Oikos 17: 169–174. Copenhagen 1966

Egg temperature and incubation rhythm of a Capercaillie (Tetrao urogallus L.) in Swedish Lapland

INGVAR LENNERSTEDT
Zoological Institute, University of Lund

Abstract

A thermistor was mounted in one of the eggs in a Capercaillie's nest, and the remaining space of the egg was filled with paraffin. Automatic registration of the electrical resistance every sixth minute throughout the last twelve days of the incubation period made calculation of the egg temperature possible. During incubation the temperature showed only minor variations, usually within the limits 34–35°C. The minimum egg temperature during absence was on average 27.7°C, the lowest recorded value being 21°C. During three days the weather conditions were severe with snow-fall and the average of the minimum egg temperatures was 2.4°C lower than that for the other days. As long as the female behaves in a normal way, i.e. the length of the absent periods are within the normal limits, even severe weather conditions do not seem to affect the embryonic development. The diurnal rhythm of incubation and absence was calculated from the temperature values. There was no concentration of periods of absence to any particular part of the day except five hours in the afternoon, 18.00–23.00, when there always occurred a period of uninterrupted incubation. These five hours obviously represent a period of rest in the diurnal rhythm of certain activities such as feeding.

Резюме

В одном из яиц кладки глухаря был смонтирован термистор, остальное пространство яйца было заполнено парафином. Температура отмечалась автоматически каждые 6 минут в течение всех 12 дней насиживания. В то время, когда птица сидела на яйцах, температура яиц колевалась в пределах 34–35°C, при отсутствии птпцы в гнезде температура яиц падала, в среднем, до 27,7°C, а максимально до 21°C. Во время трехдневного снегопада температура яиц во время отсутствия птицы в гнезде опускалась на 2,4°C ниже, чем обычно. Если время отсутствия самки в гнезде не выходит из нормальных пределов, погодные условия не влияют на развитие яиц. Периоды отсутствия самки из гнезда не приурочены к определенному времени суток, но с 18.00 до 23.00 самка всегда находилась в гнезде и, вероятно, отдыхала.

Manuscript accepted May 1966.

1. Introduction

Exhaustive studies of the ecology of the Capercaillie and other game birds have been carried out by Russian ornithologists particularly in the Lapland Reserve (68°N, 32°E) and in the Petčora-Ilyč Reserve (62°N, 57°E) by Semenow-Tjan-Šanski (1960). He gives information on, for example, egg temperature conditions and incubation rhythm as indicated by actographs. Egg temperature conditions have been studied in the Pheasant (*Phasianus colchicus*) (Huggins 1941, Westerskov 1956, Kessler 1960) and in the Willow Grouse (*Lagopus lagopus*) (Barth 1949) by means of thermocouples mounted inside the egg near the embryo, attached to the surface of the egg, or mounted between the eggs. The temperature in the nest of Hazel Hen (*Tetrastes bonasia*) has been recorded by means of thermistors (Dolbik 1962).

Incubation, sitting on the eggs, is generally regarded as a fixed behaviour pattern, "Erbkoordination". It is connected to a number of other activities such as shifting the eggs or ruffling the belly feathers (Baerends 1959). When all the mentioned activities are performed, the bird is incubating in a broader meaning. Then the egg temperature is either rising or slightly fluctuating at a certain value. When the bird is off the nest, the egg temperature is either falling or close to the air temperature at the nest. The term incubation is used in its broader meaning in this investigation.

2. Methods

The study was carried out at the nest of a Capercaillie at Ammarnäs, which lies on the eastern border of the Scandinavian mountain range in Swedish Lapland (66°N, 16°E). The nest was located just beneath the upper borderline of the pine forest region, some 500 m above sea level. The nest was built at the base of a young spruce tree. The measurements started on 3 June 1964 and continued until the hen and the newly hatched chicks left the nest on 15 June.

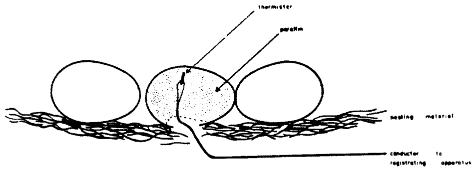

Fig. 1. Cross-section of the nest, showing the thermistor mounted inside one egg.

In one egg of the clutch the embryo was taken out through a narrow opening. A thermistor was mounted opposite the opening, 3 mm from the inside of the shell, and the remaining space inside the egg filled with paraffin (Fig. 1). The conductor was buried into the ground beneath the nest, thus fixing the egg's position in the nest. Due to the flexibility of the conductor, the egg could be moved to a certain degree. The hen accepted the arrangement without noticeable irritation. A second thermistor, for registering the air temperature, hung in the shade on the trunk of a spruce tree near the nest.

The two thermistors (type 5B, Institute of Semiconductor Research, Stockholm) had a resistance of 2,200–2,700 ohms at 25°C. They were connected to a galvanometric recorder (type ERMI, L. M. Eriksson, Stockholm). The resistances were registered every sixth minute and were checked every day by means of a Wheatstone bridge (type Norma 185RW, Norma, Vienna). The accuracy of the measurements was 0.7°C with the recorder and 0.4°C with the Wheastone bridge.

3. Egg temperature

By fixing the thermistor egg in the nest, it remained for the most part in the same position during incubation, and the temperature showed only minor variations, usually within the limits 34–35°C. It was rather constant

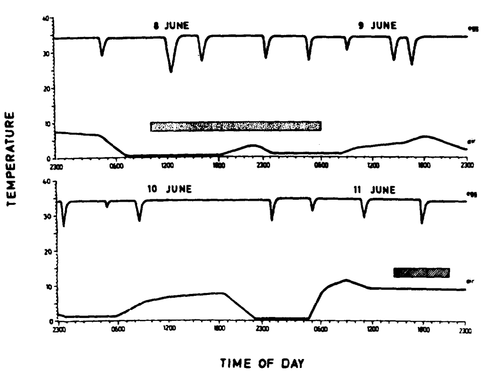

Fig. 2. Incubation temperature and air temperature during four days. A period of snow-fall is indicated by a spotted area and a period of rain by a hatched area.

during all the attentive periods. The temperature conditions during a four day period are shown in Fig. 2.

The minimum temperature during incubation depended upon the time spent off the nest. The average minimum temperature of 35 periods of absence was 27.7°C. The air temperature was usually lower during the morning hours than during the midday hours. To see if this affected the minimum temperature, the incubation periods were divided into two groups comprising the hours 23.00–9.00 and 9.00–18.00 (Tab. 1). The difference in average minimum temperatures between the two periods is slight and not statistically significant.

On 6, 8, and 9 June the weather was exceptionally cold. The snow cover was several centimeters deep. During these days there were 13 absent periods with an average minimum temperature of 26.2°C. During the remaining days there occurred 22 absent periods with an average minimum temperature of 28.6°C ($0.025 > P > 0.01$).

The lowest recorded temperature during absence with no human disturbance was approximately 21°C. This occurred on 6 June just prior to a period of snow-fall, when the hen was off the nest for 35 minutes. In the afternoon of the same day, the hen was flushed from the nest by human interference, and returned after some 80 minutes when the egg temperature slightly exceeded 14°C.

Tab. 1. Length of absent periods and minimum egg temperatures during the morning and midday hours.

Hours	2300–0900	0900–1800
Number of periods off the nest	20	15
Mean length of periods off the nest	20	27
Average minimum temperature (°C.).......	27.9	27.5

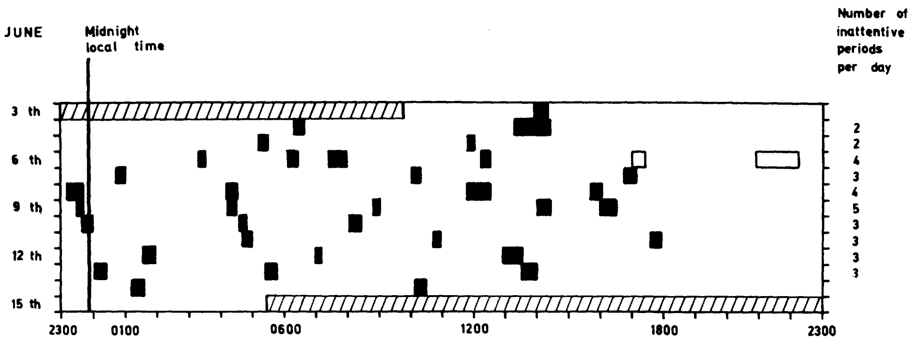

Fig. 3. The diurnal rhythm of incubation during the last twelve days. Black areas indicate periods off the nest and open areas represent absent periods caused by human interference. The periods off the nest are rather evenly distributed as to time of day except for the five evening hours, 18.00–23.00, when no natural absent period occurred. The hatched areas indicate a period before the measurements and a period after the hen left the nest with the chicks.

4. Incubation

The time distribution of the absent periods is shown in Fig. 3. The hen never left the nest during the evening hours, 18.00–23.00, except once when she was disturbed. Three times she left the nest between 23.00 and 24.00. The periods of absence during the remaining part of the day were fairly evenly distributed.

The number of absent periods per day was between 2 and 5. When the weather was severe with low air temperature and snow (6, 8, and 9 June), there were 4 or 5 absent periods. With normal conditions the number was 2 or 3. The time total for all the absent periods amounted to 4.9 per cent of the total time of measurement. The length of the individual periods varied between 10 and 65 minutes. The mean value for 35 periods was 23 minutes. The absent periods between 9.00 and 18.00 hrs. were on average 7 minutes longer than those between 23.00 and 9.00 hrs. (Tab. 1) ($0.025 > P > 0.01$).

The length of the incubation periods was highly variable. They were longest between 18.00 and 23.00 hrs. The mean value for these periods was about 11 hours, the minimum value 7 hours, and the maximum value 16 hours. These calculations do not include the last day, when the chicks were hatching. That day the hen stayed for 19 hours on the nest and then left it together with the chicks. The incubation periods of the morning and day hours lasted on the average about 5 hours though on occasion it was only one hour or as much as 9 hours.

The time of day of the absent periods was compared with the air temperature. The absent periods of the day hours, 9.00–18.00, coincided often with the highest temperature of the day, though this was not always the case. On 6, 8, and 9 June, though the air temperature was low and the ground snow-covered, the hen left the nest as usual (Figs. 2 and 3). The absent periods of the morning hours, 23.00–9.00, could not be correlated with any particular temperature condition, e.g. a rising temperature.

5. Discussion

During incubation the temperature of the egg filled with paraffin was fairly constant between 34 and 35°C. There was no rise in the average temperature during the twelve days of measurement. Owing to the heat production of the embryo, the temperature in the other eggs of the clutch may have been a little higher than that found in the thermistor egg. Experimental studies on the chemical heat regulation of domestic hen embryos during the second half of the incubation period show a slight rise in the temperature of the embryo compared with the ambient temperature. Before hatching this difference could be as much as 1 or 2°C (Romijn and Lokhorst 1955). The body temperature of the Capercaillie chicks, 10–15 sec. after hatching, was on average 2.2°C higher than the ambient temperature (Marcström 1956).

The temperature conditions in the nest of a Capercaillie were studied by Grüner (1951), who used a maximum and a minimum thermometer. The minimum temperature varied from 14.6 to 23.7°C. Though frost occurred often during the night the minimum temperature usually did not fall below 20°C, and only once did it fall as low as 14.6°C (cf. above, 14°C registered after disturbancy). Semenow-Tjan-Šanski (1960) reported eight cases of female Capercaillies leaving their nests, when the air temperature was below the freezing point. The longest period of absence was 69 minutes at an air temperature of −1.0°C. In all eight cases the embryos were unaffected.

The temperature of the incubated Pheasant egg falls within the same range, viz. 29.5–38.7°C (Huggins 1941, Westerskov 1956, Kessler 1960).

Moreng and Bryant (1955) studied the temperature tolerance of domestic hen embryos. It took approximately 3.5 hours for an egg with an initial temperature of 37.5° to cool to 0°C, when the latter temperature was the same as the ambient temperature. In one trial the eggs were rapidly cooled to 0°C and then kept at this temperature for a total of 125 minutes. No increased mortality followed this treatment except for the last days of the incubation period. Roughly the same cooling rate was recorded in Capercaillie eggs containing dead embryos (Semenow-Tjan-Šanski 1960).

In this study the average length of the absent periods was 23 minutes, minimum length about 10 minutes and maximum length about 65 minutes. Semenow-Tjan-Šanski (1960) found the length of the inattentive periods to be usually within the limits 10–35 minutes.

From this discussion the following conclusion may be drawn (cf. Semenov-Tjan-Šanski 1960). Even when extreme weather conditions prevail during the incubation period, the egg temperature does not sink to the extent that it kills or damages the embryo. This holds true as long as the female behaves in a normal way, i.e. as long as the absent periods are within the normal limits. Further support for this statement may be drawn from the studies on the population fluctuation of the Capercaillie. The causes of these fluctuations have been the object of several investigations (Semenow-Tjan-Šanski 1960, Seiskari 1962, Helminen 1963). The weather conditions during the breeding season are considered one of the main causes of population fluctuation, especially during the prelaying period (Siivonen 1957) as well as the period after hatching (Marcström 1960). The weather during the incubation period seems to have the least effect on the breeding results (Siivonen 1957).

The temperature measurements in this study gave a registration of the periods of incubation and absence, and the diurnal rhythm of the absent periods during conditions of continous day-light (66°N). There were no absent periods between 18.00 and 23.00 hrs., and these hours appear to represent a rest period in the diurnal rhythm of certain activities such as the feeding activity. The absent periods were not concentrated to any particular hours of the remaining part of the day.

Semenow-Tjan-Šanski (1960) recorded the activities at nine Capercaillie nests for a total of 98 days. He stated in the text that he did not find any particular period of rest during the darkest hours of the day, but only once a female left the nest during the hours 23.00–01.00. Tab. 68 in his treatise shows a difference between his two study areas for the time of occurrence of absent periods. In the Lapland Reserve (68°N) the least number of absent periods occurred between 19.00 and 01.00 hrs., with no particular concentration to the remaining hours of the day. This implies the same type of diurnal rhythm as that shown by the present investigation. The time for absences, registered at two nests of Willow Ptarmigan in the same reserve, often roughly coincided in two consecutive days, but there was also noted a displacement in time from day to day in the same direction, and consequently absence occurred on every hour of the day.

At the Capercaillie nests in the Pečora-Ilyč Reserve (62°N) there seemed to be a period of rest during the darkest hours and a concentration of absences between 17.00 and 21.00 hrs in the evening and 01.00 to 05.00 hrs. in the morning (Semenow-Tjan-Šanski 1960: Tab. 68). The Black Grouse (*Lyrurus tetrix*) in the same reserve rested between the hours 23.00 and 01.00 and had concentrations of absent periods during the late evening and the morning hours. The Hazel Hen rested between 22.00 and 03.00, and also in this species the absent periods were more numerous during the evening and the morning hours. The same rhythm of activity was found at the nest of Hazel Hen in central Finland about 62°N (Pynnönen 1954).

Other studies on the diurnal rhythm of activity in different game birds have usually been carried out in latitudes with dark nights. A period of rest occurs during the dark hours and absences from the nest mostly at dawn and at dusk (see Kendeigh 1952 for review, Kessler 1962, Klonglan *et al.* 1965) but also regularly during other light hours. The Pheasant of New Zealand had one absent period in the middle of the day, when the air temperature was high (Westerskov 1956).

6. Acknowledgments

Grateful acknowledgements are made to Professor P. Brinck of the Zoological Institute, University of Lund, for his advice and the supply of equipment used in this investigation, and to Professor A. Enemar of the Zoological Institute, University of Gothenburg, for encouragement during the field study and valuable suggestions in preparing the manuscript.

References

BARTH, E. K. 1949. Redetemperaturer og rugevaner. – Naturen 73: 81–95. Bergen.

BAERENDS, G. P. 1959. The ethological analysis of incubation behaviour. – Ibis 101: 357–368. London.

DOLBIK, M. S. 1962. Studying the temperature regime of brooding *Tetrastes bonasia* with the help of semi-conductor transmitting recording devices. – Ornithologija 4: 389–393. Moskwa.

GRÜNER, A. M. 1951. (Cited by SEMENOW-TJAN-ŠANSKI 1960.)

HELMINEN, M. 1963. Composition of the Finnish populations of capercaillie, *Tetrao urogallus*, and black grouse, *Lyrurus tetrix*, in the autumns of 1952–1961, as revealed by a study of wings. – Riistatieteellisiä Julkaisuja 23: 1–124. Helsinki.

HUGGINS, R. A. 1941. Egg temperatures of wild birds under natural conditions. – Ecology 22: 1–48 157. Brooklyn, New York.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. – Illinois Biol. Monogr. 22, Nos. 1–3. Urbana, Illinois.

KESSLER, F. W. 1960. Egg temperature of the Ring-necked Pheasant obtained with a self-recording potentiometer. – Auk 77: 330–336. Lancaster, Kansas.

— 1962. Measurements of nest attentiveness in the Ring-necked Pheasant. – Auk 79: 702–705. Lancaster, Kansas.

KLONGLAN, E. D., COLEMAN, I. A. and DOZICKY, E. L. 195 A Pheasant nest activity recording instrument. – J. Wildl. Manag. 20: 173–177. Lawrence, Kansas.

MARCSTRÖM, V. 1956. Om kroppstemperaturen hos tjäderkycklingar, *Tetrao urogallus* Lin., vid kläckningen och omedelbart därefter. – Viltrevy 1: 139–149. Stockholm.

— 1960. Studies on the physiological and ecological background to the reproduction of the Capercaillie (*Tetrao urogallus* Lin.). – Viltrevy 2: 1–69. Stockholm.

MORENG, R. E. and BRYANT, R. L. 1955. The tolerance of the chicken embryo to periods of low temperature exposure. – Poultry Sci. 34: 1341–1348. Urbana, Illinois.

PYNNÖNEN, A. 1954. Beiträge zur Kenntnis der Lebensweise des Haselhuhns, *Tetrastes bonasia* (L.). – Riistatieteellisiä Julkaisuja 12: 1–90. Helsinki.

ROMIJN, C. and LOKHORST, W. 1955. Chemical heat regulation in the chick embryo. – Poultry Sci. 34: 649–654. Urbana, Illinois.

SEISKARI, P. 1962. On the winter ecology of the capercaillie, *Tetrao urogallus*, and the black grouse, *Lyrurus tetrix*, in Finland. – Riistatieteellisiä Julkaisuja 22: 1–119. Helsinki.

SEMENOW-TJAN-ŠANSKI, O. I. 1960. Die Ökologie der Birkhuhnvögel (Tetraoniden). – Trudy Laplandskogo Gosudarstwennogo Zapowednika Wypusk 5. Moskwa. (Translation by Statens Naturvetenskapliga Forskningsråd, Översättningstjänsten, Nr. 106.)

SIIVONEN, L. 1957. The problem of the short-term fluctuations in numbers of tetraonids in Europe. – Riistatieteellisiä Julkaisuja 12: 1–44. Helsinki.

WESTERSKOV, K. 1956. Incubation temperatures of the Pheasant *Phasianus colchicus*. – Emu 56: 405–420. Melbourne.

Fil. lic. Ingvar Lennerstedt
Zoological Institute
University of Lund
Lund
Sweden