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Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada. Accepted for publication 16 February 1978.

INCUBATION BEHAVIOR OF THE DEAD SEA SPARROW

Y. YOM-TOV
A. AR
AND
H. MENDELSSOHN

The importance of precise regulation of egg temperature during incubation was demonstrated by Lundy (1969) in studies of the domestic fowl, in which no embryo survived continuous incubation above 40.5°C or below 35°C. Similar results were reported for pheasant, duck, quail and domestic fowl by Romanoff and Romanoff (1972). A nest temperature of 34.0°C ± 2.3°C (mean ± SD) was reported by Huggins (1941) for 37 bird species representing 11 orders, which suggests that most birds have similar thermal requirements for successful incubation. The optimal nest temperature is primarily achieved by the incubation behavior of the parents, and according to White and Kinney (1974), the nest attentiveness of some birds is a rectangular hyperbolic function of ambient temperature, where the horizontal asymptote crosses the ordinate at maximal attentiveness time (min/h) in the nest, and the vertical asymptote intersects the air temperature abscissa roughly at optimum incubation temperature. However, they mentioned only briefly the behavioral responses when ambient temperature exceeds optimal incubation temperatures, although heating above optimal temperature may be much more critical for embryonic survival than a similar exposure to cold (Romanoff et al. 1938, Drent 1976).

The aim of this paper is to report how the Dead Sea Sparrow (*Passer moabiticus*) regulates the temperature of its eggs over a range of ambient temperatures.

MATERIALS AND METHODS

The Dead Sea Sparrow, a small passerine of about 14 g, breeds along the Rift Valley in Israel, where air temperatures (Ta) during the incubation period (April–August) can exceed 45°C at noon, and relative humidity (RH) may fall to less than 10% (Rosnan 1956, Mendelssohn 1974). Their large, covered nest is generally built on dead branches of tamarisk trees, and its exterior is totally exposed to solar radiation. Occupied nests are always within 100 m of fresh water. The nest is a massive oval structure of twigs (25 × 35 cm), weighing up to 1 kg. An S-shaped tunnel leads from the top of the nest to an incubation chamber lined with soft materials in its lower part. Hence the eggs are largely insulated from direct sunlight while the nest is still well ventilated. The eggs are incubated almost exclusively by the female. During the day she leaves the nest for short periods about six times per hour. When ambient temperatures are high (Ta > 39°C), females sometimes stand at the nest opening and pant.

Egg temperatures were recorded by using fresh or dummy gypsum eggs in which a thermistor was inserted. Preliminary observations indicated no differences in temperatures of the real and dummy eggs, and the female incubated the experimental egg normally. We recorded egg temperatures (Ti) in four occupied nests and six abandoned nests in the Jordan Valley, 25 km S of the Sea of Galilee; in two occupied nests in Ein Yahav, 40 km S of the Dead Sea; and in one occupied nest at the Tel Aviv University Wildlife Research Centre (WRC). At the same time we watched and recorded indirectly (from egg temperature records) the sessions and recesses of the incubating females. Daily water losses of the eggs in the nests and eggshell water conductances were also measured, using the method suggested by Ar et al. (1974).

RESULTS AND DISCUSSION

Mean daily temperature of incubated eggs (4 nests, 24 observations) was 33.7°C ± 0.5°C (SD). This temperature is well within the range reported for other passerines (Huggins 1941, Drent 1976). Relative humidity was calculated as follows: mean daily
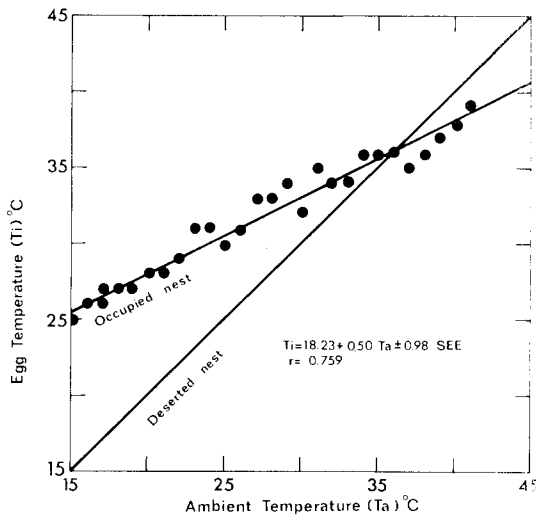
FIGURE 1. The relationship between shaded ambient temperature (Ta) and the temperature of an egg in the nest (Ti) in three occupied nests and six nests where the birds were driven out. Measurements for deserted nests have been omitted (see text). Each point represents a mean of 2–21 one-hour observations.

FIGURE 2. The relationship between shaded ambient temperature (Ta) and attentiveness in high (Yh) and low (Yc) temperatures in occupied nests. Each point represents the mean of 2–21 one-hour interval observations (see Table 1). The hyperbolic dashed line is calculated for low ambient temperature according to White and Kinney (1974). The equations predict attentiveness in percent.

water loss of two eggs was 16.52 mg H_2O/day in one nest and 16.15 in another (mean egg weight was 1.64 g). Eggshell water vapor conductance measured in the laboratory was 0.49 and 0.44 mg H_2O/day·mmHg, respectively. Thus, a mean water vapor pressure difference between the inside of the egg and the nest atmosphere of 35.1 torr was calculated. At mean nest temperature of these two nests (33.5°C), the RH in the nest is 10.5%, which, as proposed previously, is a reasonable result at this incubating temperature (Ar et al. 1974). The minimal egg temperature measured was 25°C and the maximum never exceeded 39°C over an air temperature range of 15–41° (Fig. 1). Ti in deserted nests followed Ta with a lag of a few minutes, but they did not differ in hourly mean temperatures. The Dead Sea Sparrow is able to maintain mean egg temperatures below high ambient temperatures, as are the larger White-winged Doves (*Zenaida asiatica*) in Arizona (Russell 1969).

Attentiveness and ambient temperature. Figure 2 and Table 1 summarize mean attentiveness calculated from 326 h of observation. Attentiveness (defined by min·h^{-1} or percent) is only a crude estimate of real thermoregulation because it does not describe how tightly the brood patch is applied to eggs and the amount of heat transferred to the eggs. For air temperatures below 35°C we found that the best fit to our data ($P < 0.01$) is a linear model in the form of $Yc = -1.8 \cdot Ta + 101.2$ (where Yc is the attentiveness in percent at air temperatures of 35°C and below).

A simple way to avoid overheating eggs is to incubate them continuously. The eggs should then approximate the body temperature of the parent (Russell 1969). As Ta rises, more intimate contact and attention are needed to keep egg temperature close to body temperature. Thus, at air temperatures above 35.1°C, our data take the form $Yh = 6.2 \cdot Ta -$
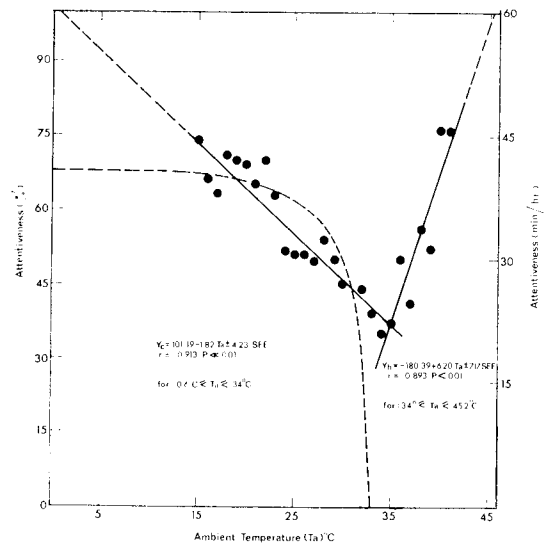
180.4 (where Yh is percent attentiveness at air temperatures above 36°C; Fig. 1).

We feel that our linear model for Yc is a better expression of real incubation behavior of the Dead Sea Sparrow than White and Kinney's (1974) rectangular hyperbolic model which describes incubation behavior of Temperate Zone birds and assumes zero attention time at Ta = Ti. Our calculated curves, besides fitting the data better ($F = 24.5$; $P < 0.01$), intersect at Ta = 35.1°C, close to the mean Ti, and predict a minimal attentiveness of 37.3% (22.4 min/h). This approximates the observed value. The fact that minimal attentiveness above zero suggests either that the birds enter the nests in order to "measure" egg temperatures or that other factors are involved. Assuming that our equations might be extrapolated to 100% attentiveness, then the limits of our model are at air temperatures approximately between 1°C and 45°C (Fig. 2), which correspond to the known breeding distribution of this species—between southern Turkey, where they have been seen nesting over snow-covered ground (Kumerloeve 1965, air temperatures were not given), and north of the Gulf of Aqaba where the mean maximum monthly air temperature during part of the incubation period is 43°C and daily maximum rarely exceeds 46°C (Rosnan 1956).

Since avian embryos tolerate overheating less than cooling, it is not surprising that a small rise in Ta above 36°C is followed by a pronounced increase in attentiveness. The slope of Yh is 3.4-fold steeper than that of Yc. Attentiveness is of minimum variability at 40°C and 41°C (Table 1). We attribute this to the parent's urgent need to attend the nest at these high Ta, in order to prevent overheating of the eggs.

Heat and water budget. High ambient temperatures require a strict heat budget, which may be ap-

TABLE 1. Daytime attendance at the nest of the Dead Sea Sparrow, in field and captivity.

Ambient temperature (°C)	No. of observations (hours)	Mean attentiveness (%)	± SE	Coefficient of variation (%)
		CAPTIVITY		
15	2	74.5		
16	2	66.5		
17	3	63.3	2.6	7.2
18	6	71.8	4.3	14.6
19	5	69.6	2.2	7.0
20	7	63.8	2.4	9.9
21	5	64.6	4.0	13.9
22	4	62.2	5.3	17.2
23	12	64.1	1.5	8.1
24	17	51.6	3.4	27.1
25	21	53.2	1.3	11.5
26	29	51.3	1.5	15.6
27	26	51.6	1.8	18.0
28	9	49.9	3.9	23.2
29	3	58.0	4.6	13.8
30	3	36.0	2.9	14.2
31	2	33.5		
		NATURAL CONDITIONS		
20	4	78.8	8.0	20.3
21	—	—	—	—
22	2	79.0	—	—
23	3	61.0	8.5	27.8
24	2	54.0	—	—
25	9	46.1	5.4	35.1
26	7	49.3	4.0	21.5
27	11	45.5	6.0	43.2
28	8	59.7	7.0	32.7
29	6	46.0	8.0	43.4
30	18	47.0	4.0	36.8
31	14	42.8	4.3	37.8
32	7	44.0	7.5	44.8
33	14	38.8	3.6	34.8
34	15	34.6	3.1	35.2
35	21	37.3	3.4	42.1
36	13	49.7	5.8	42.2
37	9	41.4	4.5	32.8
38	4	56.2	8.4	30.1
39	3	52.3	17.9	59.2
40	5	77.8	2.2	3.8
41	3	78.3	2.4	5.3

proached as follows: Assume that the rate of heating of the Dead Sea Sparrow egg in the nest is 5.2°C/°C·h, (given as the Newtonian cooling constant of the House Wren (*Troglodytes aedon*) egg of similar weight, and specific heat of an egg of 0.80 g·cal/°C; Kendeigh 1973), and that a fraction of one-third of the egg surface area is covered by the incubating female. Taking into account water evaporation from the egg, then the heat load of a typical five-egg clutch at T_a-$T_i = 2°C$ (41°C vs. 39°C, Fig. 1) would be 33 cal/h (Kendeigh 1973). The embryo's own heat production at the end of incubation is 30 cal/h (Rahn et al. 1974). The standard metabolic rate (SMR) of a 14-g passerine is 262 cal/h (Lasiewski and Dawson 1967). Heat storage, if it does exist at all, is very limited in a small bird such as the Dead Sea Sparrow; therefore if high air temperatures persist long enough, a total of (33 + 30 + 262 =) 325 cal/h must be dissipated in the form of evaporation. We may roughly estimate that an amount of 0.6 g of water is required per hour for this purpose

—a water loss of 4.5% body weight per hour. This is an outstanding rate for evaporative cooling (Rising 1969, Hinds and Calder 1973), and it requires frequent drinking. Thus, it is not surprising that we never found occupied nests far from a source of fresh water. We believe that this limitation is not due to the need for maintaining a certain humidity in the nest or for cooling the eggs by direct wetting, because the eggs lose water at a normal rate at the very low RH found in the nest.

Environmental constancy. Measurements of behavior are more variable under uncontrolled field conditions than under controlled conditions, and attentiveness is no exception. The availability of food and water, as well as factors such as wind, predators, etc., may well influence attentiveness. The birds which bred in the WRC were supplied with water and food ad libitum near the nest, were protected from predators, and had shelter from other environmental factors. From the data of Table 1, we can demonstrate that the mean nest attentiveness of the

overlapping temperature range in the field and captivity are not appreciably different. However, a Mann-Whitney U-Test shows that the coefficient of variation of attendance in captivity was significantly smaller ($P < 0.001$) than in the field (14.3% vs. 33.1% respectively). This reduction in the mean coefficient of variation of attendance in captivity to about half the field value may be attributed to the greater constancy of conditions in captivity.

SUMMARY

Incubation behavior of the Dead Sea Sparrow was observed in nature and captivity. Nest attentiveness related linearly with ambient air temperatures, increasing in both high and low air temperatures from the minimal value of 37.3% of maximum attentiveness at an ambient temperature of 35.1°C. The increase in attentiveness per degree of ambient temperature was 3.4 times greater for high temperatures than for low temperatures, indicating the importance of nest attentiveness in keeping eggs cool in a hot environment.

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Department of Zoology, The George S. Wise Centre for Life Sciences, Tel Aviv University, Tel Aviv, Israel. Accepted for publication 22 December 1977.

AN ALBINISTIC MOUNTAIN QUAIL FROM OREGON

JOHN A. CRAWFORD

Albinism is relatively common among gallinaceous birds in North America (Gross, Bird-Banding 36:67–71, 1965) and Great Britain (Sage, Br. Birds 55: 201–225, 1962; Sage, Br. Birds 56:409–416, 1963). Bobwhites (Colinus virginianus) and California Quail (Lophortyx californicus) are among the most frequently reported species (Ross, Cassinia 47:2–21, 1963; Gross 1965). Records of albinism in other North American quail are far less common. Ross (1963) reported one partially albinistic Mountain Quail (Oreortyx pictus) in the National Museum of Natural History, Washington, D.C. Deane (in Ross 1963) stated that albinistic Mountain Quail occasionally were found during the 1800's; however, the frequency of his observations was not cited.

Because of the paucity of recent data regarding albinism in Mountain Quail, I believe the following information to be noteworthy. I saw a partially albinistic Mountain Quail on 25 September 1976 and collected it on 2 October 1976. The bird was in the company of one normally pigmented quail and near a covey of approximately eight individuals on both occasions. The collection locality (Lane County, NW ¼ Sect. 33, T15S, R5E, 700 m elevation) was within