INCUBATION CONSTANCY IN THE RED-WINGED BLACKBIRD

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Avian incubation behavior is affected by a multitude of exogenous and endogenous factors. Kendeigh (1952, 1963b) and Skutch (1962) reviewed incubation in many different orders of birds and discussed factors affecting the amount of time spent in incubation. Among workers recently reporting on incubation behavior in wild passerines are Prescott (1964), Mumford (1964), Erpino (1968), Maxwell and Putnam (1972), and Morton et al. (1972). In the Red-winged Blackbird (*Agelaius phoeniceus*), Nero (1956a, 1956b) has published observations on female behavior during the reproductive cycle, but nothing was reported on the incubation constancy (percent of daylight hours spent on the nest).

I have reported (Holcomb, 1968, 1970) that female Redwings incubated normal-sized artificial eggs a mean of 19.4 days before abandoning them. This is 8.4 days beyond the normal incubation period. The present study was designed to determine the incubation constancy in the egg-laying period, to discover if it increased each day as the incubation behavior developed, and to find if there was less incubation each day as females neared the day when eggs were abandoned in prolonged incubation.

METHODS

I studied the incubation behavior of Red-winged Blackbirds near Omaha, Nebraska, in 1968 and 1969. Birds were breeding in a variety of habitats, including weed, alfalfa, and clover fields, hedgerows, ditch banks, and marshes. I visited the nesting areas nearly every day, beginning in March and ending in August. Male Redwings generally arrived in early March and females soon afterward. Pairing began in late March and continued through April and early May. Once breeding began, I searched for nests each day, with attempts made to discover nests during nest-building and to follow them daily to termination of breeding activity.

The normal incubation period of Redwings is 11 days (Allen, 1914). To prolong incubation, I placed four artificial eggs of the same size and coloration as normal eggs in nests. These eggs were made of liquid plastic or plaster-of-paris in molds of Silastic (a commercial product). The molds were cast from Redwing eggs, and the imitation eggs were painted with water-resistant acrylic paints.

Incubation constancy was studied by two methods. The first was through watching an incubating female from a small tent, six to 10 meters from a nest. The tent was usually put in place the day before beginning observation, and females appeared generally undisturbed by the presence of the tent and observer. Time intervals for on-and-off periods were recorded to the nearest one-fourth minute, and each session of observation lasted two to three hours.

The second method of recording incubation constancy was with a battery-powered con-

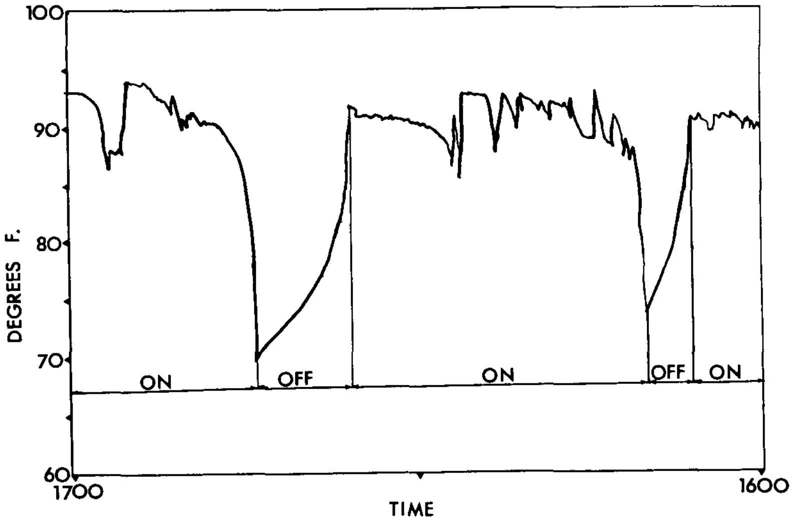

Fig. 1. A tracing of a continuous machine-recording of egg temperature (°F), indicating times the female Redwing was on or off the nest. The minor oscillations on the recording occurred when the female arose to turn the eggs, preen, or shift on the nest. (Note that the tracing proceeds from right to left, as it appeared on the original recording.)

tinuous recorder. One end of a copper-constantan wire with a thermocouple was run through the bottom of a nest and embedded in a plaster of paris egg; the latter was glued securely to the bottom of the nest. The thermocouple in the egg was either flush with or not more than one-half mm below the top surface. The recorder wire was run 25 to 400 feet to a Speedomax W Recorder (117V, 60 cycles, 30 amp) that would record temperature between 20° and 120° F (–6.7 to 48.9° C).

Temperature changes caused by presence or absence of an incubating female were relayed to the recorder with an adjustment speed of one sec. These data were recorded on chart paper, and recording was continuous. Initially, recording was at the rate of one in per hr, but this was later changed to six in per hr, so that on-and-off periods could be determined to the nearest one-fourth min. In 1968, the availability of DC current permitted a few nests to be monitored and recorded 24 hrs per day. In 1969, to give greater flexibility and selectivity, a battery was used as a power source. The battery (12 volt, 100 amp hr, 88 lbs) was changed daily, and batteries were recharged each day, giving power for 13 to 17 hrs of operation each day at full charge. I used an inverter to obtain 117 volts from the battery. Care was taken to select an inverter that would run continuously and keep constant the frequency in cycles per sec and chart speed on the recorder. The unit of the recorder, inverter, and battery was set in a box for protection from weather. A sample of the continuous record of incubation behavior is shown in Figure 1, and this record constitutes the heating curve.

The continuous recorder often ran well into the night (on occasions all night), as it recorded temperature. I checked recorded temperatures and the slope of the heating curve to discover if there was a gradual development of incubation temperature and whether

TABLE 1

INCUBATION CONSTANCY IN THE EGG-LAYING, NORMAL INCUBATION, AND PROLONGED INCUBATION PERIODS OF RED-WINGED BLACKBIRDS

	Number of females	Total hours of daytime observation	Mean (as percentage) constancy ± SE
Egg-Laying			
Day 1	5	39.9	15 ± 8
Day 2	8	48.6	24 ± 5
Day 3	14	67.7	60 ± 4
Day 4	10	41.0	68 ± 4
Day 5	1	4.7	72 —
2nd-to-last day	4	25.9	35 ± 9
Next-to-last day	9	57.2	51 ± 8
Last day	15	78.1	65 ± 4
Normal Incubation			
Day 1–3	17	226.8	71 ± 2
Day 4–6	16	279.5	72 ± 3
Day 7–9	15	272.9	69 ± 3
Day 10–12	22	325.6	64 ± 2
Prolonged Incubation			
Day 13–15	25	411.6	58 ± 3
Day 16–18	18	262.6	59 ± 3
Day 19–21	9	104.1	47 ± 7
Day 22–25	4	42.6	32 ± 11
3rd-to-last day	16	102.3	58 ± 4
2nd-to-last day	17	117.4	56 ± 4
Next-to-last day	19	153.1	48 ± 4
Last day	19	97.8	38 ± 5

differences might occur between a first nest of the season (when the incubation patch would be developing for the first time) and later nests (where the incubation patch might be partially developed or at least completely defeathered). If the female is capable of producing normal incubation temperatures, the slope of the heating curve should be steep; if her ability to warm the eggs is reduced, the slope should be more gradual.

Altogether, I monitored a total of 649 hrs of incubation behavior by direct observation and 1486.6 hrs by the continuous recorder. As the data were voluminous, I analyzed it by computer to determine the percent of time spent on the nest during egg-laying, normal incubation, and prolonged incubation. Statistical analysis was by means of a Student's t-test, with significance considered to be at the .05 level.

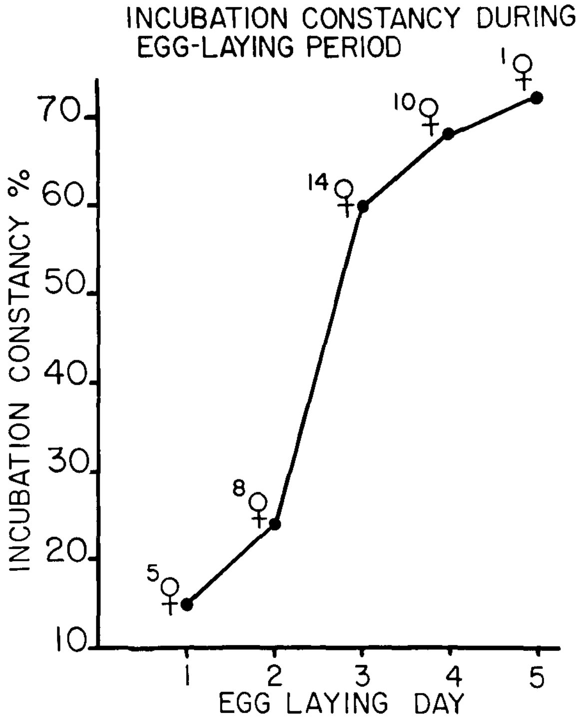

FIG. 2. Incubation constancy in Red-winged Blackbirds, demonstrating the increase from the laying of first to last egg.

RESULTS

The incubation constancy in the egg-laying, normal incubation, and prolonged incubation intervals is summarized in Table 1. Incubation begins on the first day of egg-laying, and constancy increases each day thereafter until all eggs are laid (Fig. 2). Because females lay variably-sized clutches (2–5, usually 3 or 4 eggs), incubation constancy was also calculated on the basis of second-to-last, next-to-last, and last day of egg-laying; constancy values are 35, 51, and 65 percent, respectively.

There was a significant increase in constancy from the second-to-last day of egg-laying to the last day of egg-laying. Incubation then remained high through normal incubation, with a significant decrease between days 10 to 12 and 13 to 15. It then continuously declined until birds abandoned nests.

Incubation constancy remains highest during the days of normal incubation (days one to 12). It gradually lessens during prolonged incubation, until the female abandons; days 22 to 25 show the lowest values, at 32 per-

TABLE 2

INCUBATION TEMPERATURES, ATTENTIVENESS AT NIGHT, AND SLOPE OF EGG-HEATING CURVE IN THE EGG-LAYING AND EARLY INCUBATION PERIODS IN INDIVIDUAL FEMALES

Time of reproductive cycle	Female on at night?	Temperatures of eggs during day (°C)[1]	Temperatures of eggs during night (°C)[1]	Slope of heating curve[2]
Egg-laying				
Day 1	No	30.0–32.8	—	Steep
Day 1 (3rd to last)	No	35.0–39.4	—	Steep
Day 2 (2nd to last)	Yes	35.0–39.4	Normal	Steep
Day 1 (2nd to last)	No	Peak 35.6	—	Steep
Day 2 (next to last)	No	Peak 33.9	—	Steep
Day 2 (next to last)	Yes	32.2–34.0	26.7–29.4	Gradual
Day 3 (last egg)	Yes	35.0–36.7	31.1–33.9	Gradual
Day 3 (last egg)	Yes	Normal	Normal	Steep
Day 3 (last egg)	Yes	38.3–40.0	36.1–37.2	Steep
Incubation				
Day 1	—	36.1–38.9	32.8–35.0	Gradual
Day 1	No	35.0–38.3	—	Gradual
Day 3-incub.	—	36.1–38.9	35.6–36.7	Steep

[1] Normal temperatures are 35 to 40°C.
[2] Slope of heating curve described in Methods.

cent constancy of incubation. As females usually abandon normal-sized eggs after 13 to 26 days—mean 19.4 (Holcomb, 1970), constancy values were calculated with respect to the last day before the nest was abandoned. Thus, for third-to-last, second-to-last, next-to-last, and last day of incubation, the values were 58, 56, 48, and 38 percent, respectively. There was a significant decrease in the incubation constancy between the next-to-last and last day of incubation.

No female incubated on the night after the first egg was laid (Table 2). If a clutch of three eggs were laid, a female usually incubated the night after laying the second egg; however, in one case a female did not begin incubating until laying the last egg. If four eggs were laid, a female usually did not stay on the nest at night until the third egg was laid; however, one female nesting in late May (probably her second nest) began incubating the night the second egg was laid. Another female did not incubate the night of day one of incubation. Unfortunately, there was no record available for her on the preceding night, but she incubated well on day one and continued normal incubation thereafter.

Females usually remained on the nest in the early morning until about a half-hour before sunrise. At night, they would usually get on the nest for

TABLE 3

INCUBATION TEMPERATURES, SLOPE OF EGG-HEATING CURVE, AND TIME OF DAY WHEN REDWING FEMALES ABANDONED THE NEST AFTER PROLONGED INCUBATION

Day relative to day of egg abandonment	Temperatures of eggs on day of abandonment, (°C)[1]	Temperatures of eggs on night preceding abandonment, (°C)[1]	Slope of heating curve[2]	Time of day of egg abandonment[3]
Next-to-last day	36.7–38.9	—	Steep	—
Last day	Peak 36.7	36.7–38.3	Gradual	09:40
Last day	Normal	Normal	Steep	20:53
Last day	Normal	Normal	Steep	10:05
Last day	Normal	Normal	Steep	19:05
Last day	Not above 35	Normal	Gradual	07:00
Last day	Normal	Normal	Steep	06:45
Last day	Normal	Normal	Steep	18:30
Last day	Normal	Normal	Steep	During night

[1] Normal temperatures are 35 to 40°C.
[2] Slope of heating curve discussed in Methods.
[3] Central Daylight Saving Time.

the last time 20 to 30 min after sundown, but occasionally they would get on and off the nest until well after dark.

Before abandoning a nest after prolonged incubation, a female remained on the nest all night previous to her last day (Table 3). Most of the time spent in incubation by females on the last day of incubation occurred in the early morning hours; about half the females abandoned in the morning and the others in the afternoon.

The slope of the recorded heating curve was very steep during the normal incubation period (Fig. 1). Table 2 shows that in the first nest of the year, peak egg temperature is not attained until at least day one of incubation and perhaps not until later. The slope of the heating curve was gradual until day three of incubation, suggesting that the development of the incubation patch may affect ability to heat eggs. Incubation patches in this species show some development during egg-laying, but peak development occurs during the incubation period (Selander and Kuich, 1963).

In females nesting for at least a second time, incubation temperatures and slope of heating curves during egg-laying compared closely to later incubation temperatures. It is not known to what extent the incubation patch changes in the interval after the first clutch is lost and laying begins in a renest. However, from these temperature data, it appears that vascularity changes very little. This carry-over would provide a greater ability to keep eggs warm earlier in the egg-laying period, compared to females on their first nests.

Table 3 shows that most females kept their eggs as warm on the last day of prolonged incubation as in normal incubation and that the slopes of the heating curves were usually steep. However, two females showed more gradual heating curves and less ability to keep eggs warm just prior to abandoning. It may be that these females were simply not in close contact with the eggs. However, in the direct observation studies of several females on the last day of prolonged incubation, they all appeared to sit as deep in the nest as observed previously.

DISCUSSION

Contrary to the general situation reported for passerines by Lehrman (1961), incubation by female Redwings begins during egg-laying, and effective incubation temperatures develops by the day that the last, if not second-to-last, egg is laid. This early development of incubation behavior and effective egg temperature result in the asynchronous hatching, which is believed to be important in the reproductive success of altricial birds (Ricklefs, 1965, 1968a, 1968b). Lack (1947, 1954, 1966) reported that in species of birds having asynchronous hatching, brood size may be adjusted to fluctuations in food availability. In times of food shortage the oldest and largest are fed at the expense of smaller and weaker nest-mates, insuring them among the offspring the best chance to survive. Observations on nestling growth (Holcomb and Twiest, 1971) show that brood reduction by starvation indeed occurs in Redwings, which may hatch up to 48 hours apart in a given nest.

After reviewing data from my other studies I suspect that asynchronous hatching exists in many passerine species; I have personally observed at least 24 hrs between the hatching of the first and last eggs in 25 species of passerines. Contrary to Lehrman (op. cit.), I believe that this asynchrony is due to some degree of effective incubation developing during the egg-laying period.

Recently, Eisner (1969) reported that captive Bengalese Finches (*Lonchura striata*) begin to incubate up to three days before the end of egg-laying. As in Redwings, the Bengalese Finch was found to incubate artificial eggs past normal hatching time. Prolonged incubation usually ended 10–15 days beyond normal incubation, compared to about eight and a half days in the Redwing. Eisner comments that this prolonged period corresponds to the length of time that the parents would be caring for chicks, had normal hatching taken place. The same relationship applies as well to the Redwing, as the young leave the nest at a mean of about 9 days.

Kendeigh (1952) has reported that House Wrens (*Troglodytes aedon*) incubate essentially uniformly throughout normal incubation, with a mean of 58.2 percent of the daylight time spent on the nest. Skutch (1962) reports that in most species where a single parent incubates, the eggs are covered from 60 to 80 percent of the daylight time. The 65 to 72 percent recorded for the Redwing falls well into this category. The Common Grackle (*Quiscalus quiscula*) averages slightly higher than the Redwing, at 76 percent (Maxwell and Putnam, 1972). As in the Redwing, in Grackles the constancy decreased in prolonged incubation, the average being 44 percent. For Redwings, the prolonged incubation constancy ranged from 59 to a low of 32 percent.

Kendeigh (1952) reported that age of female, a change of mate, or progression of the nesting season did not seem to govern constancy in normal incubation in House Wrens. He did find a tendency toward less incubation when ambient temperatures were higher. Drent (1973) reported that egg temperature may affect the length of attentive periods, suggesting, as did Kendeigh's data, that if eggs are cooler because of ambient temperature effects, the constancy may remain higher. Although data are not presented here for the Redwing, qualitative observations show that females do show a decreased constancy as warmer ambient temperatures develop throughout the day. However, Redwing females protect eggs from direct sunlight in the hottest portion of the day.

The temperatures of incubated Redwing eggs (Tables 2 and 3) generally range higher than those (near 35.0° C) reported by Kendeigh (1963a) for the House Wren; however, he was measuring average internal egg temperatures. The interior temperatures of eggs average less than those taken at the top of the egg, adjacent to the incubation patch (and which are reported here in the Redwing). With thermocouples placed between eggs, temperatures obtained for several species ranged from 33° to 37° C (Rolnik, 1939; Koch and Steinke, 1944; Barth, 1949; Irving and Krog, 1956; Baerands, 1959; Kessler, 1960). Temperatures measured between eggs are different from either of the two methods discussed above and may be greater or smaller, depending upon proximity of the recording probe to the incubating adult.

Emlen and Miller (1969), in studying the nesting cycle in Ring-billed Gulls (*Larus delawarensis*), suggest that the pace-setting mechanisms of the cycle change from endogenous (hormonal) to exogenous (chick) regulators early in incubation. In Redwings this shift may well also occur, as nestlings are accepted even very early in incubation in the closely related Tricolored Blackbird (*Agelaius tricolor*) (Emlen, 1941). This acceptance (and presumed shift) occurs also in the American Goldfinch (*Spinus tristis*) (Holcomb, 1967), but it may not be the same in all species. For example, Breitenbach et al. (1965) found that chicks were not accepted early in incubation in Ring-necked Pheasants (*Phasianus colchicus*), but were later when prolactin levels are higher (Breitenbach and Meyer, 1959).

It would be most interesting to discover what hormonal changes (or at least those changes in the ovary, oviduct, pituitary, and incubation patch) occur in females during prolonged incubation, as compared to their state in females involved in normal incubation or nestling care. I have noted (Holcomb, 1968), that if the nestling period is broken into two portions, there is a trend for ovaries and oviducts to be larger in the earlier portion. This would suggest a continued action of prolactin hormone, as an antigonadal agent, may extend over from the normal incubation period.

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SUMMARY

Incubation constancy behavior of Red-winged Blackbirds (*Agelaius phoeniceus*) was studied in the egg-laying, normal incubation, and prolonged incubation intervals by direct observation and use of an automatic continuous recorder. Diurnal incubation begins on day one of egg-laying and the constancy increases each day, until the last day of egg-laying. Nocturnal incubation usually begins the night just preceding the day the last egg is laid. Incubation temperature and constancy indicate that in most nests, incubation is effective before the clutch is complete, especially in the last two days of egg-laying, when incubation constancy may exceed 60 percent. In the first nest of the year, effective incubation temperature is reached somewhat more slowly than in renests. Incubation constancy remains highest throughout normal incubation (64 to 71 percent) and is in the range of 60 to 80 percent reported for passerine open-nesters; it then declines as prolonged incubation continues, reaching a low of only 38 percent on the day the nest is abandoned.

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