

Weights of the crop contents of *Tetrao urogallus*, *Lyrurus tetrix*, *Tetrastes bonasia* and *Lagopus lagopus* in Finnish Lapland in autumn and winter¹

ERKKI PULLIAINEN

PULLIAINEN, E. 1981: *Weights of the crop contents of Tetrao urogallus, Lyrurus tetrix, Tetrastes bonasia and Lagopus lagopus in Finnish Lapland in autumn and winter.* — *Ornis Fennica* 58:64—71.

The paper is based on the weights of the crop contents of 431 Capercaillie, 181 Black Grouse, 28 Hazel Grouse and 884 Willow Grouse shot in Finnish Lapland in September-May during nine successive years. The Willow Grouse had a very clear evening peak in the weights of the crop contents in October-January, and the Capercaillie and the Black Grouse in September. This peak disappeared gradually in February-April in the Willow Grouse (it was not studied in the other species). Otherwise, the crop content weights indicated alternating feeding and roosting by the birds during the light period of the day, no clear morning peaks being visible. The mean weight of the crop contents of the Willow Grouse was greatest in January, i.e. the coldest month of the winter. The data on the other species, studied in the autumn and early winter, suggest the same trend.

Erkki Pulliainen, Department of Zoology, University of Oulu, and Väriö Subarctic Research Station, University of Helsinki, SF-90100 Oulu, Finland

Introduction

The northern tetraonids, the Capercaillie *Tetrao urogallus*, Black Grouse *Lyrurus tetrix*, Hazel Grouse *Tetrastes bonasia* and Willow Grouse *Lagopus lagopus*, are sedentary birds of the taiga and subarctic parts of Finnish Lapland. In winter they are exposed to conditions of severe cold and/or windy weather, and have only a short period of daylight or twilight each day for feeding. These birds show a number of morphological and behavioural adaptations which enable them to survive in the harsh conditions, e.g. structural modifications of the digestive tract,

such as a large crop in which the birds can store considerable quantities of food, and a tendency to roost in the snow in cold and/or windy weather (reviewed in Marjakangas 1980).

When tetraonids were shot for nutritional and other studies (e.g. Pulliainen 1970, 1976, 1979, 1980a, Salo 1971, 1973), the crops were analysed at the same time. The purpose of the present paper is to discuss what light is thrown by this material on the autumn and winter feeding activity of these four tetraonid species in Finnish Lapland.

¹ Report No. 115 from the Väriö Subarctic Research Station of the University of Helsinki.

Material and methods

The fresh weights of the crop contents and the times of death of 431 Capercaillie (shot in Sept.-Dec.), 181 Black Grouse (Sept.-Nov.), 28 Hazel Grouse (Sept.-Nov.) and 884 Willow Grouse (Sept.-May) were recorded in Finnish Lapland ($66^{\circ}30'$ - 70°N) during the autumns and winters of 1966/67—1974/75. The activity of the hunters in the field was distributed fairly evenly over the period from dawn to dusk, as is apparent from Figs. 1—3. The main interest here attaches to the amounts of food found in the crops at different times of the day and in different months.

Results and discussion

All the studies carried out so far in the northern taiga on the activity patterns of the Capercaillie (e.g. Teplov 1947, Seiskari 1962), Black Grouse (e.g. Teplov 1947, Lind 1961, Koivisto & Pirkola 1961, Seiskari 1962, Koivisto 1965, Hjorth 1963, 1968, 1970), Hazel Grouse (e.g. Donaurov 1947, Pynnönen 1954) and Willow Grouse (e.g. Höglund 1980) have shown that these birds are diurnal, beginning their daily activities before sunrise at light intensities down to 0.02 lux (Hjorth 1963, 1968). Here, at and north of the Arctic Circle, these tetraonids have to cope with 24 hrs of light in summer and only 3—4 hrs of twilight around noon in mid-winter.

In autumn the Capercaillie, Black Grouse and Hazel Grouse shift from feeding on the ground to feeding in trees, a trend which, according to Seiskari (1962), is more clearly correlated with temperature than with the snow cover (cf., however, Pulliainen 1979). Willow Grouse feed on *Salix* spp. and low-growing *Betula* spp. available on the surface of the snow (e.g. Pulliainen 1976, Myrberget 1979), but may also occasionally feed in birch trees (e.g. Rajala 1966).

Lindroth & Lindgren (1950) and

Seiskari (1962) found that the Capercaillie began to feed at dawn and continued with short pauses until dusk; under long-day conditions the rhythm was bimodal with maxima in the morning and evening. Teplov (1947) reported that in mid-winter the Capercaillie has time to fill its crop only once a day. Seiskari (1962) observed that feeding activity is stimulated by cold weather and high pressure, and reduced by warm weather and low pressure.

Of the present Capercaillie killed in September, those shot between 15.00 and 21.00 had on average 2.2 times as much food in their crops as the birds shot between 05.00 and 15.00 (Fig. 1), but slight signs of bimodality (see Aschoff 1966) were evident. The corresponding data from October contained no evidence of bimodality and showed a lower mean weight for the crop contents than in September (Fig. 4). The Capercaillie had eaten abundant berries and soft leaves in September, but less in October, when the food contained a higher proportion of needles (Pulliainen 1979). Consequently, the total dry weights of the food taken in September and October may be equal, or that of October even higher. Collection of considerable amounts of food in the crop before the rest period naturally means that the bird has not been able to obtain enough energy and nutrients during the active period of the day. Young Capercaillie, especially the males, are still growing in September (Koskimies 1958), and need nutrients for this purpose. However, the mean crop contents of young and adult males shot at 15.00—21.00 were the same (juveniles: 25.1 g, range 1.6—96.0 g, $N = 6$; adults: 25.6 g, range 6.6—48.2 g, $N = 8$). Thus Capercaillie in general seem to need to store food in the evening in September.

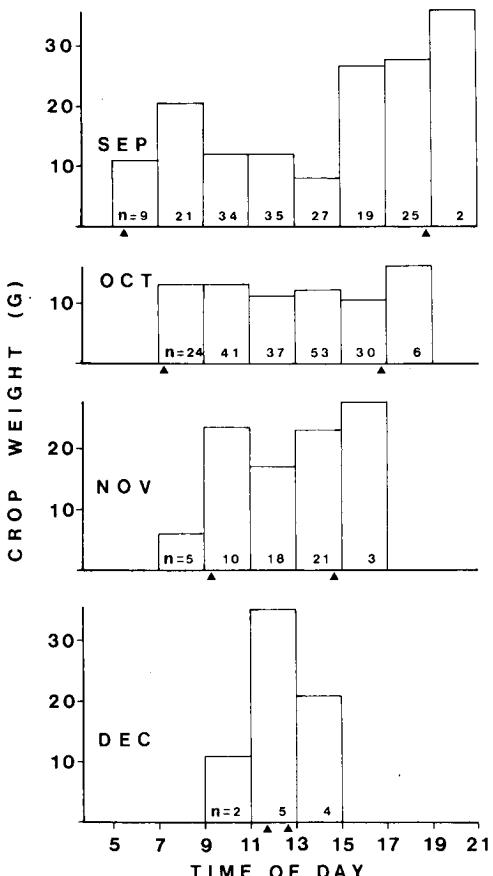


FIG. 1. Mean fresh weights (g) of the crop contents of Capercaillie shot at different times of the day in Finnish Lapland in September-December. The number of crops studied is indicated in each case, as are also the times of sunrise and sunset on the 15th day of each month at Sodankylä, in the middle of the study area.

The mean weights of the crop contents recorded in October-November (Fig. 1) do not differ in the course of the day. This pattern can be explained by such factors as alternation of feeding spells and pauses, the effects of the prevailing weather and other environmental conditions and the bird's physio-

logical state, which determines the activity pattern of each individual.

Seiskari (1962) points out that while the Capercaillie feeds fairly steadily throughout the day, the Black Grouse of northern Finland feeds for only a short period at noon. In captive Black Grouse in southern Finland, active feeding continued throughout the light period. The pattern shown by the present results appeared to be clear. The Black Grouse shot during the last four light hours of the day in September-November had considerably more food in their crops than those killed earlier in the day (Fig. 2), i.e. these birds had been feeding actively at noon and/or during the afternoon hours before roosting.

In assessing the Black Grouse data for September-October (-November), it must be remembered that the males of this species have an autumn display (see Hjorth 1970). Lind (1961) describes how their morning flights end in either display or feeding. In the first case, feeding is postponed until later in the light period of the day, and may precede the collection of food in the crop for digestion during roosting.

The Willow Grouse of the Scandinavian Mountains roost in snow burrows during the night and a large part of the day in mid-winter, being active only during the time devoted to food gathering (Höglund 1980). They thus endeavour to fill their crops with enough food to last through the next roosting period (West 1968, Höglund 1980), a habit also typical of those tits (*Parus* spp.) that overwinter north of the Arctic Circle (see Pulliainen 1980b). Willow Grouse burrow for the night in the late dusk, a considerable time after the end of civil twilight, and become active as dawn begins (Höglund 1980).

The present observations (Fig. 3) on the Willow Grouse agree with the above-mentioned Swedish data of Höglund (1980). No peaks were recorded in the weights of the crop contents in September, but an evening peak was very clear in October-January (the rather low mean weight of the four crop contents recorded at 15.00–15.30 in December may be due to unfavourable weather conditions). This peak disappeared in February-April. Crop weight data for the Alaskan Willow Grouse showed the same pattern (Irving et al. 1967b). The daily light period in autumn and late winter is probably long enough, and the environmental conditions favourable enough to make it unnecessary to gather large amounts of food in the crop for the roosting period. The numbers of empty crops recorded at different times of the day in different months (Table 1) also suggest that feeding and roosting spells alternate during the light period in autumn and late winter and before noon in mid-winter.

West (1968) studied gross activity in captive Alaskan Willow Grouse under natural conditions, and found that this was restricted to a few hours in the middle of the day in December and yielded a typical bimodal curve. He mentioned that this corresponded to observations in northern Alaska (Anaktuvuk), where the Willow Grouse had been seen roosting in willow bushes at noontime, instead of feeding (L. Irving, pers. comm.). The afternoon peak was higher than the morning peak, and it may be that this relatively low morning peak does not appear in the present crop weight data, the food taken in passing almost directly to the empty digestive tract. It is also possible that in areas of soft snow, as in northern Finland, Willow Grouse do actually alternate between feeding and roost-

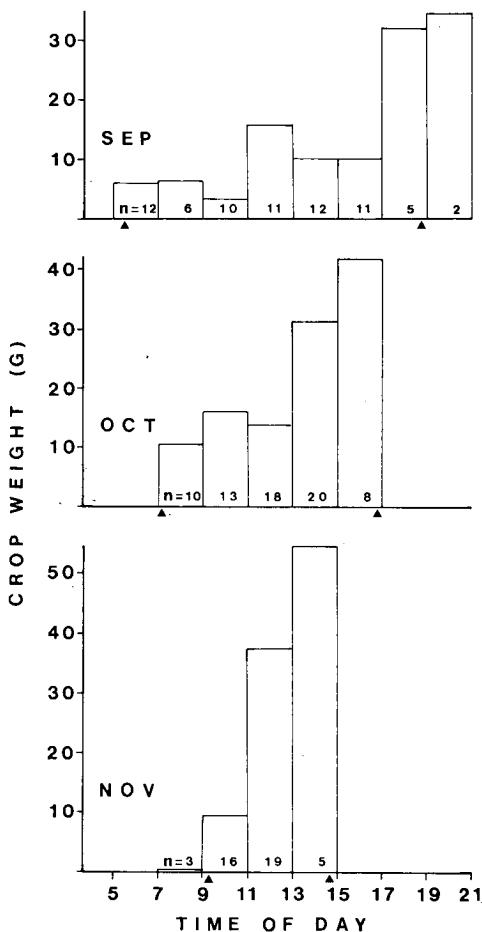
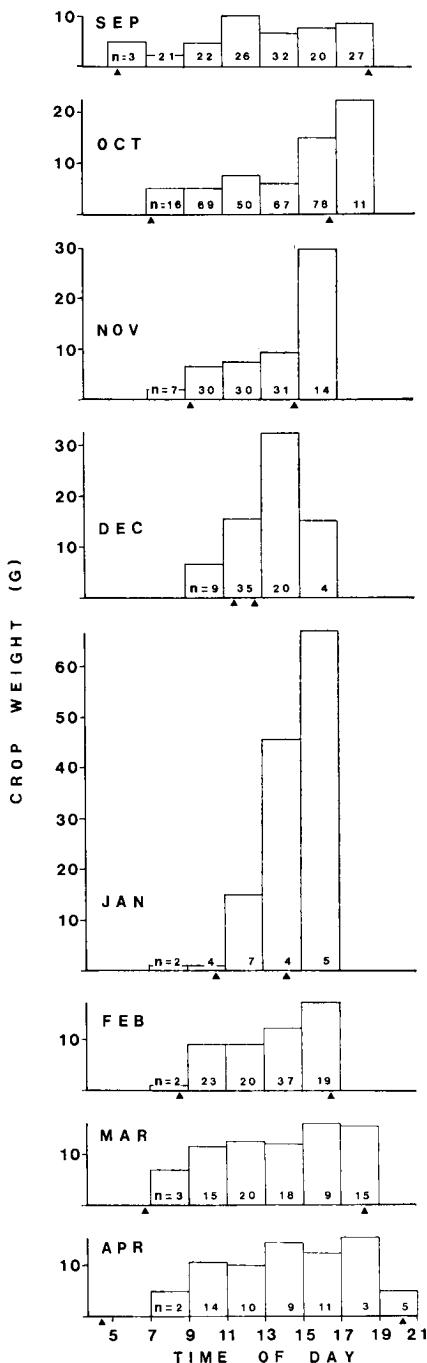


FIG. 2. Mean fresh weights (g) of the crop contents of Black Grouse shot at different times of the day in Finnish Lapland in September-November. For other explanations, see Fig. 1.

ing in the snow (see Korhonen 1980), with no appreciable peak in feeding activity in the morning in mid-winter.

Even in those Willow Grouse which undertake seasonal migrations in Alaska (Irving et al. 1967a), the amount of fat deposited is small (Irving et al. 1967b, West & Meng 1968), which suggests that the birds



have to replenish their fat reserves daily. On the other hand, there is a significant seasonal change in the Willow Grouse's insulation, for its lower critical temperature is $+7.7^{\circ}\text{C}$ in summer and -6.3°C in winter (West 1972). The temperature above the back of the bird in the snow burrows of a Willow Grouse (Korhonen 1980) or Black Grouse (Marjakangas 1980), is close to this lower critical temperature, and the difference is not very great in the case of the Capercaillie, either, for its lower critical temperature in winter is $+4^{\circ}\text{C}$ (Kendeigh et al. 1977).

Thus these tetraonids, and also the Hazel Grouse (see Andreev 1977), are really exposed to the severity of the northern winter when feeding and engaged in other activities outside their snow burrows. Fig. 4 shows that the mean weights of the crop contents of Willow Grouse in both the northern Finnish taiga and the fell area in the extreme north of Finland were greatest in January, i.e. the coldest month of the winter (the mean temperatures in 1966/67–1974/75 at Salla were 5.4° in IX, -1.5° in X, -6.8° in XI, -9.9° in XII, -13.4° in I, -12.7° in II, -6.6° in III and -2.3°C in IV; see also Helimäki 1974). The weights were lower in December, when the light (twilight) period of the day was shortest. The same pattern was recorded by Irving et al. (1967b) for Alaskan Willow Grouse. The data on the other tetraonid species, studied in September–November (–December), suggest the same trend (Fig. 4).

FIG. 3. Mean fresh weights (g) of the crop contents of Willow Grouse shot at different times of the day in Finnish Lapland in September–April. For other explanations, see Fig. 1.

TABLE 1. Distribution of empty crops of the Willow Grouse in relation to the time of day in September-May.

Time	IX	X	XI	XII	I	II	III	IV	V
05.00—06.59	1	1	—	—	—	—	—	—	—
07.00—08.59	4	1	2	1	—	—	—	—	—
09.00—10.59	3	11	3	1	2	—	—	1	—
11.00—12.59	1	2	5	2	1	2	—	2	1
13.00—14.59	2	8	2	—	—	4	—	—	—
15.00—16.59	1	6	1	—	—	—	—	—	—
17.00—18.59	2	1	—	—	—	—	1	—	2
19.00—20.59	—	—	—	—	—	—	—	—	1

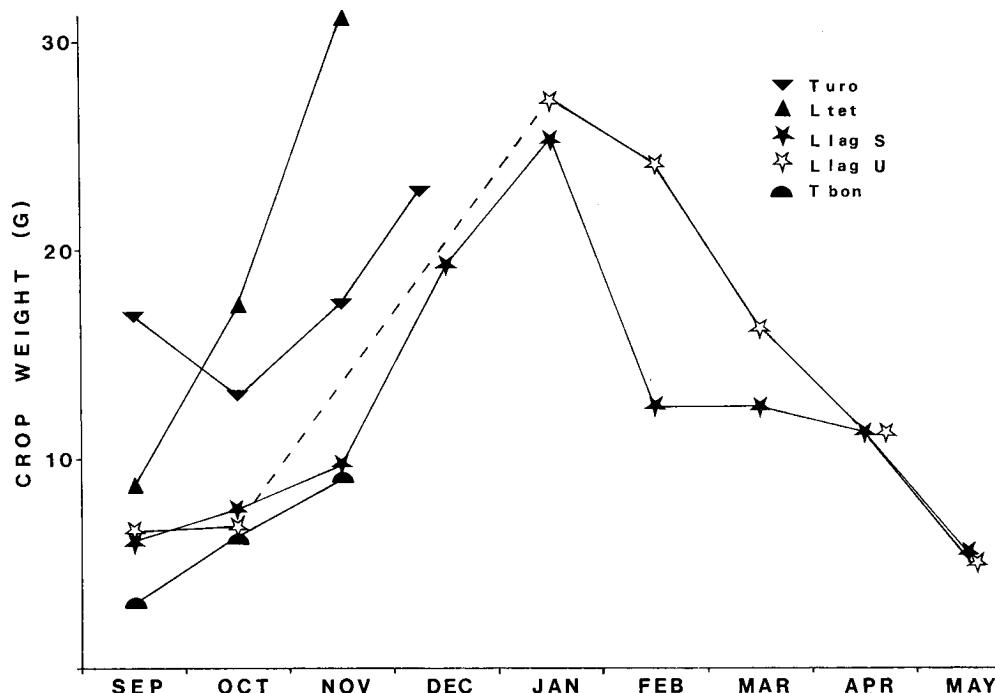


FIG. 4. Mean fresh weights (g) of the crop contents of Capercaillie (= Turo), Black Grouse (= Ltet), Hazel Grouse (= Tbon) and Willow Grouse (Llag S = taiga forests and Llag U = northern fells) shot in Finnish Lapland in September-May.

Acknowledgements. The author is grateful for technical assistance provided by Jouko Iivanainen, Kalevi Loisa, Laina Loisa and Esko Rajala, and for financial support given by the National Research Council for Agricultural and Forestry Sciences (Valtion maatalous-metsätieteellinen toimikunta), and the University of Helsinki.

Selostus: Metson, teeren, pyn ja riekon kupujen sisältöjen painoista Lapissa syksyllä ja talvella

Työssä pyrittiin selvittämään, mitä eri vuorokauden ja vuoden aikoina yhdeksänä peräkkäisenä vuonna Lapissa tapettujen 431 metson (syys-joulukuussa), 181 teeren (syys-marraskuussa), 28 pyn (syys-marraskuussa) ja 884 riekon (syys-toukokuussa) kupujen sisältöjen tuorepainot ilmaisevat näiden lintujen ruokailuaktiviteetista. Tulokset on esitetty kuvissa 1—4 ja taulukossa 1. Metsästäjät olivat liikkeellä maastossa tasaisesti kaikkina niinä vuorokauden aikoina, jolloin näki ampua, mikä näkyy myös kuvista 1—3.

Syksuussa klo 15:n ja 21:n välillä tapetuilla metsoilla oli keskimäärin 2.2 kertaa niin paljon ravintoa kuvussaan kuin aiemmin päivän aikana tapetuilla (kuva 1). Tuolloin oli havaittavissa myös hyvin lievää kaksihuippuisuutta, mistä ei ollut kuitenkaan mitään merkkiä enää lokakuussa. Metot söivät syksuussa runsaasti pehmeitä, paljon vettä sisältäviä kasvinosia, mutta lokakuussa pääasiassa männynneulasia, mikä saattaa selittää sen, että syksuussa tapetuilla oli tuorepainona mitattuna keskimäärin enemmän ravintoa kuvussaan kuin lokakuussa tapetuilla (kuva 4); kuivapainoltaan lokakuussa syödyt määräät olivat kuitenkin ehkä jopa suurempia kuin syksuussa syödyt. Loka-marraskuussa näyttäisivät ruokailu- ja lepojakset vuorottelevan päivän valoisana aikana tasaisesti kullakin yksilöllä oman rytmensä mukaan (kuva 1), mistä syystä mitään selviä huippuja ei ole havaittavissa.

Teerellä oli kupujen sisältöjen keskipainoissa syys-marraskuussa selvä huippu ilta-päivällä-ilalla (kuva 2), eli nämä linnut olivat varastoneet ravintoa vuorokauden pimeään aikaan ajoittuvaa lepotaukoa varten. Teeren syyssoitimiella, silloin kun se ajoittuu aamutunteihin, on varmastikin vaikuttusta ruokailiun siirtäen sitä päivän myöhemmille tunneille ja aiheuttaen myös tarvetta varastoida ravintoa yötä varten.

Riekoilla ei havaittu mitään huippuja sykskuussa, mutta kylläkin illan-ilta-päivän huippu loka-tammikuussa, mikä häipyi sitten vähitellen

helmi-huhtikuussa (kuva 3). Kaksihuippuisuuteen kuuluvasta aamuhuipusta ei havaittu mitään merkkejä. Riekojen kupuhiinsa varastoiman ravannon määrä oli keskimäärin suurinta tammikuussa (kuva 4), mikä on kylmin kuuksi Lapissa, mutta ei esim. joulukuussa, jolloin päivä on lyhyimmillään tällä alueella. Myös muita lajeja koskevat syys-joulukuun havaintot viittaavat samanlaiseen trendiin.

References

- ANDREEV, A. V. 1977: Temperature conditions in snow cavities of the Hazel Grouse (*Tetraastes bonasia kolymensis* But.). — *Ekologiya* 5:93—95.
- ASCHOFF, J. 1966: Circadian activity patterns with two peaks. — *Ecology* 47:657—662.
- DONAUROV, S. S. 1947: *R'abčík v Pečorskom zapovednike*. — Tr. Pečoro-Ilyčskogo zapovednika 4:77—122.
- HEIMÄKI, U. I. 1974: Lapin ilmastosta ja tuturien ilmoston erikoisuksista. — In *Lapin ilmostokirja*, pp. 23—27, Rovaniemi.
- HJORTH, I. 1963: Om orrens ankomst till lekplatserna och aggressiva beteenden. — *Zoologisk Revy* 25:16—30.
- HJORTH, I. 1968: Significance of light in the initiation of morning display of the Black Grouse (*Lyrurus tetrix* L.). — *Viltrevy* 5:39—94.
- HJORTH, I. 1970: Reproductive behaviour in Tetraonidae with special reference to males. — *Viltrevy* 7:183—596.
- HÖGLUND, N. H. 1980: Studies on the winter ecology of the Willow Grouse (*Lagopus lagopus lagopus* L.). — *Viltrevy* 11:249—270.
- IRVING, L., G. C. WEST, L. J. PEYTON & S. PANEAK 1967a: Migration of Willow Ptarmigan in Arctic Alaska. — *Arctic* 20: 77—85.
- IRVING, L., G. C. WEST & L. J. PEYTON 1967b: Winter feeding program of Alaska Willow Ptarmigan shown by crop contents. — *Condor* 69:69—77.
- KENDEIGH, S. C., V. R. DOL'NIK & V. M. GAVRILOV 1977: Avian energetics. — In J. PINOWSKI & S. C. KENDEIGH (eds.): *Granivorous birds in ecosystems*, pp. 127—204, 365—73, Cambridge.
- KOIVISTO, I. 1965: Behavior of the Black Grouse, *Lyrurus tetrix* (L.), during the spring display. — *Finnish Game Res.* 26: 1—60.
- KOIVISTO, I. & M. K. PIRKOLA 1961: Metson ja teeren soitimista sekä soidinarvioinneista keväällä 1960 kerätyn aineiston perusteella. — *Suomen Riista* 14:53—64.

- KORHONEN, K. 1980: Microclimate in the snow burrows of Willow Grouse (*Lagopus lagopus*). — Ann. Zool. Fennici 17:5—9.
- KOSKIMIES, J. 1958: Seasonal, geographical and yearly trends in the weight of Capercaillie (*Tetrao urogallus*) and Blackgame (*Lyrurus tetrix*) in Finland. — Ornis Fennica 35:1—18.
- LIND, E. A. 1961: Teeren aamulennosta ja päivääktiiviisuuden alkamisesta (Summary: On the morning flight and onset of daily activity of Black Grouse (*Lyrurus tetrix*)). — Suomen Riista 14:75—81.
- LINDROTH, H. & L. LINDGREN 1950: Metson hakomisen metsänhoidollisesta merkitykseen (Summary: On the significance for forestry of the Capercaillie, *Tetrao urogallus* L., feeding on pine-needles etc.). — Suomen Riista 5:60—81.
- MARJAKANGAS, A. 1980: Metsäkanalintujen kiepit (Summary: Snow roosting in tetraonids, *Tetraonidae*). — Memoranda Soc. Fauna Flora Fennica 56:65—70.
- MYRBERGET, S. 1979: Winter food of Willow Grouse in two Norwegian areas. — Medd. Norsk Viltforskning 3:7:1—32.
- PULLIAINEN, E. 1970: Metson talviravannon valinnasta ja koostumuksesta (Summary: Composition and selection of winter food by the Capercaillie (*Tetrao urogallus*) in northeastern Finnish Lapland). — Suomen Riista 22:67—72.
- PULLIAINEN, E. 1976: Small intestine and caeca lengths in the Willow Grouse (*Lagopus lagopus*) in Finnish Lapland. — Ann. Zool. Fennici 13:195—199.
- PULLIAINEN, E. 1979: Autumn and winter nutrition of the Capercaillie (*Tetrao urogallus*) in the northern Finnish taiga. — In: T. W. I. LOVEL (ed.): Woodland Grouse 1978, pp. 92—97, Sudbury.
- PULLIAINEN, E. 1980a: Heart/body weight ratio in the Willow Grouse *Lagopus lagopus* and Rock Ptarmigan *Lagopus mutus* in Finnish Lapland. — Ornis Fennica 57:88—90.
- PULLIAINEN, E. 1980b: Mid-winter feeding activity of Siberian Tits *Parus cinctus* and a Great Tit *Parus major* at a feeding site north of the Arctic Circle. — Ornis Fennica 57:90—92.
- PYNNÖNEN, A. 1954: Beiträge zur Kenntnis der Lebensweise des Haselhuhns, *Tetrastes bonasia* (L.). — Papers Game Res. 12: 1—90.
- RAJALA, P. 1966: Riekon ja kiirunan talvisesta kasviravannon valinnasta ja puissa ruokailusta (Summary: On the choice of plant diet and feeding in trees of the Willow Grouse (*Lagopus lagopus*) and Ptarmigan (*Lagopus mutus*) in winter). — Suomen Riista 19:79—93.
- SALO, L. J. 1971: Autumn and winter diet of the Hazel Grouse (*Tetrastes bonasia* L.) in northeastern Finnish Lapland. — Ann. Zool. Fennici 8:543—546.
- SALO, L. J. 1973: Chemical composition and caloric content of the autumn and winter diet of *Tetrastes bonasia* L. in northeastern Finnish Lapland. — Ann. Zool. Fennici 10:384—387.
- SEISKARI, P. 1962: On the winter ecology of the Capercaillie, *Tetrao urogallus*, and the Black Grouse, *Lyrurus tetrix*, in Finland. — Papers Game Res. 22:1—119.
- TEPLOV, V. P. 1947: Gluhar v Pečorsko-Ilyčskom zapovednike. — Tr. Pečoro-Ilyčskogo zapovednika 4:3—76.
- WEST, G. C. 1968: Bioenergetics of captive Willow Ptarmigan under natural conditions. — Ecology 49:1035—1045.
- WEST, G. C. 1972: Seasonal differences in resting metabolic rate of Alaskan Ptarmigan. — Comp. Biochem. Physiol. 43A:293—310.
- WEST, G. C. & M. S. MENG 1968: Seasonal changes in body weight and fat and the relation of fatty acid composition to diet in the Willow Ptarmigan. — Wilson Bull. 80:426—441.

Received January 1981