Behaviour of a Willow Grouse *Lagopus l. lagopus* at the nest

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The behaviour of a nesting Willow Grouse pair was studied mainly with the aid of a field television system with remote control in eastern Finnish Lapland (67°44' N, 29°37' E) in continuous daylight. During the laying period the hen covered the eggs with plant matter. Incubation started before the laying of the penultimate egg. Only the hen incubated. The hen could be off the nest at any time of the day. The nest was left unattended 5.7 % of the time. Snowfalls occurred during the incubation period. In continuous daylight the Willow Grouse is active for 24 hr. In cold weather the frequency of settling movements remained high, while preening, shifting, resettling and nest-building activities decreased. Exceptionally high frequencies of preening, feeding (catching) and nest-building were recorded during the hatching of the chicks, which points to displacement activity. The period from the beginning of intensive incubation to the departure of the brood was about 22 days.

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Introduction

Egg temperature, incubation rhythm and certain other aspects of parental behaviour have been studied in the Willow Grouse *Lagopus l. lagopus* by a number of investigators (e.g. BARTH 1949, SEMENOW-TJAN-ŠANSKIJ 1959, VALANNE 1966, AULIE & MOEN 1975, ALLEN et al. 1977). But no detailed studies are as yet available on the behaviour of nesting Willow Grouse under natural conditions of continuous daylight. In June 1978, an opportunity arose to study the behaviour of a pair of Willow Grouse at their nest in continuous daylight with the aid of a field TV system. The present paper reports on these observations.

Methods

The work was carried out near the Värriö Subarctic Research Station, eastern Finnish Lapland (67°44' N, 29°37' E). A nest of a Willow Grouse with 3 eggs was found on 30 May at the base of the northern slope of the Värriötunturi fell, alt. 365 m, under a small spruce sapling at the lower limit of the mountain birch forest zone.

On 2 June a TV camera with remote-controlled zoom lens and pan and tilt head was placed 3 m from the nest, the video-monitor and remote control panel being installed in a large tent at a distance of about 150 m. This same equipment had been used with success in corresponding investigations since 1971 (e.g. PULLIAINEN 1971, 1975). The female Willow Grouse did not appear to be disturbed by the movements of the camera or the monotone sound produced by it, and was never driven away from the nest. The TV system was used to study egg-laying

on 2—4 June, and for continuous monitoring in four periods of 48 hr and one of 45 hr (the last) on the following dates: 7—9, 10—12, 15—17, 19—21 and 26—28 June. Each period began at noon.

Air temperatures were recorded on a thermograph at the meteorological screen in the yard of the Research Station.

Results

Egg-laying. From the 3rd to the 9th egg of the clutch, the mean interval between two layings was 32 hr. The hen had just laid the 3rd egg when the nest was found, and had no time to cover the eggs before leaving the nest. After laying the 4th, 5th, 6th, and 7th eggs, it covered them with dry birch leaves, moss, lichens, and twigs of blueberry and cowberry, which it gathered with its bill in the immediate vicinity of the nest cup. Between the 3rd and 7th egg the hen visited the nest only in order to lay. On arrival at the nest, it did not remove the matter covering the eggs, and this then gradually fell to the bottom of the nest.

When laying the 6th egg, for instance, the hen stayed at the nest from 14.05 to 16.03, during which time it settled, resettled, ruffled and preened its plumage, moved the eggs with its feet and/or bill, and pecked different objects at the rim of the nest, but mostly sat motionless on the eggs. The last 2.5 min it spent covering the eggs. The exact moment of laying could not be recorded. The hen returned 27 hr 25 min later and probably laid the 7th egg 8 min after arrival. The 8th and 9th eggs were laid while the hen was already incubating.

Incubation rhythm. Only the hen was seen incubating. Incubation began on the night of 5 June, when there were 7 eggs in the nest. On 7—8 June, when the 9th egg was laid, the hen was off the nest 11.2 % of the time, and during the next 24 hours 8.5 %. The corresponding proportion for the whole incubation period (calculated on the basis of 235 hr 49 min of continuous observation) was only 5.7 %.

During the 9 observation days the hen was off the nest 14 times between 06.00 and 18.00 hr and 13 times between 18.00 and 06.00 hr. It left the nest both at midnight (on 8 June at 00.03) and at noon (absent at 12.00 four times during 9 days). This total of 27 departures from the nest gives an average of 3.0 times a day (range 2—4). The bird scanned the surroundings very attentively each time before leaving the nest, and then walked some 20—40 cm and took off. Once incubation had begun it no longer covered the eggs at departure. When it flew back to the nest it landed a few metres away, stalked up to the nest crouching low and sat down on the eggs again.

On 8 June a semi-domestic Reindeer *Rangifer t. tarandus* walked between the nest and the TV camera. The hen fled and was off the nest for 91 min. On 15 June the hen was off the nest when observation began at 12.00 and did not return for 129 min. The mean length of the 12 periods of absence between 06.00 and 18.00 hr was 33.0 ± 5.6 min (SD = 19.4; range 18—91) and that of the 13 periods between 18.00 and 06.00 hr 19.5 ± 1.2 min (SD=4.0; range 14—27). This difference is statistically significant (t =2,354; $0.05 < P < 0.025$). On the day of hatching, the hen left the nest three times, for periods of 18, 6 and 3 min. The mean length of the 28 absent periods recorded was 24.1 min. The mean length of the 23 spells of incubation was 460.4 ± 36.9 min (SD= 176.7; range 130—857). It is significant that the four longest incubation spells (14.3, 13.1, 12.9 and 11.4 hr) be-

gan at about noon (at 12.02, 12.09, 12.14 and 13.45). Before the hen left the nest with its chicks (at 07.49 on 28 June), it incubated for one long (15.5 hr) and two short (0.4 and 0.7 hr) spells.

The air temperatures recorded during incubation varied between —2.4° and +23.2°C. The lowest temperature at ground level was —4.5°C. The lowest mean temperature for any 24-hr period was —0.1°C (16—17 June), the highest +10.2°C (20—21 June). The ground was sporadically covered by snow, and during these periods the hen was off the nest. Now and then snow accumulated on the back of the incubating bird. When warmed by direct sunshine, it sometimes opened its bill and panted, even though the air temperature was below +10°C.

Behaviour. The hen had already moulted to summer plumage when it started incubation, and it improved its protective colouring by keeping the white primaries concealed when sitting on the eggs. The last snow was just disappearing, and the mountain birches had just come into leaf. An incubating Willow Grouse is very difficult to detect, especially as it does not fly up from the nest until the observer is within about 3 m.

The hen spent the bulk of the incubation period sitting in a certain posture on the eggs, very often closing its eyes and sleeping in this same posture. It slept for short spells at all times of the day.

In addition to sitting on the eggs, the incubating Willow Grouse shifted them, rose and sat down facing a new direction (= resettled), improved its posture by swaying its body to and fro and from side to side (= settled), ruffled and preened its plumage, pecked and removed small particles (sticks, leaves, feathers, etc.) from the rim of the nest with its bill and caught small flying insects. The settling movements often followed the other activities and achieved the highest frequency (no./24 hr) of all these activities (Table 1, Fig. 1).

TABLE 1. Frequency of shifting, preening, building, feeding, settling and resettling activities during the first (A) and second (B) halves of the incubation period.

Activity	Frequencies per day A	B
Shifting	18.5	28.7
Preening	80.3	127.7
Nest-building	9.2	11.7
Settling	184.8	150.0
Resettling	16.0	12.0
Feeding	0.8	6.3

Fig. 1 shows that the frequency of preening was at its lowest during the cold part of the first half of the incubation period and increased towards

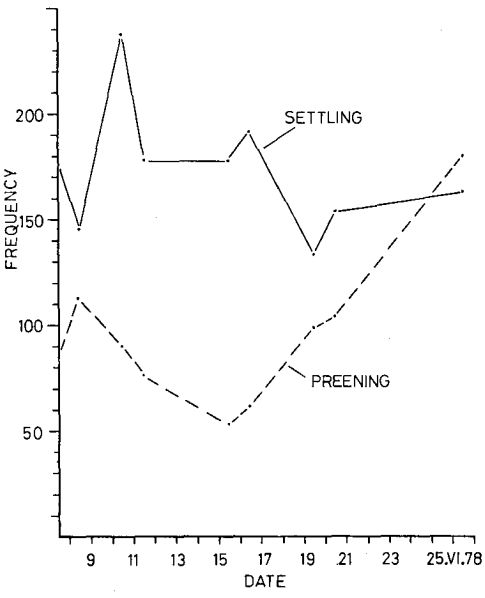

FIG. 1. Changes in the frequency of settling and preening activities of the incubating Willow Grouse hen per 24 hr.

TABLE 2. Incubation absences of the Willow Grouse in different studies.

Author	Mean length of absences (min)	Mean number of absences/day	Absences as % of total time of incubation
SEMENOV-TJAN-ŠANSKIJ (1959)	19	4	4.5
Present study	24.1	3.0	5.7
BARTH (1949)	21.5	6.4	14.5
VALANNE (1966) (captive birds)	7.3	3.4	1.7

the end. During the 20 hours of the hatching day 193 preenings were recorded, i.e. more than during any previous 24-hr period (Fig. 6). Settlings and preenings occurred throughout the day (Fig. 2), but there was a slight increase in settling in the evening hours and around midnight, concurrent with a slight decrease in preening activity.

The hen always shifted the eggs from the edge to the centre of the nest with the ventral side of the bill and the neck. Usually 2—6 eggs were moved at a time. This behaviour occurred rather evenly throughout the day and was often followed by resettling (Fig. 3). During the cold spell in the first half of the incubation period the eggs were shifted less than once an hour, on average (18.5 times/day); during the warmer latter half they were shifted more often (28.7 times/day) (Fig. 4, Table 1). Resettling was at its maximum at the beginning of the incubation period, but then decreased sharply and followed the frequency pattern of the egg-shifting (Fig. 4, Table 1). Resettling was a little more frequent in the daytime than at night (Fig. 3).

Nest-building activity occurred throughout the day with a maximum in the forenoon (Fig. 5). This activity was at a relatively high level at the beginning of the incubation period, de-

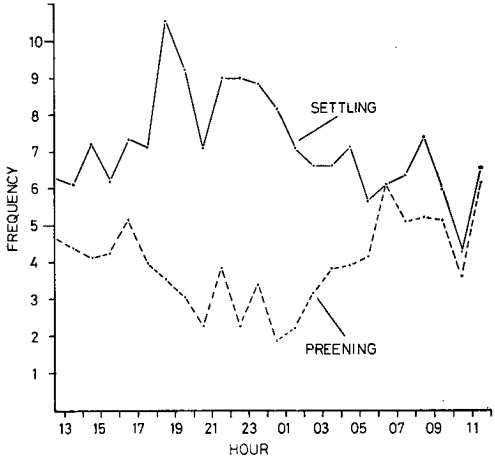

FIG. 2. Diurnal rhythm of settling and preening activities per hour in the incubating Willow Grouse hen.

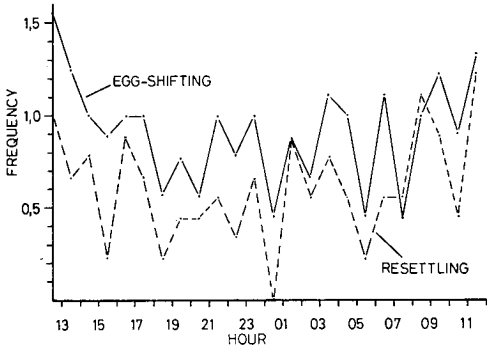

FIG. 3. Diurnal rhythm of egg-shifting and resettling activities per hour in the incubating Willow Grouse hen.

creased during the cold spell, increased afterwards and then decreased again (Fig. 4). A clear maximum was recorded during the hatching day (37 times/20 hours; Fig. 6).

The catching of flying insects was more frequent during the latter half of the incubation period (Fig. 4, Table 1), and reached a maximum (33 times/20 hr) on the hatching day (Fig. 6). It is significant that the hen was not seen feeding on the plants growing around the nest, or defecating in or near the nest, and that no droppings were observed.

The hen did not remove any eggshells from the nest.

The first chick very probably hatched on 27 June (at about 17.00), while the other chicks hatched during the evening and night. During the hatching the hen was somewhat raised up in the nest. It was very eager to catch flying insects (or at least made catching movements) and also made nest-building and preening movements (Fig. 6). The oldest chick came out of the nest about 7 hours after hatching (00.12). When the hen and the chicks left the nest on 28 June (07.49), this

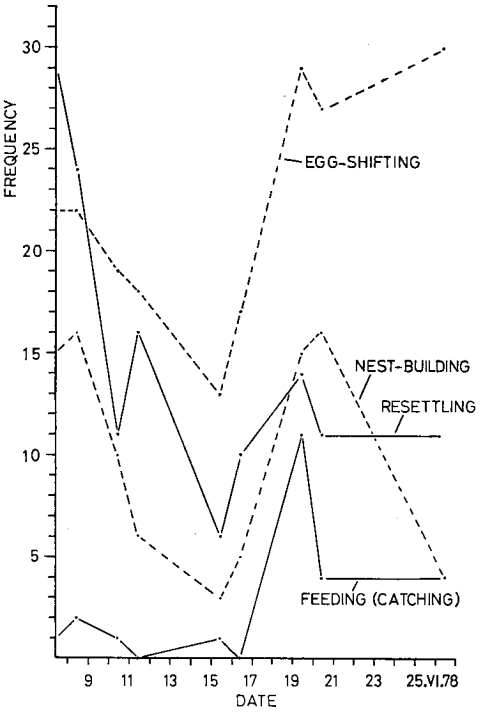

FIG. 4. Changes in the frequency of egg-shifting, nest-building, resettling and feeding (catching) activities of the incubating Willow Grouse hen in the course of incubation.

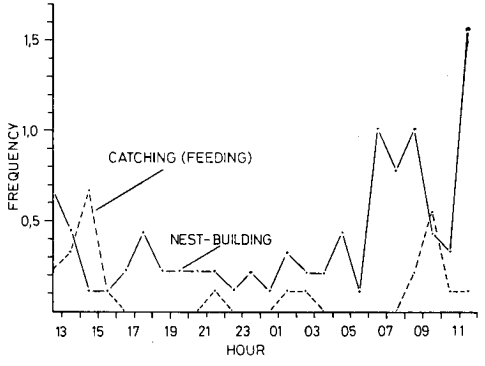

FIG. 5. Frequencies of catching (feeding) and nest-building activities per hour in the incubating Willow Grouse hen.

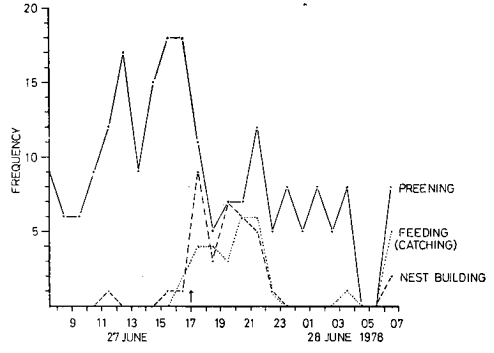

FIG. 6. Frequencies of preening, nest-building and feeding (catching) activities per hour in the Willow Grouse hen during the last 24 hours before the brood finally left the nest. The arrow shows the approximate moment of hatching of the oldest chick.

chick was about 15 hr old. The period from the beginning of intensive incubation to the departure of the brood was about 22 days and that from the laying of the 9th egg to the departure of the brood about 20.5 days.

The female and 7 chicks were seen on 28 June, between 06.32 and 06.38, walking at a distance of about 6 m from the nest. One chick and one unhatched egg containing a dead but well-developed embryo were left in the nest. Between 07.02 and 07.05 the hen and at least 3 chicks were outside the nest. The last chick came back to the nest at 07.12. At 07.47 the female left the nest for good, and the last chicks followed it at 07.49.

The female and the male with 8 chicks were seen at a distance of ca. 10 m from the nest at 9.30 on the same day, and they were still in the same place at 10.50. The mean weight of the chicks was 15.1 g.

During the egg-laying and incubation period the male moved about in its territory around the nest uttering its usual cry, but was never seen nearer than about 10 m. In this way it avoided revealing the nest site to enemies. When the hen was off the nest, it was accompanied by the cock.

When on the nest the hen reacted very sensitively to warning calls from other birds and sounds produced by man or machines (e.g. aircraft).

Discussion

WATSON & JENKINS (1964) and v. HAARTMAN et al. (1963—72) state that incubation in the Willow Grouse usually starts with the laying of the last egg, while NETHERSOLE-THOMPSON & NETHERSOLE-THOMPSON (1939) report that it may start with the penultimate egg. The present case showed that it may start even earlier. Usually only the hen incubates (see reviews by v. HAARTMAN et al. 1963—72, WATSON & JENKINS 1964, VALANNE 1966, ALLEN et al. 1977), as in the present case, although cocks have also incubated sometimes in captivity (WATSON & JENKINS 1964, ALLEN et al. 1977, ALLEN 1977). Under natural conditions an incubating cock in spring plumage with its white back would reveal the nest to enemies.

Table 2 shows that the time for which the nest of the Willow Grouse is left unattended varies under natural conditions between at least 4.5 % and 14.5 %. The corresponding range in the Capercaillie *Tetrao urogallus* is 2.7 —6.1 % (SEMENOV-TJAN-ŠANSKIJ 1959, LENNERSTEDT 1966, VALANNE 1966, PULLIAINEN 1971). These values are much lower in captivity (1.7 % and 2.4 %, respectively; VALANNE 1966).

Egg-shifting is an essential element of incubation (BAERENDS 1959). VALANNE (1966) reports on the basis of 58.5 observation hours that a captive Willow Grouse shifted its eggs more often during the first half of the incubation period (34.4 times per day) than during the second half (26.8 times per day). The present 216 observation hours give the opposite pattern, 18.5/28.7 (Table 1). The shifting was fairly evenly distributed throughout the day (Fig. 3).

BAERENDS (1959) states that retrieving, shifting and settling are part of the incubation instinct, whereas there is no evidence that preening or building are directly controlled in this way. During cold weather, and especially when it is raining, the tendency for gulls to remain sitting on the nest is so great that they are very reluctant to rise even to retrieve an egg from the rim of the nest, while warm weather causes them to sit upon the eggs less

closely or to spend less time on them. BAERENDS (1959) also mentions that shifting and settling occur when the tendency to incubate is high, whereas preening occurs mostly when the tendency to incubate is low or inhibited.

The purpose of settling movements is to bring the eggs into close contact with the brood patch (BAERENDS 1959), and one might expect this to be especially important in cold weather. The settling movements did in fact become slightly more frequent in the evening and at midnight (Fig. 2), when the temperature usually falls. The frequency of this activity also remained high throughout the cold spell (Fig. 1), when the frequency of preening, shifting, resettling and nest-building decreased (Fig. 1 and 4). These observations agree with the conclusions reached by BAERENDS (1959) on gulls, except in the case of shifting. Both egg-shifting and resettling decreased in frequency during the cold period. Thirteen shifts per day for 9 eggs (2—6 eggs shifted at a time) is probably enough for the development of the embryos, even though incubation is intensive (see DRENT 1973, ALLEN et al. 1977). The incubating bird loses contact with the eggs during egg-shifting and resettling, but egg-shifting is necessary for the development of the embryos (e.g. RANDLES & ROMANOFF 1950, NEW 1957). Nevertheless, frequent shifting in cold weather might be thought to be harmful.

A Willow Grouse nest is a hollow scraped in the plant matter on the ground, and VALANNE (1966) considers that covering the eggs with plant matter forms part of nest-building. In the present case, the hen covered the eggs until the beginning of incubation. Nest-building movements occured with varying frequency throughout the incubation period (Fig. 4). VALANNE (1966) concludes that at the end of this period nest-building must be regarded as a displacement activity. In the present case, the very frequent nest-building movements during the hatching of the chicks (Fig. 6) probably represented such activity. The same concerns at least part of the preening activity at this time (Fig. 6). The frequency of feeding (catching) movements, too, was very high during the hatching of the chicks (Fig. 6). Performed at this time, the catching movements can also be regarded as a displacement activity.

After the eggs start to chip, the hen may stay on the nest for up to 2 days until hatching is over (SEMENOV-TJAN-ŠANSKIJ 1959, WATSON & JENKINS 1964). In the present case the oldest chick was only 14.8 hr old when the hen and the chicks finally left the nest, and they stayed in its immediate vicinity for only 2 more hours.

VALANNE (1966) studied the incubation rhythm of a captive female Willow Grouse in alternating light and dark, and noted that the breaks formed three peaks in the 24-hour incubation rhythm, whereas SEMENOV-TJAN-ŠANSKIJ (1959), performing similar studies in continuous daylight, reported that these breaks were distributed evenly throughout the day. The present study gave the same result, all the essential activities of the incubating hen occurring throughout the day (Fig. 2, 3 and 5). WEST (1968), in his study of the gross activity of the Willow Ptarmigan in Alaska, observed that in a captive bird activity began at the onset of civil twilight each day throughout the year, thus continuing for 24 hr in summer. WEST (1968) also observed that the major peak in activity occurred in the morning in early summer. The present incubating hen showed peaks of this kind in its preening (Fig. 2) and nest-building (Fig. 5) activities.

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Selostus: Riekon käyttäytymisestä pesällä

Kesällä 1978 tutkittiin Sallassa Värriötunturin maastossa TV-laitteiston avulla riekkoparin käyttäytymistä pesällä ja sen läheisyydessä jatkuvassa päivänvalossa. Naaras muni pesään pienen kuusen juurella 9 munaa. Se aloitti munien hautomisen ennen 8. munan munimista. Sitä ennen se oli peittänyt munat poistuessaan pesältä, mutta ei tehnyt tätä enää hautomisen alun jälkeen. Vain naaras hautoi. Se oli poissa pesältä yhteensä 5.7 % hautomisajasta, mihin aikaan vuorokaudesta tahansa. Lumisateita esiintyi haudonnan aikana, ja lumi saattoi kasautua jopa hautovan naaraan päälle; tämä ei kuitenkaan häirinnyt hautomista.

Jatkuvan päivänvalon olosuhteissa naaraan aktiivisuus jatkui läpi vuorokauden (kuvat 2, 3 ja 5). Kylmän sääjakson aikana naaraan liikkeet munien päällä (päästäkseen tiiviiseen kosketukseen munien kanssa) jatkuivat tiheään (kuva 1), kun taas höyhenpuvunhoito (kuva 1), muniensiirtely- (kuva 4), asennonvaihto- (kuva 4) ja pesänrakennustoimintojen (kuva 4) frekvenssit pienenivät. Poikaisten kuoriutumisen aikana todettiin poikkeuksellisen innokasta höyhenpuvunhoitoa, lentävien hyönteisten saalistusta ja pesänrakennusliikkeiden suoritusta (kuva 6), mikä viittaa sijaistoimintaan.

Kahdeksasta munasta kuoriutui poikanen, yhdeksännen sisällä oli suurikokoinen kuollut sikiö. Intensiivisen haudonnan alkamisesta siihen hetkeen, jolloin emo poikasineen lähti pesästä, kului n. 22 vrk.

Muninnan ja haudonnan aikana koiras ei näyttäytynyt n. 10 m lähempänä pesää. Se liikkui reviirissään pesän ympärillä, mistä kuului aika ajoin sen ääntelyä. Naaraan poistuttua pesältä hautomisjakson aikana koiras liittyi sen seuraan, samoin se nähtiin kuoriutumisen jälkeen naaraan ja poikasten kanssa.

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