

CALCULATING THE NOCTURNAL ENERGY EXPENDITURE OF AN INCUBATING ANNA'S HUMMINGBIRD

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Recently, attention has been focused on the bioenergetics of incubating female hummingbirds (Howell and Dawson 1954; Calder 1971, 1973). Hummingbirds are homeothermic with large surface area to volume ratios and have high rates of heat dissipation. During the night when cooler air temperatures prevail and feeding is prohibited, several species become torpid, lowering body temperatures and oxygen consumption (Bartholomew et al. 1957; French 1959; Pearson 1960; Lasiewski 1963; Calder 1971). This physiological state may be carefully regulated, as for *Eulampis jugularis* (Hainsworth and Wolf 1970). For incubating female hummingbirds, high nest temperatures maintained throughout the night indicate a nontorpid condition (Howell and Dawson 1954; Calder 1971). Pearson (1954) estimated that without torpor male Anna's Hummingbirds (*Calypte anna*) would require approximately 30% more metabolic energy during a 24-hr period and over five times more at night. Calder (1971) reviewed investigations on the nesting behavior of female hummingbirds and discounted increased feeding before roosting, decreased activity due to roosting, and lower metabolic rates for females as possible energy-maintaining mechanisms. He concluded that for the Calliope Hummingbird (*Stellula calliope*) nest construction and the large overhanging limb which shields the nest from cold night skies must be important factors in nighttime energy conservation.

The purpose of this investigation was to quantify the energy conservation properties of an Anna's Hummingbird nest and nest site and provide data on feeding behavior during incubation for comparisons with similar investigations. The analysis was accomplished by simultaneously measuring nesting behavior, nest temperatures, and microclimate for a nesting *C. anna*. A model was formulated to predict the nocturnal heat transfer of the bird and nest combination and used to compute

the relative thermal advantages of nest properties and nest site.

THE MODEL

During steady-state conditions when temperatures are not fluctuating, and neglecting heat storage and work, the energy balance of an organism is given by the following equation (Gagge 1969):

$$M = E \pm R \pm C \pm K \quad (1)$$

where: M represents the metabolic heat production; R is the net radiational heat transfer between the organism and its surroundings; E is the evaporative heat exchange; C is the convective heat transfer; and K is heat exchange by conduction. Each energy exchange can be expressed in cal/cm²/min (1 cal/cm²/min = 697.45 W/m²). In the absence of solar radiation at night, this expression can be expanded as follows:

$$M + [(IR_U + IR_D)/2] + h_c(T_s - T_A) + k_N(dT/dx) - (\epsilon\sigma T_o^4) - E = 0 \quad (2)$$

where: IR_U and IR_D are the upward and downward fluxes of infrared radiation, respectively; $\epsilon\sigma T_o^4$ represents the infrared radiation in cal/cm²/min emitted from an organism with emissivity (ϵ) and absolute temperature T_o , and σ represents the Stefan-Boltzmann constant; k_N is the coefficient of thermal conductivity (cal/cm²/min/°C) for the material with which the organism may be in contact; dT/dx is the temperature-gradient through the material; h_c is the convection coefficient for the organism in cal/cm²/min (°C); and T_s and T_A are the organism surface and air temperatures, respectively, in degrees Celsius.

In order to formulate an accurate energy balance expression for the incubating Anna's Hummingbird, nest temperatures were measured as in figure 1. The conduction term in equation 2 was partitioned into heat conducted from the body core across the feather layer and into the nest (K_W), the heat conducted similarly through the body and nest but into the branch supporting the nest (K_{NB}), and the heat conducted from the body core through the feather layer to the air (K_B). The convective term was also divided into two avenues of heat exchange, one from the hummingbird's topside (C_B) and the other from the exterior of the nest (C_N). Convective heat exchange from the branch was considered negligible since the temperature of the branch surface was assumed to be near air temperature. The nighttime

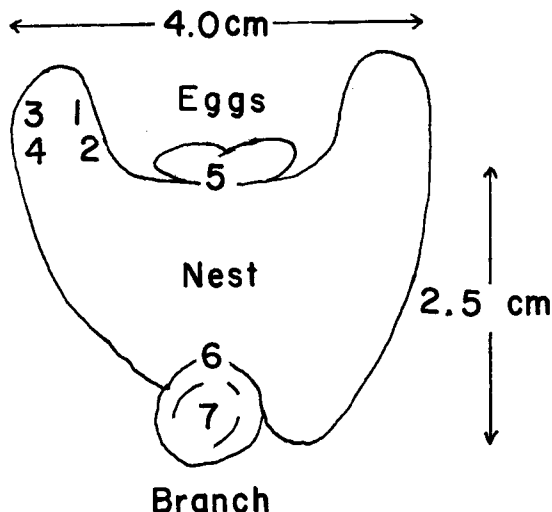


FIGURE 1. Schematic diagram of *C. anna* nest with thermocouple placement. Numbers indicate placement of numbered thermocouples. Arrows give sizes of different parts of the nest.

energy balance for the nesting Anna's Hummingbird can now be expressed as:

$$M = K_{NB} - K_W - K_B - C_N - C_B - IR_{Net} + E \quad (3)$$

where: IR_{Net} is the net infrared radiation received by the bird and nest combination. Expanding this expression to include measurable environmental and organism properties gives the following:

$$M = -([A_B k_N (dT/dx)_{NB} + A_T k_B (dT/dx)_B + A_W k_N (dT/dx)_W] - A_N hc_N (T_N - T_A) - A_T hc_B (T_F -$$

$$T_A) - [IR_D (\%SKY) - \epsilon \sigma T_A^4 (1 - \%SKY) - \epsilon \sigma T_A^4 + IR_U] / 2 + E/A \quad (4)$$

where: $(dT/dx)_{NB}$, $(dT/dx)_B$, and $(dT/dx)_{NW}$ are temperature gradients across the bottom of the nest, the insulating feather layers of the hummingbird, and the nest wall, respectively; hc_N (nest) and hc_B (bird) are the convection coefficients for a sphere with a diameter equal to the top of the hummingbird nest and a horizontal flat plate with diameter equal to the nest diameter, assuming the *C. anna*'s back lies flush with the top of the nest and fills the nest cavity, with the head protruding above the nest rim only slightly (this position was especially predominant on the cooler nights); A_B , A_N , and A_T are the fractions of the total surface area for the supporting branch, nest, and hummingbird's back which are effectively absorbing or dissipating energy; A is the total area of the bird; T_F is the feather surface temperature in °C for the back of the hummingbird; T_N is the exterior nest wall temperature in °C (thermocouple positions 3 and 4, fig. 1); and $\%SKY$ is the proportion of sky in view of the nest. The amount of downward infrared radiation from the sky was calculated by estimating the percentage of sky in view of the nest and the remaining proportion was considered radiating from the surfaces of the overhanging limbs which were assumed to be at air temperature. The evaporative energy loss was neglected due to the high nighttime relative humidities (greater than 76%) and low air temperatures. Other variables are as previously defined. Specific values assigned to the constants in equation 4 are listed in table 1.

Since neither T_C , T_F , nor M were known, an arbitrary value for T_F was chosen and M was calculated from equation 4. The body core temperature (T_C) that the assumed T_F implied was calculated from:

TABLE 1. List of standard parameter values.

Parameter	Symbol	Value
Total body surface area	A	12.8 cm ²
Total nest surface area in contact with branch	A_B	0.13 cm ²
Surface area of bird's topside	A_T	4.84 cm ²
Surface area of nest exterior	A_N	7.68 cm ²
Portion of topside exposed to sky	$\%SKY$	0.5
Thermal conductivity of feather layer	k_B	0.0126 cal/cm ² /min/(°C/cm) ^a
Thermal conductivity of nest	k_N	0.0036 cal/cm ² /min/(°C/cm) ^b
Temperature gradient across nest wall	$(dT/dx)_{NW}$	6.0/0.8 (°C/cm)
Temperature gradient across nest bottom	$(dT/dx)_{NB}$	8.0/1.3 (°C/cm)
Nest top diameter	diam.	4.0 cm
Emissivity	ϵ	0.97
Convection coefficient of topside	hc_B	$5.73 \times 10^{-3} \sqrt{\text{wind vel.}/\text{diam.}} \text{ cal/cm}^2/\text{min}/^\circ\text{C}$
Convection coefficient of nest	hc_N	$1.35 \times 10^{-3} (\text{wind vel.})^{0.5} / (\text{diam.})^{0.4} \text{ cal/cm}^2/\text{min}/^\circ\text{C}$
Stephan-Boltzman constant	σ	$8.13 \times 10^{-11} \text{ cal/cm}^2/\text{min}/^\circ\text{K}^4$
Mean interior nest temperature	T_N	
Cold night		26.2°C
Warm night		28.4°C
Mean night air temperature	T_A	
Cold night		8.1°C
Warm night		10.5°C
Wind velocity	wind vel.	50.0 cm/sec
Net infrared radiation	IR_{Net}	
Cold night		-0.075 cal/cm ² /min
Warm night		-0.010 cal/cm ² /min

^a Calculated in text.

^b Thermoconductivity of air.

$$(M)(Z) = k_B \frac{T_c - T_s}{dx_{c-s}} = k_{FT} \frac{T_s - T_f}{dx_{s-f}} \quad (5)$$

(after Porter and Gates 1969)

or

$$T_c = \frac{(M)(Z)dx_{c-s}}{k_B} + T_s \quad (6)$$

where: *Z* equals the ratio of the metabolic energy lost from the topside of the bird to the total metabolic energy, or $[Z = (K_B + C_B + T_p^4 + IR_D)/(K_B + K_{NB} + K_W + C_B + C_N - IR_{Net})]$; *T_s* is the skin temperature (thermocouple position 5, fig 1) and *k_B* and *k_{FT}* are the thermal conductivities of the fat and feather layers of hypothetical thicknesses *dx_{c-s}* (0.1 cm) and *dx_{s-f}* (0.5 cm), respectively. These values are also listed in table 1.

MATERIALS AND METHODS

MICROCLIMATE

Nest temperatures of an incubating female Anna's Hummingbird were measured with 36-gauge copper-constantan thermocouples during 16-20 April 1972, in San Diego, California. The nest was located approximately 8 ft above the ground in a leafless dead oak tree and was resting on a small branch, with a large branch only a few inches overhead. A nearby drainage (Adobe Creek) provided a large feeding area within 100 ft of the nest. Thermocouples were placed on the inside and exterior surfaces of the nest wall and bottom, and at the center of the supporting branch (fig. 1). A similar thermocouple, shielded from solar radiation, measured air temperature at the same height about 2 ft away from the nest. Total solar radiation was measured with a Moll-Gorzynski pyranometer located approximately 1 m above the tree a few meters away. Nighttime measurements of the upward and downward fluxes of infrared radiation were made using two Fritschen net radiometers, with one side of the sensing element of the instrument covered with an opaque dome. The inside of the dome was painted with 3M Black Velvet paint ($\epsilon = 0.98$). The dome temperature was recorded along with the sensor output. The radiant energy impinging on the dome-covered side of the radiometer was calculated using the Stefan-Boltzmann law $E = \epsilon\sigma T^4$ where: *T* is the absolute temperature of the inside radiating surface of the dome, and ϵ is the surface emissivity. σ is the Stefan-Boltzmann constant, 8.13×10^{-12} cal/cm²/min/°K. Hemispherical infrared flux was computed by adding the radiation from the inside of the dome to the measured output of the net radiometer. Both instruments were at the height of the nest, and exposed to the open sky, but with the same approximate horizontal influence. Periodic wind-speed measurements were made using a Hastings hot wire anemometer, and relative humidity was measured with a Honeywell relative humidity sensor. Millivolt signals from the sensor array were scanned every 10 sec and converted to appropriate units by means of a Vidar Data Acquisition System operating under programmed control of a Digital Equipment Corporation PDP 8/L computer. Nest temperatures, air temperatures, and solar radiation curves were plotted simultaneously with an on-line plotter.

BEHAVIOR

Periods of inattentiveness were determined by fluctuations in nest temperatures (thermocouple no. 5, fig.

TABLE 2. Microclimatic summary for *C. anna* during early incubation.

Date	Incubation Day	Max. Total Solar Radiation (cal/cm ² /min)	Sky	Air Temp (°C)		Nighttime Net IR (cal/cm ² /min)		Nest Temp. (°C)			
				max.	min.	max.	min.	on nest		off nest	
4/16	5	1.45	clear	26.9	6.5	-0.02	-0.04	max.	min.	max.	min.
4/17	6	1.70	part. cloudy	22.1	11.5	-0.01	-0.03	35.8	25.5	43.0	22.4
4/18	7	1.65	part. cloudy	18.5	9.3	-0.01	-0.04	33.8	27.3	37.3	16.8
4/19	8	1.55	part. cloudy	21.8	7.6	-0.02	-0.06	32.2	26.1	32.7	18.8
4/20	9	1.48	clear	22.5	4.0	-0.02	-0.10	32.9	23.5	39.3	18.8
								34.9	24.2	41.0	13.7

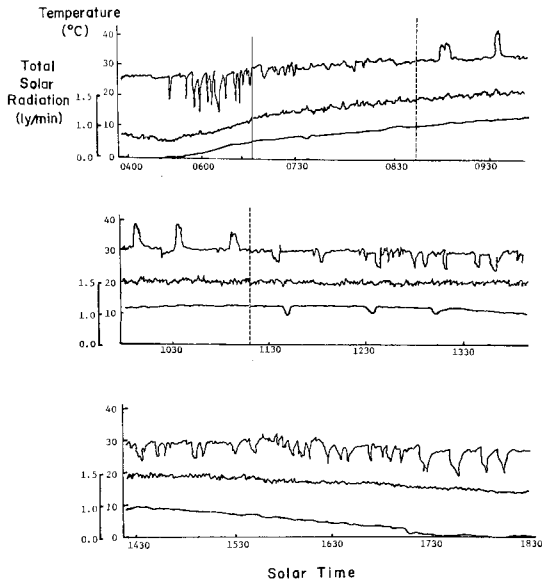


FIGURE 2. Total solar radiation, air and soil temperatures for 20 April. Top curves in each graph are nest temperatures, middle curves are air temperatures, and bottom curves are total solar radiation values. Solid vertical line represents a time scale change; dashed vertical lines denote time when nest was exposed to direct sunlight. Peaks in nest temperature are when hummingbird left the nest.

1). The accuracy of this method was tested by comparing times recorded from temperature fluctuations with visual estimates using binoculars and a stopwatch. Numerical differences using these two sampling methods during the same sampling period were statistically insignificant ($t = 1.45$, $df = 66$, $\alpha = 0.05$). Summaries were made of the total time of inattention, average time spent away from the nest per trip, and maximum times away from the nest per day over a 5-day period.

SIMULATIONS

The energy balance equation was solved for the metabolic rate (M) and body core temperature (T_c) given the surface feather temperature (T_f) of the hummingbird (Equations 3 and 4). By altering the %SKY parameter in equation 3, the relative effects of the overhanging limb were calculated. Also, by varying the thermal conductivity of the nest K_N and the nest thickness dx_N , the thermal importance of

nest structure was analyzed. The total metabolic expenditure for a given night was calculated by multiplying the area-specific metabolic rate (M) by the total body surface area (A). A was calculated by measuring the body dimensions of *C. anna* on the nest and computing the area of two cylinders approximately the area of the head and neck and main body. A was estimated to be 12.8 cm^2 for all calculations.

RESULTS

NEST MICROCLIMATE

Air temperature for the 5-day sampling period ranged from a maximum of 26.9°C to 18.5°C to a minimum of 11.5°C to 4.0°C (table 2). Nest temperatures (thermocouple position 5, fig. 1) varied from a maximum of 38.5°C to a minimum of 23.5°C during attentive periods and from 43.0°C to 13.7°C during absent periods. The mean nest temperature for attentive periods during the day was 31.9°C (29.0 – 34.7°C); the mean nest temperature during the night was 27.5°C (26.1 – 28.2°C). Net infrared radiation varied approximately $0.05 \text{ cal/cm}^2/\text{min}$ during the 5 nights sampled. Wind speeds ranged from about 10 to 100 cm/sec at night and from 50 to 450 cm/sec in the day. Relative humidity at night averaged 82.0% (76–94%). The nest was exposed to direct solar radiation only between 09:00 and 11:00; a large overhanging limb shaded the entire nest throughout the rest of the day. Figure 2 illustrates a typical daily course (20 April) of air and nest temperatures and total solar radiation recorded in the experiment.

BEHAVIOR

The general behavior of the female *C. anna* included feeding, nest maintenance, defensive behavior toward intruders, and a variety of nest movements such as quivering, turning, and nestling. Incubation lasted for 14 days; brooding, 12 days; and post brooding, 11 days. No male *C. anna* was observed in the vicinity during the nesting period.

The pattern of inattentiveness of *C. anna* is given in table 3 along with data from Calder

TABLE 3. Comparison of absence during incubation for the hummingbirds *C. anna* and *S. calliope*.

Parameter	<i>C. anna</i>	<i>S. calliope</i> ^a
\bar{x} day length (first departure to last arrival)	13:21	15:40
\bar{x} number of absences/day	75.5	100
\bar{x} min./absence	2.23	2.00
Incubation days recorded	5th–9th	8th–15th ^b
Max. min./absence	8.88	9.33
Total time absent	2.80	3.61
% of total day absent	21.0	22.9
Max. air temp. ($^\circ\text{C}$)	26.9	27.2
Min. air temp. ($^\circ\text{C}$)	4.0	0.2

^a Data from Calder (1971) for two *S. calliope* nests.

^b Last 7 days of incubation for one nest (incubation days for second nest not given).

TABLE 4. Absence versus time of day for *C. anna*.

Parameter	Solar Time		
	06:00-10:00	10:00-14:00	14:00-18:00
\bar{x} no. of absences	23.3 \pm 2.9 ^a	17.0 \pm 3.4	24.8 \pm 2.1
\bar{x} min./absence	1.8 \pm 0.23	2.1 \pm 0.16	2.6 \pm 0.18
Total time absent	39.4	33.8	64.3

^a Standard error.

(1971) for *Stellula calliope*. The total per cent time absent from the nest, corrected for differences in day length, was about 8% less for *C. anna* versus *S. calliope*. *C. anna* stayed away from the nest longer per trip but departed less frequently. Totaling the inattentive periods into three 4-hr segments showed that *C. anna* departed more frequently and was absent almost twice as long from 14:00 to 18:00 than from either 06:00 to 10:00 or 10:00 to 14:00 solar time. Air temperatures were similar for the two species in the day (maximum temperature) but cooler at night (minimum temperature) for *S. calliope*. The number of absences for *C. anna* during the morning and evening sampling period was similar, but the mean length of each departure was about 30% less in the morning (table 4). Comparable data for either *S. calliope* or *C. anna* were not found in the literature. Howell and Dawson (1954) listed similar data for *C. anna* but for only two complete incubation days just prior to hatching. These data did not show differences in either the number of absences or the duration of absences between the morning, afternoon, or evening.

During periods where the nest was exposed to direct solar radiation (09:00-11:00), *C. anna* departed less often but stayed out longer (table 5). The fewest number of departures occurred when nest temperatures rose above 40°C during an absence (16-20 April). However, the total time of absence on these occasions was greater. Nest temperatures during insolation on 20 April are plotted in figure 2.

SIMULATIONS AND SENSITIVITY TESTS

The metabolic heat production calculated for the incubating female *C. anna* during a simulated cold night ($T_A = 8.0^\circ\text{C}$, $T_C = 40.0^\circ\text{C}$,

$T_N = 26.0^\circ\text{C}$, wind vel. = 50 cm/sec, $IR_{\text{Net}} = -0.02$) was 0.440 cal/cm²/min and 0.382 cal/cm²/min on the simulated warm night ($T_A = 10.5^\circ\text{C}$, $T_C = 40.0^\circ\text{C}$, $T_N = 28.0^\circ\text{C}$, $IR_{\text{Net}} = -0.10$). Using the time between the last arrival of the evening and the first departure of the following morning as total night length (10.7 hr), the predicted metabolic expenditure was 3.62 Kcal for the cold night or 3.27 Kcal for the warm night. The thermal conductivity of the nest (k_N) was calculated to be 0.0126 cal/cm²/min/(°C/cm) where $k_N = K_W [(dT/dx)_W]/A_N$.

Varying a hypothetical average nest thickness from 1.0 cm to 2.5 cm and the thermal conductivity of the nest from 0.0 to 0.020 cal/cm²/min/(°C/cm) had the greatest effect on predicted metabolic heat production (M) (fig. 3). An increase of 0.05 cm in the average nest thickness or an increase in thermal conductivity of 0.0005 would increase M by approximately 0.0025 cal/cm²/min or 0.022 Kcal/night. Varying the body core temperature (T_C) by 0.45°C or the %SKY by 0.2 would have altered M by the same approximate amount. Decreasing the thermal conductivity of the nest by 0.01 cal/cm²/min/(°C/cm) or the nest thickness by 0.5 cm decreased the calculated metabolic heat requirement by 13% on the cold night; completely shielding the nest from the sky (%SKY = 0.0) and lowering the body core temperature by 8°C resulted in only a 6% savings in predicted nocturnal energy expenditure.

DISCUSSION

NOCTURNAL ENERGY REQUIREMENTS

Calder (1971) predicted a nocturnal metabolic heat expenditure for a nontorpid, incubating

TABLE 5. Absence and maximum nest temperatures during periods of insolation (09:00-11:00).

Date	Sky	No. of absences	Max. nest temp. (°C)	\bar{x} min/absence	Total time absent (min)
4/16/72	clear	3	43.0	4.69	14.1
4/17/72	cloudy	7	37.3	0.67	4.7
4/18/72	cloudy	10	32.7	1.27	12.7
4/19/72	cloudy	7	39.3	1.60	11.2
4/20/72	clear	4	41.0	4.59	18.4

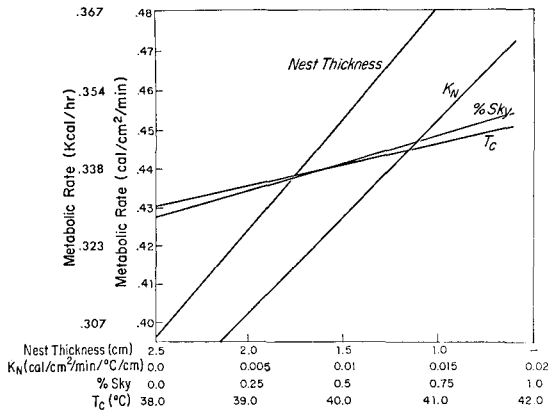


FIGURE 3. Nocturnal energy expenditure for *C. anna* at various body core temperatures (T_C), nest thicknesses, thermal conductivities (K_N), and exposures to the sky (%SKY). Each line is a plot of one of these four variables recorded along the abscissa.

female *C. anna* of 3.44 Kcal (max. and min. air temperatures 14°C and 10.6°C) based on metabolic rates for a perching male *C. anna*. The simulated results for an incubating female *C. anna* predicted a metabolic expenditure of 3.27 Kcal ($T_C = 39.96^\circ\text{C}$) for a relatively warm night (max. and min. air temperatures 13.8°C and 10.5°C) including the insulative effects of the nest. These values are somewhat lower than previously reported for *C. anna* over the same time period and at the same temperature (interpolated from Lasiewski 1963). However, his results are for resting *C. anna* and not incubating females which maintain high nest temperatures throughout the night. The effort here is not to compare absolute metabolic heat production values but to analyze the relative importance of the thermal characteristics of the nest and nest site and predict metabolic heat requirements from microclimate data. The former comparison would need more extensive microclimate measurements and a more accurate organism characterization. Of special quantitative importance is the variation in surface skin temperatures relative to the incubation patch which warms the eggs. The simulations presented here assumed skin temperatures equal to the temperatures recorded at position 5 in figure 1. This position is very near if not touching the incubation patch and most likely overestimates the average skin surface temperature over the remainder of the bird. However, the relative effects of the parameters varied in equation 6 and recorded in figure 3 are important for comparative purposes. The ultimate accuracy in predicting absolute metabolic energy requirements is limited only by the accuracy of measurements detailing body

feather morphology, skin temperature distribution, fat deposition, nest morphology, thermal conductivities, etc. Data of this nature will enable a more thorough analysis of the thermal ecology of hummingbirds.

NEST CONSTRUCTION

The most effective nocturnal heat-conserving activity for an incubating Anna's Hummingbird would be either to increase the nest thickness or to decrease its thermal conductivity. This ability to vary nest construction according to environmental conditions has been observed in hummingbirds (Wagner 1955). Decreasing the thermal conduction of the nest entails selection of materials with low thermal conductivities or construction techniques that decrease thermal conductivity by creating insulated air spaces. The nest would have to be compact enough to provide support and to prevent air flow through the nest and yet to contain a high proportion of air space. The value for K_N calculated here, 0.0126 cal/cm²/min/(°C/cm), is relatively low and approximates polar bear fur (Scholander 1955) or asbestos wool (Weast 1973).

NEST SITE

Energetically, the advantages of building the nest under a large overhanging limb are questionable. Comparing the effect of environmental variations on total metabolic energy output between the simulated warm and cold night (3.62 Kcal vs. 3.27 Kcal) reveals that the 3% savings by avoiding exposure to the cold night sky is comparatively small. However, during periods of cold stress, the importance of this saving may be amplified. The limb may play a more important role in shading the nest and preventing high nest and egg temperatures. The reluctance of *C. anna* to depart during periods when the nest was in direct sunlight (09:00–11:00) may be an attempt to prevent the eggs from getting too hot. The longer absence per departure on sunny mornings compared to absences during the same hours on cloudy mornings could be an energetic necessity since the total times absent from the nest were more similar than the average times of each departure. Again, more extensive data on nest microclimate in various geographic locations and for different types of nest sites are needed before discounting the overhanging limb as a possible aid to energy conservation during the night. Although protective overhangs have also been mentioned in respect to predation, rain, and nighttime energy conservation (Wagner 1955; Dorst 1962; Smith 1969), the thermal advan-

tages of shading the eggs while the female hummingbird is absent have not been evaluated. More quantitative data on inattentiveness are needed for nest sites exposed to direct solar radiation.

FEEDING

C. anna must store energy reserves for the night. Approximately 2.5 Kcal would be expended by *C. anna* during the night even with a significantly thicker nest, lower nest thermal conductivity, and a nest entirely shielded from the sky by an overhanging limb. Since this value represents approximately one-fourth of the total daily metabolic requirements (Pearson 1954), approximately one-fourth of the total daytime feeding should be devoted to nighttime energy storage. The 50% increase in total feeding time recorded here, in the time period 14:00–18:00, equaled approximately one-fourth of the total feeding effort. Depending upon *C. anna*'s diet, this period should be adequate to store enough energy for the night.

After corrections are made for different day lengths, the pattern of inattentiveness found here for *C. anna* was similar to data on *S. calliope* (Calder 1971). Prior data for *C. anna* showed longer durations of inattentiveness and longer maximum inattentive periods compared to *S. calliope* (Howell and Dawson 1954).

It is probable that considerable intraspecific variation occurs in the thermoregulatory aspects of nesting behavior. This variation is most likely due to varying physical and biological factors which affect the availability of food and the organism's heat balance. If the organism is to survive sudden changes in climate (a common occurrence during the spring), the ability to alter feeding behavior and possibly diet would be more energetically economical than constructing a nest that would insulate against all possible fluctuations in weather. The ability to vary nest construction and location would not compensate for short-term changes in microclimate. If the hummingbird is confined narrowly within certain bioenergetic limits, the ability to alter feeding patterns with changing microclimate would be essential. More quantitative data are needed on feeding times, diet, and microclimate in order to evaluate correctly the thermoregulatory behavior of hummingbirds. The energy balance model formulated in this paper can be used to predict hypothetical feeding and nesting behavior from microclimate studies and to predict temporal metabolic energy demands for the Anna's Hummingbird. Correlations of nesting success and microhabitat

selection could be predicted and verified by field observations. The relative importance of thermoregulatory behavior and physiology during nesting can then be evaluated.

SUMMARY

A heat-balance equation was formulated to predict the nocturnal metabolic heat requirements for a nesting female Anna's Hummingbird. Calculated estimates of metabolic heat production agreed with estimates from laboratory measurements of oxygen consumption. Sensitivity tests conducted with the model indicated that varying the thickness and thermal conductivity of the nest had the greatest apparent effect on metabolic heat requirements. Altering the amount of exposure to the sky overhead or lowering the body core temperature had the least effect.

Field observations and measurements showed that *C. anna* was absent from the nest almost twice as long during hours in the evening (14:00–18:00) than for the same period in the morning (06:00–10:00) or noon (10:00–14:00). This increased feeding effort approximated that required for nocturnal energy storage. During the morning when the nest was in direct sunlight, nest temperatures rose to over 40°C during a departure and there was a tendency for *C. anna* to depart less often. Absence patterns for this *C. anna* were more similar to those of *Stellula calliope* than patterns previously reported in the literature for another *C. anna*.

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