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Nesting behaviour of Capercaillie (*Tetrao urogallus*) females kept in aviaries

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For many bird species in captivity the best practice for incubation procedures have not been yet developed. This is hampered by a lack of cooperation between bird breeders or by reluctance to experiment on valuable eggs. The last two problems may be solved by observation of natural incubation, which technology has made a lot easier. Many studies document incubation behavior: daily time spend in the nest, preferred hours of making absences, egg turning rate and incubation temperature. Such data is scientifically interesting but also allows for better protection of endangered species through development of captive breeding programmes. The Capercaillie (*Tetrao urogallus*) is a threatened species over much of its European range and various conservation actions are being taken to save populations from global or local extinction. Our study took place in Capercaillie Breeding Centre in Wisła Forestry District and describes nesting and incubation behaviour of Capercaillie females kept in captivity. Our aim was to better document the nesting behaviour by recording egg turning rate, and the time and length of incubation recesses. Time of day and day of incubation had no significant influence on recess length, but the number of recesses was related with time of day with two peaks at 06:00 h and 18:00 h. Egg turning activity was the greatest during the first and last two days of incubation but generally consistent throughout the rest of incubation. Captive hens spent less time outside of the nest than wild ones, their absences were shorter, rarer and took place mostly in the evening. However, differences in the preferred absence hours were not as clearly marked as in the case of wild birds. We hope that this information will help improve management practises to maximise the reproductive output of captive Capercaillie.

1. Introduction

For many bird species in captivity appropriate artificial incubation procedures have not been developed. This may be due to lack of cooperation between bird breeders or reluctance to experiment on valuable eggs (Kuehler & Good 1990). Observation of natural incubation could inform artificial incubation procedures and recent technological developments have made recording incubation much easier. Incubation behavior, i.e. daily time spend in the nest, preferred hours of making absences, egg turning rate and incubation temperature have been reported, for example, for ducks (Caldwell & Cornwell 1975), pelicans (Evans 1989), passerines (Zerba & Morton 1983), and kiwis (Colbourne 2002). In other cases, e.g. falcons (Burnham 1988) and condors (Kuehler & Witman 1988), incubation procedures were investigated to improve protection of endangered species. In commercial artificial incubation, egg turning stops before hatching, but in the wild, studies show that birds turn their eggs to the end of incubation (Brua *et al.* 1996). In addition, incubation temperature in the nest has only been investigated in a relatively few species (Deeming 2008). As more bird species are threatened by human activity, there will be an increasing need for captive breeding. Thus we need to improve our understanding of incubation by captive birds and within incubators (Deeming & Jarrett 2015).

The Capercaillie (*Tetrao urogallus*) is one of the most endangered species in Poland and other western European countries (Storch 2007, Zawadzki & Zawadzka 2012). In 1995 the Capercaillie was added to the Polish Red Data Book of Animals (Głowaciński & Profus 2001), categorized as an extremely endangered species and listed in Appendix I of 79/409/EEC Bird Directive. Conservation actions for Capercaillie in Poland include *ex situ* breeding centres to produce birds for restitution or reintroduction. Around 60–100 young birds (sex ratio about 50:50) are released annually in Silesian Beskids and Beskid Sądecki, and some birds are also transferred to breeding centres in Poland, Lithuania, Ukraine, Czech Republic, Slovakia and Germany, where they become part of reproductive flocks (Rzońca 2011). Radio-transmitter studies show a 50% survival rate until the following year among the reintroduced individuals in Beskids (Rzońca *et al*. 2012). This programme was one of the factors that helped the Capercaillie population in Poland to increase from around 400 individuals in 2007 to about 700 birds in 2014 (Rzońca 2015).

The Capercaillie Breeding Centre was established in Wisła Forestry District (CBC-WFD) in 2002. It uses egg-pulling and a combination of natural and artificial incubation methods to maximise the annual reproductive output of its captive females. Towards the end of the laying season females are given clutches of eggs to incubate naturally. However, understanding of both natural and artificial incubation practises is poor for this species. Natural incubation by Capercaillie females has proved more productive than artificial incubation (unpublished data) but increasing clutch sizes incubated by birds, which could improve reproductive output, could be problematical. Wiebe & Martin (2000) showed that White-tailed Ptarmigan (*Lagopus leucurus*) females with artificially enlarged clutches spent more time off the nest by taking longer recesses off the nest, compared to the control group with a normal clutch size. Larger clutches also increased incubation costs and decreased its efficacy with a greater loss of adult body weight, higher adult energy expenditure and lower hatching success. In extreme cases, nest abandonment occurred (Coleman & Whittall 1988, Moreno & Carlson 1989, Siikamäki 1995, Thompson *et al*. 1998). In Capercaillie, it is not known to what extent the clutch size could be increased without producing an adverse effect on female condition and embryo development.

This study sought to improve the understanding of incubation in Capercaillie by providing basic information about female incubation in captivity; we tested the hypothesis that incubation behaviour in captivity would be similar to that seen in wild birds (Lennerstedt 1966, Pulliainen 1971, Storaas & Wegge 1997). In particular, patterns of attentiveness and rates of egg turning were recorded to determine whether time of day, or day of incubation, are important in determining behaviour. Such basic knowledge will allow improvements in egg management and incubation efficiency in the captive breeding Capercaillie population.

2. Material and methods

The Capercaillie Breeding Centre was established in Wisła Forestry District (CBC-WFD) in 2002. The buildings housing Capercaillie are located far from any human settlement to minimise disturbance. The basic reproductive flock is kept throughout the year in two wooden, roofed aviaries. The smaller aviary is divided into 6 sub-units, which measure 8.1 m in length × 4.0 m in width × 2.1 m in height, and the bigger one into 12 sub-units (7.2 × 3.5 × 2.3–3.3 m). Holes with a diameter of 17–18 cm, which provide only access for the females (which are smaller in size than males), are situated in the walls separating the aviary into sub-units, which can be closed if required. Every other sub-unit contains a (much larger) male and during the reproductive season females may move freely within three sub-units and choose the best male for mating and, later on, a place for nesting (Rzońca *et al*. 2012). The floor of the aviaries is covered with a 30 cm layer of sand, which is raked and sieved every day by keepers in order to remove droppings (Rzońca *et al*. 2012). Each building has a large, fenced yard with elements of the natural habitat, such as trees, blueberries, anthills and places for sand-bathing. In the breeding season, some nesting boxes are placed inside aviary although the females may also build their nests in paddock or directly in the yard.

During the entire laying period employees control the nests, supply nesting material, and collect eggs to protect them from adverse weather conditions, as well to stimulate females to lay more eggs (14–18 eggs). Towards the end of the breeding season clutches of usually 7–9 eggs (comparable to normal Capercaillie clutch size; Proctor & Summers 2002, Zawadzka & Zawadzki 2003) are returned to the same nest, or are left in nest after laying if females indicate increased interest in incubation. Removed eggs are stored for a maximum of 7 days at temperature of 10–12°C and humidity of 75–80%. The first laid eggs are either put into incubator for the entire period of embryo development, or are pre-incubated (22–23 days) by the Domestic Hens (*Gallus gallus domesticus*) and later transferred to an artificial hatcher. Such procedures should allow production of maximal number of progeny for release but the hatching success is the highest when eggs are incubated naturally by Capercaillie females (Rzońca 2015). When females start incubation, the males are removed to a temporary aviary to minimize disturbance to incubating females. Females sitting on eggs remain free to move around between sub-units and can visit other females.

This study involved five females (numbered 1 to 5) of the Western Carpathian Capercaillie population that had been hatched and reared in captivity at CBC-WFD. Females were 3–4 years-old and were accustomed to human presence. Females 1, 2 and 3 were observed during 2011 and females 4 and 5 during 2012.

Observations were carried out by watching of 24-hour recordings (at night they were made in infrared) of birds' activity during entire incubation period. Cameras (SCP-312 OVH-1/4) where placed near the nests to guarantee good observation quality of bird behaviour. The location of cameras near the nest of Female 3 and Female 5 did now allowed to count the clutch size and number of hatched chicks. Recordings were analysed on Samsung SRD 1650 recorder by the same person. In particular, the activities included: when and for how long the female was leaving the nest, the way she was leaving it (walking or rising for a flight) and what she was doing in the nest during incubation (pecking and/or eating twigs, egg turning). Hence, data were analysed from two perspectives: the effect of time of day irrespective of day of incubation; and the effect of day irrespective of the time of day. Video recordings were not available for all females on every day of the incubation period, so the number of recesses observed per hour was expressed per day observed. The recess length per hour was expressed as average number of recesses observed in that hour irrespective of day of incubation. For data recorded on a daily basis, the total recess time was summed to provide attentiveness (%) between 04:00 h and 20:00 h for each day, the number of recesses per day was counted, and average recess length which was calculated by dividing the total time by the number of recesses. Between 20:00 and 3:59 females were resting, therefore discussed behaviours were not observed. The number of egg turning behaviours were recorded on a daily basis and converted to turns per hour for 24 hours of observation.

In order to analyse the effect of air temperature on total time that females spent daily outside the nest, from March 1 to June 30 of every year the temperature was recorded at 08:00, 13:00 and 18:00 and an average daily temperature was calculated. Temperature data were provided by Dr. Grzegorz Durlo from Department of Forest Protection, Entomology and Forest Climatology, Faculty of Forestry, University of Agriculture in Kraków.

Table 1. The length of incubation, frequency and time of nest absences during entire incubation period for females kept in aviary system.

Female's activity	Means ± SD	Females min–max
Duration of incubation (days)	26.2 ± 1.3	25–28
Mean clutch size	8.2 ± 1.6	6–10
Average number of daily absences	1.7 ± 0.3	1.4–2.25
Average daily absence (min)	33.4 ± 5.9	27–42
Shortest daily absence (min)	11.6 ± 6.6	5–15
Shortest daily absence (min)	80.6 ± 14.5	61–96
Average singular absence (min)	20.0 ± 4.3	15–24
Shortest singular absence (min)	6.6 ± 5.2	2–14
Longest singular absence (min)	51.4 ± 12.8	34–66

Data were analysed using Minitab statistical software (ver. 15). We studies three response variables: egg turning rates, length and frequency of absences. This was done using general linear mixed models, with time of day, or day of incubation as a fixed effects factor, and female ID as a random effects factor. The same analyses were used to investigate relationships between of daily average air temperature, the frequency of absences during the day and time that females spend outside the nest.

All procedures performed involving animals were in accordance with the ethical standards and where approved by II Local Ethics Commission for Experiments Carried on Animals (Permit: NR 31/2010; issued on February 22, 2010). The National Forestry Wisła District got permission (DOP-OZGIZ.6401.03.171.2011.km dated on May 10, 2011 expiry date December 31, 2021) issued by the General Director of Environmental Protection, signed by Dr. Michał Keiłsznia for keeping, reproduction and collection of biological materials for experimental purposes, every year to 50 adult and 150 juvenile Capercaillie in Capercaillie Breeding Centre in Wisła Forestry District, Poland.

3. Results

Capercaillie egg incubation lasted from 25 to 28 days. Females were observed leaving their nest during daylight hours but during darkness (between 20:00 and 03:59) they all remained at the nest. Egg turning, by contrast, was observed during every hour of the 24-hour incubation period.

The length of incubation and the frequency of

Table 2. Results of the general linear mixed models on the effect of female identity (random effect), hour of a day and day of incubation on recess time, and length and frequency of absences. Significant analyses are indicated in bold text.

Responses	Time of day		Female	
	$F_{15,60}$	*p*-value	$F_{4,60}$	*p*-value
Mean recess length per hour	1.13	0.350	1.22	0.312
Number of recess per hour	**2.10**	**0.022**	1.23	0.308
	Day of incubation		Female	
	$F_{25,71}$	*p*-value	$F_{4,71}$	*p*-value
Total recess time per day	1.15	0.317	1.48	0.219
Number of recesses per day	1.15	0.317	**3.36**	**0.014**
Average recess length	0.80	0.723	0.71	0.590

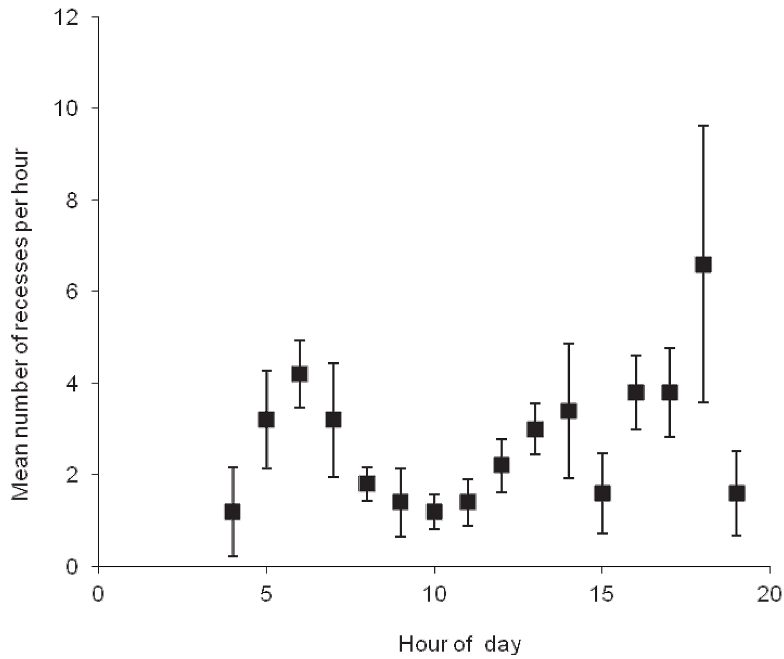

Fig. 1. Average (± SE) number of recesses during different hours of a day irrespective of day of incubation.

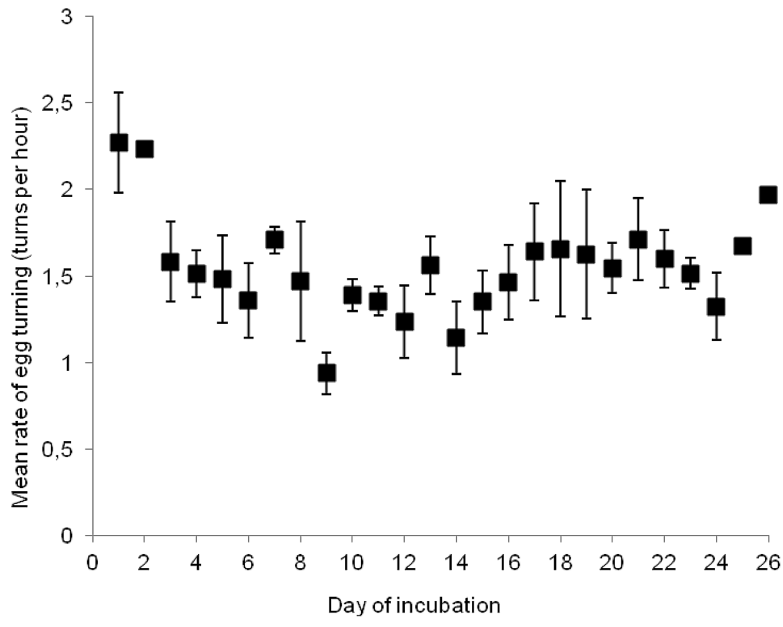

Fig. 2. Average (± SE) rate of egg turning per hour at different days of incubation.

nest absences irrespective of time of day, or day of incubation are summarised in Table 1. During the entire incubation females were very attentive to the nest. Between 04:00 and 20:00 females spent on average 97.0% of their time in the nest (SD = 0.6%; range 96.3%–97.8%), and this did not differ between incubation days (Table 2). The effects of female, day of incubation and time of a day on recess time, length and frequency of absences are shown in Table 2. The number of recesses per hour was significantly affected only by time of the day, with an apparent peak around 06:00 and increasing number of recesses at the afternoon hours, peaking around 18:00 (Fig. 1). The female as a random factor was only significantly related to the total number of recesses per day.

Table 3. Comparison of nest leaving by capercaillie kept in captivity and wildlife.

Female activity	Captivity	Wild birds (Storaas & Wegge 1997)	Wild Birds (Pulliainen 1971)	Wild Birds (Lennerstedt 1966)
Mean number of daily absences	1.74 *	2.4	1.9	(2–5)
Mean duration of singular absence (min)	20 *	27	34.7	23
Shortest duration of singular absence (min)	3	2	20	10
Longest duration of singular absence (min)	66	266	70	65
Mean duration daily of absence (min)	33.4 *	66	ca 60	–
Shortest total daily absences (min)	5	30	–	–
Longest total daily absences (min)	77	373	–	–

* Average for all females kept in Capercaillie Breeding Centre.

There was no main effect of temperature on time that females spend outside the nest ($F_{1,86}$ = 2.96, p = 0.089), but differences between females were observed (interaction between female and temperature, $F_{4,86}$ = 4.94, p = 0.001; female as a random factor, $F_{4,86}$ = 7.39, p < 0.001). Female 1 ($F_{1,21}$ = 20.97, p < 0.001), Female 3 ($F_{1,23}$ = 5.47, p = 0.029), Female 4 ($F_{1,16}$ = 5.48, p = 0.033) spent notably more time outside the nest when temperature was higher. In contrast, the incubation absences of Female 2 ($F_{1,14}$ = 1.96, p = 0.184) and Female 5 ($F_{1,17}$ = 0.46, p = 0.508) were not temperature dependent.

Rates of egg turning averaged 1.55 times per hour (SD = 0.06) over the entire incubation period. Day of incubation significantly affected rates of egg turning (day: $F_{25,74}$ = 2.19, p = 0.005) with turning rates tending to be higher at the onset and the end of incubation but quite stable during most of the incubation period (Fig. 2). Individual females also had significant effect on turning rates ($F_{4,74}$ = 15.04, p < 0.001), with one female turning eggs almost twice an hour on average, compared with only 1.3 times per hour for three other females. Interestingly, this particular female was incubating a clutch that was largely infertile.

4. Discussion

The results indicate that incubation behaviour can be female-specific in Capercaillie. Some birds appeared to be affected by external temperatures whereas others were not, and they also differed in their rates of egg turning.

Females observed in our research had similar levels of previous incubation experience but individual differences in their behaviour were shown. This could be caused by individual preferences or weather conditions in two years of observations. We can also not exclude the impact of presence of other females, including those that were not incubating, within the inter-linked aviaries. Dziedzic *et al*. (2006) observed a hierarchical system of social organization for Capercaillie females kept in captivity, but the maintenance system of our birds did not allow us to determine whether such social structure existed in our population. Capercaillie have an incubation constancy of 97%, which is typical for Galliformes (Wiebe & Martin 1997). Capercaillie spend longer incubating than for the smaller White-tailed Ptarmigan, which spend about 95% of time daily (Wiebe & Martin 1997).

Timing and duration of nest absences may be influenced by female physiological status, risk of predation, environment conditions, such as temperature or precipitation frequency and intensity. In comparison with studies of free-living Capercaillie populations (Lennerstedt 1966, Pulliainen 1971, Storaas & Wegge 1997, Zawadzka & Zawadzki 2003), we found differences in absence times, which were shorter, with fewer breaks during incubation, and a lack of a clear bimodal activity during the day (Table 3). In Norway, sensors placed in free-living Capercaillie nests indicated that the time of day and duration of absence from the nest reached two peaks during the day (Storaas & Wegge 1997). In our studies the length of time spent outside the nest during the day averaged 33.4 min, with, on average, 1.74 daily breaks during incubation. According to Pulliainen (1971), females left the nest 1.9 times a day on average, the shortest break lasted about 20 min (excluding one observation when female left the nest only for 90 sec), while the longest lasted 70 min (34.7 min on average). Lennerstedt (1966) observed a longest recess of about 65 min and a shortest of 10 min, with an average of 35 absences being 23 min. Lennerstedt (1966) found that periods of absence were not connected with particular hours and suggested that temperature influences the frequency of daily breaks. When the weather was cold the bird left 4 or 5 times a day, but only 2–3 times under warmer conditions. Three (Female 1, 3 and 4) out of five females took longer absences in incubation at warmer days, what is contrary to the observations of other authors.

According to Storaas & Wegge (1997), in natural conditions, 95% of females left the nest at the morning, between 05:01 and 06:48, and then during the evening, from 18:32 to 20:03. Pulliainen (1971) noted fewer departures during the afternoon (13:00–19:00), but the regular absences were observed between 21:00 and 01:00. Females observed in this study did not leave the nests until 04:17 at the morning (the earliest recess) and majority of nest absences took place at the evening (17:00–18:00), although it was not as well pronounced as in study conducted on wild populations (Lennerstedt 1966, Pulliainen 1971, Storaas & Wegge 1997). Female Houbara bustard (*Chlamydotis undulata*) also show a bimodal pattern in nest recess activity (Deeming *et al*. 2001). Recesses were shorter in the morning (08:00–10:00) and longer in the evening (16:00–18:00). There are no data about natural nesting behaviour for Capercaillie in central Europe (study area 49°32N 18°55'E), so there is no possible to exclude the impact of latitude, or day-length, on the length and timing of nest absences. The studies of other authors took place in north Europe 60°10'N 12°30'E (Storaas & Wegge 1997), 60°10'N 12°30'E 66°45'N 29°45'E (Pulliainen 1971) and 67°N 16E (Lennerstedt 1966).

Wild Capercaillie observed in Norway, left the nest mostly by rising to flight (Storaas & Wegge 1997), but the females kept in captivity always left the nest by walking, probably due to limited space for flying. It should be stressed that in majority of cases, before starting a recess wild females scan surroundings carefully (Pulliainen 1971), probably to minimize predation risk to females and eggs (Martin *et al.* 2000).

Many researchers point out that each individual seems to have their own incubation and rest rhythm. Birds observed in different latitudes and nests, made absences at different times of day (Pulliainen 1971, Storaas & Wegge 1997). Lennerstedt (1966) observed that the Capercaillie female never left the nest between 18:00 and 23:00 (except one time when she was flushed by human disturbance), but left the nest three times between 23:00 and 24:00. Some authors emphasize that most of birds are not willing to make breaks at night (Lennerstedt 1966, Lřfaldli 1985). This confirms behavioural flexibility observed in our females but the differences in incubation rhythm can be smaller depending the same ecosystems and regions.

Almost all bird species turn their eggs (Deeming 2002) and the importance of egg turning is well documented (Clark 1933, New 1957, Tullett & Deeming 1987, Lourens & Deeming 1999, Tona *et al*. 2001). Unturned eggs have significantly lower hatching rate, delayed hatching time and lower embryo weigh (Tazawa 1980, Tullett & Deeming 1987). Modern incubators usually turn eggs 24 times per day (Robertson 1961, Deeming 2009). In CBC-WFD the best hatching success is achieved when eggs are incubated by Capercaillie females, the worst using artificial incubation and technique elaborated for chicken eggs (unpublished observations).

Clark (1933) and New (1957) tested egg turning rate at different days of incubation and concluded that turning is more important at initial period. This conclusion is supported by our observations. Females turned eggs more intensively for the first two days of incubation (2.3 times per hour), then decreased to a constant value around 1.5 times per hour. Turning rate averages about once per hour for precocial and semi-precocial birds and but is more like five times per hour for semi-altricial and altricial birds (Deeming 2002, 2009). Capercaillie behaviour seems to be typical of other precocial species although captive birds turned their eggs twice as much as wild ones described in other reports (Valanne 1966, Pulliainen 1971). It is not known whether this difference is an effect of captivity or it just reflects natural variation within a species.

Our results confirmed the plasticity of nesting behaviour, but also showed the similarities between individuals in frequency of incubation breaks, the average time outside the nest and eggs turning rate during subsequent days of incubation. Usually, Capercaillie incubation period lasts about 26 days (Pulliainen 1971, Storch & Segelbacher 2005) and in our study we confirm this (mean incubation time for five females 26.2 days). A next step to improve incubation methods for Capercaillie would be to test whether are there better results in artificial incubation when eggs are cooled twice a day for 30 minutes or whether turning through to hatching is beneficial.

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Metsonaaraiden pesimäkäyttäytyminen vankeudessa

Moniin vankeudessa kasvatettaviin lintulajeihin soveltuvat hautomiskäytännöt vaativat kehittämistä. Vähäinen yhteistyö kasvattajien välillä, sekä haluttomuus kokeiluihin on vaikeuttanut näiden käytäntöjen kehittämistä. Luonnollisen haudontakäyttäytymisen seuraaminen – joka on helpottunut teknologisen kehityksen myötä – voisi osaltaan auttaa ongelman ratkaisemisessa. Lukuisat tutkimukset ovat selvittäneet haudontakäyttäytymistä, mm. pesässä käytettyä aikaa, pesästä poistumisen ajankohtaa, munien kääntämisen tiheyttä ja haudontalämpötilaa. Tällainen aineisto on tieteellisesti mielenkiintoinen, mutta voi myös hyödyttää uhanalaisten lajien suojelua lisääntymisohjelmien kautta.

Metso (*Tetrao urogallus*) on uhanalainen laji lähes koko esiintymisalueellaan Euroopassa; moniin suojelutoimiin on ryhdytty lajin säilyttämiseksi paikallisesti ja globaalisti. Tämä tutkimus selvittää vankeudessa kasvatettujen metsonaaraiden pesimä- ja hautomiskäyttäytymistä puolalaisessa metsojen kasvatuskeskuksessa. Tavoitteena oli kuvata pesimäkäyttäytymistä yksityiskohtaisesti: tutkimme munien kääntämisen tiheyttä sekä hautomataukojen ajoittumista ja pituutta.

Vuorokaudenajalla tai hautoma-ajan kestolla ei ollut vaikutusta hautomataukojen pituuteen, mutta taukojen lukumäärä vaihteli vuorokaudenajan mukaan: taukoja oli eniten noin klo 6.00 ja klo 18.00. Munien kääntäminen oli aktiivisimmillaan haudonnan kahtena ensimmäisenä ja viimeisenä päivänä, mutta muuten hyvin tasaista. Vankeudessa kasvatetut naarasmetsot viettivät vähemmän aikaa pesän ulkopuolella kuin luonnonvaraiset linnut. Niiden poistumiset pesästä olivat lyhyempiä, harvinaisempia ja ajoittuivat pääosin iltaan. Luonnonvaraisiin lintuihin verrattuna poistumisissa ei havaittu niin voimakasta vuorokausivaihtelua. Toivomme että tämä aineisto auttaa parantamaan vankeudessa kasvattavien metsojen hoitokäytänteitä jotta lisääntymismenestys olisi mahdollisimman hyvä.

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