

THE THERMAL AND RADIANT ENVIRONMENT OF A WINTER HUMMINGBIRD NEST

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Information on the thermoregulatory biology of birds from laboratory measurements is now abundant (Dawson and Hudson 1970; Calder and King 1974), but “. . . to know the organism it is necessary to know its environment” (Bartholomew 1958; see also Porter and Gates 1969). The nest is the center of a bird's radius of action and need for thermoregulation, so it is an ideal place for accumulating data. There is an extensive literature of nest descriptions. Traditionally, these descriptions have included materials, size, shape, type of tree or support and shelter, height, and occasionally an indication of spacing. The availability of better field instrumentation and a beginning awareness of physics, bioclimatology, and laboratory thermal biology stimulate renewed interest in the nest site (e.g., Hensley 1954; Howell and Dawson 1954; Wagner 1955; Kendeigh 1960; Dorst 1962, 1963; Horvath 1964; Hadley 1969; Orr 1970; Calder 1971, 1973a,b). What physical features govern the selection of a successful nest site? How might the bird sense or evaluate these features? What are the consequences for heat and water balance? The answers can come only from extensive field studies, particularly those in relatively extreme situations.

The smaller the bird, the more tightly it is coupled to its environment (King 1974). The thermal consequences of small size make hummingbirds especially interesting (see Pearson; 1950, 1954; Calder 1974a). The Anna's Hummingbird (*Calypte anna*) is the most northerly wintering hummingbird in North America. It has been studied extensively, perhaps more than any other hummingbird (metabolism, temperature, and torpor: Pearson 1950; Lasiewski 1963, 1964; time-energy budget: Pearson 1954; Stiles 1971; courtship: Bent 1940; Hamilton 1965; territoriality: Pitelka 1942; Stiles 1971; breeding ecology: Woods 1927; Legg and Pitelka 1956; molt and testicular cycles: Williamson 1956; and food supply and annual cycle: Stiles 1973).

The Anna's Hummingbird nests in California and Baja California. Those seen in southeastern Arizona have been thought to depart for the breeding range in late December or

January (Williamson 1956; Phillips 1947; Phillips et al. 1964). The range of Anna's Hummingbird has expanded recently (Zimmerman 1973). However, territorial males can be observed singing and displaying from November to April in Romero Canyon, Santa Catalina Mountains, north of Tucson. I saw a female feeding a recent fledgling there on 20 March 1974. The California breeding season extends from December to June (Williamson 1956). On 12 February, Theodore Parker discovered a nesting Anna's Hummingbird near the mouth of Sabino Canyon, also in the Santa Catalina Mountains. That nest was the subject of this study.

Howell and Dawson (1954) recorded nest and air temperatures at an Anna's nest in Los Angeles, California, in April. The climate there was relatively mild, with a minimum air temperature (T_a) of 10°C. The daylength for feeding was 14 hr. In comparison, the Arizona nest was exposed to a subfreezing T_a after a cold front passed. The daylength for the hen's energy-intake was 2.5 hr shorter and her nocturnal fast was consequently that much longer. Despite this, the nest was successful. Hence, it seems worthwhile to describe the nest site, temperature ranges, and radiant environment of this possibly extreme situation.

TECHNIQUES

The nest site (figs. 1 and 2) near the mouth of Sabino Canyon was in riparian habitat where the principal trees were *Populus fremontii*, *Platanus wrightii*, and *Fraxinus velutina*. The elevation was 829 m.

I recorded the nest temperature from a 36 ga. type T-thermocouple in a synthetic egg, and the air temperature from a thermistor in a Wheatstone bridge circuit. These were connected to battery-powered potentiometric recorders, readable to $\pm \frac{1}{2}^\circ\text{C}$ (Calder 1971). A mercury maximum-minimum thermometer ($\pm 1^\circ\text{C}$) registered extremes. The nest was 1.6 km from the Sabino Canyon official National Weather Service Station (NOAA), so the temperature data could be further supplemented.

Radiation temperatures of the sky, rocks,

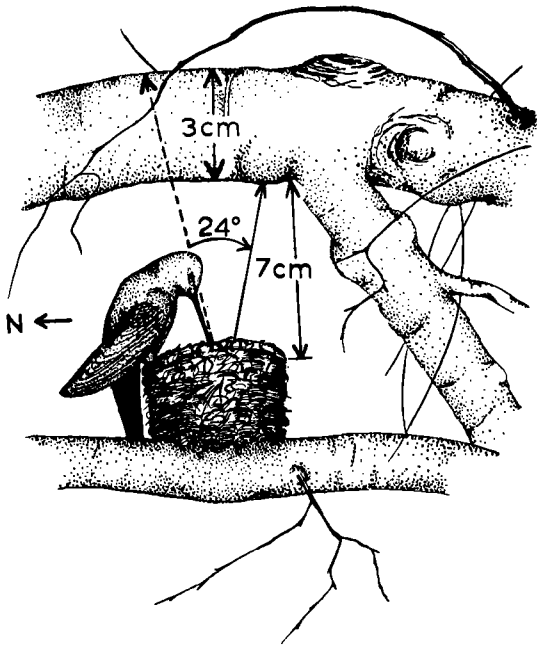


FIGURE 1. The nest site of an Anna's Hummingbird: a, female feeding chicks, viewed obliquely from 10 m distance on ground; b, viewed from beneath. The nest was in the center of the circle. The branch extending diagonally to top center from the main branch was approximately 30° west from the celestial meridian over the nest (see text).

ground, and vegetation samples were obtained with an infrared radiometric-thermometer (Barnes PRT-10). The calibrated range of this instrument is -10° to +60°C, but lower

temperatures can be sensed by offsetting the calibration, i.e., the radiometer was set to read +20°C when pointed at a +10°C black-body reference block. Because of the non-linear scale, a -20°C reading would be obtained from a somewhat colder sky segment (manufacturer states ±10% of target temperature).

The net radiation is the difference between radiation from the bird and radiation from the environment. The radiation from the bird was not measured, but was probably similar to that from the nesting Broad-tailed Hummingbird (*Selasphorus platycercus*) of similar body size and in a similarly chilling climate in the Rocky Mountains, estimated to be 39.2 mW cm⁻² (Calder 1974b). I will follow Mechtly (1969), Tucker (1972), and Barrow (1973) in using S.I. units. Conversion to more familiar units is: 1 mW = 0.014 cal min⁻¹ = 0.86 cal hr⁻¹.

The radiation influx would be described by the Stefan-Boltzmann equation:

$$\dot{H}_r = \sigma \epsilon \overline{K}^4$$

Where \dot{H}_r = rate of radiation influx per cm²

σ = Stefan-Boltzmann constant, 5.68 × 10⁻⁹ mW cm⁻² °K⁻⁴

ϵ = emissivity, assumed to be 1.0

\overline{K} = mean hemispherical surface temperature (°Kelvin).

Note that distance is not a factor in the radiation flux.

Azimuth and altitude angles of prominent skyline features were obtained with a pocket transit from which a rough outline was plotted with an electronic calculator-plotter (HP 9100B, 9125). The details were added from projections of a 35-mm slide panoramic series aligned to the transit-points on the plot. From the master plot, copies were traced, and cut into strips of 5° altitudinal angles. Proportions of sky and terrain were determined through gravimetric integration on an analytical balance using a conversion factor for paper samples of known area. These proportions were then multiplied by a factor representing the proportionate part of the surface area of a hemisphere of unit radius for each 5° interval, using the equation: Surface ∝ 2π (sin[θ + 5°] - sin θ). The percentages of the hemisphere in which radiation exchange was with the cold sky and with the relatively warm rocks and canyon hillsides could then be obtained by summation of the 5° intervals.

To relate to the heat-stress when the nest

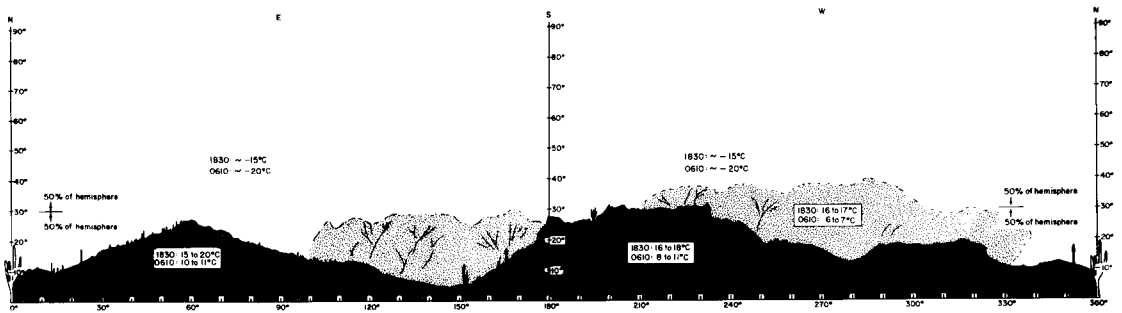


FIGURE 2. A panoramic silhouette viewed from the Anna's Hummingbird nest. Sample radiation temperatures (26–27 February; T_a decreased from 18 to 5.5°C) are indicated for early evening and early morning hours. Solid black = rock and earth of canyon walls. Stippled = canopies of trees on flood plain (in foreground of canyon walls).

was unshaded in the early afternoon during unusually warm weather in the week before fledging, data for the total hemispherical solar radiation flux at a point 17 km WSW of the nest site and 62 m lower in elevation (University of Arizona campus) were obtained through the courtesy of the Department of Atmospheric Physics.

RESULTS AND DISCUSSION

Chronology. The Anna's nest was observed intensely from 17 February until fledging, 14 March. The chicks hatched 18 February. The incubation period for the Anna's Hummingbird is 14–18 days (Bent 1940). Therefore incubation must have begun between 31 January and 4 February when the solar day-length would have been 10 hr 40 min.

Nocturnal brooding of the chicks continued until they were 12 days old (1 March: solar day = 11 hr 30 min). Afterward, the female only fed them. The chicks fledged 14 March and were seen in the general vicinity the following day.

The nest environment. Air temperatures from the end of incubation to fledging ranged from 4°C to 32.5°C, while the temperature at the Sabino Canyon NOAA weather station T_{NOAA} 1.6 km to the south ranged from -4.5 to 34.4°C in the nesting period (fig. 3). On the morning of 3 February, the low T_{NOAA} was 24°F (-4.5°C). This was before recording at the nest began, but from later comparisons of nest site T_a and T_{NOAA} minima, T_a at the nest site might have been 2°C warmer than T_{NOAA} (fig. 3). Temperatures of the synthetic egg in the nest were 26°C or higher, similar to or somewhat warmer than mean nest temperatures recorded from an Anna's nest by Howell and Dawson (1954) in the milder climate of Los Angeles. A typical recording is seen in figure 4.

Interesting thermal behavior of the female included a bath in 11.5°C shallow stream water at 06:46 when T_a had not risen above the minimum of 5.5°C for that day. At the other extreme, the hottest day (9 March) necessitated shading of the postbrooding chicks when T_a reached 32.5°C during a mid-afternoon period when direct sunlight hit the nest. Hemispherical solar radiation at the Atmospheric Physics facility at the University of Arizona campus was 75.9 mW cm⁻² at that time. The chicks had been panting (gaping, without gular flutter) prior to arrival of the female for shading.

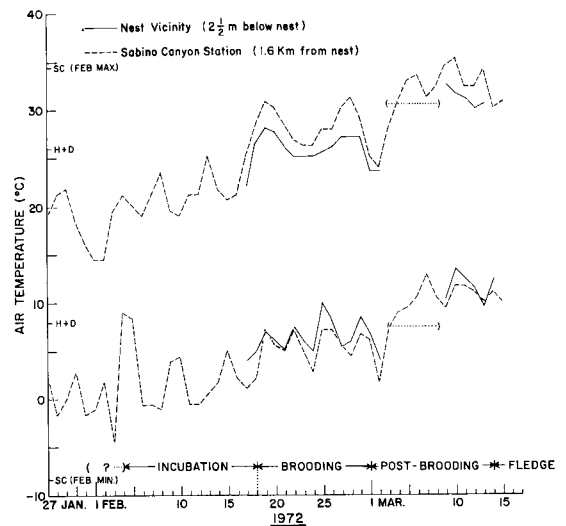


FIGURE 3. Maximum and minimum air temperatures during nesting of the Anna's Hummingbird. Temperatures were recorded from 17 February until fledging. Estimated from date of hatching, incubation began 1–3 February when the monthly minimum temperature was attained. Data from the Sabino Canyon Weather Station (NWS-NOAA) 1.6 km from nest have been included to approximate conditions prior to the beginning of this study. H + D = maximum and minimum air temperatures recorded at UCLA during the period of study of Howell and Dawson (1954).

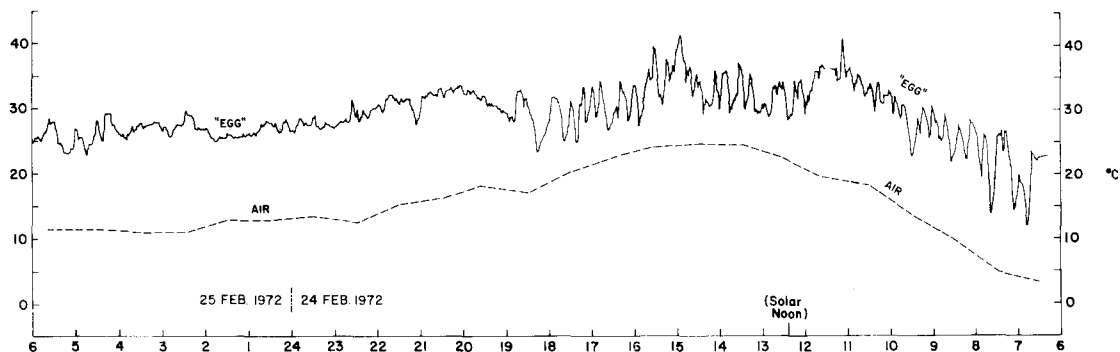


FIGURE 4. Nest temperatures (solid trace) monitored from a synthetic egg in the nest of an Anna's Hummingbird during the sixth day of brooding. Air temperatures are shown in the lower (broken) trace.

To aid in a thermal description of the nest site, the temperature of the artificial egg in the empty nest was monitored for a day without the hen's influence (fig. 5). This was 2 days after fledging, when the maximum T_a was 29°C (3.5° less than on 9 March) but the total hemispherical radiation recorded for the day (University of Arizona) was 10% higher than on 9 March. Thus the conditions were similar but not exactly the same in this comparison.

Nocturnal radiation. The nesting micro-environment can be subdivided for (speculative) analysis as follows:

- I. Above nest walls
 - A. Radiative exchange
 1. Influx from hemisphere
 - a. Cold sky
 - b. Topographical blocking of celestial hemisphere
 - c. Surfaces of vegetation—leaves, branches

(Note a, b, and c together are 100% of hemispherical "surface.")

2. Emissions from exposed body surfaces

- B. Convective loss

- II. Through nest walls—conducted losses from that portion of the body surfaces contained within nest cup.

The cold sky temperature was -19°C or colder, as determined with the IR radiation thermometer. The rocks and ridges bordering the valley floor constituted 29.6% of the hemisphere (see fig. 2). Solar radiation during the day had warmed the rocks, and though they cooled during the night, they were still warmer than the pre-sunrise T_a , and considerably warmer than the cold sky. Thus, they contributed a more intense long-wave influx than the portion of the sky which they blocked. The branches and leaves of the trees

lagged on the warm side of T_a by $1-2^\circ\text{C}$. I estimated the contribution of the branches as follows: 7 cm directly above the nest (circled in fig. 1b) was a branch 3 cm in diameter. Simplified as a cylinder, this would block an angular field of 24° across the celestial meridian. A second higher branch (seen across upper left side of fig. 1b) extended about 30° west from the meridian for perhaps one-third of this arc, blocking about 3% more of the sky. Nearby sycamore, cottonwood, and ash trees also shielded part of the radiation hemisphere, at a guess 10%. Together, the rocks and vegetation appear to make up slightly more than half of the radiation-hemispherical field.

Applying the appropriate temperatures to these proportions, the hemispherical long-wave influx can be crudely estimated. Table 1 gives the results of calculations for early evening (post-sunset, maximum from warm surfaces) and early morning (pre-sunrise,

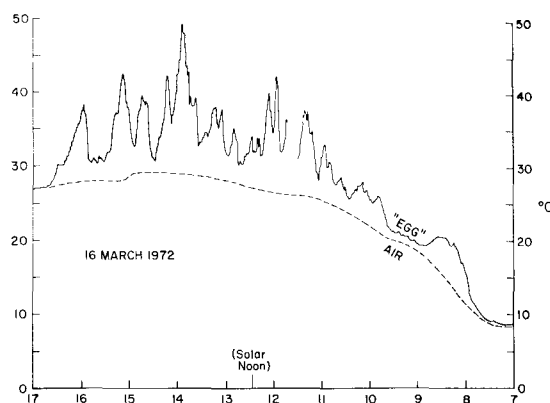


FIGURE 5. A temperature "signature" of the empty Anna's Hummingbird nest for a day similar to the warmest pre-fledging day. At the University of Arizona campus 17 km WSW from the nest, peak hemispherical radiation flux was 90.1 mW cm^{-2} and during the sunstruck period it was 81.2 mW cm^{-2} , compared to 85.2 and 75.9 mW cm^{-2} , respectively, for the warmest pre-fledging day (10 March).

TABLE 1. Estimated nocturnal radiation influx (\dot{H}_r) at a winter nest of the Anna's Hummingbird.

Time	Component	Radiation temp. ($^{\circ}\text{C}$)	$\dot{H}_r = \sigma \text{ } ^{\circ}\text{K}^4$ (mWatt cm^{-2})	% of hemisphere ^a	$\dot{H}_r \times \%$ (mW cm^{-2})
Maximum influx, Post-sunset					
18:30	Rocks	+ 17¼	40.24	29.6	11.9
26 Feb. '72	Trees	+ 16½	39.82	13 + 3 + 10 = 26	10.4
	Sky	- 15	25.12	100-55.6 = 44.4	11.2
			Total = 100% =		33.4
			Total if 100% unobstructed sky =		25.1
			Savings =		8.3
Minimum influx, Pre-sunrise					
06:10	Rocks	+ 10	36.36	29.6	10.8
27 Feb. '72	Trees	+ 6½	34.60	26	9.0
	Sky	-20	23.23	44.4	10.3
			Total = 100% =		30.1
			Total if 100% unobstructed sky =		23.2
			Savings =		6.8

^a See text.

minimum from rocks and other surfaces cooled overnight). Thus in the course of the night, the influx declined from 33.4 mW cm^{-2} to 30.1 mW cm^{-2} , 33-29% greater than that from an unobstructed hemispherical sky.

It would be necessary to have the surface temperature of the female hummingbird for estimating her radiant efflux, but this could not be measured at this nest. In a similar thermal and radiant environment, the female Broad-tailed Hummingbird had a surface T of 15.3 $^{\circ}\text{C}$, which would emit 39.2 mW cm^{-2} (Calder 1974b). This borrowed value suggests that the average net radiation loss from the Anna's Hummingbird might be 39.2 - 31.8 = 7.4 mW cm^{-2} . To put this value into perspective, it is just twice the basal flux for the species in a metabolic chamber (3.7 mW cm^{-2} , obtained from Lasiewski 1963, converting units and, assuming that the surface area is 10 $\text{g}^{0.67}$, following Drent and Stonehouse 1971). The savings provided by the topography and vegetation in the form of reduced net radiation losses are 2.2-1.8 times the basal flux, so that the worst possible nest site under an unobstructed celestial hemisphere would result in a net radiative loss four times the basal flux. To this would be added the convective heat loss from the above-nest portion of the bird, not measured in this study.

Much of the bird is not exposed to radiative and convective losses, being insulated by the nest cup. The upward-facing projection of hummingbird museum specimens, excluding remiges and rectrices, is one-fourth of the 10 $\text{g}^{0.67}$ = 28.5 cm^2 surface, so that the other three-fourths might be within the nest, where recorded nest temperatures were generally within the thermoneutral range reported by

Lasiewski (1963). Consequently, for the three-fourths of the bird inside, the nest would lose heat at a much slower rate.

Thus the energetic cost of thermoregulation during nesting can be reduced by nest-site selection as well as by the insulation provided by the nest composition and construction. The absolute value of the nest placement cannot be stated without measurements of total heat loss at the natural nest site or roost. Enclosed within a metabolic chamber, an open nest would no longer be exposed to its natural radiation and convection environment. At present, I can only state that the long-wave, nocturnal, radiant influx seems to have been better than if she had nested upstream or downstream where more sky was visible. The estimated hemispherical radiation was almost identical to that of a Broad-tailed Hummingbird nesting in the Colorado Rockies, at a cool 2910 m elevation (Calder 1974b), but the Anna's Hummingbird was exposed to this chilling environment for a longer night after a shorter day for foraging. The temporal aspects of this energetic problem will be discussed elsewhere (Calder 1974c).

CONCLUSIONS

The female Anna's Hummingbird appears to be as capable of meeting the challenge of cold stress as those species which nest farther north in the Rocky Mountains. Successful nesting of the Anna's Hummingbird in winter rules out low air temperature as a limiting factor in its northern or altitudinal distribution.

The canyon walls may be quite significant in reducing heat loss by radiation. Thus topography must be considered to have

ecological significance for thermoregulation in addition to previously suggested effects.

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