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EGG-LAYING BEHAVIOR IN TITS[1]

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Like most passerines, tits lay their eggs early in the morning. Traditionally, ornithologists determine laying times indirectly by checking the nest content at different times of the day. Only a few persons seem to have actually witnessed the egg-laying itself. Haftorn (1966) gave a preliminary description in Norwegian of egg-laying behavior in tits. Subsequently, Flanagan and Morris (1975) published photos of a female Blue Tit (*Parus caeruleus*) during egg-laying. Over the years I have observed egg-laying in many females of several tit species and am therefore able to give a more comprehensive quantitative description of this phenomenon.

METHODS

The survey was carried out at Maalsjøen in Klaebu, Norway (63°15′N, 10°26′E) during the period 1962–1981 and includes four species: the Great Tit (*Parus major*), Willow Tit (*P. montanus*), Marsh Tit (*P. palustris*), and Coal Tit (*P. ater*). They nested in wooden nestboxes, except for the Willow Tit which bred in self-made or artificial holes in decayed tree stumps. Portable observation huts were used initially to watch birds at nest through glass walls of specially constructed nestboxes (Haftorn 1965). From 1970 onwards, closed-circuit TV was used (Haftorn 1972) and later on infrared light. I observed 66 egg-laying acts (20 in the Great Tit, 11 in the Marsh Tit, 17 in the Willow Tit, and 18 in the Coal Tit).

RESULTS

TIME OF EGG-LAYING

On average, eggs were laid 1–43 minutes after sunrise (02:58–03:38); range 33 minutes before sunrise (02:07) to 118 minutes after sunrise (04:33) (Table 1). Time of egg-laying did not differ between species (Kruskal-Wallis test, $P = 0.19$). It is nevertheless noteworthy that egg-laying in the Willow Tit occurred on average 42 minutes earlier in the morning than in the Great Tit, in spite of the fact that the mean laying dates of the two species were almost identical (Table 1).

BEHAVIOR DURING EGG-LAYING

All four species behaved similarly during egg-laying. Initially the female stood motionless in the nest cup. The first sign of approaching egg-laying was usually intensified breathing, occasionally with rhythmic opening and closing of the bill that pointed either horizontally forwards or more or less upwards. The head was drawn in and the body feathers were somewhat fluffed out; the Coal Tit in addition raised its crown feathers. The tail was kept horizontal or elevated up to about 45°. Then the tip of the tail started nodding movements synchronously with rhythmic depressions of the rump. These movements which apparently were caused by throes of parturition when the egg traveled down the oviduct, were almost invisible to begin with but gathered in strength and ended with a sudden elevation of the rump (Fig. 1, top) that marked the moment of egg-laying. Then the bird "froze" in a motionless posture, termed "recovery phase" (Fig. 1, bottom). This last rise of the rump clearly indicated that the egg had just been laid.

I never succeeded in seeing the egg itself leaving the cloaca because the rump was hidden in the nest cup at that moment, but on several occasions I heard the faint sound when the egg fell down and collided with the other eggs. The eyes were usually closed during this process. During the last forceful throes of egg-laying, the bird sometimes rotated its head in a highly withdrawn position, evidently caused by the great effort needed to press the egg out of the cloaca. Occasionally the bird adopted a sleeping posture up to the moment of oviposition, with the head turned backwards and the bill hidden among the scapulars. This was observed in the Great and Willow Tits; one Willow Tit kept the posture even during the moment of egg-laying. Usually the bird was absolutely silent during the egg-laying process, but two Great Tits made extremely faint guttural sounds every time the bird opened its bill during the throes of egg-laying. Such sounds, combined with rhythmic opening/closing of the bill, I have heard at other times only from birds in an emergency, for example from newly caught birds held in hand or from mortally wounded birds. On the other hand, shortly before and after the egg-laying process the female Great Tit commonly communicates loudly with the singing male residing in the vicinity.

The number of visible throes varied greatly, from about 5 to 30. The period from the first visible throe until the moment of oviposition lasted about 10–77 seconds, mostly 20–30 seconds, with 30 (Coal Tit), 55 (Great Tit), 67 (Marsh Tit), and 77 seconds (Willow Tit) as upper extremes.

During the recovery phase the female stood motionless and silent. This phase lasted 24–435 seconds, mostly 30–90 seconds, with 130 (Coal Tit), approximately 300 (Great Tit), 431 (Marsh Tit), and 435 seconds (Willow Tit) as upper extremes.

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TABLE 1. Egg-laying time relative to sunrise, and date of egg-laying. Means are based on mean values of each nest.

	Time (minutes)		Date		Number of	
	Mean	Range	Mean	Range	nests	eggs
Great Tit	43.0	−32–118	22 May	12 May–12 June	9	19
Marsh Tit	22.1	−1–49	13 May	8–20 May	4	11
Willow Tit	1.3	−23–19	21 May	14–30 May	4	17
Coal Tit	11.0	−33–35	12 May	3–20 May	5	15

FIGURE 1. Female Great Tit during egg-laying on 19 May 1996 at 03:30. Top photograph: elevation of the rump immediately after the egg was laid. Bottom photograph: the same bird during the "recovery phase" following egg-laying.

The first activity performed after the end of the recovery phase was either bill-pressing (or bill-pulling) at the nest rim (63% of 35 observations), tremble-thrusting (20%) or preening (17%; Haftorn and Slagsvold 1995). From the moment of oviposition until the female left the nest at least 12 minutes elapsed, mostly 20–40 minutes, with 41 (Marsh Tit), 44 (Coal Tit), 87 (Willow Tit), and 94 minutes (Great Tit) as upper extremes.

No statistical differences between species were found with respect to duration of egg-laying, the following recovery phase and the period spent in the nest between oviposition and departure (Kruskal-Wallis test, all *Ps* > 0.15).

Occasionally the male brought food to the female before she left the nest for the first time in the morning. Such morning visits combined with courtship feedings may take place even before the start of egg-laying.

In the egg-laying period, tits regularly cover the eggs with nesting material during the daytime although some species are more careless than others. The covering process may begin early in the morning before the start of egg-laying, but the main part of the work occurs after the egg has been laid and just before the female is leaving the nest. However, egg covering may be postponed to the morning hours after the departure of the female (Haftorn and Slagsvold 1995).

DISCUSSION

The behavior of tits during egg-laying is very similar to that previously described for the Prairie Warbler (*Dendroica discolor*) (Nolan 1978) and the Goldcrest (*Regulus regulus*) (Haftorn 1978). Duration of egg-laying varies a great deal even within species. Nolan (1978) observed opening and closing of the bill and rhythmic movements of the back and tip of the tail repeatedly for up to 4 minutes in the Prairie Warbler, presumably corresponding to the duration of egg-laying. For 3 eggs of the Goldcrest only 8–9 seconds elapsed between the first visible sign of pressure and the moment of egg-laying (Haftorn 1978). In tits this period varied from about 10 to 77 seconds, mostly 20–30 seconds. The Cuckoo (*Cuculus canorus*) which is a brood parasite, is known to lay the egg remarkably swift, usually within 10 seconds with a lower limit of only 3–4 seconds (Wyllie 1981). Presumably this short duration is an adaptation to its parasitic behavior.

The recovery phase immediately following egg-laying is probably caused by great physical strain during laying which calls for a rest. Nolan (1978) described the condition of the Prairie Warbler immediately after laying to be "trance-like." The Goldcrest also goes through a recovery phase after laying. The recovery phase in this species lasts 39–53 seconds. The female then gradually "revives," making slight head and body movements which last for another 28–42 seconds before she becomes active (Haftorn 1978). In tits the recovery phase lasts mostly 30–90 seconds.

The mean laying dates of the Great and Willow Tits were almost the same. Nevertheless, egg-laying in the latter occurred on average 42 minutes before that of the Great Tit. I have no good explanation for this possible discrepancy (statistically insignificant). Maybe it is a result of the size difference and that the smaller Willow Tit is able to produce an egg quicker than the Great Tit.

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