be expected to show a numerical response to any change in food quality, similar to that of voles. In the study of Selås & Steel (1998), unsuccessful breeding attempts were omitted. The pattern observed could therefore not be due to annual variations in egg or nestling predation, caused by fluctuating populations of small mustelids.

The re-analysis of the data collected by Grasaas supports the idea that not only predation, but also food quality, influence the population dynamics of capercaillie in Norway. The challenge for further research then is to test if bilberry production actually influences the chemical composition and thus the nutrient value of this plant, and to study the direct effects of any changes in bilberry quality on individuals of grouse and other herbivorous species. If such effects are apparent, then we also need to reveal the importance of food quality in relation to the effects of predation (e.g. Marcström et al. 1988, Lindström et al. 1994) on different grouse populations.

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References

Ahnlund, H. & Helander, B. 1975: The food of the hazel grouse (Tetrastes bonasia) in Sweden. - Viltrevy 9: 221-240.

Angelstam, P. 1983: Population dynamics of Tetraonids, especially the black grouse Tetrao tetrix L., in boreal forests. - PhD thesis, Uppsala University, 275 pp.

Angelstam, P., Lindström, E. & Widén, P. 1984: Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. - Oecologia 62: 199-208.

Angelstam, P., Lindström, E. & Widén, P. 1985: Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. - Holarctic Ecology 8: 285-298.

Atlegrim, O. 1991: Interactions between the bilberry (Vaccinium myrtillus) and a guild of insect larvae in a boreal coniferous forest. - PhD thesis, Swedish University of Agricultural Sciences, Umeå, 144 pp.

Brittas, R. 1988: Nutrition and reproduction of the willow grouse Lagopus lagopus in Central Sweden. - Ornis Scandinavica 19: 49-57.

Christiansen, E. 1983: Fluctuations in some small rodent populations in Norway 1971-1979. - Holarctic Ecology 6: 24-31.

Erikstad, K.E., Pedersen, H.C. & Steen, J.B. 1985: Clutch size and egg size variation in willow grouse Lagopus l. lagopus. - Ornis Scandinavica 16: 88-94.

Grasaas, T. 1955: Skogsfuglundersøkelsene i Vegårshei 1955. - Jeger og Fisker 84: 417-429. (In Norwegian).

Grasaas, T. 1956: Skogsfuglundersøkelsene i Vegårshei i 1956. - Jeger og Fisker 85: 402-405. (In Norwegian).

Grasaas, T. 1957: Skogsfuglundersøkelsene i Vegårshei 1957. - Jeger og Fisker 86: 370-376. (In Norwegian).

Grasaas, T. 1958: Skogsfuglundersøkelsene på Vegårshei 1958. - Jeger og Fisker 87: 464-468. (In Norwegian).

Grasaas, T. 1960: Skogsfuglundersøkelsene og jaktavkastingen i Vegårshei. - Jakt, fiske og friluftsliv 89: 128-131. (In Norwegian).

Grasaas, T. 1961: Viltet i Vegårshei 1960. - Jakt, fiske og friluftsliv 90: 200-202. (In Norwegian).

Grasaas, T. 1962: Skogsfuglundersøkelsene i Vegårshei 1961. - Jakt, fiske og friluftsliv 91: 196-200, 230. (In Norwegian).

Grasaas, T. 1963: Skogsfuglundersøkelsene i Vegårshei. - Jakt, fiske og friluftsliv 92: 544-551. (In Norwegian).

Grasaas, T. 1971: Skogsfuglundersøkelsene i Vegårshei. - Jakt, fiske og friluftsliv 100: 338-342. (In Norwegian).

Grasaas, T. 1972: Skogsfuglundersøkelsene i Vegårshei 1971. - Jakt, fiske og friluftsliv 101: 222-223. (In Norwegian).

Grasaas, T. 1973: Skogsfuglundersøkelsene i Vegårshei 1972. - Jakt, fiske og friluftsliv 102: 36-38. (In Norwegian).

Grasaas, T. 1977: Storfuglen og klimaet. En 50 års oversikt fra Vegårshei. - Jakt, fiske og friluftsliv 106 (10,11): 12-15. (In Norwegian).

Grasaas, T. 1978: Halvparten av leikene var tomme for fugl. Fra skogsfuglundersøkelsene i Vegårshei i 1977. - Jakt, fiske og friluftsliv 107 (9): 20-22. (In Norwegian).

Grasaas, T. 1980: Merkbar framgang i høststammen. Fra skogsfuglundersøkelsene i Vegårshei 1979. - Jakt, fiske og friluftsliv 109 (3): 16-17. (In Norwegian).

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Guglielmo, C.G., Karasov, W.H. & Jakubas, W.J. 1996: Nutritional costs of a plant secondary metabolite explain selective foraging by ruffed grouse. - Ecology 77: 1103-1115.

Hagen, Y. 1952: Rovfuglene og viltpleien. - Gyldendal, Oslo, 622 pp. (In Norwegian).

Hanssen, I., Pedersen, H.C. & Lundh, T. 1991: Does intense herbivory from microtine rodents induce production of plant estrogens in the spring food plants of willow ptarmigan Lagopus l. lagopus? - Oikos 62: 77-79.

Hanssen, I. & Utne, F. 1985: Spring phenology, egg quality and chick production in willow grouse Lagopus l. lagopus in northern Norway. - Fauna Norvegica Series C, Cinclus 8: 77-81.

Hansson, L. 1985: Clethrionomys food: generic, specific and regional characteristics. - Annales Zoologici Fennici 22: 315-318.

Hansson, L. & Larsson, T-B. 1978: Vole diet on experimentally managed reforestation areas in northern Sweden. - Holarctic Ecology 1: 16-26.

Hewitt, C.G. & Kirkpatrick, R.L. 1997: Ruffed grouse consumption and detoxification of evergreen leaves. - Journal of Wildlife Management 61: 129-139.

Hjeljord, O. 1980: Viltbiologi. - Landbruksforlaget, Oslo, 318 pp. (In Norwegian).

Höglund, N.H. 1964: Über die Ernährung des Habichts (Accipiter gentilis Lin.) in Schweden. - Viltrevy 2: 271-328. (In German).

Hörnfeldt, B. 1978: Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. - Oecologia 32: 141-152.

Hörnfeldt, B., Löfgren, O. & Carlson, B-G. 1986: Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. - Oecologia 68: 496-502.

Hudson, P.J. 1992: Grouse in space and time. The population biology of a managed gamebird. - The Report of the Game Conservancy's Scottish Grouse Research Project & North of England Grouse Research Project, 218 pp.

Jonasson, S., Bryant, J.P., Chapin, F.S. & Andersson, M. 1986: Plant phenols and nutrients in relation to variations in climate and rodent grazing. - American Naturalist 128: 394-408.

Kaasa, J. 1959: En undersøkelse over næringen hos orrfuglen (Lyrurus tetrix (L.)) i Norge. (In Norwegian with English summary: On the knowledge of the food of the black grouse (Lyrurus tetrix (L.)) in Norway). - Papers of the Norwegian State Game Research, 2. serie no. 4, 116 pp.

Karban, R. & Baldwin, T. 1997: Induced responses to herbivory. - The University of Chicago Press, Chicago, 319 pp.

Laine, K. & Henttonen, H. 1983: The role of plant production in microtine cycles in northern Fennoscandia. - Oikos 40: 407-418.

Laine, K. & Henttonen, H. 1987: Phenolics/nitrogen ratios in the blueberry Vaccinium myrtillus in relation to temperature and microtine density in Finnish Lapland. - Oikos 50: 389-395.

Lima, S.L. & Dill, L.M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. - Canadian Journal of Zoology 68: 619-640.

Lindén, H. 1983: Metson ja teeren muna- ja pesyekoon vaihtelusta. (In Finnish with English summary: Variations in clutch size and egg size of capercaillie and black grouse.) - Suomen Riista 30: 44-50.

Lindén, H. 1989: Characteristics of tetraonid cycles in Finland. - Finnish Game Research 46: 34-42.

Lindroth, R.L. & Batzli, G.O. 1986: Inducible plant chemical defences: a cause of vole population cycles? - Journal of Animal Ecology 55: 431-449.

Lindström, E., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P-A., Martinsson, B., Sköld, K. & Swenson J.E. 1994: Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. - Ecology 75: 1042-1049.

Lindström, E., Angelstam, P., Widén, P. & Andrén, H. 1987: Do predators synchronize vole and grouse fluctuations? - An experiment. - Oikos 48: 121-124.

Lindström, J. 1994: Tetraonid population studies - state of the art. - Annales Zoologici Fennici 31: 347-364.

Lindström, J., Ranta, E., Lindén, M. & Lindén, H. 1997: Reproductive output, population structure and cyclic dynamics in capercaillie, black grouse and hazel grouse. - Journal of Avian Biology 28: 1-8.

Marcström, V., Kenward, R.E. & Engren, E. 1988: The impact of predation on boreal tetraonids during vole cycles: an experimental study. - Journal of Animal Ecology 57: 859-872.

Moksnes, A. 1972: Bestandssvingninger hos småviltarter i Trollheimsområdet. - Naturen 5: 315-319. (In Norwegian).

Moss, R. 1972: Food selection by red grouse (Lagopus lagopus scoticus (Lath.)) in relation to chemical composition. - Journal of Animal Ecology 41: 411-428.

Myrberget, S. 1970: On the part played by predation in short-term variations in the population of willow grouse, Lagopus lagopus, in Norway. - Transactions of IX International Congress of Game Biology, Moscow, pp. 458-464.

Myrberget, S. 1974: Variations in the production of the willow grouse Lagopus lagopus (L.) in Norway, 1963-1972. - Ornis Scandinavica 5: 163-172.

Myrberget, S. 1977: Bestandsvekslinger hos skogsfugl og ryper i Norge, 1932-1971. (In Norwegian with English abstract: Fluctuations in Norwegian tetraonid populations 1932-1971). Foredrag Nordisk Skogsfuglsymposium 1976. - Viltrapport 5: 19-21.

Myrberget, S. 1982a: Variationer i produktionen av vilda bär i Norge. (In Swedish with English summary: Production of some wild berries in Norway.) - Fauna och flora 77: 261-268.

Myrberget, S. 1982b: Bestandsvariasjoner hos mus i Norge i 1932-1971. (In Norwegian with English abstract: Popu-

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lation fluctuations in Norwegian microtines 1932-1971). - Fauna 35: 29-32.

Myrberget, S. 1984: Population cycles of willow grouse Lagopus lagopus on an island in northern Norway. - Fauna Norvegica Series C, Cinclus 7: 46-56.

Myrberget, S. 1986: Annual variation in clutch sizes of a population of willow grouse Lagopus lagopus. - Fauna Norvegica Series C, Cinclus 9: 74-81.

Nordhagen, R. 1928: Rypeår og bærår. Bidrag til diskusjonen om vår rypebestands vekslinger. (In Norwegian with English summary: Grouse peak years and berry peak years. Contribution to the discussion on the variation in our grouse population.). - Bergens Museums Årbok 1928, Naturvidenskapelig rekke, no. 2, 52 pp.

Oksanen, L., Oksanen, T., Lukkari, A. & Sirén, S. 1987: The role of phenol-based inducible defense in the interaction between tundra populations of the vole Clethrionomys rufocanus and the dwarf shrub Vaccinium myrtillus. - Oikos 50: 371-380.

Pulliainen, E. & Tunkkari, P.S. 1991: Responses by the capercaillie Tetrao urogallus, and the willow grouse Lagopus lagopus, to the green matter available in early spring. - Holarctic Ecology 14: 156-160.

Ranta, E., Lindström, J. & Lindén, H. 1995: Synchrony in tetraonid population dynamics. - Journal of Animal Ecology 64: 767-776.

Seldal, T., Andersen, K-J. & Högstedt, G. 1994: Grazing-induced proteinase inhibitors: a possible cause for lemming population cycles. - Oikos 70: 3-11.

Selås, V. 1997: Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. - Oikos 80: 257-268.

Selås, V. 1998a: Mast seeding and microtine cycles: a reply to Lennart Hansson. - Oikos 82: 595-596.

Selås, V. 1998b: Does food competition from red fox influence the breeding density of goshawk? Evidence from a natural experiment. - Journal of Zoology, London, 246: 325-335.

Selås, V. & Steel, C. 1998: Large brood sizes of pied flycatcher, sparrowhawk and goshawk in peak microtine years: support for the mast depression hypothesis. - Oecologia 116: 449-455.

Sinclair, A.R.E., Krebs, C.J., Smith, J.N.M. & Boutin, S. 1988: Population biology of snowshoe hares. III. Nutrition, plant secondary compounds and food limitation. - Journal of Animal Ecology 57: 787-806.

Slagsvold, T. & Grasaas, T. 1979: Autumn population size of the capercaillie Tetrao urogallus in relation to weather. - Ornis Scandinavica 10: 37-41.

Smedshaug, C.A., Selås, V., Lund, S.E. & Sonerud, G.A. 1999: The effect of a natural reduction of red fox Vulpes vulpes on small game hunting bags in Norway. - Wildlife Biology 5: 157-166.

Spidsø, T.K. & Stuen, O.H. 1988: Food selection by capercaillie chicks in southern Norway. - Canadian Journal of Zoology 66: 279-283.

Spidsø, T.K., Wegge, P. & Storaas, T. 1984. Renesting in capercaillie in southern Norway. - In: Hudson, P.J. & Lovel, T. (Eds.); Proceedings of 3th International Grouse Symposium, York, pp. 278-293.

Sulkava, S. 1964: Zur Nährungsbiologie des Habichts Accipiter gentilis. - Aquilo Serie Zoologica 3: 1-103. (In German).

Sørensen, O.J. 1977: En fellingsstatistikk på skogshøns fra Hurdal 1953-1975. (In Norwegian with English abstract: Hunting-bag reports on tetraonids from Hurdal 1953-1975). Foredrag Nordisk Skogsfuglsymposium 1976. - Viltrapport 5: 39-47.

Tast, J. & Kalela, O. 1971: Comparisons between rodent cycles and plant production in Finnish Lapland. - Annales Acadademiae Scientiarum Fennicae (A, IV) 186: 1-14.

Thingstad, P.G. 1997: Birds as indicators of studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher. - PhD thesis, University of Trondheim, 126 pp.

Watson, A. & Moss, R. 1979: Population cycles in the Tetraonidae. - Ornis Fennica 56: 87-109.

Wegge, P. 1979: Skogsfugltakseringer - nyttige og populære. En rapport fra lokalforeningers samarbeid med viltforskningen. - Jakt Fiske Friluftsliv 108 (7): 28-30, 46. (In Norwegian).

Wegge, P. 1980: Distorted sex ratio among small broods in a declining capercaillie population. - Ornis Scandinavica 11: 106-109.

Wegge, P. 1984: Naturlig dødelighet hos storfugl gjennom året på Østlandet. - In: Myrberget, S. (Ed.); Skogsfuglprosjektet 1980-84. Viltrapport 36: 76-80. (In Norwegian).

Wegge, P., Larsen, B.B., Gjerde, I., Kastdalen, L., Rolstad, J. & Storaas, T. 1987: Natural mortality and predation of adult capercaillie in southeast Norway. - Proceedings of 4th International Grouse Symposium, Lam, West Germany, pp. 49-55.

Wegge, P. & Grasaas, T. 1977: Bestandsstudier av storfugl på Sørlandet. (In Norwegian with English abstract: A population study of capercaillie (Tetrao urogallus) in South Norway.) - Foredrag Nordisk Skogsfuglsymposium 1976, Viltrapport 5: 22-39.

Wegge, P., Rolstad, J. & Gjerde, I. 1991: Bestandsskogbruket og faunaen: En foreløpig oppsummering fra et forskningsprosjekt om storfugl i Varald statsskog i Hedmark. - Faginfo, Statens fagtjeneste for landbruket, report no. 23, pp. 189-215. (In Norwegian).

Wegge, P. & Storaas, T. 1990: Nest loss in capercaillie and black grouse in relation to the small rodent cycle in southeast Norway. - Oecologia 82: 527-530.

Widén, P. 1987: Goshawk predation during winter, spring and summer in a boreal forest area of central Sweden. - Holarctic Ecology 10: 104-109.

Widén, P., Andrén, H., Angelstam, P. & Lindström, E. 1987: The effect of prey vulnerability: goshawk predation and population fluctuations of small game. - Oikos 49: 233-235.

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