THE TIMING OF MATERNAL BEHAVIOR OF THE BROAD-TAILED HUMMINGBIRD PRECEDING NEST FAILURE

WILLIAM A. CALDER

ATTACHMENT to nest or contents is strong in birds, as is exhibited by the vigorous defense by a female hummingbird, despite her being several orders of magnitude smaller than the intruder. Although cause and effect may not be positively distinguished, profound physiological changes in birds coincide with the stages of the breeding season (Eisner, 1960; Lehrman, 1961; Yapp, 1970). At this time of the year, the reproductive objectives appear to dominate every aspect of the bird's behavior. Therefore, observation of the breakdown of such a compelling pattern should be of interest.

The literature on incubation, parental behavior, and nesting success is extensive. However, I find little information on the behavior of females just prior to the abandonment of nests, eggs, or chicks except for information on the incubation of infertile eggs (Kelly, 1956; Skutch, 1962). Maintenance of the individual (maternal welfare) may compete with maintenance of the species (welfare of potential offspring) when time or resources are limiting. Maternal behavior may entail sacrifices made only when there is a good chance that chicks or eggs will survive. If the nest fails, continued sacrifice of maternal welfare is without benefit, and a return to the pattern of self-maintenance will come, abruptly or gradually. How does an incubating or brooding bird budget her time as nest failure becomes inevitable? Davis (1955) stated: "Problems of animal behavior exist in the relation of perception of the contents of the nest to behavior." How does timing of behavior reflect her perception of the situation?

I report here continuous recordings of sessions and recesses (Skutch, 1962) obtained from sensors in synthetic eggs, during a study of thermoregulation and microhabitat selection of hummingbirds (Calder, 1971; 1972; 1973*a*,*b*). I have analyzed recordings of activity preceding abandonment of seven nests of the Broad-tailed Hummingbirds (*Selasphorus platycercus*). One of these nests was abandoned after 23 days of incubation of infertile eggs (normal incubation is 15 to 19 days). One was abandoned after death of the young. The other five were apparently abandoned because of a food crisis, coinciding with the decline of flowers used by hummingbirds and with the invasion by migrant Rufous Hummingbirds (*S. rufus*), competing for the dwindling resources.

MATERIALS AND METHODS

I have modified the technique of Howell and Dawson (1954) and Kendeigh (1963) to monitor presence and absence of female hummingbirds at their nests. Nest temperatures

were sensed from synthetic eggs (Silastic 382, Dow Corning) within which either a thermocouple or a thermistor had been implanted (Calder, 1971, 1973*a*). The "egg" sensors were then placed in the nests of the Broad-tailed Hummingbird without removal of natural eggs. These were tolerated well. From the "egg," leads extended to recording potentiometers (EA 171B, ICA 400, L & N Speedomax W, or Bristol Dynamaster) for continuous recording. Each departure of the female was thus clearly recognizable by an abrupt cooling of the "egg," and her return was recorded as rewarming.

I observed 41 completed nests during the summers of 1971 and 1972 at the Rocky Mountain Biological Laboratory, Gothic, Colorado, elev. 2900 m. The outcome was determined for 35; temperature/activity recordings were obtained from 17 of the nests. Since a maximum of five recorders were operational at a time, they had to be shifted from nest to nest as cycles were completed or nests abandoned. Obviously, a smaller proportion of 18 active nests could be monitored in mid-season than when eight or fewer were active in late July. The nests with sensors were 41 percent successful, those without recorders; 59 percent. This difference does not represent disruption by the technique, but rather a consequence of the bias due to equipment limitations. Most of the nestings were terminated before 2 August, with 53 percent success (one or two chicks fledged) for those nests, but there was only 20 percent success for nests terminated after 2 August. Thus the recorder sampling was proportionately greater from the failure-prone late nests. Also, recorder-nests which failed did so an average of 18 days after the sensor was placed in the nest, during which interval, attentive behavior and hatching (from fertile eggs) were normal. Four nests of other species of hummingbirds have been similarly monitored, following which all chicks fledged successfully.

The nests were numbered in sequence of discovery, with exceptions to preserve the numbering of the previous season when possible. Thus nest 3-72 occupied the same branch in 1972 as nest 3-71 in 1971.

Times of first departure from the nest in the morning and last return in the evening are expressed relative to almanac sunrise (0° horizon; Anon., 1971, 1972). The local topography intercepted the sunrays and cast shadows on the various nest sites considerably later than sunrise and earlier than sunset times in the almanac.

RESULTS AND DISCUSSION

Abandonment of Infertile Eggs.—Nest 3-72 was approximately 11 m up on a crook of an aspen branch (*Populus tremuloides*). Nest construction extended from 1–3 June atop the remains of nest 3-71 (which was successful; see Figure 3 in Calder, 1973*a* for an illustration; and Calder, 1972, for other natural history of this site). Incubation began 4 June. A temperature sensor was placed in the nest on 9 June. Normal incubation behavior was sustained until the 23rd day (27 June), with the first departure from the nest between ½ and 14 minutes before almanac sunrise, the last arrival 9 to 52 minutes before sunset until the 21st day, with all absences less than 10 min each. During mid-day the warmer air temperature and sunlight plus a gradual pushing of the synthetic egg into the nest wall and thus further from the brood-patch, abolished the cooling spikes, so that the number of feedings could no longer be counted in mid-day. The longest successful incubation period I have recorded from this species was 19 days, and the shortest was 16

days. Skutch (1962) stated: "Most birds seem to remain faithful to their eggs for an interval at least 50 percent longer than is normally required to hatch them. . ." For this hummingbird the "margin of safety" was only 21 to 44 percent, and far short of the record of 95 days attentiveness by a female Anna's Hummingbird (*Calypte anna*) with sterile eggs (Kelly, 1956).

On 27 June, the female began lengthening her recesses to 10, 10, 20, 13 min, a period of normal shorter trips and a series of 36, 21, 78, 22, and 3 min duration. The last trip ended slightly late, 4 min after sunset, as had been the case for the previous two nights. She incubated overnight and departed 9 min before sunrise for 6 min. The trips which insued were 71, 6, 30, 3, and 23 min. At 08:50 she departed, never to return. The eggs were collected; one was infertile. The other had been finely pierced; conceivably, she might have inserted her bill and extracted some of the nutrients within.

It is interesting to compare timing of nesting at site 3 in 1972 with 1971. The snow melted out unusually early in 1972, hummingbirds began to nest earlier, and their flowers commenced blooming earlier. Nest 3-72 was 17 days earlier than 3-71. With reference to the local population, the first incubation of 1972 was 22 days earlier than in 1971. The mean hatching and fledging dates were 9 and 11 days earlier, respectively, in 1972. If the onset of flowering of *Delphinium nelsoni*, the first major hummingbird flower in Gothic, is influenced by the disappearance of snow, and, if hummingbird nesting is in turn related to the nectar supply of *D. nelsoni*, an early season could conceivably instigate nesting before the mates were completely ready, physiologically, leading to such infertility. One of two eggs in next nest to be discussed was also infertile; that nest was also early. Two other nests were found with abandoned eggs, one on 6 June and one on 12 July.

Abandonment of a Dead Nestling.—Nest 5-72 was ⅓ m above ground in a small spruce (*Picea engelmanii*) in an open wet-meadow. It was discovered and outfitted with a sensor-egg on 5 June. The hen became hypothermic at 02:45–05:00 on 9 June (see Calder and Booser, 1973, for ecological correlations). One egg hatched 20 June. The other was infertile when found later beneath the nest. The one chick developed normally for 10 days. At this age, the normal clutch of two are homeothermic, at least when their calorigenic capacities are consolidated by huddling. The female no longer broods them at night. On the tenth night (1 July) the lone chick possibly entered torpor, as the "egg" registered a low of 4°C which is below minimum body temperatures for spontaneous arousal in adult hummingbirds (Lasiewski, 1963, 1964; Dawson and Hudson, 1970). At 05:35 the nest began warming more rapidly than would be likely from air temperature rise.

Recordings for 1–3 July suggest that either the female came and brooded

several times daily or that the chick was still capable of thermoregulation, intermittently contacting the sensor "egg." On 4 July the chick was dead when examined for the first time in several days. From 12:15–15:45, the nest was brooded with periodic departures of normal feeding duration. From 15:45 to 18:50 the nest was unwarmed, but at 18:50 the nest was rewarmed, interrupted by five departures and abandoned for the night. At 05:38, normal for onset of activity (10 min before sunrise), the sensor was steadily rewarmed from −1°C to 25°C in 15 minutes, before solar radiation could have had any significant effect at that location. There were two cooling spikes (foraging?) before final abandonment at about 06:50, after which the "egg" went to 2°C and followed air temperature with the addition of any direct solar radiation.

Late Season Abandonments of Live Chicks.—Nest 17-72 was being built on 27 June, 12⅔ m above the ground on a crook in an aspen branch, the highest nest discovered in this study. A temperature sensor was placed in the nest on 29 June. The nest was not warmed overnight. The hen returned at 05:30 on 30 June to warm the nest. The record was somewhat irregular for two hours, with departures about 30 min apart. After 07:30, a regular session/recess pattern was exhibited. Thus it appears that the second egg was laid that morning, followed by onset of incubation. Young were being fed by the adult on 20 July and had probably hatched 2 or 3 days previously.

The attentive behavior of the female appeared normal through the morning of 28 July, the first feeding departures were 23, 20, and 23 min before sunrise on 26, 27, and 28 July, respectively. The temperature began dropping at about 17:45 on 28 July and appeared to follow ambient temperature thereafter. The nest was collected 31 July. Both chicks were dead, with one partially eaten, apparently by insects.

Two other nests were abandoned on 31 July, nests 28-72 and 35-72. Both were low nests in stream-side spruce trees. Behavior at 28-72 was apparently normal on 27 July when the chicks were 9 days old. Recorder batteries ran down on 28 July and were replaced at 16:52. The following absence was nearly 2 hr in duration, with a gradual cooling, a rewarming, a last trip and a warm nest until about 01:00. Then, a period of hypothermia began, consisting of apparently exponential cooling for 1½ hr to a stable minimum of 7 to 7½°C for 1¼ hr, and an exponential rise to a normal 29°C in the morning. This was followed by 6 recess periods of 13 to 45 min duration, then by 10 hr of stable warmth, whether from the chicks metabolism or brooding by the adult. There was one more exponential cooling-rewarming cycle of about 65 min before 3 hr of nocturnal homeothermy. Then, ca 00:45, on 30 July, a 3½ hr cycle of hypothermia occurred again. As in the preceding night, the pattern was typical of energy-crisis hypothermia reported by Calder and Booser (1973). This was followed by inattentive-coolings of 15, 35,

and 90 min, a 09:40 warming and slow decline to apparent equilibrium with air temperature the rest of the day and overnight. At 06:17 on 31 July, the sensor was suddenly and rapidly rewarmed from 5° to 25°C in 15 min, then left to cool for 38 min, rewarmed and finally abandoned permanently. At 20:32 the nest was examined. One chick was dead, the other cold and lethargic but alive. An attempt was made to hand-rear it. When rewarmed, it gaped eagerly and was fed an improvised diet for two days over which it gradually weakened and died.

Recording began on 23 July at nest 35-72. The eggs hatched on 26 July. Live young were abandoned on 31 July. The temperature record preceding abandonment appears normal through the morning of 31 July. At 05:46, the hen was feeding the chicks upon return from her first trip of the day. At 12:40, she departed and the nest equilibrated to the air temperature. She did not return. At 20:06, the abandoned chicks were transferred to a thermoregulated chamber for hand-rearing which was unsuccessful.

The abandonment of live chicks, which are still capable of gaping when warm, is difficult to understand, but this occurred at two other nests also.

Nest 8-71 was under a crook in the trunk of a large aspen (see Figure 4, Calder, 1973*a*), about 2½ m above the ground. The second egg was laid and incubation commenced on 21 July. The eggs hatched on 5 August, 19 days after the latest egg date for Broad-tailed Hummingbirds in Colorado cited by Bent (1940). A normal pattern for attentive and feeding behavior was recorded through 7 August. The recorder malfunctioned 8 August. The first departure on 9 August was on time, but was followed by abnormally and progressively longer absences (Fig. 1). The female abandoned the chicks at 15:12, made a brief appearance without feeding them at about 19:15. At 06:30 on 10 August, the chicks were still alive, having chilled to 6°C from peak overheating of 44.5°C in the unprotected nest on 9 August. Attempts to hand-rear the chicks were unsuccessful.

The gilia and larkspur flowers, from which the adult fed, had been fading rapidly in the nearby meadow. The lengthening recesses may reflect the need to range farther and farther in search of an energy supply. Higher in the mountains where flowers were still spectacularly abundant, there was intense agonistic behavior between abundant hummingbirds. The Rufous Hummingbirds had established territories as described by Armitage (1955). Thus even if a brooding female could visit distant flower patches, she would have to compete there with territorial birds at a severe disadvantage. Having to return to the nest frequently, she would not be able to continuously defend her food supply.

Nest 36-72 was located 1½ m above the ground in an isolated spruce in an aspen-forb ecotone. The nest was discovered on 23 July and was being

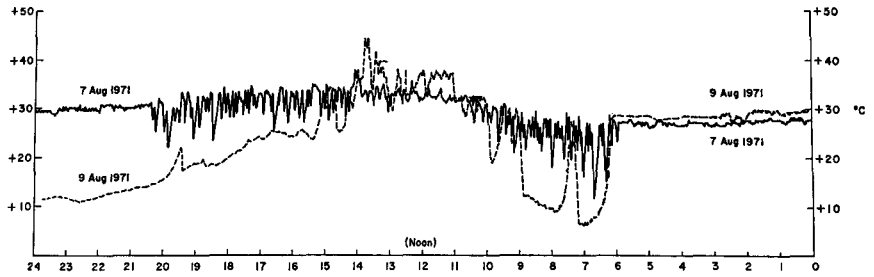

FIG. 1. Records of normal behavior (Nest 8-71, 7 August, solid trace, chicks 2 days old) and pre-abandonment behavior (9 August, dashed trace) superimposed for comparison. Note that the overnight nest temperature was normal for the brooding of chicks, and that first feeding departure was on schedule on 9 August. This was followed by three prolonged inattentive, cooling periods of presumed foraging, overheating of the nest during mid-day sunlit period, some brooding before abandonment at 15:12. The warming spike at 19:30 was an artifact.

incubated then. A sensor was placed in the nest and recording began on 1 August. The eggs hatched on 5 August. Normal temperature cycles continued until about 17:00 on 13 August, at which time the nest temperature dropped to ambient. The chicks were found dead but intact on the ground beneath the nest at 17:39.

When last checked previous to this (14:54, 11 August) the nest wall had been torn open. Very frequently the hens repaired their nests when they returned from feeding to incubate or brood. That this damage to 36-72 went unrepaired leads me to speculate that there was late-season weakening of brooding behavior, the lack of maintenance making the nest less safe for the young. Predators, on the other hand, would probably have eaten part or all of the chicks.

CONCLUSIONS

The behavior of birds prior to abandonment of nesting failures does not appear to have been described with reference to the dimension of time, nor is it likely that any one will bother to acquire a large sample of such observations in the near future. Hence an attempt to generalize or to see any pattern in this fortuitously-recorded behavior seems justifiable.

Of 26 nests, 53 percent which were terminated before 29 July were successful, while only 29 percent were successful after that date in 1972. This excludes nests which were not completely built or at which the success or failure was undetermined. Nesting was later in 1971 than in 1972, with no observed fledging until 29 July, and all fledging completed by 2 August 1971. Pooling the two years, 53 percent were successful on or before 2 August, but

only 20 percent thereafter. The greater liklihood of failure of late nesting is not correlated with significant temperature changes. The only abiotic factor is that the daylength for foraging purposes has decreased about 38 min, but a winter-nesting Anna's Hummingbird of similar size was successful in weather as cold but with much shorter daylengths (Calder, unpubl.). It appears likely that biotic factors cause this greater likelihood of failure. Dramatically obvious are the disappearance (going to seed) of the tubular flowers that the Broad-tails used and the abundance of Rufous Hummingbirds which compete for the same flower patches, even claim them with aggressive behavior. Counts were not made of flowers or Rufous Hummingbirds, but the qualitative facts were inescapable to the casual observer. (A scientist who shall remain nameless confessed to killing a Rufous Hummingbird because it was so domineering at his feeder!)

With that background, the recorded nest failures can be divided into early (27 June, 4 July) and later (29 July–9 August) abandonments. In both early abandonments (3-72, 5-72), there was a persistence in attentiveness after the reality of failure. Infertile eggs were incubated 4 days beyond the longest observed incubation period for that species, and a dead chick was brooded at least intermittently for one day or more after its death. The persistence can be regarded as a safety factor that precludes abandonment if there is any chance of success (Skutch, 1962).

Of the later failures, the records for two show no hint of abandonment or irregularity beforehand (17-, 35-72), the cessation of attentiveness being sudden, as if the result of predation or other disaster to the adults. The other two (8-71, 28-72) showed a lengthening of inattentive periods, as did the earlier incubator of sterile eggs, indicative of a gradual cessation of broodiness. In the cases of the latter two, I suspect that the lengthened recesses represent longer foraging trips in unsuccessful attempts to attain energy balance. The hypothermia two nights in a row at 28-72 is further circumstantial evidence of an energy crisis.

SUMMARY

The temporal behavior of female Broad-tailed Hummingbirds is described for the period preceding natural abandonment of nests. Nesting failure can be considered in two classes: early and late failures. The early failures were due to infertile eggs and the death of a chick. Attentiveness persisted four days beyond normal incubation period and at least one day after the chick was dead. In the latter nest, abandonment was preceded by a lengthening of the recess periods.

Of the late failures, three hens abandoned suddenly, while the other two exhibited a series of lengthened recesses. One of the latter two became hypothermic for a portion of the two nights preceding abandonment. The lengthened recesses are thought related to the declining food supply. Live chicks remained in both of those and one of the suddenly-abandoned nests.

ACKNOWLEDGMENTS

This research was supported by NSF Grant GB13249 and by an instructional staff position at R.M.B.L. I am indebted to Joanna Booser and Nickolas Waser for assistance in the field.

LITERATURE CITED

ANONYMOUS. 1971, 1972. The Air Almanac. U.S. Naval Observatory, Washington.

ARMITAGE, K. B. 1955. Territorial behavior in fall migrant Rufous Hummingbirds. Condor, 57:239.

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U.S. Natl. Mus. Bull., 176:420–429, 387–398.

CALDER, W. A. 1971. Temperature relationships and nesting of the Calliope Hummingbird. Condor, 73:314.

CALDER, W. A. 1972. Piracy of nesting materials from and by the Broad-tailed Hummingbird. Condor, 74:485.

CALDER, W. A. 1973*a*. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology, 54:127–134.

CALDER, W. A. 1973*b*. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comp. Biochem. Physiol., (in press).

CALDER, W. A., AND J. BOOSER. 1973. Hypothermia of Broad-tailed Hummingbirds during incubation in nature with ecological correlations. Science, 180:751–753.

DAVIS, D. E. 1955. Breeding biology of birds. p. 288 in Recent studies in avian biology (A. Wolfson, Ed.). Univ. Illinois Press, Urbana.

DAWSON, W. R., AND J. W. HUDSON. 1970. Birds. pp. 223–310 in Comparative physiology of thermoregulation. I. Invertebrates and non-mammialian vertebrates (G. C. Whittow, Ed.). Academic Press, New York.

EISNER, E. 1960. The relationship of hormones to the reproductive behavior of birds, referring especially to parental behavior: a review. Anim. Behav., 8:155.

HOWELL, T. R., AND W. R. DAWSON. 1954. Nest temperatures and attentiveness in the Anna Hummingbird. Condor, 56:93–97.

KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren, *Troglodytes aedon*. Proc. XIII Internatl. Ornithol. Congr., 884–904.

KELLY, J. W. 1956. Prolonged incubation by an Anna Hummingbird. Condor, 58:163.

LASIEWSKI, R. C. 1963. Oxygen consumption of torpid, resting, active and flying hummingbirds. Physiol. Zool., 36:122–140.

LASIEWSKI, R. C. 1964. Body temperatures, heart and breathing rate, and evaporative water loss in hummingbirds. Physiol. Zool., 37:212.

LEHRMAN, D. S. 1961. Sex hormones and parental behavior in birds and infra-human mammals. pp. 1268–1382 in Sex and internal secretions, vol. 2 (W. C. Young, Ed.). Williams and Wilkins, Baltimore.

SKUTCH, A. F. 1962. The constancy of incubation. Wilson Bull., 74:115–152.

YAPP, W. D. 1970. The life and organization of birds. pp. 77, 101–104, 123–124. American Elsevier Publishing Co., New York.

DEPARTMENT OF BIOLOGICAL SCIENCES, UNIVERSITY OF ARIZONA, TUCSON, ARIZONA 85721 AND ROCKY MOUNTAIN BIOLOGICAL LABORATORY, CRESTED BUTTE, COLORADO 81224. 26 FEBRUARY 1973.