MODIFICATION OF BODY TEMPERATURE BY ACTIVITY IN BRAZILIAN HUMMINGBIRDS

By Peter Morrison

Hummingbirds, together with certain shrews and bats, represent the smallest homeothermic animals. They have a correspondingly large thermal conductance and therefore face a more difficult task of thermoregulation than larger animals. Observations on the level and variation of their body temperature and of their energy balance are consequently of much interest. Hummingbirds are, moreover, one of the few groups of birds in which lowered body temperature has been observed. Pearson has described torpor in both a Californian species, *Calypte anna* (1950 and 1954) and an Andean species, *Oreotrochilus estella* (1953). Bartholomew, Howell and Cade (1957) have also described torpor in the Anna Hummingbird. Ruschi (1949), in his extensive report on the Brazilian Trochilidae, listed temperatures for nine different species with afternoon values ranging from 39.5° to 44.6° C. and night values (sleep) ranging from 36.6° to 40.5° C. He also observed torpor in all these species at body temperatures ranging from 32.0° to 36.6° C. The present study extends our knowledge of body temperatures in hummingbirds as represented by three Brazilian species with emphasis on the daily cycle and the influence of various types of activity.

ACKNOWLEDGMENTS

This study was supported by a grant from the National Science Foundation (G–7073) and a Senior Postdoctoral Fellowship. Logistic support was provided through a contract with the Office of Naval Research, United States Navy (Nonr–2247 (00)). I am indebted to Professor Roberto Santos for use of facilities in his laboratories; to Dr. Jose Simoes, Jr., for assistance in local arrangements; and to Dr. Edegard Santos, Rector of the Universidad da Bahia in Salvador, Brazil, for his generosity and support. Dolores Perez Gonzales, of Professor Paulo Sawaya's laboratory in São Paulo, Brazil, kindly translated the article by Ruschi. The identification of birds was provided through the kindness of Dr. Emmet Blake, of the Chicago Natural History Museum.

MATERIALS AND METHODS

Eight "small" hummingbirds (*Chlorestes notatus cyanogenys* and *Hylocharis cyanus cyanus*), averaging 3.0 gm. (2.7 to 3.5 gm.), and four "large" ones (*Amazilia leucogaster bahiae*), averaging 4.1 gm. (3.8 to 4.4 gm.), were used in this study. They were obtained in a group from a local dealer in Salvador, Brazil, and maintained in the laboratory on a mixture of diluted honey fortified with powdered milk and peptone. The room temperature was fairly uniform during this period, ranging from 24° to 28° C. The four specimens of *Amazilia* were more active than the other birds and often engaged in aggressive behavior toward them. The small hummingbirds tended to perch quietly except when shifting position to feed.

Body temperatures were measured with a thermister thermometer using fine probes, either plastic coated or enclosed in a 22-gauge hypodermic needle. Temperatures were measured under the wing, where the bare area provides direct access to the warm body core yet is shielded from heat loss by the insulation of the wing. The optimal position was fairly critical, but it could be checked easily by moving the probe back and forth. This axillary location was considered preferable to a cloacal or esophageal insertion, at least in our inexperienced hands, because of the delicacy and excitability of these small birds. It is possible that there is an appreciable differential between the axillary and internal temperatures, but this seems unlikely because of their very small size. Moreover our values agree with throat temperatures taken by Ruschi (1949). Body temperature for the two smaller species, which did not differ within the combined variability, were pooled to provide enough values for analysis of the several influences.

In making these measurements it was soon apparent that the ordinal sequence could be correlated with the resultant values. The second bird taken from the cage always had

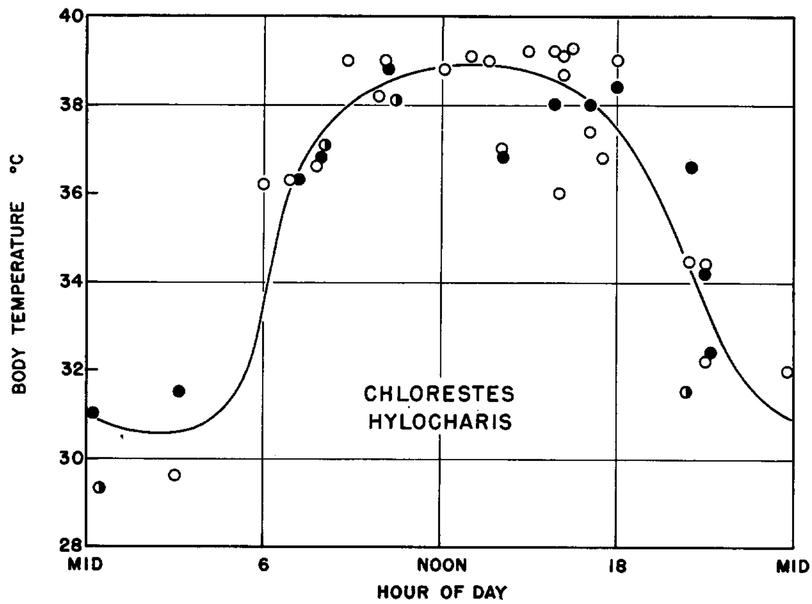

Fig. 1. Daily variation of body temperature in "smaller" hummingbirds (*Chlorestes* and *Hylocharis*). Open circles, first bird; half-circles, second in series (value, —1.0°C.); closed circles, third in series (value, —2.0°C.). Ambient temperature, 26°C.

a higher temperature than the first, and the third still higher. Average values (mean, standard deviation, sample size) for these increases were: 1.06° C. ± 0.3° (10) in *Chlorestes* and *Hylocharis* and 1.10° C. ± 0.5° (12) in *Amazilia*. In figures 1 and 2, which relate body temperature to hour of day, the second and third measurements are corrected for this effect using the average value of 1.1° C.

RESULTS

Body temperatures in *Chlorestes* and *Hylocharis* are summarized in figure 1. These birds were much less active than *Amazilia* and almost always remained on the perches unless actually feeding. The cycle in temperature with an amplitude of 8.0°C. is striking. The 24-hour period can be divided into two subdivisions (8 a.m. to 10 p.m., and 10 p.m. to 8 a.m.), representing general activity and quiescence, with mean values of 38.5°C. ± 1.01° (22) and 33.8°C. (18), respectively. The body temperature of birds in torpor averaged 32.0°C. (11). A similar plot of the data for *Amazilia* is given in figure 2. For this species the mean value for the active period (7 a.m. to 7 p.m.) was somewhat higher, 39.4°C. ± 0.82° (28), as was also the value for the torpid animals, 32.4°C. (5). Mean values from figures 1 and 2 are summarized in table 1.

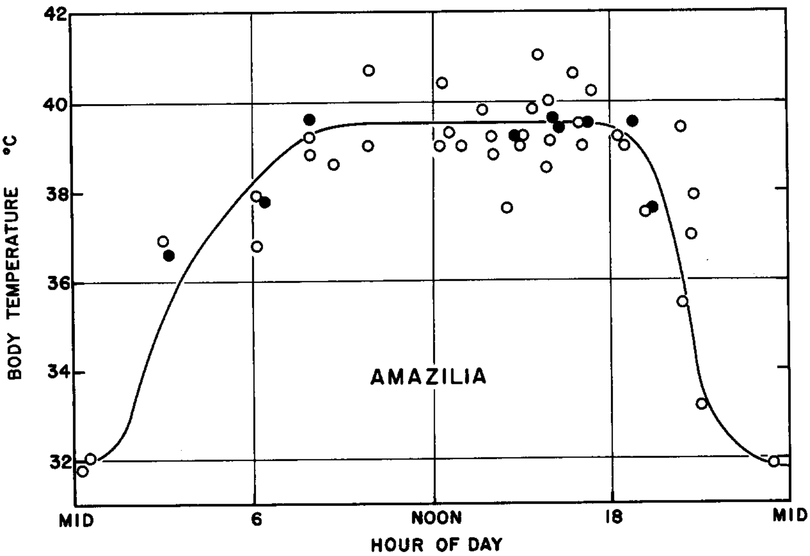

Fig. 2. Daily variation of body temperature in "larger" hummingbirds (*Amazilia*). Symbols as in figure 1.

Figure 3 relates the body temperature to the activity level of the bird prior to measurement. This activity was graded on a scale ranging from 0 to 4+, representing conditions of complete inactivity in sleep or torpor (0); quiet but awake (1+); moving on perch, shifting on perches or feeding from perch (2+); short or intermittent flights (3+); vigorous, continued flight or attacking other birds (4+). Three curves are presented; one for day, one for night, and one for the initial day's measurements (June 24). These latter values were not plotted in figures 1 and 2 since they were clearly higher than subsequent values (June 25 to July 4). They are presented here to show the superposition of the added factor of "general excitement" which resulted in a higher temperature level under each condition of activity. The slope of the curve for *Amazilia* in figure 3A (0.83° = body temperature change per unit of "activity" change) was close to that for the other curves, but values were displaced above the daytime curve by an average of 1.0°C. A similar slope (0.75°) was seen in the data for *Chlorestes* and *Hylocharis* (fig. 3B) and although the comparative data were not so extensive, an average increment of 1.1°C. was seen in relation to the daytime curve. Since these small birds were much less active than the larger ones, no activity levels above 1+ were observed at night. However, the observed increment of change between day and night was the same in both groups (1.5° and 1.4°C.).

The transition from sleep or torpor (0) to quiet (1+) was reflected in a larger

Table 1

Levels of Body Temperature (°C.) in Hummingbirds

	Amazilia	*Chlorestes* and *Hylocharis*
Torpid	[1]32.4 ± 0.8 (4)	31.2 ± 1.2 (8)
(Transitional)	35.5 (1)	34.3 (3)
Sleeping	37.4 ± 0.4 (10)	36.7 ± 0.6 (12)
Awake	39.4 ± 0.6 (32)	38.8 ± 0.4 (17)

[1] Mean, standard deviation, and number of records.

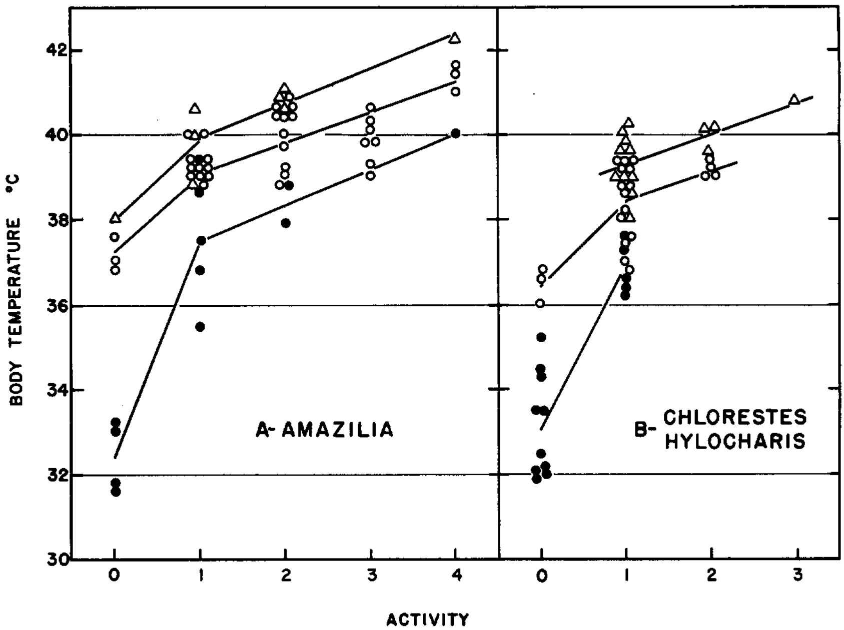

Fig. 3. Modification of body temperature in hummingbirds by spontaneous activity. Triangles, data of June 24; circles, June 25 to July 4; open symbols, day values; closed symbols, night values.

temperature increment than for the other steps. In this analysis, birds with closed eyes were considered to be in sleep during the day and in torpor at night. Since some values undoubtedly represented birds in transition from a more active condition, these increments, substantial as they were, should be even larger. The lowest four values (figs. 1 and 2) which give means of 30.5° and 31.5°C. for *Amazilia* and for *Chlorestes* and *Hylocharis*, respectively, may represent the best estimate of the temperature in torpor. Mean values by activity level are summarized in table 2.

TABLE 2

INFLUENCE OF ACTIVITY ON MEAN BODY TEMPERATURE IN HUMMINGBIRDS

Activity	June 24 24-hr. period	June 25–July 4 7 a.m. to 7 p.m.	7 p.m. to 7 a.m.	24-hr. period
Amazilia				
0	38.0 (1)	37.3 (3)	32.4 (4)	35.0 (7)
1+	39.8 (3)	39.3 (11)	37.5 (5)	38.6 (16)
2+	40.8 (3)	39.9 (11)	38.4 (2)	39.6 (13)
3+	42.2 (1)	39.9 (7)	....	39.9 (7)
4+	......	41.3 (3)	40.0 (1)	41.0 (4)
Mean temperature	40.3	39.2	36.1	38.7
Mean activity	1.5 (8)	1.9 (32)	1.1 (12)	1.7 (47)
Chlorestes and *Hylocharis*				
0	......	36.4 (3)	33.0 (10)	33.9 (13)
1+	39.2 (10)	38.4 (14)	36.8 (4)	37.8 (21)
2+	40.0 (3)	39.2 (4)	......	39.2 (4)
3+	40.8 (1)	....	......	....
Mean temperature	39.5	38.3	34.1	36.6
Mean activity	1.3 (14)	1.0 (21)	0.3 (14)	0.8 (38)

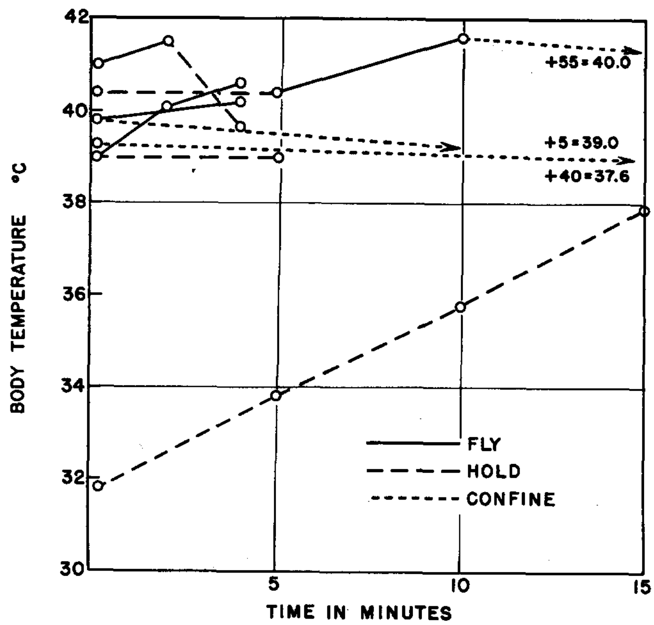

Fig. 4. Modification of body temperature in hummingbirds by forced activity or restraint.

Figure 4 shows some results of forced activity—or inactivity—on the body temperature, principally in the larger *Amazilia*. The maximum observed increase was 1.1°C. in two minutes. A temperature of 40°C. appeared quite compatible with short flights, and where initial values were at this level, smaller increases were produced by flying. Confinement apparently resulted in sleep in one case (body temperature, 37.6°C.), in other cases the level was maintained at or reduced to the resting (1+) level of 39° to 40°C. The lower curve (fig. 4) is of particular interest. This represents data for one of the *Chlorestes* which was found lying on its side in torpor on the cage floor. When picked up, however, the bird fed and over the next 15 minutes showed a constant warming at the rate of 0.4°C. per minute. This increment is equivalent to about 5 cc.O_2 per gram-hour.

TABLE 3

EFFECT OF CONFINEMENT IN THE COLD ON BODY TEMPERATURE OF HUMMINGBIRDS

Species		Initial	12°C. ambient for 1 hr.	7°C. ambient for 1 hr.
Chlorestes and *Hylocharis*		39.2	39.1	
		39.2	32.2	
		39.8	38.2	
		39.1		37.0
	Aver. =	39.3	36.5	37.0
Amazilia		40.3	38.5	
		38.5	34.5	
		40.4	38.2	
		40.6		38.5
	Aver. =	40.0	37.0	38.5

Table 3 summarizes a few experiments at low temperature. The birds were confined for one hour in containers set in a cold waterbath. Three individuals of each of the two groups were measured at 12° ambient temperature and one of each group at 7°. In each case, two birds maintained their body temperature in the normal range for "quiet" birds, and one went into torpor. At 7° both individuals maintained a temperature within, but at the bottom of, the normal daytime range.

DISCUSSION

There are only a few temperature measurements of hummingbirds from the northern hemisphere. These are summarized in table 4 and include seven values for five species measured after shooting (Wetmore, 1921). Available also are "normal" values for 9 species of Brazilian hummingbirds (Ruschi, 1949). These two groups of values average 39.7° and 41.5°C., respectively, but we have no indication of the activity level represented by these values reported in the literature beyond the fact that the birds were not sleeping. They probably represent moderate to extreme activity in the day and compare to values of 38.8° and 39.9°C. for our daytime birds at 2+ and 3+ activity.

Ruschi (1949) described "hibernation" as lasting from 8 to 14 hours, and he stated that "hibernation" was more common in winter than in summer. The present study was conducted in winter, but at a low latitude (13°S) and in a coastal location so that there was as little daily variation as 2°C. in the ambient temperature, which maintained itself near 26°C. Nonetheless, although our data during these hours are not extensive, the

TABLE 4

REPORTED TEMPERATURES OF DIFFERENT SPECIES OF HUMMINGBIRDS

Species	Mean	No.	Range	References
Archilochus alexandri	39.4	(6)	38.8–40.2	Wetmore, 1921
A. colubris	38.9	(3)	38.2–41.1	
Cynanthus latirostris	41.1	(3)	40.7–41.4	
Selasphorus rufus	39.0	(2)	38.8–39.2	
S. platycercus	38.7	(1)		
Calypte anna	41.9	(1)		Bartholomew, Howell and Cade, 1957
6 North American species	39.8			
16 individuals	39.9			
Agyrtria viridissima	43.0	(1)		Groebbels, 1932
1 *Lophornis magnificus*	39.5			Ruschi, 1949
2 *Colibri serrirostris*	42.5			
3 *Thalurania furcata*	39.6			
4 *Polytmus guainumbi*	41.0			
5 *Clytolaema rubricauda*	42.2			
6 *Melanotrochilus fuscus*	42.2			
7 *Aphantochroa cirrochloris*	44.6			
8 *Eupetomena macroura*	40.6			
9 *Thalurania glaucopis*	41.2			
10 South American species	41.6			
16 species	40.9			
*Oreotrochilus estella**	37.3	(5)	36–39.5	Pearson, 1953

* Night value at 14°C. ambient temperature corresponds to the average value of Ruschi (1949) for "sleeping" birds at 10 p.m. Other values in table represent "awake" birds.

birds apparently experienced torpor regularly at night. We also observed the bristling of the feathers described by Ruschi which exposed the skin, particularly at the neck, and facilitated heat dissipation and torpor. This condition was remarkably like that observed in small shrews (*Sorex cinereus*) although in shrews the heat dissipation "posture" is conditioned by high body temperature since these smallest of mammals have not been observed to hibernate (Morrison, Ryser, and Dawe, 1959).

During torpor the hummingbirds were quite helpless and when removed from their perches were unable to regain a grip. Rewarming from torpor took place fairly rapidly (fig. 4) at about 0.4°C. per minute. Flight was not possible below 36°C. and even at 38°C. the birds appeared handicapped. Another individual could not stand at a body temperature of 34.5°C. although Bartholomew, Howell and Cade (1957) described their birds as appearing "normally active" at a body temperature of 35.5°C. This compares to a critical temperature for flight of about 34°C. in the Poor-will (*Phalaenoptilus*), a hibernating caprimulgid (Miller, 1950; Marshall, 1955; Bartholomew, Howell and Cade, 1957). Accordingly, the tropical hummingbirds appear more sensitive to lowering of the body temperature than do temperate birds. This is the opposite of the situation described by Eisentraut (1956) in bats in which tropical species could function at body temperatures well below those for temperate species. It is of interest to compare these stages to those observed in small bats, which are the prototype for a "daily hibernator" and are closely analogous to the hummingbird in size, capacity for flight, and daily torpor. In an Australian species of *Miniopterus* the minimum temperature for walking was about 28°C., and for flying it was 30° to 31°C., or about 5° less than in the hummingbird (Morrison, 1959). But at activity levels of 1 to 3+, the body temperature in this bat is within a degree of that of the hummingbird. The maximum increase in body temperature observed in hummingbirds during flight was 0.55°C. per minute, and decrease following flight was 0.9°C. per minute. These values compare to values of +0.85° and −0.32°C. per minute, respectively, in *Miniopterus* which warmed more quickly and cooled more slowly than these hummingbirds. Similarly, the maximum increase in body temperature during rewarming from torpor is two and one-half to three times greater in bats than that observed in the hummingbirds of this study, but Bartholomew, Howell and Cade (1957) reported comparable rates of warming in the Anna Hummingbird (0.93° and 1.50°C. per minute).

TABLE 5

SUMMARY OF INFLUENCES ON BODY TEMPERATURE

Condition	*Amazilia* Change in degrees C.	*Chlorestes* and *Hylocharis* Change in degrees C.
Removal of prior bird	1.10+	1.06+
Excitement of first day	1.0 +	0.9 +
Activity (maximum)	2.3 +	2.2 +
Night (*vs.* day)	1.4 −	1.5 −
Sleep (*vs.* awake)	1.8 −	2.0 −
Torpor (*vs.* awake)	4.9 −	3.8 −

It is of interest that the warming curve was linear, that is, the bird did not produce heat more rapidly as it became warmer, so there was no "Q_{10}-effect," the increase in rate characteristic of many biological systems as temperature is raised. A similar situation has been observed in developing opossums in which a considerable reduction in body temperature does not reduce the (maximum) heat production (Petajan and Morrison, MS). This warming rate of 0.4°C. per minute was equivalent to the "ordinal" increase in temperature of 1.1°C. experienced over 2 to 3 minutes by the second bird measured and is, in a like manner, not accompanied by obvious muscular activity.

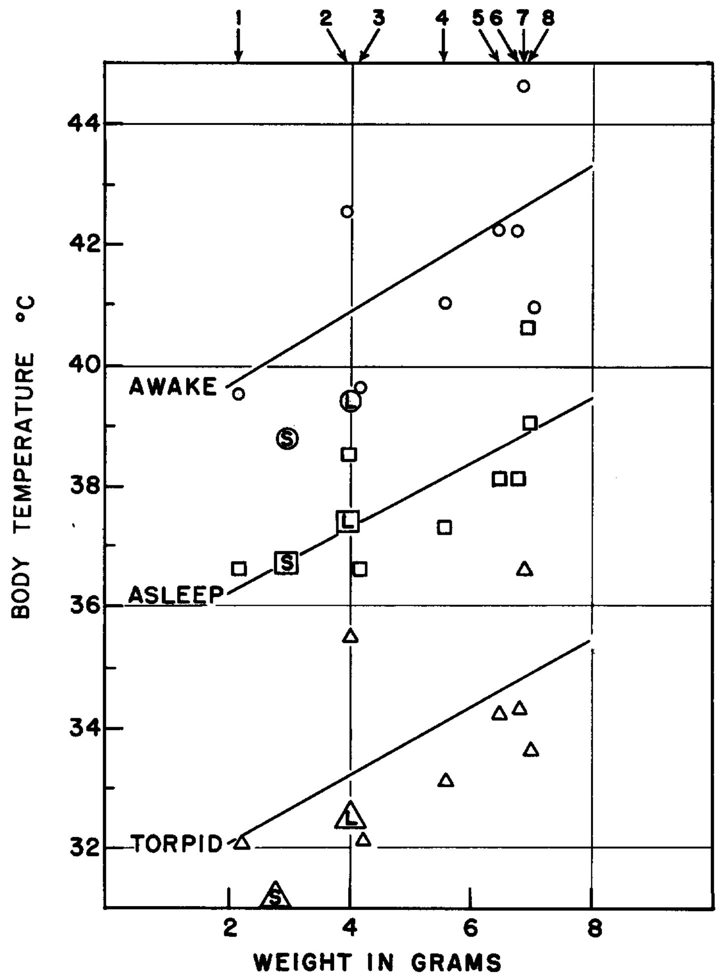

Fig. 5. Relation between body temperature and weight in hummingbirds. Numbers indicate species studied by Ruschi as listed in table 4. S (*Chlorestes* and *Hylocharis*) and L (*Amazilia*) indicate species of present study. Slopes of curves 0.56° (0.53–0.60°) per gram in contrast with general observation that body temperature in larger birds is lower than in smaller birds (Wetmore, 1921).

Pearson (1950) has also described torpor in a Californian hummingbird (*Calypte anna*) on the basis of metabolic measurements. In his experiments, birds measured at ambient temperatures of 24° and 12°C. reduced their oxygen consumption from about 14 cc. per gram-hour to 1.5 and 0.75 cc. per gram-hour, respectively. Since these measurements indicate a Q_{10} of about two we might expect torpor in the present study to reduce the metabolism by about three-fold, of which two-fold would represent the elimination of thermoregulation thus reducing the level to basal; and 1.5-fold would represent the Q_{10}-reduction of the basal metabolic rate.

SUMMARY

The body temperatures of three species of Brazilian hummingbirds (*Chlorestes notatus*, *Hylocharis cyanus*, *Amazilia leucogaster*) and their modification by a variety of factors have been described. Basal temperatures (not sleeping) were 38.4° to 39.3°C. Mild disturbance increased the temperature of a resting bird by a degree within 2 to 3 minutes. The night level was 1.5°C. lower than the day level at comparable activity. The maximum range of activity (rest to vigorous flight) gave a 2.2°C. increase, whereas sleep and torpor resulted in 2° and 4° to 5°C. decreases, respectively. By taking account of each of these several factors, the extreme variability may be accounted for; it is not an instability or lack of thermoregulation but is the sum of several influences.

LITERATURE CITED

Bartholomew, G. A., Howell, T. R., and Cade, T. J.
1957. Torpidity in the white-throated swift, Anna hummingbird, and poor-will. Condor, 59:145–155.

Eisentraut, M.
1956. Körpertemperaturen bei tropischen Fledermäusen und Schuppentieren. Säugetierk. Mitt., 4:64–67.

Groebbels, F.
1932. Der Vogel. Vol. 1 (Gebrüder Borntraeger, Berlin).

Marshall, J. T., Jr.
1955. Hibernation in captive goatsuckers. Condor, 57:129–134.

Miller, A. H.
1950. Temperatures of poor-wills in the summer season. Condor, 52:41–42.

Morrison, P.
1959. Body temperatures in some Australian mammals. I. Chiroptera. Biol. Bull., 116:484–497.

Morrison, P., Ryser, F. A., and Dawe, A. R.
1959. Studies on the physiology of the masked shrew *Sorex cinereus*. Physiol. Zool., 32:256–271.

Pearson, O. P.
1950. The metabolism of hummingbirds. Condor, 52:145–152.
1953. Use of caves by hummingbirds and other species at high altitudes in Peru. Condor, 55:17–20.
1954. The daily energy requirements of a wild Anna hummingbird. Condor, 56:317–322.

Ruschi, A.
1949. Observacoes sobre Trochilideos. Bol. Mus. de Biol., Santa Thereza, 1, No. 7.

Wetmore, A.
1921. A study of the body temperature of birds. Smiths. Misc. Coll., 72, No. 12:1–52.

Hospital das Clinicas, Universidad da Bahia, Salvador, Brazil, and *the Departments of Zoology and Physiology, University of Wisconsin, Madison, Wisconsin, June 29, 1961.* (This is paper 1 of a series describing results from the Wisconsin South American Physiological Expedition, 1959–60.)