THE CONDOR

VOLUME 52 JULY-AUGUST, 1950 NUMBER 4

THE METABOLISM OF HUMMINGBIRDS

By OLIVER P. PEARSON

Physiologists have made few studies on hummingbirds despite the attention that these birds deserve because of their small size and their ability to fly in a small container. By measuring oxygen consumption I have been able to calculate their rate of metabolism at rest and in flight and their energy needs over a 24-hour period. It has also been possible to measure the depth of the torpidity that some investigators have suspected occurs and to make a rough estimate of the non-stop flight range of hummingbirds.

METHODS

Five Anna (*Calypte anna*) and two Allen (*Selasphorus sasin sasin*) hummingbirds were studied. These were captured as nestlings or as adults and were fed either a mixture of water, sugar, milk, and Mellon's food, or a mixture of water, sugar, and canned strained liver. Rate of metabolism was measured by oxygen consumption in a closed circuit volumetric apparatus similar to that described by Morrison (1947). For determinations during which no flying was wanted, the animal chamber used was a bell jar 5 inches in diameter and 3 inches high (inside measurements). For determinations during which the bird was expected to fly, a bell jar 6 inches in diameter and 10 inches tall was used. Suitable surfaces of soda lime and calcium chloride were exposed in each, and the large bell jar was equipped with a fan to stir up the air and thus speed absorption of carbon dioxide and water vapor. These chambers were connected to a spirometer of oxygen and when in use were submerged in a water bath to keep the temperature inside them constant. Food was provided for the birds in the bell jars except in a few special cases. When a bird was confined in the apparatus for several hours, it was weighed both before and after, and the weight used for calculation of metabolic rate at any period during the experiment was arrived at by interpolation. On shorter experiments the animal was weighed only at the end. The oxygen consumptions reported in this paper are expressed in cubic centimeters of gas at 0°C. and 760 mm. pressure.

Acknowledgment.—I am much indebted to Mr. and Mrs. Eric C. Kinsey for supplying me with the Allen Hummingbirds used and for much valuable advice on caring for hummingbirds in captivity.

METABOLISM AT REST

The metabolic rate of animals varies inversely with their size. In general, the larger an animal, the slower its rate of metabolism per gram of body weight. It is of interest, therefore, to establish the rate for hummingbirds, the smallest of all birds. The Allen and Anna hummingbirds used in this study weigh less than half as much as the smallest birds heretofore measured.

The rates of metabolism of two resting, adult birds of each species are presented in table 1. These are not to be considered basal determinations. The environmental temperature may not have been within the zone of thermal neutrality (this zone has not been defined for hummingbirds), and the birds were not necessarily post-absorptive because food was available to them at all times. Attempts to achieve post-absorptive conditions result either in increased activity or a drop in the body temperature. Because of this lability of temperature, basal measurements would be of doubtful value. Each of the measurements recorded in table 1 is the lowest of many measurements made on that bird in the daytime.

The measurements from table 1 are graphed in figure 26 where they may be compared with other metabolic rates measured within 3°C. of the same temperature and in similar fashion. It will be seen that the various species of shrews tend to have a higher rate of metabolism than mice and that birds have even higher rates than shrews. The Allen and Anna hummingbirds metabolize faster than any of the other forms shown. In fact, their resting metabolism is higher than that of any other organism that has been studied. The rate of the House Wren (*Troglodytes aëdon*) was computed from data by Kendeigh (1939), the widow bird (family Ploceidae) from data by Terroine and Trautman (1927), and the Cliff Swallow (*Petrochelidon albifrons*) from my own measurements on a 22-gram male at 21°C. The curves for mice and shrews are from Pearson (1948).

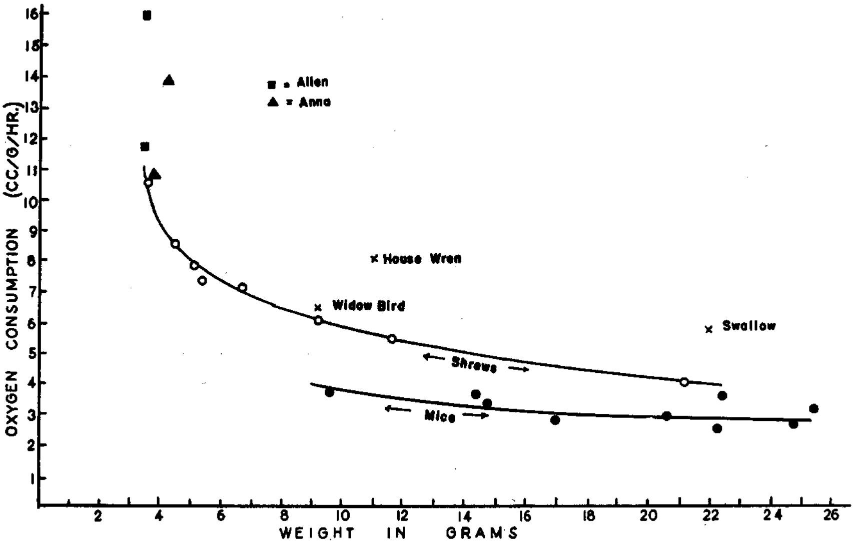

Fig. 26. A comparison of the metabolic rates of several species of mice, shrews, and small birds.

Table 1

Oxygen Consumption of Resting Hummingbirds

Species	Sex	Weight	Temp.	Length of measuring period	Rate
Anna	♀	3.82 g.	24°C.	19 minutes	10.7 cc/g/hr.
Anna	♂	4.32	24	64	13.9
Allen	♀	3.57	22	11	16.0
Allen	♂	3.49	22	10	11.8

The capture of a pair of nestling hummingbirds estimated to be 9 days old made it possible to study the change in rate of metabolism from this age to maturity. Even at 9 days the young were as heavy as adults and had good temperature control. With the room at 25°C. a thermometer thrust between them as they huddled together in the nest registered 39.4°. Nevertheless, their rate of metabolism, even allowing for heat conservation due to huddling, had not reached the adult level (fig. 27). When 11 days old, they were left in the apparatus, except for two feedings, from 2:15 p.m. to 5:30 a.m. The environmental temperature was 24°. They disclosed no drop in metabolism during the night. There was also no appreciable lowering of metabolism at night when 17 and 25 days old. The high point at 26 days in figure 27 was obtained on a run from 5:55 p.m. to 8:34 p.m. with the environmental temperature at 15°. Were there a tendency toward poikilothermy in this 26-day individual, the metabolism at this cold temperature would have been depressed rather than elevated.

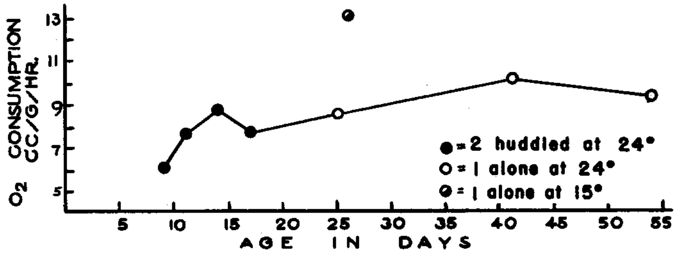

Fig. 27. Rate of metabolism of young Anna Hummingbirds.

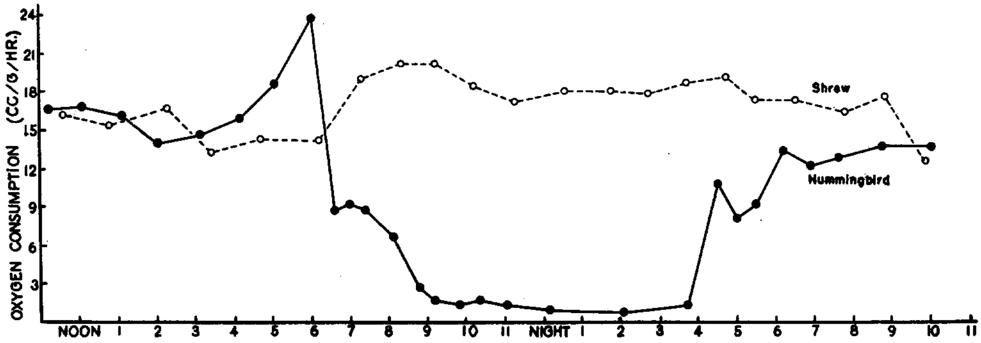

Fig. 28. The rate of metabolism of a male Anna Hummingbird and of a shrew (*Sorex cinereus*) recorded over a 24-hour period.

TORPIDITY

Aviculturists, as pointed out by Huxley, *et al.* (1939), have long known that hummingbirds occasionally become torpid, but this knowledge has not been widespread among zoologists. McAtee (1947) has published a valuable bibliography of torpidity in birds, but upon reading the articles to which he refers, it soon becomes apparent that really sound observations substantiated by actual measurements of body temperature or rate of metabolism are extremely rare for all birds.

Torpidity in the wild.—A female Anna Hummingbird found torpid on a lawn in Oakland, California, in the daytime during a cold spell in February, 1949, subsequently recovered in captivity and was used for some of the measurements of the metabolism of flight. The male Anna whose 24-hour metabolism is presented in figure 28 was captured in the following manner. He was observed as he alternately fed and perched at 5:55 p.m. on September 12, 1949. At 6:05 he flew 50 feet and perched on a small naked branch 8 feet above the ground and about 3 feet out from the trunk of an alder tree.

He remained about 2 minutes, then left to feed nearby until 6:10 when he returned to the same spot on the same branch. He did not fly again before I stopped watching at 6:50, when it was nearly dark. I returned at 3:00 a.m. and found him at the same place. When picked up he gave a few slow, wheezy squeaks not unlike those uttered by hibernating bats when they are disturbed. He felt slightly warm to the touch, but was quite incapable of flight. The air temperature was 15°. He was carried indoors at once to a temperature of 21° and put on the floor of a cage, but he did not revive sufficiently to fly until 3:11. At 7 a.m. he was awake and normally active.

Torpidity in captivity.—Aldrich (1939) kept two immature male Allen Hummingbirds in captivity and remarks: "In all instances, regardless of the temperature, the birds seemed to go into a torpor or coma from which they could not be readily awakened. This type of behavior, which probably is accompanied by a lowering of body temperature, was more pronounced on colder nights. On warm nights the birds were more easily awakened."

I noted the condition of my Allen Hummingbirds between 2 and 4 a.m. on 6 nights between May 2 and May 10. The female was torpid on one night and the male on five. Activity until 10 p.m. in the room in which they were kept may have prevented the male from entering torpidity on the sixth occasion. Notes on the emergence from torpidity on two occasions are as follows:

May 5, 3:40 a.m. Female awake and flew when approached; male torpid on perch, feels cool, squeaks when touched.
3:41. Temperature in throat of male 18.7°; room 16°.
3:42. Rectal temperature (shallow insertion) 21.5°.
3:48. Lying on ground, feathers fluffed, panting 240 per minute.
3:50. Able to fly.
3:51. Skin temperature of abdomen 30.5°.
May 8, 2:36 a.m. Female flew at once. Male torpid, feathers slightly fluffed.
2:37. Respiration 132 per minute.
2:39. Cannot fly.
2:40. Feathers much fluffed, shaking.
2:44. Cannot fly, feathers fluffed.
2:45. Respiration 210 per minute.
2:47. Lowered feathers, cannot fly.
2:48. Respiration 150 per minute.
2:49. First flight, awkward.

A single 24-hour run in the metabolism apparatus was carried out using a 4.32-gram adult male Anna Hummingbird. He was confined on September 16 in the large bell jar with a supply of food arranged so that he had to fly to feed. The water bath was kept at 24° and only natural daylight was allowed to reach him so that his normal activity cycle would not be disturbed. A record of this run is given in figure 28 where each point represents the average metabolism over a period of 18 minutes or more. Long measuring intervals were used during the daytime to even out the wide fluctuations introduced by alternate periods of flight and rest and at night because changes from hour to hour were slight. Short intervals were used at dusk and at dawn to show in greater detail the course of metabolism at these crucial periods. It will be seen that the metabolism rose to a peak at dusk. This reflects a period of frequent flying, feeding, and wing-buzzing just before going to sleep. Between 5:28 and 6:28 p.m. these activities resulted in an average oxygen consumption of 23.7 cc/g/hr. The last flapping of the wings was at 6:24. Not more than 20 minutes later the rate of metabolism had dropped to 8 cc/g/hr., a level much lower than that reached during resting periods in the daytime. It is possible that this was a period of sleep comparable to that of humans during which metabolism may drop 10 or 15 per cent below the basal level. Between 7:30 and 8:00 another change became apparent which resulted in a descent into deep torpor before 9 p.m. This drop in metabolism was probably accompanied by a profound drop in body temperature. The lowest point was reached between 1:24 and 3:03 a.m. when the average oxygen consumption was 0.84 cc/g/hr. Arousal from the 7-hour torpor occurred before daybreak and without any apparent outside disturbance. Almost the entire return to daytime level was accomplished between 4:30 and 4:48 a.m. The meaning of the drop in metabolism after the initial early morning rise is not clear.

A record of the 24-hour metabolism of a small mammal (data from Pearson, 1947) has also been plotted in figure 28 for comparison with the hummingbird. The shrew (*Sorex cinereus*) involved is about the same weight as the hummingbird and has approximately the same rate of metabolism during the daytime, but notice the difference in their records due to the hummingbird's period of torpidity at night. In the depths of torpidity the hummingbird was using only one twenty-eighth as much oxygen as during the active period late in the afternoon, whereas the metabolism of the shrew never fell to even half the peak level. As a consequence, the average rate of metabolism for the day of the hummingbird (9.8 cc/g/hr.) is much lower than that of the shrew (15 cc/g/hr.)

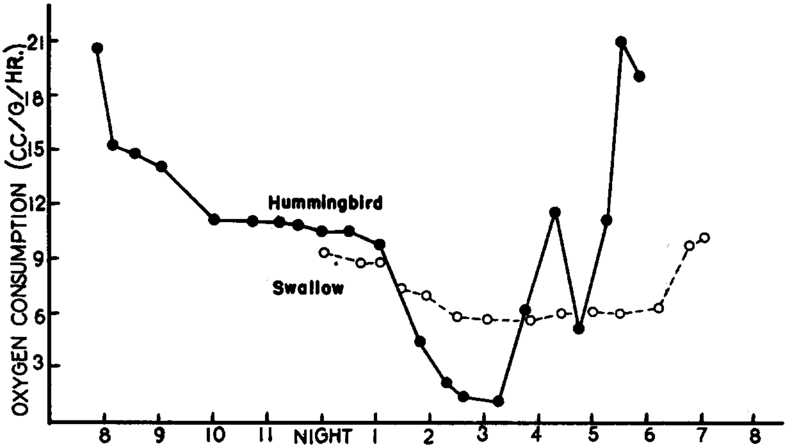

Fig. 29. Metabolism of an Allen Hummingbird at night compared with that of a Cliff Swallow in which no period of torpidity occurred.

The animals with metabolic characteristics most closely resembling those of hummingbirds are bats. Although bats are nocturnal instead of diurnal, their daily loss of control of body temperature and accompanying entrance into torpidity indicates similar physiological characteristics and results in similar metabolic personalities.

The 24-hour metabolism of hummingbirds in the wild would differ somewhat from the record shown in figure 28. Night temperatures lower than 24° would be encountered in the wild and would cause an even lower metabolism during the torpid period. More flying would be necessary in order to feed in the wild, and this would result in a higher rate of metabolism during the day than that indicated in figure 28.

The only metabolism record of an Allen Hummingbird during the night is reproduced in figure 29. The male was weighed (3.175 g.) and put into the apparatus at 22° with a supply of food at 7:35 p.m. It will be seen that his rate of metabolism did not drop as abruptly to a "sleeping" level as did that of the Anna Hummingbird. By 10 o'clock, however, a "sleeping" level was reached at about 11 cc/g/hr., corresponding to the level at 8 cc/g/hr. reached by the Anna much earlier in the evening. The descent into torpidity did not occur until 1 o'clock. The lowest rate was 1.24 cc/g/hr. for the period between 2:58 and 3:28 a.m. As in the case of the Anna, recovery from torpidity was spontaneous at about 3:30 and was followed by a short relapse.

In comparing the two series of measurements, it becomes apparent that the process of entering and emerging from torpidity is similar in the two genera. Torpidity was shorter in the Allen and, despite 2° lower air temperature, did not become quite as deep as in the Anna. These differences are probably individual ones, however, and not generic. Metabolism of the Allen would probably have dropped further had this bird become torpid earlier in the evening.

METABOLISM OF FLIGHT

Careful measurements are available of the rate of metabolism of flying insects. These indicate a flight metabolism of about 95 cc/g/hr. for blowflies (Davis and Fraenkel, 1940), 21 cc/g/hr. for fruit flies (Chadwick and Gilmour, 1940), and 100 cc/g/hr. for butterflies (Krogh, 1941). These were 190, 13, and 170 times, respectively, the resting rate of each species. The most reliable figures for a bird are those of Zeuthen (1942) who, taking cognizance of air resistance and other aerodynamical factors and assuming an efficiency of 25 per cent, calculated that the rate of metabolism of a pigeon flying at 43 miles per hour must be about 27 times the resting rate, or 42 cc/g/hr.

Hummingbirds are able to fly when confined in a small space. This ability has made them suitable subjects for the first actual measurements of the rate of metabolism of a flying vertebrate. The experimental procedure was as follows. A bird was placed in the larger bell jar as though for an ordinary metabolism determination, but a vial of food suspended near the top of the bell jar made it necessary for the bird to fly in order to feed. After the bell jar had been submerged in the water bath and temperature equilibrium had been reached, a careful watch was kept of the bird's actions. Under favorable circumstances the bird would sit motionless for about 10 minutes, then, after a few tilts of its head to locate the food vial, would take off and hover while feeding for perhaps fifteen seconds, then return to its perch and again sit motionless for many minutes. Having timed the duration of the flight with a stop watch, and knowing the resting rate of metabolism immediately before and after the flight, it is possible to select an interval including the period of flight and calculate the amount of oxygen the bird would have used during the quiet part of that interval. Any increase in oxygen consumption over this calculated amount must be due to 15 seconds of flight.

The measuring interval usually extended from just before the flight, or flights, to 3 or 4 minutes after. The chamber reached temperature, water vapor, and carbon dioxide equilibrium in less than 2 minutes after flight. I found no indication of oxygen debt following flight.

It must be admitted that most flights did not follow the pattern outlined above. Some of the birds did not like to fly in the bell jar and would make dozens of short flights instead of one or two long ones. Some would sit on the perch and buzz their wings at inconvenient times. Others would try to cling to the vial while feeding, and finally, the experimenter sometimes bungled. Consequently, hundreds of measurements had to be discarded. There remain, however, dozens of measurements that I consider satisfactory.

The best flight measurements were obtained with the Allen Hummingbirds. Not only did these birds perform better in the bell jar, but at the time that they were studied the technique and apparatus were closer to perfection than in the earlier studies. The average of the twenty-two most satisfactory determinations is 85 cc/g/hr., or approximately six times the resting level. The readings varied from 165 cc/g/hr. to 23. This low value was only half the next lowest, yet I can find no good reason to discard it. The most satisfying series of determinations was obtained from the female Allen on one afternoon when six of the seven readings fell between 82 and 95 cc/g/hr., and the seventh was 51 cc/g/hr. For the Anna Hummingbirds the average of the ten best measurements was 68 cc/g/hr., or about 5½ times the resting rate. Needless to say, the hovering hummingbird consumes oxygen at a much faster rate than has been recorded for any other vertebrate.

The ability of hummingbirds to maintain a high rate of metabolism for a considerable time was revealed on two occasions when the bird could not locate the feed vial in the metabolism chamber. On one of these occasions a male Allen made hundreds of short flights with few rest periods and averaged 31 cc/g/hr. over a period of 157 minutes. At the end of this time he was completely exhausted. On the other occasion the same bird averaged 41 cc/g/hr. for 50 minutes.

Some people have expressed doubt that linear flight is as strenuous as hovering, for it seems likely that a hummingbird could derive lift from forward motion as does an airplane and as a result might be able to keep itself aloft with less exertion than by hovering. However, this could be true only within a certain speed-range. At less than five miles per hour the lift from forward motion would be negligible and linear flight at this speed would certainly be more strenuous than hovering. Likewise, at very high speed so much power would be needed to overcome resistance that linear flight would of necessity be harder work than hovering. Between these extremes it is possible that there are speeds at which linear flight would result in a lower metabolism.

FLIGHT RANGE

A controversy has existed over whether small birds, including Ruby-throated Hummingbirds, migrate non-stop across the Gulf of Mexico, or whether they go by easier stages around the margins of the Gulf. Knowing the approximate rate of metabolism of flight, it is possible to make a rough estimate of the flying range of a hummingbird and thus get some idea of whether it is physiologically possible for them to make the crossing. Because our knowledge is so incomplete, one must make several assumptions, but despite this it seems worthwhile to approach this interesting question from a new direction.

Assume a flight speed of 50 miles per hour (based on observations by Allard, 1934, and Hayes, 1929), a metabolic rate at this speed of 80 cc/g/hr., and ability to carry and utilize one gram of fat as fuel (based on published records of weights of Ruby-throats: the heaviest is a bird on September 28 weighing 3.5 grams, and the lightest is one in July weighing 2.5 grams. I have assumed that the difference of one gram might be made up entirely of fat in a migrating bird). Assume also a caloric equivalence for one gram of fat of 9 Calories, and for one liter of oxygen consumed, 4.69 Calories (standard physiological procedure). Finally, using the weight of the bird in mid-passage as an average (3.0 grams) it is possible to calculate an energy expenditure of 1.17 Calories per hour. On one gram of fat this could last 7.7 hours, which at an air speed of 50 miles per hour would allow the bird to cover 385 miles. The shortest possible distance across the Gulf is more than 500 miles.

SUMMARY AND CONCLUSIONS

The rate of oxygen consumption of Allen and Anna hummingbirds resting in daytime is higher than that of any other animal measured under comparable conditions. This high rate is in part balanced in both species by a period of torpidity at night during which body temperature falls and metabolism at 24° environmental temperature drops as low as 0.84 cc/g/hr. In captivity recovery from torpidity occurred spontaneously before daybreak. This torpidity did not occur in young Anna Hummingbirds. Over a 24-hour period the metaboic behavior of hummingbirds is reminiscent of that of bats but reversed with respect to day and night.

The rate of metabolism of hovering Allen Hummingbirds averaged 85 cc/g/hr., which is about 6 times the resting rate. The rate for Anna Hummingbirds was about 5½ times the resting level. During one 50-minute period of much activity one Allen consumed oxygen at an average rate of 41 cc/g/hr.

After making several assumptions it was estimated that the Ruby-throated Hummingbird, a migratory species suspected of making long over-water flights, has a flight range of 385 miles.

LITERATURE CITED

Aldrich, E. C.
1938. Natural history of the Allen hummingbird (*Selasphorus alleni*). Thesis for the degree of Master of Arts, University of California, Berkeley.

Allard, H. A.
1934. Speed of the ruby-throated hummingbird's flight. Auk, 51:84.

Chadwick, L. E., and Gilmour, D.
1940. Respiration during flight in Drosophila repleta Wollaston: the oxygen consumption considered in relation to the wing-rate. Physiol. Zool., 13:398-410.

Davis, R. A., and Fraenkel, G.
1940. The oxygen consumption of flies during flight. Jour. Exp. Biol., 17:402-407.

Hayes, S. P., Jr.
1929. Speed of flying hummingbird. Auk, 46:116.

Huxley, J. S., Webb, C. S., and Best, A. T.
1939. Temporary poikilothermy in birds. Nature, 143:683-684.

Kendeigh, S. C.
1939. The relation of metabolism to the development of temperature regulation in birds. Jour. Exp. Zool., 82:419-438.

Krogh, A.
1941. The comparative physiology of respiratory mechanisms. Phila., Univ. of Penna. Press.

McAtee, W. L.
1947. Torpidity in birds. Amer. Midl. Nat., 38:191-206.

Morrison, P. R.
1947. An automatic apparatus for the determination of oxygen consumption. Jour. Biol. Chem., 169:667-679.

Pearson, O. P.
1947. The rate of metabolism of some small mammals. Ecology, 28:127-145.
1948. Metabolism of small mammals, with remarks on the lower limit of mammalian size. Science, 108:44.

Terroine, E. F., and Trautman, S.
1927. Influence de la température extérieure sur la production calorique des homéothermes et loi des surfaces. Ann. Physiol. et Physicochim. Biol., 3:422-457.

Zeuthen, E.
1942. The ventilation of the respiratory tract in birds. Det Kgl. Danske Videnskabernes Selskab, Biologiske Meddelelser, 17:1-51.

Museum of Vertebrate Zoology, Berkeley, California, December 14, 1949.