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THE DAILY ENERGY REQUIREMENTS OF A WILD ANNA HUMMINGBIRD

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The daily energy requirements of wild, unfettered birds are difficult to estimate because the metabolic costs of flying, hopping, scratching and other common activities are not known, and were they known, it would still be almost impossible to divide a bird's day neatly into periods spent at the different energy levels. Hummingbirds, however, spend almost their entire active day at only two metabolic levels, hovering and perching, and their rate of metabolism during these activities is known. Therefore, to calculate the energy expenditure of a wild hummingbird, one has only to watch a hummingbird all day and record with a stopwatch how much time is spent in the air and how much is spent perching. I shall report below two such attempts to watch a male Anna Hummingbird (*Calypte anna*) on September 3 and September 8, 1953, in the botanical gardens of the University of California at Berkeley.

METABOLIC GROUNDWORK

Before calculating the energy balance of this bird for the day, it is necessary to estimate his rate of metabolism while hovering and while perching. On the basis of previous work (Pearson, Condor, 52, 1950:145), I shall assume that Anna Hummingbirds while hovering consume oxygen at the rate of 68 cc per gram of body weight per hour. In the absence of evidence to the contrary, the energy cost of linear flight will be assumed to be the same as for hovering. Should this assumption prove to be unsound, only a slight error will have been introduced because only a small fraction of the air-borne time is spent in linear flight.

For calculating the metabolism of hummingbirds perching at the temperatures encountered in the wild, two 24-hour recordings of oxygen consumption of captive Anna Hummingbirds are available (fig. 1), one at 24°C. and one at 12°. The 24° run has been reported earlier (Pearson, *op. cit.*). These records were obtained in a modification of the apparatus described by Morrison (Jour. Biol. Chem., 169, 1947:667). The bird was confined under a belljar whose inside dimensions were six inches in diameter and four inches high, a space too small to permit flight. Containers of soda lime and calcium chloride served to absorb the water vapor and carbon dioxide produced by the bird, and a generous supply of food was provided. The belljar with the bird inside was submerged in a water bath of appropriate temperature and was connected to a floating spirometer that supplied oxygen at atmospheric pressure. The chamber was illuminated by natural daylight. The bird was weighed at the beginning and end of each 24-hour run and his weight at any time during the run was estimated by interpolation. Results are given in cubic centimeters of oxygen consumed per gram of body weight per hour. The volume of oxygen has been corrected for water vapor and temperature and therefore corresponds to dry gas at 0°C. For conversion to Calories, I have assumed each liter of oxygen consumed to be equivalent to 4.8 Calories, a value appropriate to the respiratory quotient of actively digesting small birds (Kendeigh, Jour. Exp. Zool., 96, 1944:1).

From the data on which figure 1 is based, I calculate that the daytime perching

metabolism (including activities such as preening) at 24° is 16.3 cc/gm/hr and at 12° is 21.0 cc/gm/hr. The mean hourly daytime temperature in the shade on the observed hummingbird's territory on September 3 was 17.3°, and on September 8, 18.1° (fig. 2). The resting metabolism at these temperatures was calculated by linear interpolation between 16.3 and 21.0 cc./gm/hr. Body weight was estimated at 4.0 grams.

Finally, before calculating the total energy expenditure of this wild hummingbird for a 24-hour period, one must assign a metabolic rate for overnight. It has been shown

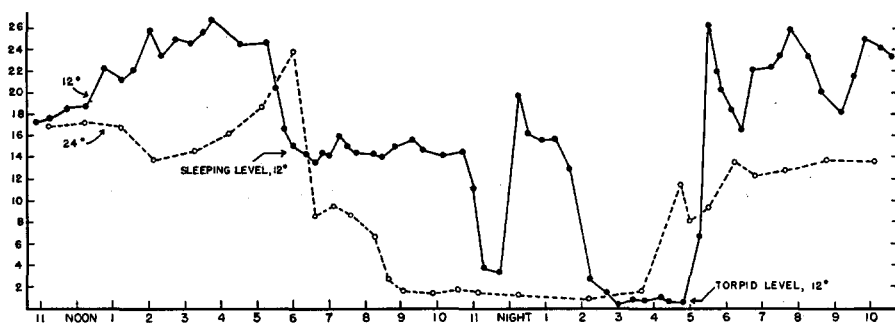


Fig. 1. The 24-hour metabolism of two male Anna Hummingbirds, one at 12°C. and one at 24°. The bird at 12° reached a sleeping level of 14.5 cc/gm/hr at about 6 p.m. and continued at this level until it dropped abruptly into torpor at 11 p.m. However, before reaching the minimal level, its metabolism reversed and the bird, for no apparent reason, emerged from torpor only to drop a short time later to a level of only 0.76 cc/gm/hr. During the 24° as well as the 12° run the birds emerged from torpor spontaneously before daybreak. The torpid level at 12° is somewhat lower than at 24°, but close comparison cannot be made because the accuracy of the apparatus is not great at such low levels of oxygen consumption.

that Anna Hummingbirds frequently pass the night in a condition of torpor at an extremely low metabolic level (Pearson, *op. cit.*, and fig. 1), but on the other hand an incubating female observed by Howell and Dawson (Condor, 56, 1954:93) did not become torpid. It is probable, furthermore, that many hummingbirds in the wild spend part of the night torpid and part merely sleeping, as did the bird whose metabolism was measured at 12° (fig. 1). Therefore, I have made two sets of calculations, one assuming that the night was spent entirely at the sleeping level at an environmental temperature of 12°, and one assuming that the night started as in the 12° run illustrated in figure 1, but that metabolism dropped to the 0.76 cc/gm/hr torpid level at 8 p.m. and remained there until the pre-dawn rise at 5 a.m.

RESULTS

Early in September, when the observations were made, male Anna Hummingbirds vigorously defend a small feeding territory. The territory of the male under observation was only 50 feet in diameter. He rarely left this territory except to chase other hummingbirds, and he drove off every hummingbird that he saw on his territory, regardless of its sex. At dusk, however, he flew off more than 300 feet to his night roosting place.

Figure 3 reveals that he was especially active in the mornings and in the evenings and relatively inactive during the early afternoon. He was flying only 10 per cent of the time early in the afternoons but as much as 30 per cent of one hour just before dark. During his active day, which was 12 hours and 52 minutes long on both days, he averaged 18.7 per cent of the time flying on September 3 and 17.9 per cent on September 8. The longest perching period was between 1:05 and 1:35 p.m. on September 3, although

during a brief observation period on September 1 I noted that he remained perched for as long as 34 minutes between 1:27 and 2:01 p.m.

Using the metabolism data given earlier, one can calculate the daily energy values presented in table 1 and illustrated in figure 4. Assuming torpidity at night, the energy exchange of this bird for 24 hours of normal life in the wild was 7.55 Calories (average of two days), and assuming sleep at night, 10.32 Calories. This is, of course, a consider-

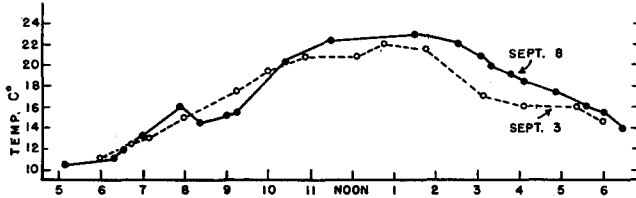


Fig. 2. Shade temperatures on September 3 and 8 on the territory of the hummingbird under observation.

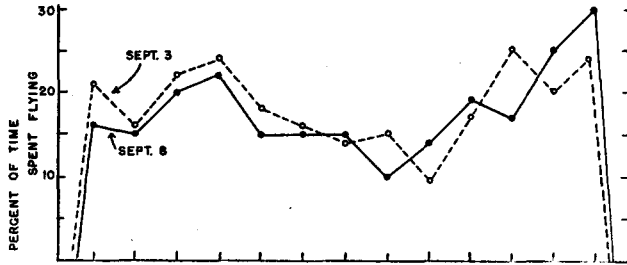


Fig. 3. Per cent of each hour spent airborne. Same male Anna Hummingbird on two days.

ably higher metabolic rate than that of the birds confined in the metabolism apparatus, which totalled 4.88 Calories at 24° and 6.77 Calories at 12°. Agreement is good, however, with the results of some feeding experiments reported by van Riper (*Nature Mag.*, 54, 1953:135). He found that a 4.3-gram Broad-tailed Hummingbird (*Selasphorus platycercus*) removed 7.31 Calories of sugar solution from a feeder each day.

The male Anna Hummingbird's day (fig. 4) can be divided into three major metabolic levels that are at the same time crude categories of activity: daytime perching, flying, and night roosting. If the bird spends the night at the sleeping level, rather than in torpor, then one-third of his 24-hour energy budget is spent in each of these three activities, although his time is spent in an entirely different ratio.

The category "flying" can be subdivided successfully into the following activities: 1. Nectar flights. By far the largest part of his flying time and flying energy could be assigned to this category. 2. Insect-catching flights. These consisted of forays of only a few seconds, similar to the insect-catching flights of flycatchers. The prey was usually gnats. 3. Territory defense. Usually chases in which an intruding hummingbird was pursued, but occasionally flights to the edge of the territory to forestall trespass by a nearby hummingbird. 4. Perch changes. Short flights to a nearby perch for no obvious reason. 5. Disturbances. Short flights of a few yards to avoid workmen and visitors in the botanical gardens. 6. Unclassified flying. The bird was out of sight during 1.5 to 2.0 per cent of each day. After each disappearance an estimate was made of the prob-

Table 1
Time and Energy Values for Two Days of Activity of a Male Anna Hummingbird

	Basic data		Per cent of daytime activity		Per cent of 24 hours		
	Time	Energy	Time	Energy	Time	Energy assuming torpidity	Energy assuming sleep
Daytime activity	12 hr. 52 min. (12.52-12:52)	6.88 Cal. (6.95-6.80)	100	100	53.7 (53.7-53.7)	91.2 (91.3-91.1)	66.6 (66.8-66.4)
Perching	10 hr. 32 min. (10:28-10:36)	3.81 (3.82-3.80)	81.8 (81.4-82.2)	55.5 (55.0-55.9)	43.8 (43.6-44.1)	50.5 (50.1-50.9)	36.8 (36.7-37.0)
Flying	2 hr. 21 min. (2:24-2:18)	3.07 (3.13-3.00)	18.2 (18.7-17.9)	44.6 (45.1-44.2)	9.8 (10.0-9.6)	40.7 (41.2-40.2)	29.7 (30.1-29.3)
120 (120-119) nectar- feeding flights	1 hr. 53 min. (1:58-1:49)	2.46 (2.55-2.37)	14.6 (15.2-14.1)	35.7 (36.7-34.8)	7.85 (8.15-7.55)	32.5 (33.4-31.7)	23.8 (24.5-23.1)
Chasing 78 (108-62) insects	4.45 min. (5.50-3.40)	.094 (0.110-.077)	0.54 (0.65-0.44)	1.34 (1.58-1.10)	0.30 (0.35-0.24)	1.22 (1.44-1.00)	0.90 (1.06-0.75)
50 (47-53) territory defenses	13.76 min. (10.00-17.52)	0.305 (.230-.379)	1.8 (1.3-2.3)	4.48 (3.34-5.61)	0.96 (.70-1.22)	4.08 (3.05-5.11)	2.96 (2.22-3.70)
60 (70-50) perch changes	2.75 min. (3.37-2.13)	.058 (.072-.043)	0.36 (.44-.28)	0.85 (1.04-0.66)	0.19 (.23-.15)	0.78 (.95-.60)	0.55 (.69-.42)
39 (64-14) dis- turbances	0.65 min. (1.07-.23)	.014 (.024-.005)	.08 (.14-.03)	0.20 (.32-.09)	.04 (.07-.01)	0.18 (.29-.08)	0.14 (.23-.05)
Unclassified flying	6.87 min. (7.50-6.25)	0.148 (.163-.134)	0.89 (.97-.81)	2.17 (2.35-2.00)	0.45 (.47-.43)	1.97 (2.14-1.81)	1.44 (1.57-1.31)
Night roosting (torpid)	11 hr. 8 min. (11:08-11:08)	0.672			46.5 (46.5-46.5)	8.91 (8.83-9.00)	
Night roosting (asleep)	11 hr. 8 min. (11:08-11:08)	3.446			46.5 (46.5-46.5)		33.3 (33.1-33.6)

able time spent flying, the estimate depending upon what the bird was doing when it disappeared and how soon it returned. All such estimates of flying time were then added to make up the "Unclassified Flying" category. Figure 4 and table 1 divide the bird's day into these activities. In table 1 the average figure for the two days is given as well as, in parentheses, the separate value for September 3 followed by that for September 8. The values for the two days agree surprisingly well.

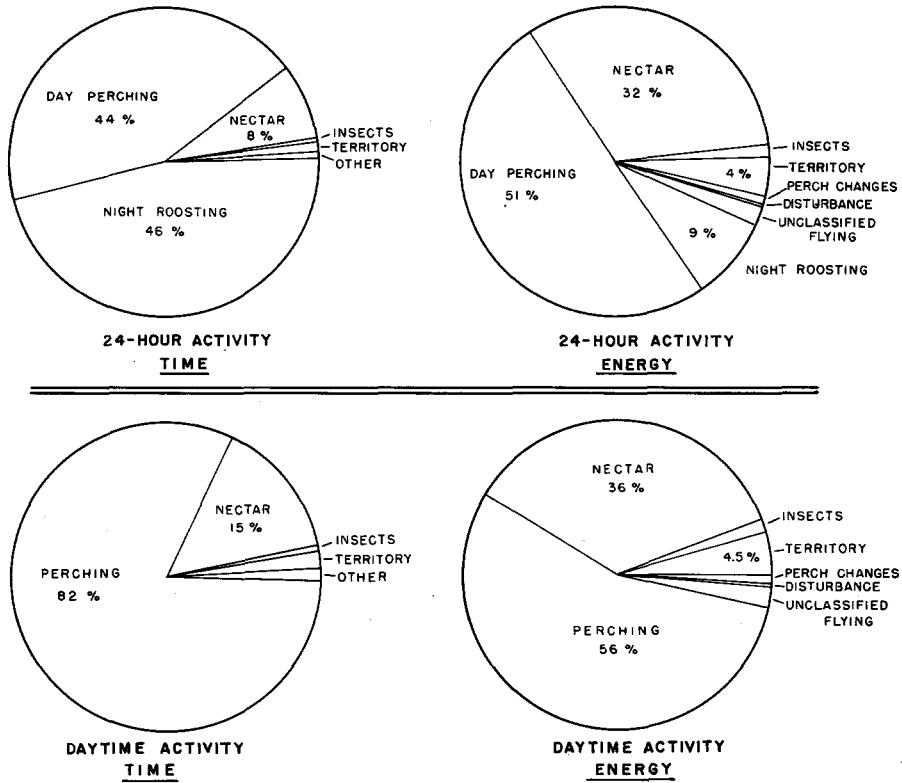


Fig. 4. Upper. Expenditure of time and energy by a hummingbird for 24 hours; average of September 3 and 8. The energy diagram was constructed assuming that the bird became torpid at night.

Lower. Expenditure of time and energy during the 12-hour, 52-minute active day. Same observations as above but the night period at unknown metabolic level has been omitted.

The hummingbird under observation did approximately 90 per cent of his nectar feeding from the blossoms of a single large bush of *Fuchsia macrostemma*. On a few occasions when his attention was directed elsewhere another bird managed to feed for a short period on these blossoms. If we assume that this pilfering just balances the nourishment that the resident bird obtained feeding on insects and on other flowers, then it becomes possible to say that the 7.6 (assuming torpidity at night) to 10.3 Calories (assuming no torpidity) required every day by this bird could be supplied by nectar from the 1022 blossoms available on this bush.

The value of defended territory to an individual bird or to a species is difficult to measure and to put into quantitative terms, yet the concept of territories is basic in the

study of bird behavior and avian ecology. It is probably safe to assume that the true value of territorial defense to an individual or species is greater than the cost, otherwise the habit would have been eliminated through centuries of evolution. If, then, one can calculate how much energy a bird spends defending its territory, one has a minimal estimate of the value received by the bird as a result of its expenditure. In figure 4 and table 1 can be seen the cost of territorial defense to this hummingbird. The cost is expressed in Calories, an international currency that lends itself to comparison of the territorial defense costs of the same individual on different days, at different seasons, or even of comparing the defense costs of widely different species. The male Anna Hummingbird watched on September 3 and 8 devoted 1.8 per cent of his 12-hour 52-minute active day to an average of 50 flights in defense of his territory. This amounts to 0.305 Calories, 4.48 per cent of his daytime energy expenditure, or 4.08 per cent of his 24-hour metabolic needs (assuming torpidity at night). In more tangible units this represents the energy derived from 42 blossoms of *Fuchsia macrostemma* (4.08 per cent of 1022). This is the expense of active defense of his territory. Probably a small fraction should be added for the cost of territorial singing. Perching of the bird in conspicuous places where he can be seen by birds on neighboring territories can also, like singing, be considered a kind of territorial advertisement, but unless such perches require more energy to reach than do alternate perches no allowance need be made for this territorial display because it does not necessitate increased metabolism.

It will be seen from figures 3 and 4 that only about one-fifth of the daytime is spent on the wing. Of the remaining four-fifths, a small fraction is necessary for preening to keep the plumage in serviceable condition and probably a small fraction is required for rest, but the remainder of the perching time is available for more strenuous activity should occasion demand. At some seasons the territory must be considerably larger to allow gathering of sufficient food, and at such seasons more time and energy would be spent feeding and less perching. During the early spring considerable energy must be expended in the spectacular diving display, thereby necessitating more feeding. Each hour of flight not only subtracts that much time from the perching time, but necessitates approximately 15 minutes more of flying to replace the *additional* food consumed during the hour of flight. Accordingly figure 4 may be expected to have a quite different appearance if plotted for other seasons of the year. It is my impression that early September, despite vigorous territorial defense, is a time of abundant food, small territories, and relative inactivity. It is a season of leisure for the Anna Hummingbird.

SUMMARY

A male Anna Hummingbird watched on September 3 and 8 flew on the average 18.7 per cent of the time. His energy exchange for 24 hours of normal life in the wild was calculated to be 7.55 Calories (assuming torpidity at night) or 10.32 Calories (assuming sleep at night). During his 12-hour 52-minute active day, most of his energy expenditure was distributed as follows: perching, 3.81 Calories (56 per cent); nectar flights, 2.46 (36 per cent); insect-catching flights, .09 (1.3 per cent); and defense of territory, .30 (4.5 per cent). The nectar secretion of about 1022 *Fuchsia* blossoms can supply this daily need.

Museum of Vertebrate Zoology, Berkeley, California, August 13, 1954.