NEST TEMPERATURES AND ATTENTIVENESS IN THE ANNA HUMMINGBIRD

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Recent investigations of the energy metabolism of hummingbirds (Pearson, 1950) have documented quantitatively the existence of torpidity in the family Trochilidae. Should this phenomenon occur in nesting females, it would have considerable effect on incubation and brooding temperatures and so would be important at a critical stage in the life history of the young. The lack of data on nesting temperatures for any trochilid prompted us to take advantage of an opportunity to study the Anna Hummingbird (*Calypte anna*), one of the species for which metabolic data are available.

MATERIALS AND METHODS

In April, 1952, Dr. Waldo H. Furgason of the Department of Zoology, University of California, Los Angeles, informed us that a female Anna Hummingbird was building a nest outside a window of his residence in West Los Angeles. The location of the nest made possible continuous observation and use of a temperature recording instrument without disturbing the female. Nest temperatures were measured with a thermocouple of 30-gauge, copper-constantan duplex wire inserted through the bottom of the nest so that the junction lay between the two eggs which the nest contained. Air temperatures were measured with another thermocouple placed near the nest, which was located on the north side of the house and never received direct sunlight. A stepping switch driven by a synchronous electric motor, in conjunction with a Brown Electronik Recording Potentiometer, allowed us to measure and record the temperature of the thermocouple inside the nest for 17 minutes and the temperature of the thermocouple outside the nest for 3 minutes out of every 20. Thus, it was possible to obtain essentially continuous records of air and nest temperatures over long periods of time. The position of the thermocouple in the nest was unchanged at the termination of the study, despite the movements of the parent and of the young.

We are grateful to Dr. Waldo H. Furgason for calling our attention to this nest and for his kindness in allowing us full use of his residence during the study period.

RESULTS

Temperatures were recorded from 1 to 8 p.m. on April 28, from 10 a.m. on April 29 to 12 noon on May 1 (fig. 1), and from 5 p.m. on May 1 to 5 p.m. on May 4, 1952. The eggs hatched on May 3. Records were again obtained in the period from 11 a.m. on May 16 to 5 p.m. on May 18, 1952, at which time the young were in their 13th to 15th days (fig. 2).

Departures of the female from the nest in the period before and shortly after the eggs were hatched resulted in a rapid decline in nest temperature, whereas her returns resulted in a rapid rise. These events made it possible to determine from the temperature record the number and duration of inattentive periods. These inattentive periods are tabulated in table 1. Inattentive periods of the female were generally less than 20 minutes, and the longest was less than 40 minutes. Since the thermocouple in the nest was between the eggs, and infrequently in contact with the skin of the parent bird, its temterature was usually somewhat below skin temperature. This thermocouple, therefore, measured the temperature at the outer surface of the eggs, in which there was continuous slight variation. Consequently, the points plotted in figure 1 represent the approximate average temperature in the nest during each hour. The extent of the temperature variation during any given interval provides a rough index of the activity of the female. The maxima usually indicate that the skin of the parent came close to or in contact with the thermocouple as she shifted around on the nest, and the minima indicate absence of the parent. In general, the lower the minimum temperature, the longer was the inattentive period. Minute to minute variation in air temperature was very slight during the study periods except when occasional gusts of wind caused sudden changes of several degrees.

Table 1

Number and Duration in Minutes of Inattentive Periods

	April 28		April 29		April 30		May 1		May 2		May 3		May 4	
Time (to nearest hour)	No.	Min.	No.	Min.	No.	Min.	No.	Min.	No.	Min.	No.	Min.	No.	Min.
4–5 a.m.					3	36.5	2	7.1	2	4.1	2	5.3	4	14.2
5–6					7	10.0	5	13.0	7	14.7	3	3.7	5	5.9
6–7					7	8.2	8	10.0	5	12.3	3	5.0	4	13.0
7–8					7	11.7	6	10.0	3	16.4	3	6.5	3	10.6
8–9					3	12.3	4	29.4	1	3.55	5	11.7	3	13.5
9–10					3	9.4	2	5.3	0	0	2	4.7	1	4.7
10–11			3	4.7	3	7.1	1	2.35	2	6.45	1	1.76	2	13.0
11–12			3	12.3	8	13.0	2	8.8	5	10.0	4	13.0	3	18.2
12–1 p.m.			1	10.6	7	8.8			2	11.2	0	0	2	11.2
1–2	2	1.76	2	2.95	4	10.0			2	10.6	1*	8.2	3	13.0
2–3	4	5.3	3	11.2	3	18.2			2	9.4	3†	16.4	0	0
3–4	4	4.1	2	2.95	3	9.4			1	8.8	3	13.5	3	13.5
4–5	4	9.4	2	6.5	3	9.4			2	11.7	4	15.2	3	11.0
5–6	3	8.8	2	8.8	4	8.8	4	10.6	2	20.0	5	9.4		
6–7	0	0	0	0	0	0	0	0			1	2.95		
Total time recorded (minutes)	295		457		843		488		793		838		725	
Per cent inattentive	10.0		13.1		20.5		19.8		17.6		14.0		20.1	

* One newly-hatched young was seen at 1:45 p.m.
† The second egg was hatched at 2:30 p.m.

The nest temperatures from May 16 to May 18 are presented in figure 2. By the time the young were 12 days old they filled the nest and the parent no longer was near the thermocouple during her visits. Therefore, data on attentive and inattentive periods at this time are lacking, and the temperature fluctuations indicate activity of the young and not the parent. During this period, the young were not brooded day or night by the female.

There was no evidence of torpidity in the parent bird while incubating. As shown in figure 1, nest temperature always remained about 10°C. above air temperature at night. In fact, on April 30 nest temperature rose between 6 and 10 p.m. (from 27 to 29°C.) while air temperature fell (from 18 to 13°C.). The temperatures to which the female was exposed were lower than some at which Pearson (1950) observed torpidity to occur in a male Anna Hummingbird. However, there was no indication that the body temperature of the female closely approached the environmental level at any time. Nighttime observations during June, 1953, of another nest of an Anna Hummingbird also failed to reveal any signs of torpidity in the incubating female, even though air temperatures were again as low as some at which torpidity has been reported.

In the first few days after hatching, the nestlings exhibited no apparent capacity for homoeothermy—their temperatures rose when they were brooded and fell sharply when the parent left the nest. By May 16, when they were about 13 days old, the nestlings could maintain their temperatures well above that of the environment. As shown in figure 2, the nest temperature averaged 30°C. or above at this time, with only slight changes in accordance with environmental temperature. The older nestlings exhibited no tendency toward torpidity, which is consistent with Pearson's (1953) observations on young of other species of hummingbirds.

DISCUSSION

Kendeigh (1952:285) gives 16 to 17 days as the duration of incubation in the Trochilidae, and that of the Anna Hummingbird is given in Bent (1940) as 14 to 18 days. Several authors quoted by Bent express surprise that the incubation period in *Calypte anna* is as long as has been reported. As Nice (1953) states, "a firm conviction has existed that little birds must have short incubation periods" and that "humming-

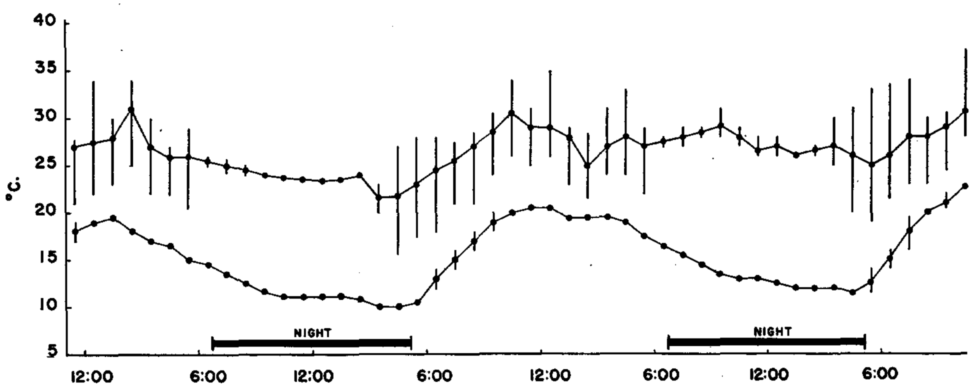

Fig. 1. Nest temperatures (upper) and air temperatures (lower) from April 29 to May 1, 1952, before eggs hatched. Points indicate approximate average temperature during each hour; vertical lines indicate extent of variation, if any, in temperature during each hour.

birds must have even shorter periods." We therefore paid close attention to the possibility that the "slow" development within the egg might be caused by low incubation temperatures at night as a result of the parent becoming torpid. As mentioned previously, however, we found no evidence of torpidity in the parent bird.

The data given by Kendeigh (1952:table 51) show that members of several families of small passerines exhibit incubation periods as long or longer than those reported for trochilids—e.g., the Pipridae (19-21), Troglodytidae (14-19), Regulidae (14-17), and the Parulidae (11-17). On the other hand, some families of larger passerines have shorter incubation periods than some of the smaller forms—e.g., the Mimidae (12-13), Turdidae (12-14), and the Alaudidae (11-12). In the absence of a consistent correlation between body size and length of incubation period in altricial birds, the duration of hummingbird incubation is not surprising.

The House Wren, *Troglodytes aëdon,* weighing between 9 and 10 gms., is the next smallest bird for which incubation temperatures over long periods of time are available (Baldwin and Kendeigh, 1932). These temperatures average about 37°C., which is several degrees higher than those which we obtained from the Anna Hummingbird. This discrepancy may be in part due to differences in technique, for Baldwin and Kendeigh placed the thermocouple inside the egg so that it was in contact with the embryo. Our figures for average nest temperature are undoubtedly somewhat lower than the true incubation temperature, for the thermocouple was at the outer surface of the eggs. However, even when the parent bird presumably came in contact with the thermocouple, the highest temperature recorded was 37°C., and it appears likely that the true incubation temperature of the Anna Hummingbird is slightly lower than that of the House Wren.

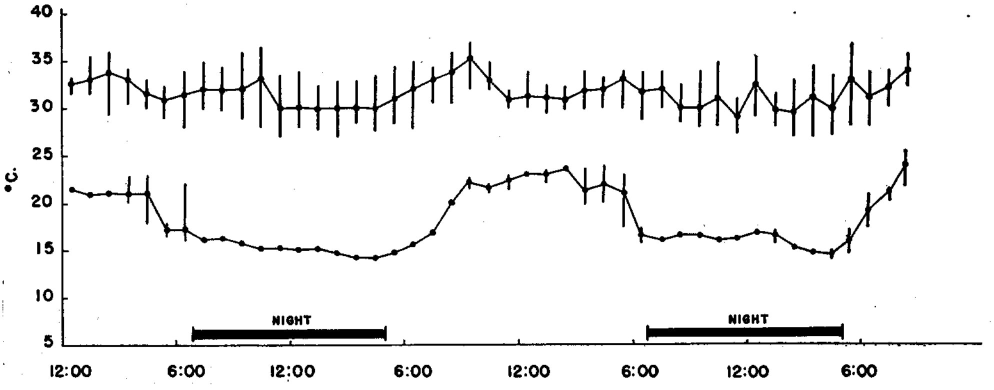

Fig. 2. Nest temperatures (upper) and air temperatures (lower) from May 16 to May 18, 1952, when young were 13 to 15 days old. Points indicate approximate average temperature during each hour; vertical lines indicate extent of variation, if any, in temperature during each hour.

The apparent absence of torpidity in incubating female hummingbirds is of interest from the standpoint of bioenergetics. Several factors may possibly enable the birds to maintain body temperatures and consequently nest temperatures above the environmental level at night when they are unable to procure food. Perhaps, as Pearson (1953) has suggested, intensive feeding before roosting might permit hummingbirds to sustain their rapid rates of energy metabolism through the night. However, with one exception (the evening of May 2, 1952), the records for this hour during six consecutive evenings fail to reveal that the nesting female studied by us spent unusually long periods away from the nest. Although on May 2 it was away for 20 minutes, presumably feeding, the average duration of its absences from the nest in the last active hour of the afternoon on the other five days was only 8.0 minutes (range: 2.9 to 10.6), which was often exceeded during the middle of the day. The presence of "feeders" nearby and the profusion of flowering plants in the immediate vicinity of the nest may have made these brief periods adequate. However, this female usually went away from the nest area to feed.

It is possible that the females of this species have a lower rate of energy metabolism than the males. Pearson found that the resting rate at 24°C. for the one male *Calypte anna* he studied was 13.9 cc. O_2/gm./hr., whereas that at 24°C. for the one female available was 10.7 cc. O_2/gm./hr. The reverse was true in two individuals of *Selasphorus sasin,* however, and additional data might also give a reverse picture in *Calypte anna.*

Another alternative is that the incubating female, which spends most of the day sitting quietly on the nest, may have more energy reserves than non-incubating individuals as a result of reduced activity. The energy stores thus conserved might permit the incubating female to maintain a relatively rapid metabolic rate overnight.

Food intake may be elevated in incubating individuals, but our data on inattentive periods do not indicate that this is likely. If it does occur it could provide the parent with the energy reserves necessary to maintain a warm nest at night.

If any of the above factors are operative in allowing the female Anna Hummingbird to maintain a relatively high rate of heat production at night, they most certainly work in combination with the protection afforded to the adult bird by the nest. Hummingbird nests are tightly constructed and provide effective insulation for the ventral surface of the body. Since this is the surface from which the greatest amount of heat loss probably occurs, because of the position of the viscera and the large pectoral muscles, the insulation provided by the nest must function importantly in retarding heat loss from the incubating individual.

SUMMARY

Essentially continuous records of temperatures inside the nest of an Anna Hummingbird and of air temperatures nearby were obtained during several stages of the development of the young. Periods of inattentiveness by the parent female were usually less than 20 minutes and never more than 40 minutes in duration. This bird did not become torpid at any time while incubating the eggs or brooding the young. The nest was generally maintained about 10°C. warmer than the surrounding air. In the first few days after hatching, the young exhibited little capacity for homeothermy. However, they maintained their temperatures well above that of the environment at all times 13 days after hatching. *Calypte anna* is compared as to incubation period with members of various passerine families, and the means by which incubating female hummingbirds might avoid torpidity at night are discussed.

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