

TEMPERATURE RELATIONSHIPS AND NESTING OF THE CALLIOPE HUMMINGBIRD

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Environmental challenges to homeostasis can be most severe to the smallest homeotherms. This is a consequence of the inverse relationship of surface/volume ratio to body mass ($M^{0.67}/M^{1.0} = M^{-0.33}$) and of thermal conductance to body mass ($M^{-0.5}$; Herreid and Kessel 1967; Lasiewski et al. 1967). When the climate becomes inhospitable, the smallest mammals, shrews, can retreat to moderate subsurface microclimates beneath logs, rocks, and in underground burrows. Comparably small birds are not fossorial and hence are exposed to more variable and extreme conditions. This is particularly true for those hummingbirds which breed at higher elevations and latitudes.

The Calliope Hummingbird (*Stellula callope*) is the smallest bird on the North American continent north of México, weighing only 2.6–3.4 g. It breeds in the Cascade, Sierra, and Rocky Mountains from British Columbia and Alberta south to Wyoming, Utah, and northern Baja California, the second most northerly distribution of a hummingbird (Bent 1940; weights from Lasiewski 1963). The Calliope Hummingbird is often exposed to cold night temperatures during the breeding season in the mountains. These conditions seem particularly threatening to this species, which has the highest thermal conductance and metabolic requirements, yet the smallest thermal mass among the North American avifauna (Lasiewski and Dawson 1967; Lasiewski et al. 1967).

Hummingbirds generally become torpid at night for energetic economy (Huxley et al. 1939; Pearson 1950, 1953; Bartholomew et al. 1957; French 1959; Hainsworth and Wolf 1970). However, two female Anna's Hummingbirds (*Calypte anna*) maintained homeothermy throughout the night when incubating eggs (Howell and Dawson 1954). From this it has been generally assumed that all female hummingbirds are nocturnally homeothermic throughout the nesting period (Welty 1962; Thomson 1964). Such an assumption needs verification with smaller hummingbirds and in more extreme environments.

The Anna's Hummingbird cited above was exposed to mild nights, the minimum air temperature being 10°C. The species weighs 3.4–

5.8 g (Lasiewski 1963). In contrast, the smaller Calliope Hummingbird nests in night air temperatures which often approach freezing at Jackson Hole, Wyoming. The Calliope Hummingbird should therefore be of considerable interest for studies of nest microclimate, nocturnal egg temperatures, nest attentiveness, and energy budget estimation. Such a field study seemed a valuable opportunity in view of the wealth of excellent background information from the laboratory on the metabolism and other aspects of hummingbird physiology, contributed by Pearson, Bartholomew, Lasiewski, and their associates.

MATERIALS AND METHODS

The Calliope Hummingbird was studied at the Jackson Hole Biological Research Station near Moran, Wyoming. The station is located at 2077 m in a small stand of lodgepole pine (*Pinus contorta*) surrounded by sagebrush (*Artemisia*) with grassland to the north and east, willow-bordered streams and wet meadows to the west, and the Snake River channel on the south. Females nested in lodgepole pines, while the males defended territories in thickets of willow and alder bordering adjacent water-courses.

Temperatures were monitored continuously from two nests by means of thermocouples connected to recording potentiometers (Leeds and Northrup "Speedomax W" and Esterline Angus T-171 B). Initial recordings from a bare thermocouple junction were erratic. More stable and representative recordings came from copper-constantan thermocouples (36 ga.) embedded in synthetic eggs made of elastomer with a thermal conductivity similar to that of egg [Dow-Corning "Silastic" 382; "typical" thermal conductivity 5.25×10^{-4} cal/(cm sec °C) vs. 4.2×10^{-4} cal/(cm sec °C) for duck egg; Kashkin 1961]. A synthetic egg (hereafter designated by "egg," "egg temperature") was added to each nest without removing a natural egg.

Nest 1 was discovered during its construction 20 June 1970, located ca. 2.5 m out a limb of lodgepole pine, 12 m above the ground. Incubation began 23 June. The "egg" was placed 31 July by means of a 3-m pole with a string-controlled releasing pin. Temperatures were recorded for the last seven days of incubation, the entire brooding and post-brooding periods, and five days past fledging to obtain a temperature profile of the empty nest.

Nest 2 was located on the third day of incubation (assuming a 15-day incubation), 2 m above the ground in lodgepole pine on a steep bank of the Snake River, but 2 m vertically below the level of the top of the bank. Temperatures were recorded until two days after fledging.

TABLE 1. Absence of female Calliope Hummingbird from nest during incubation and brooding, summer 1970.

	Incubation			Brood		
	Nest 1	Nest 2	Both	Nest 1	Nest 2	Both
Day ^a	11	10		20	21	
No. absences	111	107	109	74	95	85
\bar{x} no. absences/day ^b	100	99	100	71.2	97	84.1
\bar{x} min./absence	2.24	1.77	2.00	3.35	3.84	3.60
No. days recorded	5	9	14	9	6	15
Max. min./absence	7.8	10.85	9.33	8.98	8.00	8.49
Total time absent (hr)	4.14	3.07	3.61	4.13	6.08	5.11
% of day ^c absent	26.1	19.7	22.9	26.0	39.3	32.7
Max. air temp. (°C)	28.0	26.3	27.2	23.9	21.7	22.8

^a Hatching = day 15.

^b Average of all totals recorded for stage under consideration.

^c Mean day length (first departure to last arrival) = 15 hr, 40 min; range = 15:51-15:29.

Each departure and arrival of the female hummingbirds was recorded as a cooling-warming pen displacement. By increasing the chart speed (120 mm vs. the usual 20 mm/hr, calibrated), the duration of periods on and off of the nest, day length, and night length (from first departure and last arrival) could be estimated with a vernier caliper. Stopwatch timing provided a check on this estimation. The errors from caliper measurement of chart advance were random and counter-balanced to less than 3 per cent (6 sec error/trip; individual errors as high as ± 26 sec tending to cancel).

RESULTS

GENERAL OBSERVATIONS

The nesting of the Calliope Hummingbird consisted of 15 days of incubation, 11-12 days of brooding and feeding young, and, finally, 10-11 days of post-brooding in which the female came to the nest only in the daytime to feed the homeothermic young. The sequence began 23 June 1970 at the first nest, and fledging occurred upon my approach to the second nest on 14 August.

Observation records for the Calliope Hummingbird in the Grand Teton National Park extend from 4 June-12 August (Charles McCurdy, Chief Park Naturalist, pers. comm.). There was no seasonal trend in air temperatures towards either warmer or cooler temperatures, but a cycling of warm and cold periods, with dawn temperatures 3°C or lower in all stages of nesting. On 30 June, during incubation but before a thermocouple was placed successfully in Nest 1, light snow was falling without accumulating in the mid-morning. Mean maximum air temperatures were 25.2°C during incubation, 24.3°C during brooding, and 25.1°C during the post-brooding period.

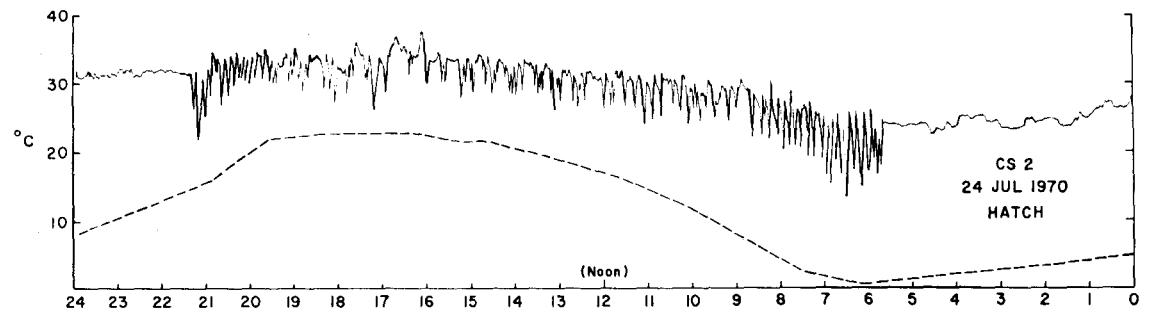
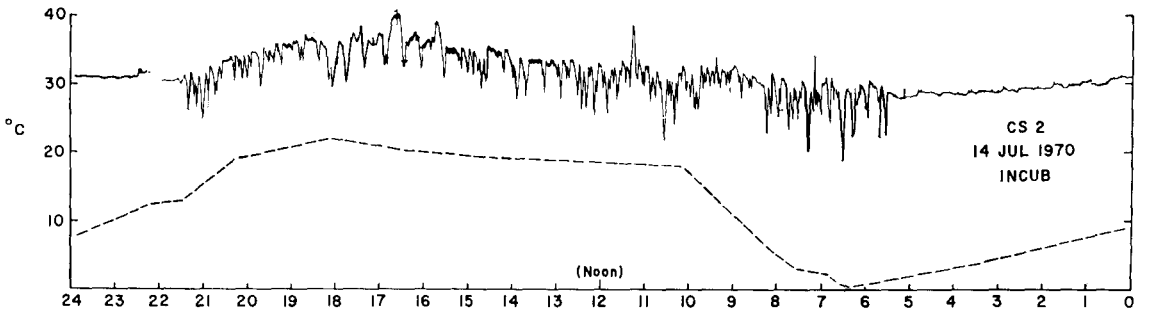
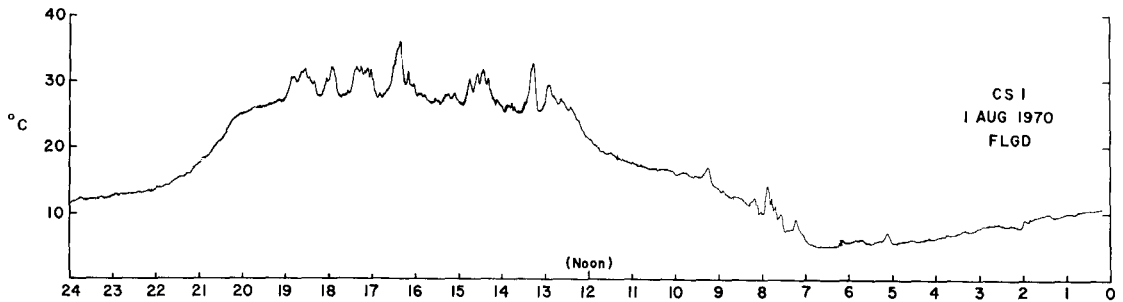
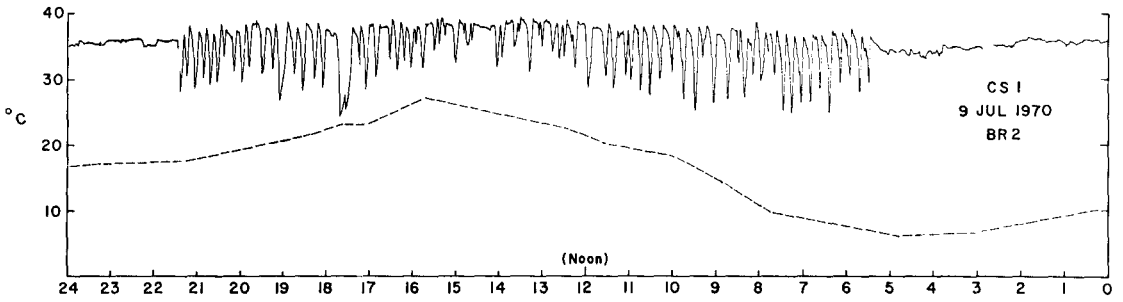
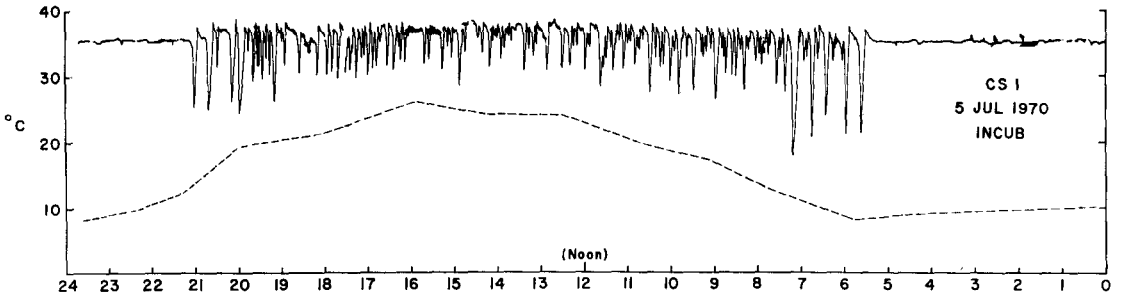
Male Calliope Hummingbirds were already engaged in territorial disputes on 13 June, the first day of this study. Courtship displays as

described in Bent (1940) were seen 21 and 22 June in a willow-alder thicket adjacent to the lodgepole pine stand. The intensity of the males' territorial defenses subsided in July, and the last observation of a male was on 24 July, the date of the first hatching in nearby Nest 2.

DAYTIME ACTIVITY

The temperature-sensing "eggs" were tolerated and remained in the nest. Maintenance and/or improvement of the nest walls by the females resulted in burying the thermocouple leads in the sides of the nests. Data on nest absences (temperature changes of the synthetic "eggs") of the two females are summarized in table 1. Sample recordings are shown in figure 1. The nestlings attained a mid-day homeothermy when eight days old, indicated by absence of cooling during the inattentive periods (mid-day air temperatures rising to 26.7° and 23.3°C).

The patterns of inattentiveness of the two *S. calliope* hens were quite different. The one-third decrease in frequency of departure of the female from Nest 1 was a clear trend, the sequences for six days before and seven days after hatching being 91, 111, 102, 110, 85, 85, hatching, 75, 75, 69, 72, 74, 67, and 66 trips per day (until thermogenesis of the young made counting of trips from the strip-chart recording unreliable). The female of Nest 2 nearly doubled the total inattentiveness by departing as frequently, but for longer durations during brooding as compared with incubation. The number of trips ranged from 87 to 111 per day during incubation, and from 86 to 110 trips per day during brooding. The difference may have been related to the distance to food sources. No relationship between the frequency or duration of inattentive periods and environmental temperature was



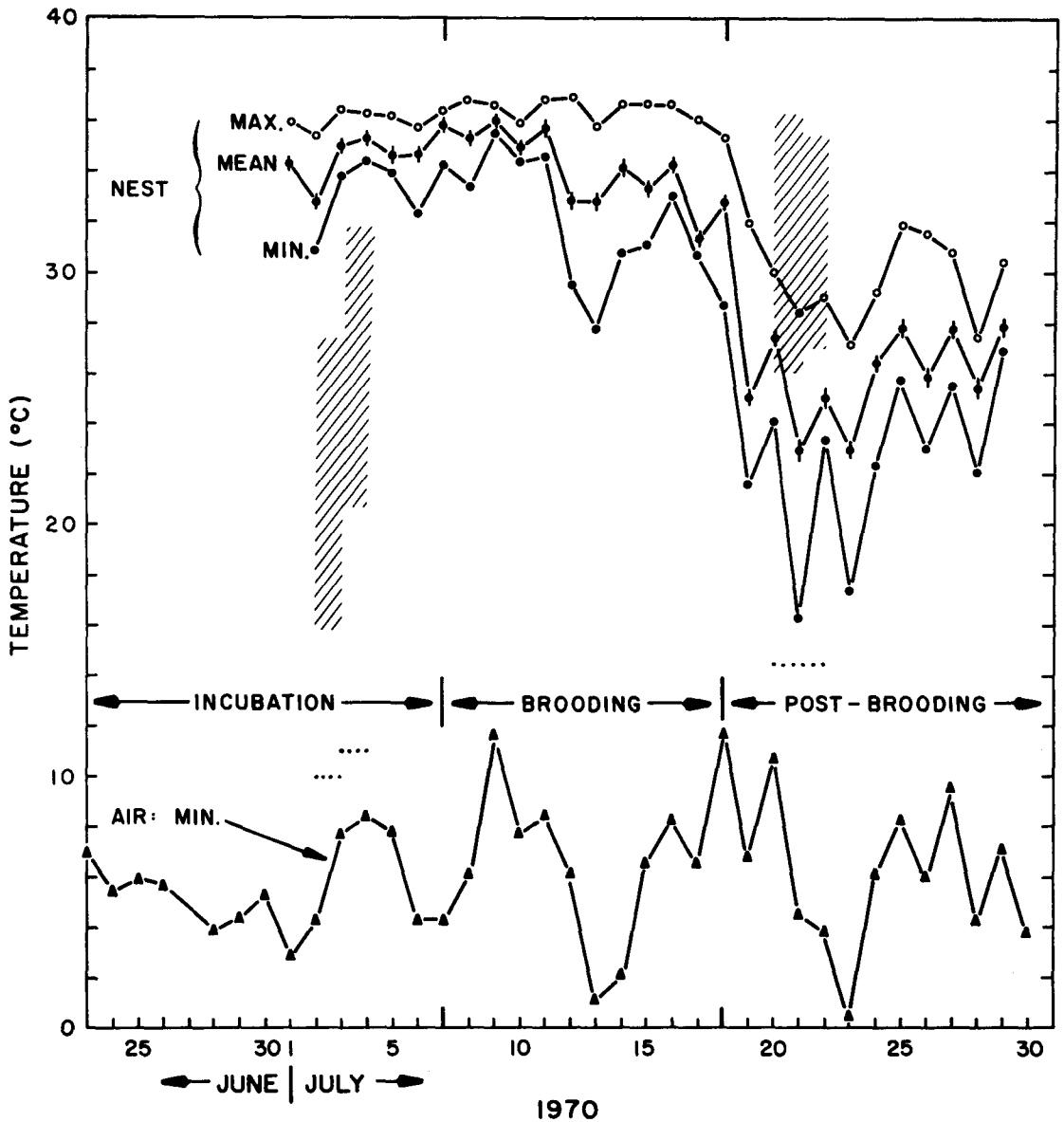


FIGURE 2. Upper: Daily temperatures of artificial egg, Calliope Hummingbird Nest 1. Cross-hatching = ranges in a nest of Anna's Hummingbird at the same stage of development (Howell and Dawson 1954). Lower: minimum air temperatures during nesting of the Calliope Hummingbird. Note that these were generally much colder than the minima for the Anna's (dotted lines beneath cross-hatched bars of upper portion of graph).

obvious as in other birds (Baerends 1959), but the Calliope hens seemed not to depart on a succeeding trip until nest temperature returned to a rather consistent temperature range, gen-

erally 34-37°C in Nest 1, rarely lower. As noted above, the "egg" was further from the thermal center of Nest 2, so the departures coincided with lower recorded temperatures.

FIGURE 1. Sample temperature recordings from Calliope Hummingbird nests, from top to bottom: line 1, day 13 of incubation (Nest 1); line 2, day 2 of brooding (Nest 1); line 3, a nest temperature profile two days after fledging (Nest 1); line 4, day 6 of incubation (Nest 2); and line 5, hatching date of first chick (Nest 2). Solid traces = temperature of artificial egg; lower, broken curves = air temperatures determined at ¼-4 hr intervals, by calibrated mercury thermometers. Air temperature extremes were recorded with max-min thermometers 2 m below nest level in the same tree (Nest 1) or at same height in an adjacent tree (Nest 2). Spikes in the post-fledged nest recording are from direct sunlight.

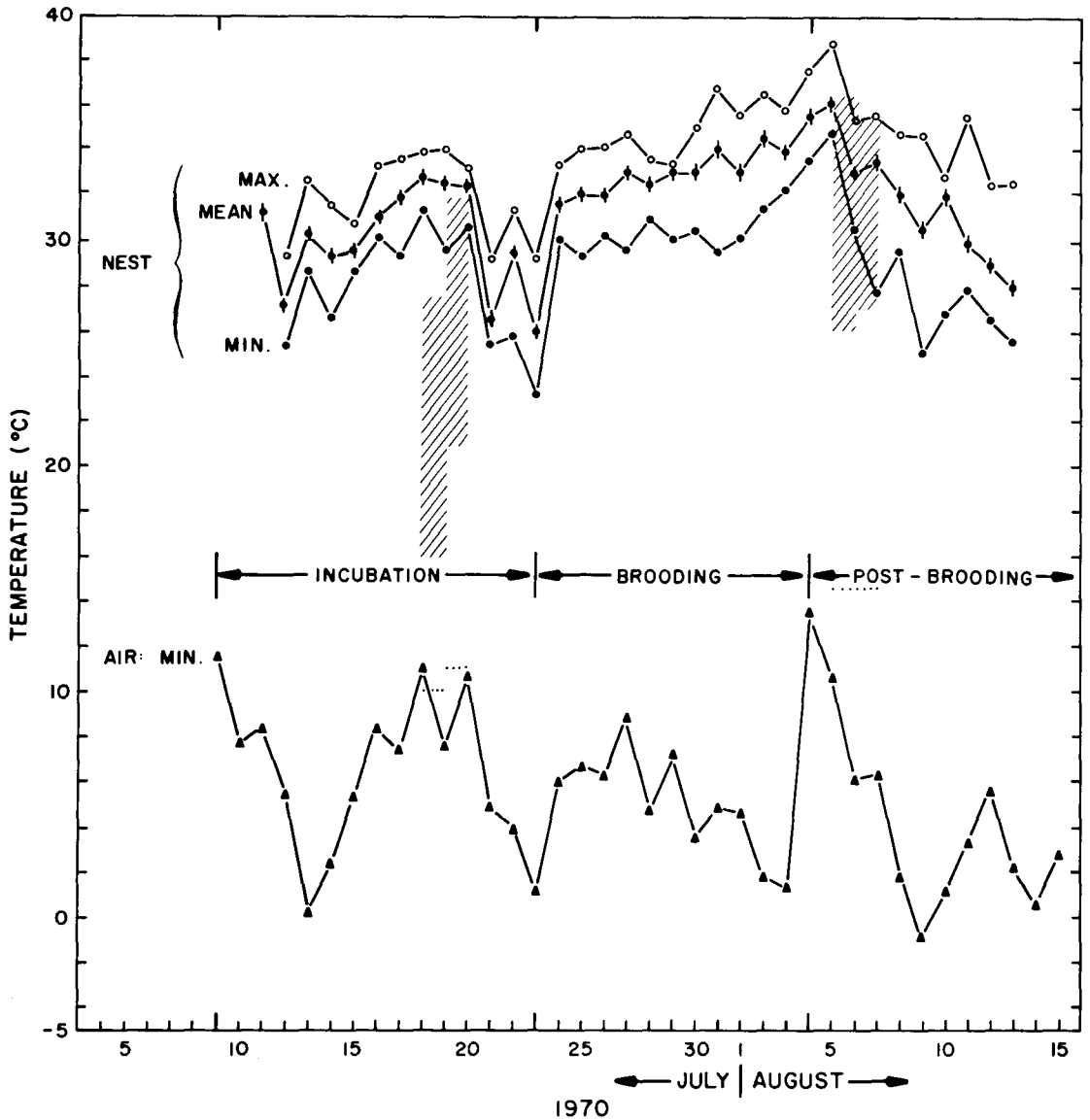


FIGURE 3. Daily temperatures from Calliope Nest 2. Upper: "egg" temperatures; lower: minimum air temperature. Comparison with the data from the Anna's Hummingbird nest as in figure 2.

In neither pattern was there support for the suggestion that the quiet of nest-attentiveness constitutes sufficient energy savings to fuel the nocturnal thermoregulation.

Significantly, the females did not feed the young following the last trip of the evening. Food of the last trip was apparently allocated to the hen's metabolic budget for the 8 hr to 8 hr 50 min of nocturnal fasting.

NOCTURNAL TEMPERATURES

The air cooled to an average of 5.9°C before sunrise and to extremes of 0.2°C during incubation, 1.2°C during brooding, and -0.9°C during post-brooding. The artificial eggs were

located somewhere along the gradient from hen to ambient air, probably cooler than the bird's body. These "egg" temperatures also fluctuated with her position changes but are clearly not those of nocturnal torpidity. In seven recorded incubation nights of Nest 1, the minimum "egg" temperatures ranged from 22 to 29.8°C above the minimum air temperature, while in 11 incubation nights at Nest 2, they were 19.9–28.3°C higher (figs. 1, 2, and 3). The mean nocturnal "egg" temperatures were 34.6°C for seven incubation nights in Nest 1, and 30.8°C for 11 incubation nights in Nest 2. Upon collection of the nests at the end of the season, I noted that the cooler "egg" in Nest 2

appeared to have been pushed against the side of the nest towards which the hen customarily pointed her tail; it thus had less thermal proximity to her brood patch.

DISCUSSION

TIMING

There is a trend towards shorter incubation and nestling stages of birds with increasing latitude, perhaps the result of greater photoperiods for feeding (Irving and Krog 1956; Welty 1962). However in the adverse climate and food supply of the Andes, the hummingbird *Oreotrochilus estella* has a slower development, 22–23 days of incubation and a proportionately longer nestling period, than other hummingbirds (Dorst 1962).

Despite the cold night temperatures, and even some cool days with the possibility of light snow, the Calliope Hummingbird's 15-day incubation and 11–12 days of brooding are of about the same duration as those of hummingbirds that breed in warmer climates. The Allen's Hummingbird (*Selasphorus sasin*, 3.7 g) also has a 15–16 day incubation and the Anna's Hummingbird (4.8 g), 14–18 days. Brooding is discontinued when the nestlings of both species are 12 days old, the 13-day-old chicks being homeothermic (Orr 1939; Bent 1940; Howell and Dawson 1954; weights from Lasiewski et al. 1967). Neither the smaller size of the Calliope nor the cooler climate surrounding the nest seems to have influenced these durations.

The "egg" temperatures recorded in the nest of *S. calliope* during the cool nights noted above are remarkably similar to egg temperatures of much larger birds in warmer environments. The average egg temperature was 34.3°C during attentive periods of birds from 11 orders, ranging in size from warblers to swans, 34.2°C for passerines only (Huggins 1941). The "egg" temperature of *S. calliope* was maintained at an average 34.6°C in Nest 1 and 30.8°C in Nest 2, the latter average also falling within Huggin's range despite its peripheral location. Similar nest temperatures were recorded from nests of arctic birds by Irving and Krog (1956).

The minimum nocturnal nest temperatures for *S. calliope* were 19.9–29.8°C above the corresponding minimum air temperatures. Differences between temperatures of nest thermocouples and outside air for *C. anna* ranged from 10 to 16°C, the basis of subsequent generalization, such as: "In the hummingbirds . . . the incubating bird does not become torpid at night" (Thomson 1964:829). The nest tem-

peratures for *S. calliope* confirm this generalization. The lower temperatures from the nest of *C. anna* are probably the result of the method of thermocouple placement rather than a tendency to maintain a cooler nest.

Given the same developmental rates and incubation temperatures but a greater heat loss potential from nest to ambient air, eggs and nestlings of *S. calliope* would seem to be more restricted in the duration of exposure that they can tolerate. Further comparisons with *C. anna* suggest that the inattentive periods may be shorter. The *C. anna* averaged 2.9 min per absence from incubation, and 3.9 min per absence from brooding, while the two *S. calliope*s had averaged absences of 2.0 and 3.6 min, respectively. Maximum inattentive periods were "less than 40 min" for *C. anna* and 10.8 min for *S. calliope* (Howell and Dawson 1954). On the other hand, during 3 incubation days, *S. sasin* had a mean absence duration of 1.4 min, with longest absences (3 min) considerably shorter than the maximum for *S. calliope* (Orr 1939). These latter inattentive durations probably reflect distance to food source, as the *S. sasin* was in a grove of blooming *Eugenia* trees which provided abundant nectar.

While *S. calliope* may be restricted to somewhat shorter inattentive periods, the hen must meet her energy needs with a considerable "per cent inattentive" time, (19.7–39.3 per cent of the time; mean, 27.8). For comparison, *C. anna* was absent 10–20.5 per cent (mean, 16.9) of the observation periods (Howell and Dawson 1954) and *S. sasin* was absent from incubation 50, 26.9, and 22.9 per cent of the morning observation periods (Orr 1939).

ENERGY BALANCE

Nocturnal torpor is important for energy conservation (Pearson 1950, 1954). The female hummingbird's non-entry into nocturnal torpor during incubation has raised questions about the bioenergetic budget. Howell and Dawson (1954) suggested the following factors that could contribute to an energy balance over the nocturnal fast, and which can be re-examined with respect to *S. calliope*: 1) elevated food intake and storage late in the day, 2) a sex difference in metabolic rates, 3) energy savings of reduced activity during incubation, and 4) insulative value of the nest. For *C. anna*, they found no evening elevation of food intake above mid-day feeding intensity. Evidence for a sex difference in metabolism was equivocal. They concluded that energy conservation through reduced activity and reduction in heat loss by the insulating nest were the significant factors in the energy budget in nesting *C. anna*.

TABLE 2. A comparison of daily energy estimates for hummingbirds* (*Stellula calliope* and *Calypte anna*).

Bird	Activity	Duration (hr)	Energy cost (kcal)	Energy cost per g body wt.	Air temp. (°C)	
					Max	Min
Daytime						
<i>S. calliope</i> ♀	On nest ^b	11.66	2.32	0.771	28	4.4
	Absent, non-fly. ^c	1.03	0.26	0.088	28	4.4
	Total, non-fly.	12.69	2.58	0.859	28	4.4
<i>C. anna</i> ♂	Perched	10.53	3.81	0.952	23	10.6
<i>S. calliope</i>						
♀ #1	Flight, inattentive ^d	3.10	2.97	0.989	28	4.4
♀ #2	Flight, incub. pd. ^d	2.30	2.20	0.734	26.3	7.3
♀ #2	Flight, brood. pd. ^d	4.56	4.38	1.461	21.7	4.7
<i>C. anna</i> ♂	Flight	2.35	3.07	0.767	23	10.6
<i>S. calliope</i> ♀ #1	Total ^e	15.79	5.29	1.760	28	4.4
<i>C. anna</i> ♂	Total	12.87	6.88	1.720	23	10.6
Nighttime						
<i>S. calliope</i> ♀ #1	Non-torpid	8.20	1.85 ^f	0.616 ^f	12	4.4
<i>C. anna</i> ♂	If non-torpid	11.13	3.44	0.861	14	10.6
	Torpid	11.13	0.67	0.168	14	10.6
Total						
<i>S. calliope</i> ♀ #1		23.99	7.40 ^f	2.46 ^f	28	4.4
<i>C. anna</i> ♂	With torpor	24.01	7.55	1.89	23	10.6
	With homeothermy	24.01	10.33	2.58	23	10.6

* Data for *C. anna* (4 g) from Pearson 1954. Data for *S. calliope* #1 on eleventh day of incubation, for *S. calliope* #2 on presumed tenth day of incubation and sixth day of brooding. *S. calliope* wt. (3 g) and metabolic rates from Lasiewski 1963 (flight time estimates for *S. calliope* #2 given for comparison only, not used in calculating totals).

^b Estimated as 1.5 times resting metabolism at existing ambient temperatures.

^c Assuming 1/4 of time absent from nest.

^d Assuming 3/4 of time absent from nest, metabolic rate for hovering flight given by Lasiewski (1963).

^e Daytime total = on nest + absent, non-flying time + flight, inattentive.

^f Neglecting insulative effect of nest on energy conservation.

Using Pearson's (1954) estimate of the energy requirements of a wild male *C. anna*, and information on the metabolic rates of *S. calliope* (Lasiewski 1963), the energy requirements of a nesting Calliope hen can be estimated and compared with *C. anna*. Differences in species, season, and habitat must be acknowledged, but this is still instructive in absence of other data for such a comparison (table 2).

The nesting Calliope hen spends as much or more time flying as the *C. anna* male did in defending his feeding territory. The assumption that three-fourths of the inattentive period is spent in flight is not entirely subjective but is based upon sample timings under ideal viewing conditions. Nest 2 was located below the river bank in a solitary tree with an essentially uniform background with the water surface of the river extending to several clumps of red *Castilleja* (Indian paintbrush) across the river, from which the hen fed extensively. This made it possible to evaluate the proportion of flying and perching in several inattentive periods.

The seemingly quiet routine of an incubating or brooding hummingbird entails a daytime metabolic expenditure (column 5, table 2) quite similar to that of a male hummingbird defending a territory when comparison is made

per gram body weight (necessary because of size difference). This indicates no metabolic savings that could be applied to the cost of overnight thermoregulation. That nocturnal cost would amount to the energy in 0.2 g of fat or 0.44 g of carbohydrate (using and extrapolating from Lasiewski's 1963 resting metabolic rates for *C. stellula*, and neglecting the insulative value of the nest). The similarity in total metabolic estimates for Anna's and Calliope suggests that the specialization of labor in hummingbirds might have evolved to an even split in the overall work load, although intraspecific comparisons of the sexes are needed to confirm this.

Thus, of the factors suggested by Howell and Dawson (1954) to explain the hummingbird's bioenergetic balance, the insulation provided by the nest stands as the most plausible. In a study of the breeding biology of hummingbirds exposed to low temperatures in the mountains of México (3100 m, temperatures of -8 to 15°C), Wagner (1955) correlated adaptations in nest thickness and composition with environmental conditions. Doubtlessly a crucial factor in the thermoregulatory success of incubating hummingbirds, such as the Calliope, is the nest itself.

In addition to the protection afforded by the

nest material and construction, nest location must be of great significance. Wagner (1955), Dorst (1962), and Smith (1969) have pointed out the importance of protective overhangs and orientation to receive early morning sun, to hummingbirds living in the cool climates of high mountains such as *Oreotrochilus chimborazo* and *O. estella* of the high Andes and *Selasphorus platycercus* in Mexican highlands. *O. estella* also nests in the more moderate nocturnal environment of caves (Pearson 1953).

The high thermal conductance and insignificant thermal inertia of its tiny body and the large temperature difference between bird and nocturnal air must place *S. calliope* at or near the maximum limits for its thermoregulatory capacity. Therefore, we might expect that natural selection has maximized the thermal or energetic economy in the behavioral patterns associated with nest site and material selection and nest construction. The Calliope Hummingbird nests on an old pine cone base, on a branchlet immediately below a larger branch, or else under the canopy of foliage. Such location "serves to protect the nest from overhead" (Bent 1940). In Jackson Hole, I observed only the under-branch nesting site. The branch shields the nest so that it does not "face" the heat sink of the cold night sky. This must be of great significance in reducing the nocturnal heat loss by radiation, in addition to the protection from raindrops and predators which it affords.

SUMMARY

The smallest bird in temperate North America, the Calliope Hummingbird, incubates her eggs while exposed to nocturnal temperatures which approach freezing in northwestern Wyoming. Temperatures were recorded continuously from thermocouples imbedded in synthetic eggs placed in two Calliope nests. The small size and large heat loss potentials do not appear to be compensated by adaptive modification in the duration of incubation and brooding, the "per cent inattentiveness," the metabolic cost of activity, or the nocturnal body temperatures. Duration of inattentiveness is slightly shorter than in the Anna's Hummingbird. The incubating Calliope Hummingbird does not become torpid at night. Nest sites and construction which minimize heat loss are indicated as the major factors in the thermal success of the nesting Calliope Hummingbird.

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