

# DAYLENGTH AND THE HUMMINGBIRDS' USE OF TIME

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PHYSIOLOGICAL homeostasis is maintained with energy that a bird must extract from its environment. Effective investment of the bird's time in exchange for the necessary energy must be the objective of maintenance strategy. If the rate of intake is less than the metabolic rate over a period of time, homeostasis is impossible.

The temporal aspects involved in attainment of energy balance by a diurnal bird include duration of adequate light for effective foraging, cyclic availability of food, flight time to a food source or successful prey capture, duration of the nocturnal fast, and the daily environmental temperature cycle that will influence the overall energy cost. In summer the length of daylight for foraging increases with latitude, and the duration of the nocturnal fast decreases. In winter, the ratio of feeding time to fasting time is reduced with increasing latitude.

The endurance of fasting would be directly proportional to the amount of energy in reserve and inversely related to the rate of degradation of the reserves:

$$\text{Time} = \text{energy} \div \text{metabolic rate} \quad (1)$$

Fasting endurance time is one form of physiological time, a stimulating discussion of which is found in a paper by Hill (1950) pointing out that the physiological time scale is highly dependent upon body size. This is apparent when equation (1) is examined allometrically. The primary energy storage is in the gut. The amount of energy yielding food that the digestive tract can contain at the end of a day's feeding should be a function of the size or mass of the stomach plus intestines. Brody (1945) derived the relationship:

$$\text{Gut mass} = 0.0997 m^{0.985} \quad (2)$$

where  $m$  = body mass in grams. Quiring's tabular data (1950: 516) for birds yield, similarly:

$$\text{Gut mass} = 0.096 m^{1.003} \quad (2a)$$

Thus maximum gut energy storage is essentially a linear function of body size. From feeding experiments Hainsworth and Wolf (1972c) found that crop volume of tropical hummingbirds weighing 2.7 to 10.1 g was also linearly related to body mass.

The metabolic rates of birds are proportional to mass to the 0.72 to 0.73 power at thermoneutrality and to the 0.42 to 0.53 power at 0°C

(Lasiewski and Dawson 1967; Kendeigh 1969; Aschoff and Pohl 1970a, 1970b; Calder 1974). Substituting this information in equation (1):

$$\text{Fasting endurance time} \propto m^{0.985} \div m^{0.73} = m^{0.26} \quad (1a)$$

or, at 0°C,

$$\text{Fasting endurance time} \propto m^{1.003} \div m^{0.42} = m^{0.58} \quad (1b)$$

Thus fasting endurance increases with body size. Qualitatively the same conclusion comes from consideration of maximum fat reserves, and Kendeigh's (1945) data show that fasting survival time at colder temperatures was proportional to  $m^{0.59}$ . Expressions for other physiological times range from  $m^{0.19}$  to  $m^{0.33}$  (Calder 1974). Somehow these must be compensated for as each animal, large or small, couples to the daily cycle of the earth's rotation.

Visual and auditory conspicuousness makes birds useful for studies of physiological time scales. The sequence of onset and cessation of songs of different birds has been recorded in the eastern United States (e.g. Wright 1913, Allard 1930, Leopold and Eynon 1961), and similar sequences, of genera if not always the same species, have been recorded in the Rocky Mountains in Colorado (Steiker and Gaffney MS) but no consistent size influence was shown. Nice (1943) related time of first activity to light intensity for the Song Sparrow (*Melospiza melodia*). The roosting of Starlings (*Sturnus vulgaris*) has also been correlated with light intensity (Davis and Lussenhop 1970). The temporal organization or "temporal niche" of birds has been investigated extensively (excellent review: Aschoff 1967, also Aschoff and Pohl 1970a, 1970b). Aschoff examined the influence of light intensity in a continuous environment on the length of endogenous cycles and the component phases of activity and rest. He also related this to factors of latitude and season, but described no effect of body size.

Energy demanding, chilling climates occur in winter and at higher elevations in summer. Consequently we have an opportunity to gain insight into time use by comparing hummingbird species of similar sizes and short fasting endurance, breeding in similar climates, but with considerable difference in available daylength. Breeding in the summer in Colorado and Wyoming, Broad-tailed (*Selasphorus platycercus*) and Calliope (*Stellula calliope*) Hummingbirds have 29 to 40% more time per day than does an Anna's Hummingbird (*Calypte anna*) breeding in Arizona in the winter. The latitude and season of my observations of the Anna's Hummingbird probably approach the minimum daylength any nesting hummingbird would ever experience.

## METHODS

The times of first and last activity were recorded by three methods, and from them the length of the birds' daytime activity ( $\alpha$ ) and nocturnal ( $\rho$ ) phases were determined. Electronic recordings of nest temperatures show cooling and warming deflections for each departure and arrival, so that first and last trips could be determined (for details see Calder 1971, 1973). Visual observations and timing of some of the arrivals and departures provided an accurate check on the recordings as well as additional data at nests, at flower patches, and at feeders with 25% sucrose solutions. The flight sounds produced by the primary feathers of male Broad-tailed Hummingbirds are audible for considerable distances, so that times of first and last flights were easily detected.

Other species studied included the Calliope, Anna's, Costa's (*Calypte costae*), Broad-billed (*Cyananthus latirostris*), and Black-chinned (*Archilochus alexandri*) Hummingbirds. Study sites were: Jackson Hole Biological Research Station, Moran, Wyoming (elevation 2060 m: Calliope); Rocky Mountain Biological Laboratory, Gothic, Colorado (2900-3020 m: Broad-tail); Santa Catalina Mountains, north of Tucson (865-1310 m: Anna's, Costa's, Broad-bill); and in Tucson, Arizona (800 m: Black-chin).

Watches were synchronized with National Bureau of Standards Radio Station WWV, Fort Collins, Colorado. Sunrise, sunset, and civil twilight times were calculated from "The air almanac" (Anon. 1970, 1971, 1972), and related to field notations of local topographic sunrise.

Light intensities were measured with an incident light meter with a cosine-correction diffuser disc (Photo-Research FC-200A). Temperatures were obtained with mercury thermometers and a thermocouple recorder (36 ga type T thermocouples connected to a recording potentiometer (L & N Speedomax W) on 2 mV = -10 to +40 °C span). The data were analyzed with an electronic calculator system (HP 9100B-9125).

## RESULTS AND DISCUSSION

*Onset and cessation of activity.*—Earliest and latest activity data are given in Table 1. The cool climate of the Rocky Mountains would seem to be an incentive to feed as early and late as possible. In the following, references to sunrise and sunset are almanac times, not appearance above local topography. The diffuse or scattered light overhead should be essentially independent of topography. Males and prenesting females of the Broad-tailed Hummingbird are similar in beginning their feeding about 20 min before sunrise and, on the average, beginning the nocturnal fast 13½ min after sunset. Incubating females left the nest 5½ to 9 min later in the morning and returned about 12 min earlier in the evening than before nesting, apparently sacrificing feeding time in favor of additional warming of the eggs.

The smaller Calliope Hummingbirds, which breed farther north where the solar daylength is 35 min longer, got up earlier and retired later relative to sun times than did the Broad-tails during incubation. Thus the

TABLE 1  
EARLIEST AND LATEST ACTIVITY OF HUMMINGBIRDS RELATIVE TO ALMANAC SUNRISE

Species	Daylength <sup>1</sup> (h)	First active (min before sunrise) <sup>2,3</sup>			Last active (min after sunset) <sup>2,3</sup>		
		Nonnesting <sup>4</sup>	Incubating	Brooding	Nonnesting <sup>4</sup>	Incubating	Brooding
Calliope ♀	14.53-15.45	—	14.6 ± 7.29 (n = 20, 2 ♀)	18.0 ± 4.64 (n = 23, 2 ♀)	—	10.4 ± 6.69 (n = 17, 2 ♀)	16.4 ± 5.65 (n = 18, 2 ♀)
Broad-tail ♂ '71	13.95-14.90	19.8 ± 4.68 (n = 14)	—	—	10.3 ± 4.79 (n = 7)	—	—
Broad-tail ♂ '72	13.83-14.92	21.7 ± 2.45 (n = 43)	—	—	16.6 ± 4.80 (n = 19)	—	—
Broad-tail ♀ '71	13.95-14.90	—	11.1 ± 11.25 (n = 41, 5 ♀)	13.6 ± 8.26 (n = 25, 4 ♀)	—	-1.9 ± 14.23 (n = 46, 5 ♀)	2.0 ± 15.13 (n = 22, 4 ♀)
Broad-tail ♀ '72	13.83-14.92	20.1 ± 2.55 (n = 11)	14.5 ± 5.53 (n = 62, 11 ♀)	18.5 ± 4.10 (n = 38, 9 ♀)	13.6 ± 4.39 (n = 4)	-1.4 ± 14.63 (n = 66, 11 ♀)	6.8 ± 6.78 (n = 39, 9 ♀)
Anna's ♂	10.37-11.08	13.3 ± 10.06 (n = 89, 1 ♂)	—	—	0.8 ± 13.63 (n = 38, 1 ♂)	—	—
Anna's ♀	11.08-11.50	—	17.3 ± 1.06 (n = 2, 1 ♀)	19.6 ± 2.49 (n = 12, 1 ♀)	—	3.0 ± 4.24 (n = 2, 1 ♀)	6.5 ± 5.36 (n = 9, 1 ♀)
Black-chin ♀	13.42-13.70	—	12.3 ± 3.91 (n = 12, 1 ♀)	—	—	-22.5 ± 12.52 (n = 13, 1 ♀)	—
Broad-bill ♀ <sup>4</sup>	12.28-13.15	—	12.3 ± 7.27 (n = 4, 2 ♀)	—	—	—	—
Costa's ♀ <sup>4</sup>	12.52-13.08	—	3.3 ± 4.60 (n = 2, 1 ♀)	—	—	—	—

<sup>1</sup> All values ± SD; sun times from "The air almanac" for dates and location of observations.

<sup>2</sup> Mean ± SD; n = number of observations; number of individuals contributing data indicated if known.

<sup>3</sup> Cooling deflections on potentiometric recorder, except as noted. Numbers in parentheses are deflections of sufficient duration for feeding.

<sup>4</sup> Direct observation.

incubating Calliope hen had 37 min more per day in which to feed (Figs. 1 and 2). After the eggs hatched, both species increased their feeding daylength relative to solar daylength by about 9 min.

The winter-breeding Anna's female tended to rise earlier and retire later, relative to sun times, than did the Calliopes and Broad-tails in summer, but the values fell within the highly variable ranges for the Broad-tails, so this difference was not significant. The male Anna on a territory faced the shortest daylengths represented in the data but appeared later, relative to sunrise time, than the female (see Fig. 3). The high variability of the male data and the site of acquisition (suburban sprawl, availability of other feeders unknown) suggest that he was using alternative feeding sources. In late autumn and early winter, the male Anna's first appearance at the feeder tended to be earlier when temperatures were lower, reflecting higher energy requirements (Fig. 4).

Hummingbird activity as a function of time has been mentioned only incidentally farther to the north. The earliest and latest visits of the Ruby-throated Hummingbird (*Archilochus colubris*) to a feeder were 0430 and 2140, an active daylength of 17.17 h (Miller and Miller 1971). The solar day at 53° 38' N is 16.33 h.

*Daily use of time.*—The time between sunrise and sunset was 65% of the 24-h cycle during Calliope incubation in Wyoming, 61% for the nesting Broad-tail in Colorado, but only 46% for the Anna nesting in the Arizona winter. Thus the Calliope fasted 33% of the cycle, the Broad-tail 39%, and the Anna's 52%. The Ruby-throat at 53° 38' N fasts only 6.83 h, only 28.5% of the daily cycle (calculated from Miller and Miller 1971 and "The air almanac"). Breeding at a high latitude has an advantage for hummingbirds.

The number of recesses or absences from the nests was highly variable. Distance to food supply was probably a major factor. The eggs cool during the recess and, if the food supply is nearby, short trips might be preferable. The amplitude of the egg temperature would be reduced at the price of incomplete filling of the crop. With a greater distance to food it would seem more economical to fill to capacity and thereby maximize the ratio, energy intake/energy expended (see Wolf and Hainsworth 1971; Wolf et al. 1972; Hainsworth and Wolf 1972a, 1972b for excellent discussions of the energetics of feeding in hummingbirds). The Anna's Hummingbird in the present study usually traveled out of sight to feed, as no flowers bloomed near the nest. A garden of introduced red *Aloe* was 1.6 km distant and beyond the canyon mouth in the direction of many departures. On one occasion I watched the female fly up the canyon until

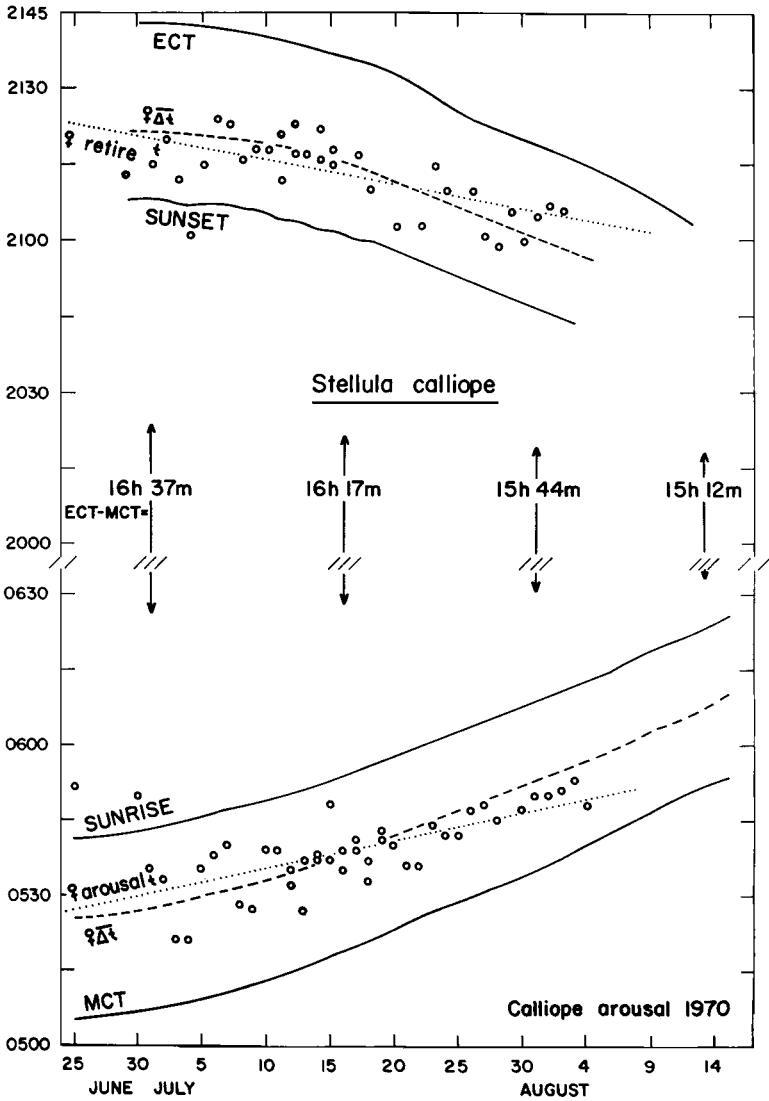


Fig. 1. First departure from nest and last arrival times of two female Calliope Hummingbirds with almanac sun and twilight times. Dashed lines indicate mean difference from sunrise and sunset times; dotted lines signify least square regressions ( $P < 0.001$  for both departures and arrivals). Twilight to twilight daylengths are indicated in the mid-break.

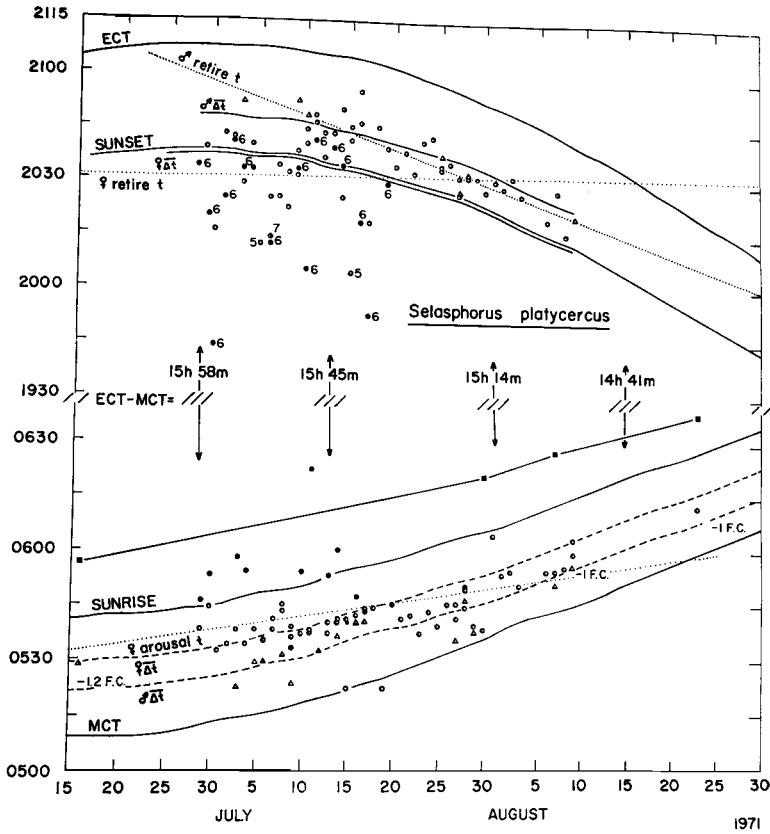


Fig. 2. First and last activity times for the Broad-tailed Hummingbird in 1971. Top: Last arrival at nest (○ = female Broad-tail; numbers where indicated are females from nests 5, 6, and 7) and latest observations (△ = male Broad-tail), almanac sunset and evening civil twilight (ECT). Shorter solid lines are mean differences from sunset time for females and males. Dotted lines are least squares regressions for females (not significant,  $P > 0.1$ ) and male Broad-tails ( $P < 0.001$ ). Bottom: First departure from the nest (○ = female Broad-tailed Hummingbird; ● = female of nest 6) or first appearance (△ = male Broad-tail) relative to morning civil twilight (MCT) and sunrise ("The air almanac" times) and the time at which the sun first illuminated a local landmark (Gothic Peak, 3860 m, ■—■). Lower dashed line indicates mean difference between male Broad-tail arousal and sunrise; upper dashed line is the mean difference for females. Dotted line is a least squares linear regression on female arousals ( $P < 0.001$ ). Middle: Almanac day-length. Except for the scatter of early retirement times for females, the data for 1972 were similar (see Table 1).

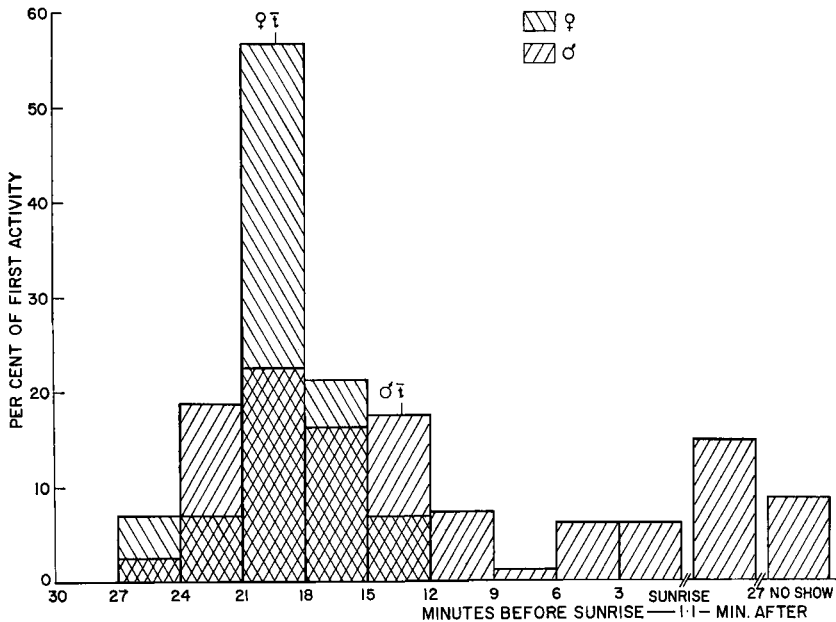


Fig. 3. Distribution of times relative to almanac sunrise at which male and female Anna's Hummingbirds were first active on winter mornings near Tucson, Arizona. Calculated as 100% = activity before sunrise for each sex (days for the male when arrival was after sunrise or not at all were not included in a calculator program plotting 10 equal time classes).

she was too small to see (10× binoculars; after a 42-sec climbing flight in one direction against a clear sky). She returned after a 20-min absence, possibly used for feeding on manzanita (*Arctostaphylos pringlei*) higher in the mountains.

A further source of variability in the number of recesses per day is the subjective decision as to which cooling deflections of the nest temperature record were feeding trips. Many brief trips could have been for preening, defense of nest site, or interaction with male hummingbirds, which I noted at several nests. The recess numbers in parentheses in Table 2 are those long enough, and presumed to be feeding trips.

The sum of recess durations for Broad-tails, Calliopes, and the Arizona Anna's were remarkably similar during incubation. Total absence was greater in the brooding stage, but interspecifically similar, despite differences in daylength and number of recesses. Thus compared to others, the Anna's had a shorter daylength but similar time away and a lower daytime percent constancy (attentiveness). The Anna's studied by Howell



TABLE 2  
COMPARISON OF USE OF TIME BY NESTING FEMALE HUMMINGBIRDS IN NORTH AMERICA COMPARED WITH TERRITORIAL MALES

Species	Location	Month	Air temp. range (°C)	Solar day (min) <sup>1</sup>	Activity daylength (min) (n)	Recesses (day <sup>-1</sup> ) <sup>2</sup>	Time away (min) (n)	Constancy (♀) or perched (♂) (% of day) <sup>3</sup>
<b>Incubation</b>								
Calliope	Wyoming	Jun.-Jul.	4.4-28	942	967 17	99.5	216.6 1	77
Broad-tail	Colorado	Jun.-Jul.	1.4-26.2	878	887 41	90.6 (60.1)	190.8 5	78
Anna's <sup>4</sup>	Arizona	Feb.	4.0-22	665	689 2	33	210.3 1	69
Anna's <sup>4</sup>	California	Apr.	10 -22	812	843 1	65	173 1	79
Black-chin	Arizona	Apr.	11 -36	814	804 12	65.4 (49.6)	—	—
<b>Brooding</b>								
Calliope	Wyoming	Jul.-Aug.	4.7-23.9	940	974 18	84.1	306.6 2	67
Broad-tail	Colorado	Jul.-Aug.	3.7-25.5	874	890 22	83.4 (59.8)	330.6 2	62
Anna's <sup>5</sup>	Arizona	Feb.	5 -25	677	701 13	53(38)	328.4 2	53
Anna's <sup>5</sup>	California	May	—	813	838 1	40	117 1	86
<b>Feeding: territorial males</b>								
Anna's <sup>6</sup>	Arizona	Oct.-Feb.	(-)7-36	644	658 40	—	—	—
Anna's <sup>6</sup>	California	Sep.	10.5-22	772	772 2	—	—	82
<b>Breeding: territorial males</b>								
Anna's <sup>7</sup>	California	Jan.	—	615	639 1	—	—	81
Anna's <sup>7</sup>	California	Mar.	—	731	759 1	—	—	80
Broad-tail	Colorado	Jun.-Jul.	—	878	910 1	—	—	76

<sup>1</sup> Mean for period of observation from "The air almanac" (Anon. 1970, 1971, 1972).  
<sup>2</sup> Determined by direct observation for Anna's and by electrical recording and sample direct observation for Calliope, Broad-tail, and Black-chin. Larger value is total for cooling deflections in recorder trace, while values in parentheses are of sufficient duration for feeding, based upon sample observations and subjective evaluation.  
<sup>3</sup> Percent of active daylength spent on the nest.  
<sup>4</sup> Howell and Dawson (1954).  
<sup>5</sup> Date of hatching.  
<sup>6</sup> Pearson (1954).  
<sup>7</sup> Stiles (1971).

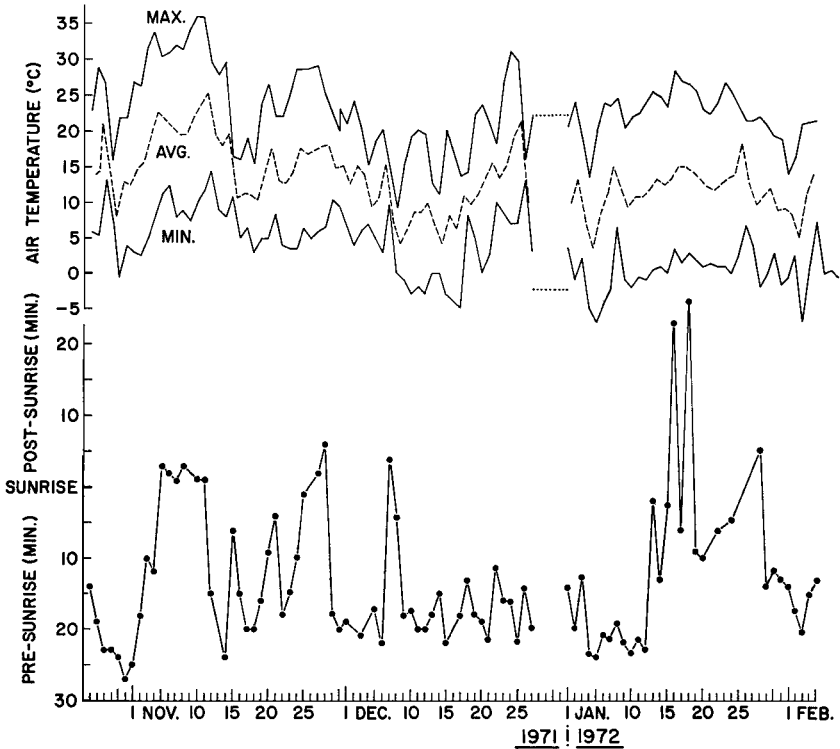


Fig. 4. Maximum, mean, and minimum air temperatures correlated with time of first arrival of Anna's Hummingbird at a feeder containing a  $\frac{1}{4}$  sucrose solution.

and Dawson (1954) in California was in an urban environment where domestic plants could have provided an unnaturally rich or nearby food supply while the temperature was not so cold at night, reducing the energy cost of thermoregulation.

*Light intensity.*—The vision of hummingbirds has been studied with regard to field of view and color preference, but apparently not for light sensitivity (Pumphrey 1961, Grant and Grant 1968, Miller and Miller 1971, Raven 1972). I find no information on the minimum illumination necessary for effective foraging so perhaps my field observations are relevant in this regard.

The onset of activity by mid-latitude birds at daybreak as indicated by song has been closely correlated with light intensity, while other environmental factors such as temperature and wind only serve to inhibit or modify this (Allard 1930, Nice 1943, Leopold and Eynon 1961). The

TABLE 3  
COMPARISON OF LIGHT INTENSITIES OF FIRST AND LAST ACTIVITIES IN LONG DAY AND SHORT DAY BREEDING OF HUMMINGBIRDS

Conditions	Broad-tail		Anna's		Broad-tail		Anna's	
	(lux)	(n)	(lux)	(n)	(lux)	(n)	(lux)	(n)
♂, prenest <sup>1</sup>	15.2 ± 8.10	11	99.2 ± 140.39 <sup>2</sup>	30	39.4 ± 44.50	11	—	—
♂, breeding <sup>1</sup>	9.6 ± 7.47	24	—	—	25.1 ± 15.43	8	—	—
♀, prenest <sup>1</sup>	14.5 ± 3.68	8	—	—	32.5 ± 21.36	3	—	—
♀, incubating <sup>2</sup>	—	—	—	—	—	—	—	—
nest 1-72	6.2 ± 3.47	5	17.3 ± 0.35	2	21	1	114	1
nest 3-72	39.3 ± 21.81	13	—	—	—	—	—	—
nest 9-72	36.8 ± 35.71	2	—	—	—	—	—	—
♀, brooding <sup>2</sup>	—	—	—	—	—	—	—	—
nest 9-72	5.9 ± 2.92	11	6.1 ± 3.67	12	34	1	123.1 ± 109.2	10
nest 23-72	6.4 ± 2.66	7	—	—	18.5 ± 16.21	2	—	—

<sup>1</sup> Measured under open sky.  
<sup>2</sup> Highly variable, as if using alternative food sources, minimum 9L (see Fig. 4).  
<sup>3</sup> Measured beneath nest tree.

hummingbirds in this study seem to be no exception to this correlation (Table 3).

Light intensity measured in the open (unforested meadows) at the time of first feeding flights was similar for male and female Broad-tailed Hummingbirds when the females had not yet begun to incubate. The light intensity at last flight or feeding in the evening was slightly more than twice that of first activity at daybreak.

Once incubation began, both sexes were active at slightly lower light intensities than previously. Light intensities were then measured at the nest or beneath it, so the light intensity for the first departure from one of three incubated nests and at two nests monitored during brooding were lower than that recorded earlier under the open sky where males were first noted. The nocturnal roosts of the males were not located, so it was not possible to compare light intensities at their respective points of departure. The apparent variability between nests (light intensities between 6.2 and 39.32) is only a range of 0.6 to 3.9 footcandles (10.76 lux = 1 footcandle). No statistical significance can be claimed for the difference between incubation and brooding with regard to the light intensities of first and last activity, although in both years the females tended to depart with a slightly greater lead before sunrise and to return with a slightly greater lag at sunset after the eggs hatched.

Just as the female Anna's Hummingbird became active with a greater lead on sunrise time than the male, she was also departing at a lower light intensity (Fig. 5).

The interesting point is that the winter-nesting Anna's Hummingbird, with longer night fasts and shorter foraging days, did not or could not extend foraging when light intensities were lower than those used by female Broad-tails. The Broad-tails are similar in size but have the advantage of longer summer days. The hummingbirds in both circumstances were perhaps foraging at something approaching minimal light intensity. The minimum light intensities for the two sexes of the two species were: Broad-tail male, 4.0 lux in open (AM), 6.8 lux (PM); Broad-tail female, 1.6 lux at nest (AM); Anna's male, 9.0 lux in open (AM); Anna's female, 2.5 lux beneath nest (AM).

*Energy budget estimates for the Anna's Hummingbird.*—Pearson (1954) applied laboratory data for metabolism during hovering, perching, sleep, and torpor to the time budget of a male Anna's Hummingbird on his feeding territory. This estimate appears to have been the original time energy budget account for free-ranging metabolism. Stiles (1971) drew up time energy budgets of male Anna's on breeding territories.

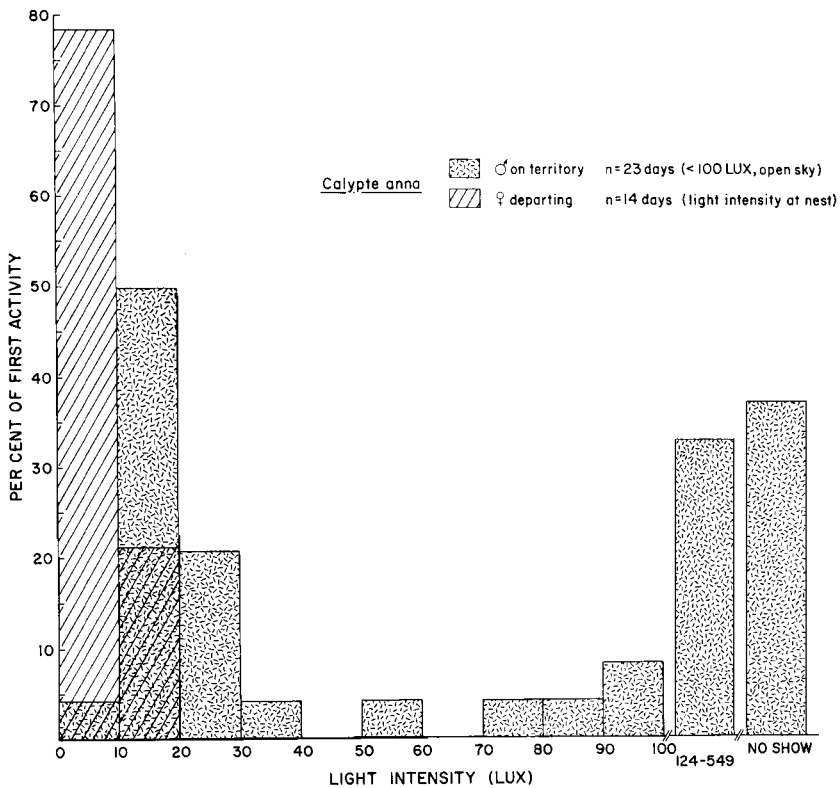


Fig. 5. Distribution of light intensity readings at the time of first morning activity near Tucson in the winter. The roost of the male was not located, and light intensities are those recorded under open sky in the vicinity of a feeder, 24 December–5 February. Light intensity at the time of female departure was recorded 3 m beneath the nest, 17 February–3 March. Thus the values for the two sexes are not strictly comparable. 100% = arrivals at light intensities < 100 lux (before sunrise).

I calculated a crude budget for the female Calliope Hummingbird from nest temperature recordings (duration of cooling in recesses) and direct observations of departure and arrival times. I converted times to energy units with Lasiewski's (1963) metabolic data for the Calliope. The total energy budget was similar to that of the Anna's males studied by Pearson, despite sexual differences in habits (Calder 1971). My speculative comparison of sexes also involved size and species differences and ignored the possible energy conservation provided by nest insulation. Time analysis of the female Anna's Hummingbird permits refinement of the speculation. For the metabolic effort of thermoregulation, I considered one-

half of the body to be exposed to the air temperature and the other half enclosed in the nest temperature (Table 4). Unfortunately I could not maintain continuous surveillance of the bird (a suspected food source was 1.6 km distant). In limited periods when she did remain in view, portions of the recess periods were devoted to bathing, preening, and perching between bouts of catching small insects in flight. Hence I assumed that one-fourth of the recess was spent perching and three-fourths flying. There was nothing to substantiate this guess, and estimates with those proportions reversed (one-fourth time in flight) reduced the total budget 22 to 31% (Table 4). The local food sources, gnat swarms and small flowers, would probably necessitate feeding during hovering. Incubation and brooding can be accomplished only when the hen is on the nest. Thus it seems unprofitable to spend as much as three-fourths of the recess perching away from the nest, so perhaps the latter estimates show rather extreme effects of error in assumption. Obviously more observations would be desirable, but Anna's Hummingbird is rarely discovered nesting in southern Arizona (Zimmerman 1973).

The total estimates will also vary depending upon which published metabolic data are used in the calculations. For comparing the sexes, this does not matter so long as one is consistent. I have recalculated from time energy budgets of Anna's (Pearson 1954, Stiles 1971) using Lasiewski's (1963) data.

"T"-tests between males and females indicate a similarity in the energetic requirements of the two sexes if the males go torpid at night and if the females are in flight three-fourths of the time when absent from the nest ( $0.5 < P < 0.6$ ). Even if the female spends only one-fourth of her recess in flight, the difference from night torpid males was not significant at the 0.95 level.

The role, if any, of the male hummingbird beyond insemination of the female has not been explained, at least for temperate species. Wolf and Stiles (1970) studied the tropical Fiery-throated Hummingbird (*Panterpe insignis*) and found that it was to the advantage of the male's reproductive potential if he defended a territory from which females could feed his offspring. Perhaps time energy budgets merit further study with regard to specialization of the sexes in hummingbirds.

In conclusion, the earliest and latest activities of hummingbirds appear to be determined by light intensity, probably relative to levels necessary for effective foraging. Facing the constraints of short daylength (45% of 24-h day) and prolonged nocturnal fast, the winter-nesting Anna's Hummingbird attains energy balance during recess periods of a total similar to that of the summer-nesting Broad-tail. In 24 h, time on the

TABLE 4  
ESTIMATES OF ENERGY BUDGETS FOR ANNA'S HUMMINGBIRD

Sex and status	Date	Activity	Duration (h:min)	Energy cost (kjoule/day) <sup>1</sup>	Total/basal
♂, feeding territory <sup>2,3</sup>	3-8 Sep.	Perched	10:32	11.48	
		Flying	02:21	7.96	
		Sleep, nontorpid	11:08	10.38	
		Total	24:00	29.82	3.24
		Sleep, torpid	11:08	2.81	
		Total	24:00	22.25	2.42
♂, breeding territory <sup>2,4</sup>	Jan.	Perched	08:38	13.64	
		Flying	02:01	7.77	
		Sleep, nontorpid	13:21	12.45	
		Total	24:00	33.86	3.68
		Sleep, torpid	13:21	2.43	
		Total	24:00	23.84	2.59
♂, breeding territory <sup>2,4</sup>	22 Mar.	Perched	10:00	16.91	
		Flying (F, ic, A, f)	02:31	9.68	
		Sleep, nontorpid	11:29	10.70	
		Total	24:00	37.30	4.05
		Sleep, torpid	11:29	2.09	
		Total	24:00	28.47	3.09
♀, incubating <sup>5</sup>	17 Feb.	On nest	20:30	15.02	
		Flying	02:38	10.74 ( 3.58)	
		Absent, nonflying	00:52	0.65 ( 1.95)	
		Total	24:00	26.45 (20.54)	2.87
♀, brooding <sup>5</sup>	22 Feb.	On nest	18:27	12.89	
		Flying	04:09	16.99 ( 5.67)	
		Absent, nonflying	01:24	1.03 ( 3.09)	
		Total	24:00	30.91 (21.64)	3.36
♀, brooding <sup>5</sup>	24 Feb.	On nest	18:36	12.03	
		Flying	04:03	16.56 ( 5.52)	
		Absent, nonflying	01:21	1.00 ( 3.01)	
		Total	24:00	29.60 (20.57)	3.22
♀, incubating <sup>6</sup>	30 Apr.	On nest	21:07	12.98	
		Flying	02:10	8.83 ( 2.94)	
		Absent, nonflying	00:43	0.53 ( 1.59)	
		Total	24:00	22.35 (17.52)	2.43

<sup>1</sup> Energy in S.I. units, 1 kcal = 4.184 kJoules, 1 kJ = 0.24 kcal (see Mechtly 1969, Tucker 1972, Barrow 1973).

<sup>2</sup> Using values of Lasiewski (1963); 42.4 ccO<sub>2</sub>/g hour for hovering flight, 458 ml/day for standard metabolism, lower critical temperature = 27°C, 0.44 ccO<sub>2</sub>/g hour °C for heat transfer coefficient ("thermal conductance"), body mass = 4.8 g. Combining Stiles (1971) categories for feeding at flowers, insect catching, territorial aggression, miscellaneous flight, and out-of-contact.

<sup>3</sup> Recalculated from Pearson (1954).

<sup>4</sup> Recalculated from Stiles (1971). Using his symbols, f = miscellaneous flying, ic = insect catching, A = territorial aggression, and F = feeding at flowers.

<sup>5</sup> This study; night and daytime at resting metabolic rate for average of nest and air temperatures (one-half of bird in nest, one-half of bird in air), but with minimum daytime metabolism of 1.5× basal metabolism (standard metabolic rate in thermoneutrality). I assume that three-fourths of absence is in flight, one-fourth perched at 2× standard metabolism. Numbers in parentheses are for the converse assumption, one-fourth flight, three-fourths perched.

<sup>6</sup> Calculated from data of Howell and Dawson (1954) using assumptions as in (2) and (5) above.

nest is nearly the same. The female's energy budget may be similar to that of the male whose responsibilities and activity patterns are quite different, but more extensive observational data are needed to confirm this.

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