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Winter nutrition of the willow grouse (Lagopus lagopus L.) in the extreme north of Finland[1]

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The winter food of the willow grouse and its crude protein and ether extract composition were studied in two areas in the extreme north of Finnish Fjeld Lapland in February — early May 1972—1975 and 1981. The contents of 918 crops (empty crops excluded) were examined. In both areas the most important food plant was *Betula* spp. (almost entirely *pubescens* ssp. *tortuosa*), constituting 77.3—97.8 % of the dry weight of the crop contents in the various years. Its frequency of occurrence varied between 88 and 100 %. In 1973 there were a lot of birch catkins available in both areas, and these were also utilized by the willow grouse in large quantities. Willows (*Salix* spp.) constituted 0.9—22.5 % of the dry weight of the crop contents, their frequency of occurrence and their proportions being lowest at times when the consumption of birch catkins was highest. The rest of the diet consisted of plants available in snowless places, where grit was also taken in. There were no significant differences between age or sex. The frequent consumption of protein-rich birch catkins shows that the willow grouse tend to obtain relatively nutritious food even in winter.

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1. Introduction

The winter nutrition of the willow grouse (*Lagopus lagopus* L.), which inhabits the northernmost areas of Europe, has recently been studied by a number of investigators (e.g. Voronin 1978, Myrberget 1979, Uotila et al. 1980a, b, Helle 1980, Bryant & Kuropat 1980). One of the aspects involved is the speculation as to whether forage proximal nutritional quality or avoidance of plant secondary constituents are of primary importance in forage selection patterns (reviewed in Bryant & Kuropat 1980). This paper forms a part of a series of investigations on the nutrition of *Lagopus* species in northern Finland and adaptive radiation in their organs (Pulliainen et al. 1968, Tanhuanpää & Pulliainen 1969, Pulliainen 1970, 1976, 1980, Pulliainen & Salo 1973).

2. Material and methods

The data were collected from two areas (Enontekiö and Utsjoki) in Finnish Fjeld Lapland (see Fig. 1). The former area (alt. 350—700 m) is characterized by treeless summits of fells and mountain birch forests (*Betula pubescens* ssp. *tortuosa*). Dense birch stands are to be found especially on the banks of rivers (e.g. Lätäseno). The mean depth of snow on March 15 is approximately 60 cm, but patches with little or no snow occur on the summits and on the banks of lakes and ponds.

The Utsjoki area (alt. 100—250 m) is also characterized by treeless summits and mountain birch forests, the area of the former being smaller than in Enontekiö. The depth of snow is approximately 50 cm, with snowless patches occurring in places similar to those in Enontekiö. Some of the mountain birch forests were destroyed by *Epirrita autumnata* caterpillars in the 1960s (see Kallio & Lehtonen 1973).

A total of 907 willow grouse with food in their crops were captured, mainly by snaring, in February — early May 1972—1975. The material for the snaring fences was taken from each capture site. Only a few specimens were killed by shooting. The birds were caught by the same people in the same areas every year.

The willow grouse were sexed and their ages estimated from the amount of pigment in the three outermost primaries (see Bergerud et al. 1963, Myrberget et al. 1969, Myrberget 1974), a method which permits an accuracy of more than 96 %. Age was also confirmed by examination of the bursa Fabricii.

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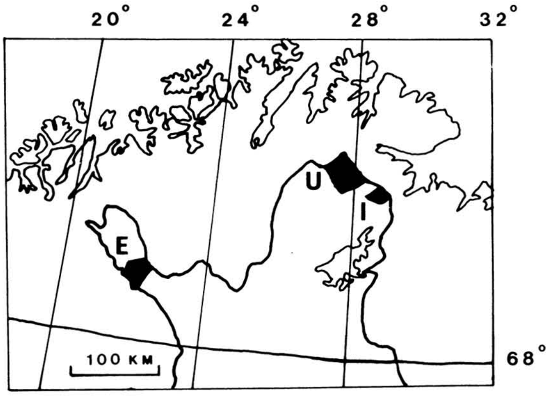

Fig. 1. The study areas in the extreme north of Finland. E = Enontekiö, U = Utsjoki and I = Inari.

The contents were removed from the crops and dried in an oven (at 65°C). Leaves, catkins, berries, stems, shoots, buds and other recognizable plant remains were sorted out from these dried samples. The crop samples were classified according to the sex and age of the bird.

An additional 11 willow grouse were shot in northeastern Inari, approximately 50 km southeast of the Utsjoki study area, in February—March 1981. The contents of their crops, together with the previous material, were used for determination of crude protein (6.25 × nitrogen) and ether extract contents by Viljavuuspalvelu Oy (for methods, see Pulliainen 1973).

Table 1. Frequency of occurrence (%) of different food items and grit in the crop contents of 415 willow grouse captured in Enontekiö in the winters of 1972—1975.

Food item or grit	1972 (*N* = 167)	1973 (*N* = 90)	1974 (*N* = 99)	1975 (*N* = 59)
Betula spp.				
twigs	98.2	98.9	100.0	84.7
catkins	65.3	97.8	90.9	84.7
buds	73.1	78.9	97.0	71.2
Salix spp.				
twigs	46.7	18.9	35.4	88.1
buds	42.5	14.4	28.3	76.3
Vaccinium vitis-idaea				
berries	4.8	2.2	3.0	—
leaves	4.8	2.2	—	1.7
V. myrtillus				
berries	—	—	3.0	—
stems	3.6	—	—	—
V. uliginosum				
berries	0.6	—	1.0	—
leaves	1.2	—	—	—
Empetrum nigrum				
berries	15.6	3.3	4.0	3.4
leaves	2.4	1.1	—	1.7
Andromeda polifolia				
leaves	2.4	—	1.0	1.7
buds	—	1.1	—	—
Juniperus communis				
shoots	—	—	1.0	—
Grit	2.4	2.2	4.0	1.7

3. Results

In both main study areas the most important food plant of the willow grouse was birch, almost entirely mountain birch (Fig. 2, Tables 1 and 2), which constituted between 77.3 % (Enontekiö 1975) and 97.8 % (Utsjoki 1973) of the dry weight of the crop contents (Fig. 2). Its frequency of occurrence was once 88 % (Enontekiö 1975), three times 97—99 % and three times 100 % (Enontekiö 1973 and 1974; Utsjoki 1974). Shoots of the birch were always consumed frequently and abundantly by the willow grouse, and the catkins and buds were also found in the contents of the majority of the crops (Tables 1 and 2), although their proportions of the dry weight varied considerably (Fig. 2). In 1973 a lot of catkins were available in both areas (see also Järvinen & Pietiäinen 1981), and large numbers of these were consumed by the willow grouse (Fig. 2). Some dry leaves which had remained on the birches were also accepted in Utsjoki in 1974.

The birch diet of the present willow grouse captured in Enontekiö and Utsjoki consisted of 63.5 % shoots (both short and long), 34.0 % catkins and 2.4 % buds (both loose and attached to shoots).

Table 2. Frequency of occurrence of different food items and grit in the crop contents of 492 willow grouse captured in Utsjoki in the winters of 1972—1974.

Food item or grit	1972 (*N* = 142)	1973 (*N* = 190)	1974 (*N* = 160)
Betula spp.			
twigs	96.5	96.3	99.4
catkins	79.6	94.2	93.1
buds	81.0	81.1	71.9
leaves	—	—	3.1
Salix spp.			
twigs	36.6	11.1	21.3
buds	35.9	11.1	15.6
leaves	—	—	1.3
Vaccinium vitis-idaea			
berries	7.7	7.4	8.3
leaves	6.3	6.3	6.3
V. myrtillus			
berries	1.4	2.6	1.9
stems	6.3	3.2	1.3
V. uliginosum			
berries	0.7	—	—
Empetrum nigrum			
berries	16.9	11.6	12.5
leaves	5.6	6.3	1.9
Andromeda polifolia			
leaves	5.6	5.3	0.6
buds	—	2.1	—
Ledum palustre			
leaves	2.1	—	—
buds	2.1	1.6	0.6
Loiseleuria procumbens			
leaves	—	0.5	—
Grit	0.7	2.6	11.3

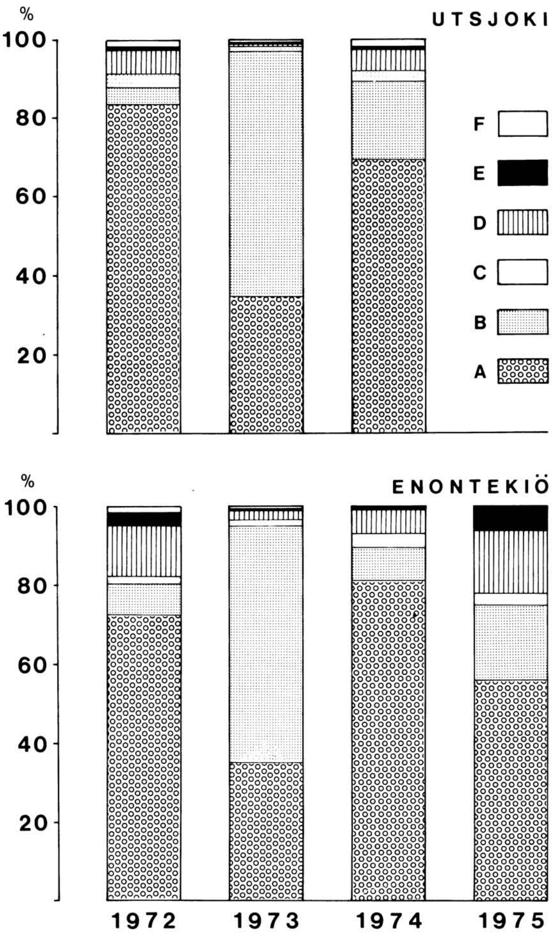

Fig. 2. Principal constituents of the diet of the willow grouse in the Enontekiö study area in the winters of 1972—75 and in the Utsjoki study area in the winters of 1972—74. A = shoots of *Betula* spp. (mainly *pubescens* spp. *tortuosa)*, B = catkins of *Betula pubescens* ssp. *tortuosa*, C = buds of *Betula* spp., D = shoots of *Salix* spp., E = buds of *Salix* spp. and F = other food items.

The average crop contained 443 shoots, 133 catkins and 36 buds of *Betula* spp.

Willows (*Salix* spp.) constituted between 0.9 % (Utsjoki 1973) and 22.5 % (Enontekiö 1975) of the dry weight of the crop contents (Fig. 2). Their frequency of occurrence (Enontekiö 18.9 % and Utsjoki 13.2 %) and their proportions of the dry weight of the crop contents (3.0 and 0.9 %, respectively) were lowest when the consumption of birch catkins was greatest, in 1973 (Fig. 2). Their other frequencies of occurrence varied between 21.9 % (Utsjoki 1974) and 88.1 % (Enontekiö 1975). The willow biomass identified comprised 81.6 % shoots and 18.3 % buds.

Table 3. Comparison of the proportions of *Betula* spp. and *Salix* spp. in the crop contents of the sex and age groups of willow grouse captured in Enontekiö and Utsjoki.

Age group and/or sex	Number of crops	Proportion of *Betula* spp.	Proportion of *Salix* spp.
Juv. females	199	88.4 %	9.2 %
Ad. females	196	89.3 %	9.3 %
Juv. males	199	87.5 %	11.4 %
Ad. males	313	89.9 %	8.6 %
Females	395	90.1 %	8.2 %
Males	512	89.2 %	9.5 %
Juveniles	398	88.6 %	9.9 %
Adults	509	89.2 %	9.3 %

The remainder of the diet (0.2—2.5 %; Fig. 2) consisted of plants which were available in places where the wind or the reindeer (*Rangifer t. tarandus* L.) had removed the snow. This list (see Tables 1 and 2) comprises plants which are accepted by the willow grouse in late autumn and early spring (see Semenov-Tjan-Šanskij 1960, Voronin 1978, Helle 1980).

Table 3 shows that there were no significant differences between the age and sex groups in the composition of the winter diet. The same finding was made by Pulliainen (1970) in the rock ptarmigan (*Lagopus mutus* Montin).

Some grit may be available in wind-swept places, and Tables 1 and 2 show that this opportunity was exploited by the willow grouse.

The average dry weight of the present crop contents (grit excluded) was 10.93 g and the average number of food items per crop (empty crops excluded) was approximately 700 (calculated from the total weight of each food item and the average weight of one particle). Myrberget (1979), studying the same aspects at Senja, northern Norway, at a latitude of 69°15′N, which lies between the latitudes of the present study areas at Enontekiö and Utsjoki, found the average dry weight of the crops to be 9.0 g and the average number of food items to be about 500.

4. Discussion

The present data confirm earlier findings (e.g. Olstad & Lid 1923, Holmboe 1924, Nordhagen 1928, Semenov-Tjan-Šanskij 1960, Höglund 1970, 1980, Pulliainen 1976, Voronin 1978, Myrberget 1979, Uotila et al. 1980a, b) that *Betula* spp. (especially *pubescens* ssp. *tortuosa*) constitute the most important winter food of the willow grouse in the mountain birch forests of the Scandinavian Mountain range and other parts of the extreme north of Europe, although if other food items such as ground herbs or willows are available, these are also accepted.

The variation in the availability of food items acceptable to the willow grouse in the present study areas was caused by the uneven distribution of the snow, accumulation of the snow on the ground and on the birch trees, and year-to-year variation in the yield of birch catkins. Each increase in the depth of the snow cover brings new parts of the mountain birch within reach of the willow grouse moving on the snow surface, although the birds may also feed by moving about in the trees (see also Semenov-Tjan-Šanskij 1960, Höglund 1966, Rajala 1966). The accumulation of snow on the branches of the birches will also bend them down towards the snow surface, and sometimes cover them up, thus reserving them for feeding in late winter, when they are freed from their snow burden.

The present willow grouse browsed heavily in the few willow stands available in the areas. The frequencies of occurrence of willow shoots and buds in the crop contents were also relatively high (Tables 1 and 2), but their proportions of the total dry weight remained relatively low (Fig. 2). When a lot of birch staminate catkins were available, however, this item was preferred to the willow diet, the incidence of which simultaneously decreased (Fig. 2, Tables 1 and 2). Another factor might also be involved, namely the feeding level. Birds looking for catkins in birches do not move along the snow surface, which is where the willow shoots are to be found. This cannot be the sole explanation, however, because the willow grouse did feed simultaneously on herbs in snowless places even when there were a lot of birch catkins available (Tables 1 and 2).

The feeding on herbs in wind-swept spots observed here (Fig. 2, Tables 1 and 2) is in accordance with our earlier observations (see Salo 1971). The winter of 1967 was exceptional in Finnish Lapland, since, after early heavy falls of snow had produced a continuous snow-cover of 40—50 cm, a warm spell melted almost all the snow at the lower elevations, and the field layer of the forest vegetation became exposed, allowing the willow grouse to resume its typical autumn diet of berries and green stems of *Vaccinium myrtillus*.

In Fjeld Lapland, the rock ptarmigan mainly inhabits the alpine summits of the fells, feeding largely on the herbs available on the wind-swept heaths (Pulliainen 1970, Uotila et al. 1980a, b), while the willow grouse mainly lives in the mountain birch forests on the slopes, with their thicker snow cover. Even so, the rock ptarmigan may also fly into the mountain birch forest zone to feed on birch staminate catkins (Pulliainen 1970, Uotila et al. 1980a, b) and the willow grouse may visit the summit areas. Uotila et al. (1980b) studied the composition of the winter nutrition of the latter in the extreme northwest of Enontekiö (alt. 560—800 m), 80—90 km NW of the present Enontekiö study area, and recorded the following diet: tall *Salix* 30.9 %, *Betula pubescens* ssp. *tortuosa* 27.0 %, *B. nana* 16.0 % and *Salix herbacea* 14.9 %, the proportion of browsed material being 91 %, that of berries 5 % and that of herbs 4 %. Thirty-five per cent of these willow grouse had grit in their crops, and thus Uotila et al. (1980b) suggest that they were either searching for grit or attending the display of the rock ptarmigan. The present relatively low frequencies of occurrence of grit in the crops (Tables 1 and 2) support the first alternative.

The rock ptarmigan certainly does not fly to the mountain birch forest zone to pick up grit. Pulliainen (1970) shows that the mountain birch catkins, when available, are greatly preferred by this species, and these comprised 74 % of their food in the Saariselkä fell area in the early winter of 1966/67 and 65 % in the Paistunturit fell area in March—April 1967. Uotila et al. (1980b) found a positive correlation between the consumption of mountain birch catkins and their yield in the area. On the one hand, the rock ptarmigan must also move in the mountain birch forest zone in order to know that birch catkins are available there, and on the other hand, they must be highly preferred as food by this species, just as they are by the willow grouse (Fig. 2). The use of this favourite food resource by the two *Lagopus* species may be so intense that it becomes exhausted during the course of the winter, as happened in the winter of 1966/67 in the Saariselkä fell area (Pulliainen 1970).

Comparing the midwinter nutrition of *Lagopus lagopus, L. mutus* and *L. leucurus* (Richardson), Moss (1975) states that the dominant species tends to have diets of higher palatability, digestibility and nutritive quality than the subdominant one. Moss (1974) found the following ranking of the expected digestibility and nutritive quality of the midwinter diets of the Alaskan *Lagopus* species: *L. lagopus* > *L. mutus* > *L. leucurus, L. lagopus* feeding preferentially upon willows (Irving et al. 1967), *L. mutus* on *Betula nana* staminate catkins (Weeden 1969) and *L. leucurus* on *Alnus crispa* staminate catkins (Moss 1973).

On the basis of their review of the winter diets of the *Lagopus* species of Alaska, Iceland and Fennoscandia, Bryant & Kuropat (1980) suggest that the palatability, digestibility, and nutritive quality of *Salix* buds and internodes > *Betula nana* staminate catkins > *Betula nana* foliar buds > non-resinous *Betula nana* internodes > *Alnus* staminate catkins > resinous *Betula nana* internodes > *Alnus* foliar buds and internodes. In the present study areas there are no *Alnus* available and most of the *Betula nana* stands are covered by snow in mid-winter. Here the staminate catkins of *Betula pubescens* ssp. *tortuosa* are even more obviously preferred by the willow grouse and the rock ptarmigan (see also Gardarsson & Moss 1970) than *Salix* shoots and buds. It is worth remembering that *Betula pubescens* staminate catkins are also the preferred winter food of *Tetrastes bonasia* (Salo 1971) and *Lyrurus tetrix* in Finnish Lapland (Pulliainen unpubl. data).

The digestibility of *Salix* by *L. lagopus* is approximately 45 % (Moss 1973), that of *Vaccinium myrtillus* stems 31 % (Pulliainen et al. 1968), that of *Betula* approximately 27 % (Moss 1973) and that of *Vaccinium vitis-idaea* berries 81 % (Pulliainen et al. 1968). We have no data on the digestibility of *Betula* catkins, but due to their loose structure it must be relatively high, although less than that of the typical summer food (see Gasaway 1976b). Bryant & Kuropat (1980) conclude that *Lagopus* forage preferences are not correlated with the proximal nutrient content of their winter browsed material, due to the lower proximal nutritional quality of *Salix* compared with *Betula* and *Alnus*. Instead, the negative correlation between *Lagopus* winter forage preferences and the gross energy content of browsed material is said to be a consequence of resin avoidance.

In the terminology used by Bryant & Kuropat (1980), the ether-extractable fraction of woody browsed material is referred to as resin. Resins may inhibit protein digestion (Moss 1974) and may also inhibit *Lagopus* caecal microbes (Moss 1973, Bryant & Kuropat 1980). The main question is whether the ether extract content of *Betula* catkins is in fact markedly lower than that of *Salix* shoots and buds (see also Moss & Hanssen 1980). Table 4 shows that this is not the case, the latter being below 5 % and the former over 9 % in Fennoscandia. On the other hand, the crude protein content of the favoured birch catkins is approximately 17 %, while that of *Salix* shoots and buds is below 12 % (Table 4). In an experiment in which only *Vaccinium myrtillus* stems (crude protein content 8.1 %) were offered to captive willow grouse, it was observed that the birds had a slightly negative nitrogen balance (Pulliainen et al. 1968). Taking into account the different digestibilities, a few additional per cent in the crude protein content may be very important to the animal. Gasaway (1976a) found that the crude protein content of the summer food of the rock ptarmigan varied between 18 and 23 % and that of the late autumn and winter diet between 10 and 14 %.

Table 4. Chemical composition (% of dry weight) of some major winter food items recovered from crops of the willow grouse in different parts of its range. Abbreviations: A = according to Gasaway (1976b) in Alaska, B = according to Myrberget (1979) in Norway and C in the present study.

Food item	Crude protein A	B	C	Ether extract A	B	C
Betula spp.						
catkins	13.1	16.9	17.1	8.2	9.8	9.8-16.4
buds	13.3	15.6	13.8	18.6	15.5	15.5
shoots	—	11.9	9.8	—	7.0	3.0
buds + shoots	—	13.8	—	—	9.3	—
Salix spp.						
shoots	9.4	—	—	9.4	—	—
buds	14.8	—	—	3.8	—	—
shoots + buds	—	11.9	12.4	—	4.8	1.6

Bryant & Kuropat (1980) report that *Salix* buds are less resinous than *Betula* buds, as was also recorded here (Table 4). Myrberget (1979) found that the willow grouse either discarded or lost a large number of mountain birch buds during the eating process. Here the reason may be avoidance of resinous matter, because the resin content of the birch buds may exceed 30 % (Salo 1973). Even so, an average of 36 *Betula* spp. buds was found in each crop (approx. 5 % of the food particles). It would have been easy for a bird to discard each loose bud.

If the nutritive value of the diet, such as the optimal crude protein content, were of some importance to the nesting result, a high percentage of juveniles could be expected in the study populations after the 1973 breeding season. In fact, the highest percentages of juveniles in the two study populations during the winters of 1972—74 were recorded after the 1973 breeding season, in 1974, as shown in the following (see also Pulliainen 1975):

Study area	1972	1973	1974
Enontekiö	13.2 %	40.0 %	59.6 %
Utsjoki	37.3 %	38.4 %	76.2 %

Furthermore, the corresponding percentage of juveniles in the Enontekiö population was high (55.9 %) in the winter of 1975, even though the proportion of *Betula* catkins in the diet had been low during the previous winter (Fig. 2). Several factors are, of course, responsible for the nesting result and survival of these birds in the course of the year.

The willow grouse of northern Fennoscandia can survive the long subarctic winters on diets which may be very poor in total protein (Myrberget 1979, Moss & Hanssen 1980, the present study), and may lack some essential amino acids (Mortensen & Tindall 1978). Under such conditions a bird can catabolize its own body protein (Sturkie 1976) and possibly also recycle nitrogen in its body (for further details, see Mortensen & Tindall 1978, 1981). The present study shows that on certain occasions and within certain limits a willow grouse can obtain relatively protein-rich food in winter (i.e. birch catkins). In such a case food selection will scarcely operate via the avoidance of ether extract, as suggested by Bryant & Kuropat (1980). From the standpoint of the bird, the net result obtained is decisive; the grouse may simultaneously avoid too resinous a diet (e.g. it may discard resinous buds to some extent) and try to obtain protein-rich items like birch catkins. The difficulty involved in such selection may even, per se, explain the great year-to-year fluctuations in the abundance of northern willow grouse populations, but these can hardly be explained solely on the basis of the avoidance of an excessively resinous diet. Correspondingly, Finerty (1980:120), when discussing the reasons for fluctuations in small mammal populations, concluded that the role of toxic secondary compounds in plants, although conceptually interesting, seems as yet unproven (see also Schlesinger 1976).

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