Body Temperatures, Heart and Breathing Rate, and Evaporative Water Loss in Hummingbirds

Author(s): Robert C. Lasiewski

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BODY TEMPERATURES, HEART AND BREATHING RATE, AND EVAPORATIVE WATER LOSS IN HUMMINGBIRDS[1]

ROBERT C. LASIEWSKI

Department of Zoölogy, University of Michigan

INTRODUCTION

RECENT studies on the metabolism of hummingbirds (Lasiewski, 1963) have revealed that, although the energetic cost of small size in hummingbirds is high, it is not as high as had been previously reported. These studies outlined the responses of the metabolism of torpid, resting, active, and flying hummingbirds to temperature. The results showed that hummingbirds are not "indifferent" homeotherms, as suggested by Pearson (1960), but have the ability to maintain homeothermy all night over a wide range of ambient temperatures, thereby qualifying as "stubborn homeo-

therms." The present paper is concerned with the effects of ambient temperature (T_A) on the interrelated aspects of body temperature (T_B), heart and breathing rate, and evaporative water loss. Some information is already available concerning these responses in hummingbirds through the studies of Odum (1941), Ruschi (1949), Pearson (1953), Bartholomew, Howell, and Cade (1957), and Morrison (1962).

Over forty individuals of seven species of hummingbirds were used in this study, and the birds were maintained in the laboratory for periods as long as 17 months. The species studied were Costa's hummingbird (*Calypte costae*), Anna's hummingbird (*C. anna*), black-chinned hummingbird (*Archilochus alexandri*), ruby-throated hummingbird (*A. colubris*), rufous hummingbird (*Selasphorus rufus*), Allen's hummingbird (*S. sasin*) and calliope hummingbird (*Stellula calliope*).

MATERIAL AND METHODS

The capture, maintenance, and transportation of hummingbirds has been treated elsewhere (Lasiewski, 1962) and need not be considered here. The birds studied were captured in Riverside County, California, and Ann Arbor, Michigan.

Body temperatures (T_B's), heart rates, and breathing rates were recorded simultaneously. The hummingbird was placed in a restraining flannel jacket, and a 40-ga. copper-constantan thermocouple, prepared by butt welding, was sewn into

the deep pectoral musculature. Temperatures of the bird and the surrounding air were monitored continually by a Brown recording potentiometer.

Three electrocardiographic electrodes, fashioned from fine, stainless-steel insect pins, were placed in the thoracic musculature, two medio-laterally, one dorsally. The leads from these electrodes were connected to a high-gain, a.c. preamplifier, which was used with a channel of a recording oscillograph (Sanborn, Model 1154). From the recordings obtained it was usually possible to determine both heart and breathing rates. The birds were placed in a darkened constant-temperature cabinet, and T_B's and heart and breathing rates during rest and torpor were recorded. Arousal from torpor was initiated by switching on the light, by raising the temperature of the cabinet, or by loud hand-clapping.

During measurements of evaporative water loss, the birds were housed in 1-gal. cans fitted with an airtight, 3.5-inch glass port for illumination and viewing of the bird, and with exit and entry ports for air. The bottoms of the chambers were covered with 1 cm. of mineral oil to entrap the feces as they were voided and thereby prevent their contributing water to the system. The birds were placed on perches in the chambers and were separated from the oil by a floor of $\frac{1}{2}$-inch wire mesh, installed 1 inch above the surface of the oil. The gallon cans were placed in temperature control cabinets, in which the temperature was maintained within 0.5° C. of the desired level. Dried air was passed through the chambers at a rate of 120 cm³ air/min, and then through two light-weight drying tubes filled with fresh Drierite. The birds were allowed to equilibrate 2 hours in the darkened chambers before measurements of evaporative water loss were begun. Water loss during torpor was obtained by placing the hummingbirds in the darkened chambers and monitoring their oxygen consumption with a Beckman G-2 paramagnetic oxygen analyzer used in conjunction with a Brown recording potentiometer. When the bird entered torpor, and had reached a stable level of oxygen consumption, the light-weight drying tubes, filled with Drierite, were connected into the air train. The drying tubes were weighed to the nearest milligram before and after the test period (1 hour for torpid birds, 2 hours for birds resting in the dark). Blank tests were performed periodically to check the system for possible leakage.

All temperatures are expressed in degrees Centigrade.

RESULTS AND DISCUSSION

A constant record of T_B was obtained while heart and breathing rates were being studied. Only rarely were electrocardiograms and breathing movements recorded simultaneously, although both were often obtained during the course of a single experiment. The best heart rates were obtained when the birds were torpid, or at T_A's within the zone of thermal neutrality. Muscle potentials often obscured deflections on the oscillograph representing electrocardiograms or breathing, particularly if the bird was regulating its T_B at T_A's below the lower critical temperature, or was emerging from torpor.

The data on heart and breathing rates and on T_B's are not strictly comparable to the data obtained on the metabolism of hummingbirds (Lasiewski, 1962), since it was necessary to confine the birds in flannel jackets during the oscillographic measurements. Hummingbirds have such small bodies, and relatively powerful muscles, that it was not possible to obtain these measurements without the use of restraining jackets. While such jackets

obviously alter the insulative character-istics of the bird being studied, I believe that the changes of heart and breathing rate with temperature are nevertheless instructive and valuable in the respects with which they are comparable to studies of larger birds and mammals. The data obtained from restrained birds are similar to the few values in the literature from unrestrained hummingbirds.

be even higher. The duration and level of T_B regulation depends largely upon the condition of the bird and upon external factors such as temperature. Birds with little or no energy reserves may drop into torpor soon after they are placed in the dark. Others may regulate their T_B at 40° or higher, for periods exceeding 8 hours at relatively low T_A. Still others may regulate at slowly decreasing T_B's,
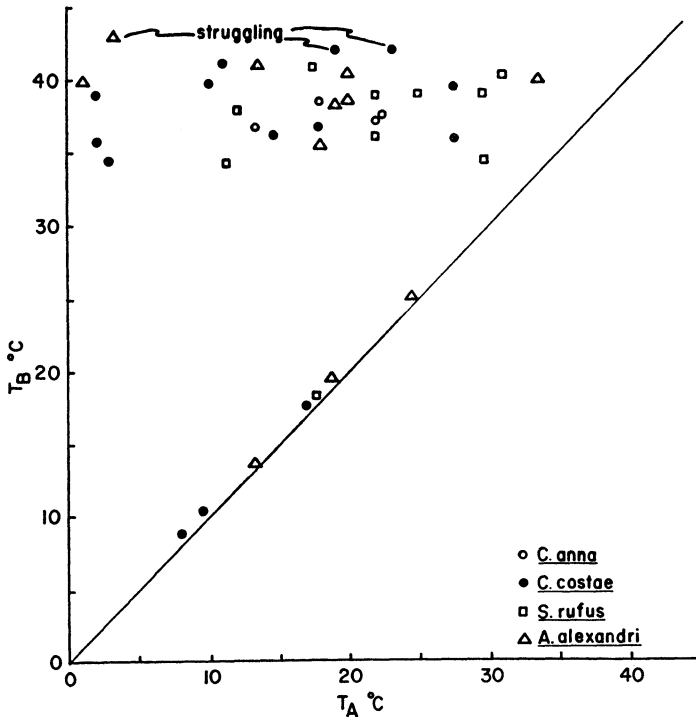

FIG. 1.—The relation between core body temperature and ambient temperature in hummingbirds of four species, resting in the dark, struggling, or torpid. Body temperatures were obtained with fine thermocouples implanted in the deep pectoral musculature from birds restained in flannel jackets.

BODY TEMPERATURES

The core T_B's of torpid and home-othermic hummingbirds, restrained in flannel jackets, are shown in Figure 1. The T_B's of torpid birds are within 1.2° of T_A over the temperature range stud-ied. Hummingbirds resting in the dark, in a postabsorptive state, may regulate their T_B's at levels between 34.4° and 41.2°, while the T_B's of active birds may

starting around 40°, and after 5 or 6 hours dropping as low as 34.4°. If dark-ness continues, the bird may abandon homeothermy, with the result that T_B declines to near the temperature of the environment. Birds entering torpor do not necessarily start at T_B of 35°–36° but may do so directly from levels as high as 40.2°.

No stable levels of T_B intermediate

between those of torpid and homeother-
mic birds have been recorded in direct
measurements of core T_B's, which is con-
sistent with data obtained from oxygen-
consumption studies (Lasiewski, 1963)
and heart rates reported below.

T_B's of restrained hummingbirds in
the light have been found to be between
39.6° and 43°. It has not been possible to
obtain recordings of core T_B from active
hummingbirds, since the vigorous move-
ments of the bird break the fine thermo-
couple junction that is normally sewn
through the pectoral musculature.

The core T_B's of restrained birds in
this study compare favorably with cloa-
cal temperatures of nine genera of Brazil-
ian hummingbirds (Ruschi, 1949), with
crop temperatures of Calypte anna (Bar-
tholomew et al., 1957), and with body
temperatures (obtained from under the
wings) of three genera of Brazilian hum-
mingbirds (Morrison, 1962). Ruschi com-
pared the cloacal temparatures of hum-
mingbirds during the day (39.5°–44.6°)
to those at night when the birds are
asleep, but not torpid (36.3°–40.5°). He
states that "to enter hibernation [torpor]
the temperature of the bird must drop
seven degrees below the normal daily
temperature, as was the case in all the
examples we have investigated." The
T_B's from which the Brazilian humming-
birds entered torpor were 32.0°–36.3°.

It was not necessary for the birds
studied here to drop their T_B's 7° before
entering torpor. While many of the birds
studied did regulate T_B at levels of 35°–
36° before entering torpor, at least four
cases were recorded in which humming-
birds (Archilochus alexandri and C. cos-
tae) abandoned homeothermy from T_B's
of 38.1°–40.2°.

Bartholomew et al. (1957) recorded
T_B's as low as 8.8° ($T_A = 8.2°$), and rates
of arousal of 1.0°–1.5° per minute in C.
anna. Similar rates of arousal were re-
corded in this study, and the T_B of 8.8°
for an unrestrained bird would fall di-
rectly in line with the other T_B's of torpid
birds in Figure 1.

The hummingbirds studied by Morri-
son (1962) exhibited a diurnal cycle of
T_B of at least 8°, which is the approxi-
mate range found for birds regulating in
the dark in this study. It is unclear, how-
ever, whether the birds which were classi-
fied as torpid by both Ruschi (1949) and
Morrison were torpid in the sense of a
lack of homeothermy. Morrison states:
"In this analysis, birds with closed eyes
were considered to be in sleep during the
day and in torpor at night," and Ruschi
may have used similar criteria. The T_B's
of "torpid" birds reported by Morrison
were 32.4° ± 0.8° for Amazilia, and 31.2°
± 1.2° for Chlorestes and Hylocharis,
while those of the nine genera of "hiber-
nating" birds reported by Ruschi ranged
from 32.0° to 36.3°. The torpid humming-
birds studied by Pearson (1953), Bar-
tholomew et al. (1957), and this author
generally had T_B's within 1.2° of T_A.
Presumably, Ruschi and Morrison were
referring to a deep sleep, in which the
hummingbirds were homeothermic.

Hummingbirds, the most diminutive
of the birds, appear to have a diurnal
cycle of T_B of at least 8°, excluding tor-
por. King and Farner (1961) have point-
ed out that the order of magnitude of the
diurnal variation of T_B in birds is "at
least in part an inverse function of body
size." The ability of hummingbirds to
regulate their T_B's at night, at levels
considerably lower than normal daytime
levels, is of adaptive value in lowering
their energetic commitments. If the Q_{10}
of 4.1 obtained from the relation between
oxygen consumption and T_A in torpid
hummingbirds (Lasiewski, 1963) is ap-
plicable, lowering the T_B by 5° would
halve the energy costs of maintaining
homeothermy at night. If energy re-

serves are insufficient for the mainte-
nance of homeothermic T_B's, humming-
birds are able to abandon warm-blooded-
ness and enter a state of torpor, thereby
further reducing energy expenditures.
The amount of energy saved by entering
torpor increases with decreasing T_A (Las-
iewski, 1963).

HEART AND BREATHING RATES

The minimal recorded heart rates of
torpid and resting hummingbirds, along
with those of birds that were awake but
active, are plotted in Figure 2. Generally,
heart rates of birds regulating in the dark
increase with decreasing T_A. Minimal
heart rates of homeothermic birds range
from 480 beats/min at T_A of 32°, to 1,020
beats/min at 1.0°. Yapp (1962) suggested
that the upper limit of the rate of beat of
a bird's heart is around 1,000/min on the
basis of available data. The maximum
rates recorded in this study were 1,200
beats/min, but it seems unlikely that
this represents the upper limit of heart
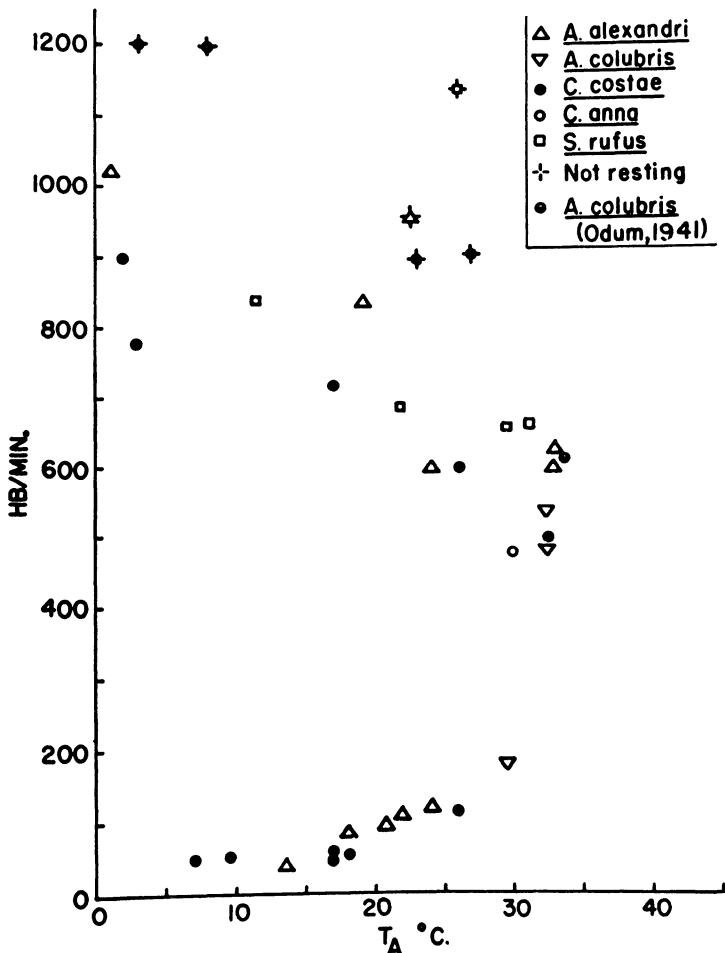action in hummingbirds. Electrocardio-

FIG. 2.—The relation between heart rate and ambient temperature in hummingbirds of five species, and a point from Odum (1941) for *A. colubris*. The resting and torpid rates plotted here are the lowest obtained at each temperature. The hummingbirds were confined in flannel jackets and placed in darkened temperature control cabinets. Values designated by a superimposed + are the highest recorded in particular experiments and represent struggling or excited birds.

grams of struggling birds are often obscured by extensive somatic potentials, and it has not yet been possible to record the heart rates of hummingbirds during, or shortly after, flight. The values reported here for *Archilochus alexandri, A. colubris, Selasphorus rufus,* and *C. costae* are in close agreement with those reported by Odum (1941) for *A. colubris* (550–650 beats/min), and by Morrison, Ryser, and Dawe (1959) for the small shrew, *Sorex cinereus* (600–1,320 beats/min).

Heart rate decreases with T_A in torpid birds, with values ranging from 48 beats/min at T_A of 7°, to 180 beats/min at 29.6°. There is too much variability in the heart rate of torpid birds to calculate a meaningful Q_{10} of the change in rate with temperature. As with T_B's and oxygen consumption, there is no indication of any intermediate steady-state levels of regulation, between the heart rates of torpid and resting birds. There is a marked hiatus between the lowest recorded resting rate and the highest recorded torpid value, but this is undoubtedly due in large part to failure to obtain records from torpid birds above T_A of 29.6°.

The interval between heart beats is not always uniform in torpid birds, and heart rates calculated from short-term records may be misleading. However, representative rates could be obtained from records extending over several minutes. Atrio-ventricular dissociation occurred in two hummingbirds forced into torpor at T_A's below 3°. It developed in *C. costae* at T_B of 11.5°, and in *A. alexandri* at T_B of 7°. Both birds died minutes after the *A-V* dissociation occurred. French and Hodges (1959) observed hummingbirds that were torpid at T_A's as low as 5°, and acclimatization may be important in allowing T_B's to drop to these low levels without lethal effects.

The birds studied here were maintained in captivity at T_A's of 19°–24°.

Respiratory rate increases with decreasing T_A (Fig. 3), with values for homeothermic birds ranging from 180 breaths/min at 31°, to 460 breaths/min at 3°. From the data available, it appears that individuals of *C. costae* may have a lower breathing rate than birds of the other species, but more observations are needed to verify this. Bartholomew *et al.* (1957) visually recorded a maximum respiratory rate of 273/min from an excited *C. anna* at T_A of 22°. Respiratory rates as high as 600 breaths/min were recorded electronically in the present study.

Torpid hummingbirds all breathed sporadically, with long periods of apnea occurring at lower temperatures. Regular breathing was not recorded from torpid birds in this study. Bartholomew *et al.* (1957) found "periods of cessation of breathing of five minutes in duration" at T_B's of 9°–12°. It is uncertain from their data whether or not these birds were completely torpid.

Although oxygen consumption (Lasiewski, 1962), respiratory rates, and heart rates all increase with decreasing T_A in birds resting in the dark, the changes (per cent increase above basal levels) per degree Centigrade differed. This may, in part, be due to the insulative effects of the flannel jackets which were used to restrain the birds during recordings of heart and respiratory potentials, although it may also reflect actual changes in the characteristics of breathing and heart action with decreasing temperature. It will nevertheless be instructive to compare the oxygen utilized at different temperatures per heart beat and per breath (Table 1). The oxygen consumed per heart beat, and per breath, increases as the T_A decreases, possibly reflecting a more efficient utili-
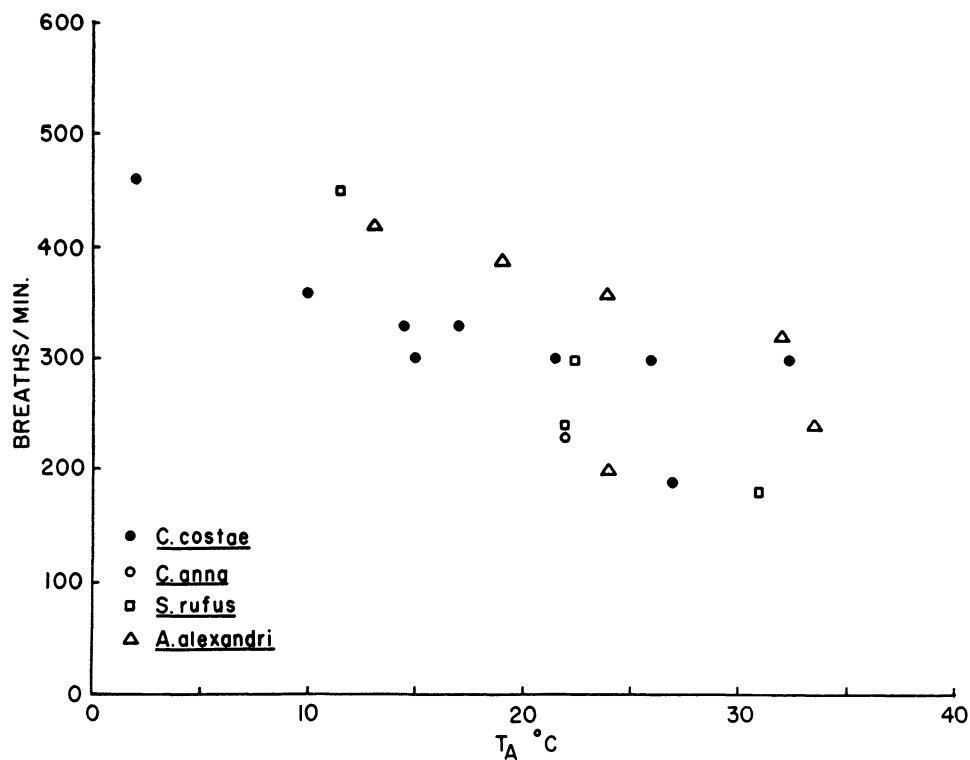
FIG. 3.—Breathing rates of hummingbirds of four species resting in the dark, as a function of ambient temperature. The birds were confined in flannel jackets, and the values shown here are the lowest recorded at particular temperatures. Respiratory rates as high as 600 breaths/min were recorded in excited birds.

TABLE 1

NET OXYGEN UTILIZED AS A FUNCTION OF HEART AND BREATHING RATE

| | T_A (° C.) | METABOLISM | | HEART RATE (BEATS/ MIN) | BREATHING RATE (BREATHS/ MIN) | NET OXYGEN UTILIZED | |
		Cm³ O₂/ Gm Hr	Cm³ O₂/ Min			μl O₂/ Beat	μl O₂/ Breath
Calypte costae (postabsorptive and resting in dark).......	$\begin{cases}32.5\\ 2.0\end{cases}$	2.8 17.4	0.14 .87	500 900	180* 460	0.28 .97	0.78 1.9
Calypte costae (torpid).......	$\begin{cases}26.0\\ 12.0\end{cases}$	0.83 0.10	.042 .005	114 52*	....	.36 .096	....
Sorex cinereus† ("basal" conditions).....................	....	9.8	0.049	606	650	0.80	0.75

* Approximate.
† From Morrison, Ryser, and Dawe (1959).

zation of oxygen as the metabolic demands increase.

The basal value for *C. costae* of net oxygen utilized per heart beat (0.28 μl O_2/beat) is considerably less than that obtained for a shrew, *Sorex cinereus*, of similar size (0.80 μl O_2/beat) by Morrison *et al.* (1959). Since the heart rates of the two animals are similar, this difference is accounted for largely by the higher oxygen consumption of *Sorex*.

The basal value of net oxygen utilized per breath by *C. costae* (0.78 μl O_2/breath) is essentially the same as that calculated for *S. cinereus* (0.75 μl O_2/breath) from the data of Morrison *et al.* (1959). The higher metabolism of *S. cinereus* is offset, in these comparisons, by an increased breathing rate in this shrew.

Heart rate in torpid birds does not drop as markedly with decreasing T_A as does oxygen consumption. Hummingbirds therefore utilize less oxygen per heart beat at 12°, than at 26°. The oxygen utilized per heart beat in torpid humming birds at T_A of 26° (0.36 μl O_2/beat) is well within the range observed in postabsorptive hummingbirds regulating in the dark (0.28–0.97 μl O_2/beat). The relatively low value of 0.096 μl O_2/beat for a torpid bird at 12° allows one to explain the occurrence of periods of apnea at low T_A. The diffusion of oxygen from the external air to the lung surfaces may account for a considerable portion of the oxygen needed to sustain metabolism in torpid hummingbirds, particularly at lower temperatures.

EVAPORATIVE WATER LOSS

The amount of water vapor added by each bird to the system used for evaporative water loss measurements (see "Material and Methods") varies with T_A as do the different carrying capacities of the air. It was possible to calculate the approximate relative humidities in the chambers from the following formula:

$$\text{Relative humidity} = 100\left[\frac{MRT}{V(0.621)e_s}\right],$$

where

M = mass of water vapor (gm/min)

R = gas constant (2.87×10^6 erg/° K.)

T = ambient temperature (° K.)

V = cm³ air/min

0.621 = constant

e_s = 1,333 dynes/cm² $\times$ saturated vapor pressure

TABLE 2

REPRESENTATIVE RELATIVE HUMIDITIES IN CHAMBERS AT VARIOUS AMBIENT TEMPERATURES DURING STUDIES OF EVAPORATIVE WATER LOSS IN RESTING HUMMINGBIRDS

T_A (° C.)	Species	Relative Humidity (Per Cent)
10	*Stellula calliope*	51.7
10	*Calypte costae*	64.7
10	*C. anna*	56.5
15	*C. costae*	41.9
23	*C. anna*	28.7
35	*Calypte costae*	17.7
39.5	*C. costae*	17.6
41.2	*C. costae*	37.8

Representative relative humidities at different temperatures are presented in Table 2.

Evaporative water loss was measured over a wide range of T_A's in six species of hummingbirds; *Calypte costae*, *C. anna*, *Selasphorus sasin*, *S. rufus*, *Archilochus alexandri*, and *Stellula calliope*. Water loss through evaporation, for birds resting in the dark, increases slowly with increasing temperature (Fig. 4), with values ranging from 6.2–33.6 mg H_2O/gm hr. In almost all cases, the evaporative water loss per unit was lower in the heavier *C. anna* (4.7–5.7 gm.) than in the other five species.

An immature male *C. costae* lost 33.6 mg H_2O/gm hr through evaporation at a T_A of 41.2°. If this rate of evaporative water loss were maintained over a 24-hour period, it would amount to over 81 per cent of the body weight per 24 hours! After 1 hour at this temperature the *C. costae* showed signs of what appeared to

More average values were around 30 per cent body weight per 24 hours. Bartholomew and Dawson (1953) demonstrated that evaporative water loss at 23°–27° increases sharply in birds weighing less than 40 gm. The rates of evaporative water loss in hummingbirds constitute some of the highest recorded for birds,
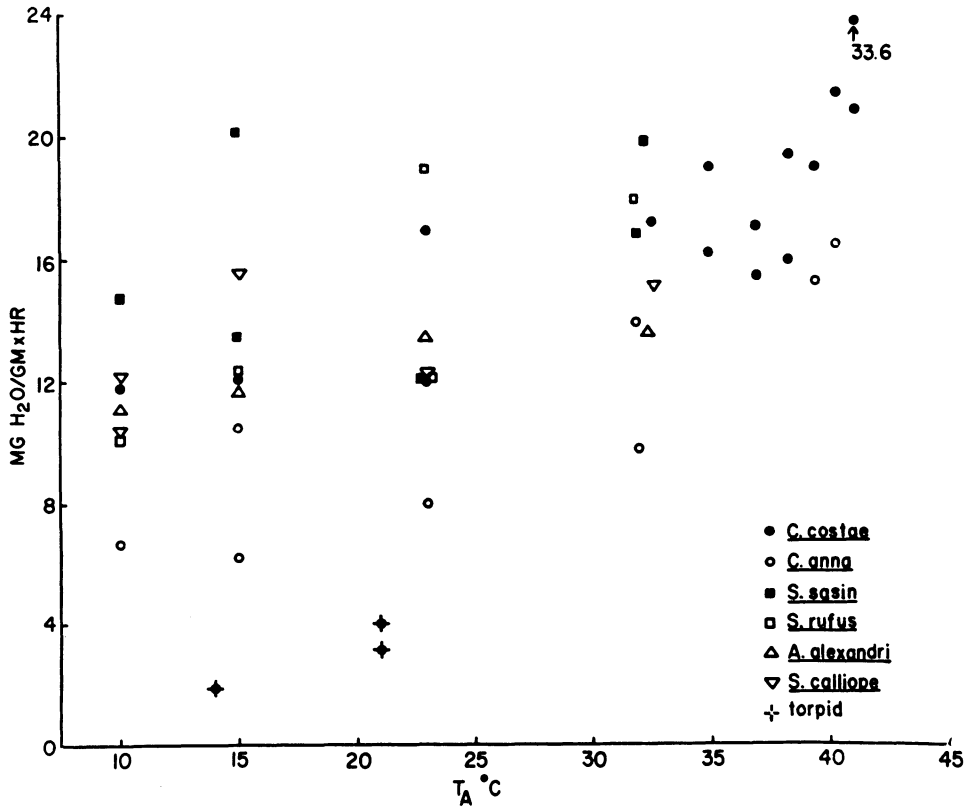

Fig. 4.—Evaporative water loss in hummingbirds of six species as a function of ambient temperature. Water loss of torpid birds is designated by a + superimposed over the species symbol. All other values represent birds resting in the dark in a postabsorptive state.

be heat prostration (it was not possible to measure T_B). Specimens of *C. costae* were used at the higher temperatures, since this species is found in hotter and drier areas than the others studied.

Water loss was high even at relatively mild T_A. At 23°, evaporative water loss ranged from 18.3 per cent body weight per 24 hours in *C. anna*, to 45 per cent body weight per 24 hours in *S. rufus*.

and the values are consistent with those predicted by the body-weight–respiratory-water-loss curve for birds in Bartholomew and Dawson (see their Fig. 1, p. 165). It should be noted that the range of temperatures of 23°–27° used to obtain this curve may have different effects on different sized birds. While 24° is well within the zone of thermal neutrality for larger birds, it is below the

lower critical temperatures of the hummingbirds studied here.

In view of the increasing rates of oxygen consumption and respiration with decreasing T_A, the reasons for decreasing rates of water loss are unclear. While $C.$ $costae$ loses 2.1 mg H_2O/cm^3 O_2 at 23°, only 0.92 mg H_2O/cm^3 O_2 are lost at 10°. Decreasing evaporative water loss with decreasing T_A was also found in the cardinal, $Richmondena$ $cardinalis$, by Dawson (1958), and the cardinal exhibited a much lower rate of water loss per unit oxygen consumed that did the hummingbirds. Dawson reported losses of 0.9 mg H_2O/cm^3 O_2 consumed at 25°. Rates of water loss in hummingbirds and in the cardinal greatly exceed those of the heteromyid rodents of desert regions, which evaporate as little as 0.50–0.59 mg H_2O/cm^3 O_2 consumed at 25° (Schmidt-Nielsen and Schmidt-Nielsen, 1950). The greater water loss per unit metabolism by the cardinal "reflects a higher rate of respiratory water loss owing to expiration of warmer air of greater moisture-carrying capacity than that expired by rodents" (Dawson, 1958), and a comparable situation may exist in hummingbirds. The decreased evaporative water loss with decreased T_A could be due to a change in the characteristics of breathing at different temperatures. Also, air may be expired at lower temperatures with a consequent decrease of moisture-carrying capacity as the T_A decreases.

Although oxygen consumption and evaporative water loss were not measured simultaneously, it is possible to estimate corresponding values at a given temperature and thereby provide an approximation of the role of evaporative cooling in the heat economy of hummingbirds. At 10°, evaporation accounts for only 11.1 per cent of the heat produced (Table 3). With increasing T_A, the heat dissipated by evaporative cooling

offsets progressively larger proportions of the metabolic heat produced. In the zone of thermal neutrality, evaporation may dispose of as much as 65 per cent of the heat produced, but never completely offsets heat production. At higher temperatures, where a favorable gradient for loss does not exist, these birds would be forced to store heat. This situation is similar to that found in the cardinal by Dawson (1958). Hummingbirds are able to dissipate a higher proportion of their metabolic heat at high T_A's by evaporative cooling, than most other birds. King and Farner (1961) have compiled data

TABLE 3

ROLE OF EVAPORATIVE COOLING IN HEAT
ECONOMY OF "CALYPTE COSTAE"

T_A (° C.)	Heat Production (Cal/ Gm Hr)	Evaporative Cooling (Cal/ Gm Hr)	100(Evap. Cooling/ Heat Product)
10.....	61.9	6.9	11.1
15.....	48.4	7.0	14.5
23.....	26.8	7.0	26.2
35.....	14.4	9.4	65.3
39.5...	18.2	11.2	61.6

on the per cent of resting heat production lost via respiratory evaporation at high ambient temperatures for a number of representative species of birds (see their Table 7, p. 263). Evaporative cooling in these species (mostly passerines) accounts for 27.6–50.4 per cent of the resting heat production at high T_A's. The higher value for $Calypte$ $costae$ (65.3 per cent at T_A of 35°) is, in large part, due to the high evaporative water loss per unit weight.

It was possible to measure evaporative water loss during torpor in three individual Costa's hummingbirds, $C.$ $costae$, as shown in Figure 4. As might be predicted from the greatly decreased oxygen consumption and breathing rates, torpidity also lowers the amount of water

lost through evaporation. Water loss during torpor decreases with decreasing T_A, with recorded levels of 3.2 and 4.0 mg H_2O/gm hr at 21°, and 1.9 mg H_2O gm hr at 14°. There is a three- to sixfold difference between the evaporative water loss of torpid and homeothermic hummingbirds. Since hummingbirds are characterized by relatively large evaporative water losses while homeothermic, torpor is obviously important in terms of water conservation as well as energy conservation. We might expect a hummingbird to enter torpidity when its energy reserves were low, and/or when its water balance was precarious.

Evaporative water loss is only a portion of the total water turnover in hummingbirds, and fecal and urinary water losses were not measured in this study. With such a high rate of water turnover, it is apparent that the availability of sufficient water may be as important as sufficient energy in limiting the distribution of hummingbirds. Water may be obtained by drinking, through the oxidation of foodstuffs, and as free water in the food (mainly insects and nectar). Hummingbirds utilize each of these sources. Since fresh nectar may be 75 per cent water, it can contribute importantly to the water economies of hummingbirds that utilize it. During certain seasons, some hummingbirds exist almost exclusively on insects (Wagner, 1946; Lasiewski, unpublished observations), which may be important both as an energy and a water source.

SUMMARY

The effects of temperature on cardiac and respiratory rates, body temperature regulation, and evaporative water loss of hummingbirds were investigated in the following species: Costa's hummingbird, *Calypte costae;* Anna's hummingbird, *C. anna;* rufous hummingbird, *Selasphorus rufus;* Allen's hummingbird, *S. sasin;* black-chinned hummingbird, *Archilochus alexandri;* ruby-throated hummingbird, *A. colubris;* and Calliope hummingbird, *Stellula calliope.* Although some species differences were demonstrated (i.e., evaporative water loss was lower in the larger *C. anna*), many more measurements would be needed for a valid differentiation of species-specific responses.

Torpid hummingbirds have body temperatures within 1.2° of ambient temperature. Homeothermic birds resting in the dark in a postabsorptive state may regulate body temperatures at levels between 34.4° and 41.2° for considerable periods of time over a wide range of environmental temperatures.

Heart rates of torpid birds vary directly with temperature, ranging from 48–180 heartbeats/min between 7° and 29.6°. The heart rates of hummingbirds resting in the dark vary inversely with ambient temperatures, with recorded values ranging from 480 beats/min within the zone of thermal neutrality to maximum values of 1,200 beats/min.

Breathing rates of homeothermic birds also vary inversely with temperature, with values ranging from 180 breaths/min in the zone of thermal neutrality to maximum recorded rates of 600/min. Breathing of torpid birds is irregular, with long periods of apnea occurring at lower temperatures.

Evaporative water loss increases slowly with increasing ambient temperatures, with rates for the heavier *C. anna* consistently being somewhat lower than those for the other species. Panting at temperatures above 41° causes a sharp increase in water loss, with recorded rates for 1 hour being sufficient to cause a loss of water equivalent to 81 per cent of the body weight in water per 24 hours.

Evaporative water loss of torpid *C. costae* decreases with decreasing environ-

mental temperatures, with recorded levels of 3.2 and 4.0 mg H_2O/gm hr at 21° and 1.9 mg H_2O/gm hr at 14°. There is a three- to sixfold difference between comparable torpid and homeothermic values of water loss. Torpidity may be important in conservation of water, as well as in conservation of energy.

LITERATURE CITED

BARTHOLOMEW, G. A., and DAWSON, W. R. 1953. Respiratory water loss in some birds of southwestern United States. Physiol. Zoöl., 26:162–66.

BARTHOLOMEW, G. A., HOWELL, T. R., and CADE, T. J. 1957. Torpidity in the white-throated swift, Anna hummingbird, and poor-will. Condor, 59: 145–55.

DAWSON, W. R. 1958. Relation of oxygen consumption and evaporative water loss to temperature in the cardinal. Physiol. Zoöl., 31:37–48.

FRENCH, N. R., and HODGES, R. W. 1959. Torpidity in cave-roosting hummingbirds. Condor, 61:223.

KING, J. R., and FARNER, D. S. 1961. Energy metabolism, thermoregulation and body temperature. Pp. 215–88 in Biology and comparative physiology of birds, Vol. II, ed. A. J. MARSHALL. New York: Academic Press.

LASIEWSKI, R. C. 1962. The capture and maintenance of hummingbirds for experimental purposes. Avicult. Mag., 68:59–64.

———. 1963. Oxygen consumption of torpid, resting, active, and flying hummingbirds. Physiol. Zoöl., 36:122–40.

MORRISON, P. R. 1962. Modification of body temperature by activity in Brazilian hummingbirds. Condor, 64:215–23.

MORRISON, P. R., RYSER, F. A., and DAWE, A. R. 1959. Studies on the physiology of the masked shrew, Sorex cinereus. Physiol. Zoöl., 32:256–71.

ODUM, E. P. 1941. Variations in the heart rate of birds: a study in physiological ecology. Ecol. Monog., 11:299–326.

PEARSON, O. P. 1953. Use of caves by hummingbirds and other species at high altitudes in Peru. Condor, 55:17–20.

———. 1960. Torpidity in birds. Bull. Mus. Comp. Zoöl., 124:93–103.

RUSCHI, A. 1949. Observations on the Trochilidae. Bull. Mus. Biol. Prof. Mello-Leitao, Santa Teresa, Brazil, No. 7. (Seen in translation prepared by C. H. Greenewalt.)

SCHMIDT-NIELSEN, B., and SCHMIDT-NIELSEN, K. 1950. Pulmonary water loss in desert rodents. Amer. Jour. Physiol., 162:31–36.

WAGNER, H. O. 1946. Food and feeding habits of Mexican hummingbirds. Wilson Bull., 58:69–93.

YAPP, W. B. 1962. Some physical limits on migration. Ibis, 104:86–89.