PHYSIOLOGICAL RESPONSES OF THE BLUE-THROATED AND RIVOLI'S HUMMINGBIRDS

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Because of their small size and consequent high rates of physiological activities, hummingbirds have intrigued generations of biologists. Within the past 30 years, physiologists have studied many aspects of the responses of these diminutive homeotherms (Huxley *et al.*, 1939; Odum, 1941; Ruschi, 1949; Pearson, 1950, 1953, 1954; Howell and Dawson, 1954; Bartholomew *et al.*, 1957; Shellabarger *et al.*, 1961; Morrison, 1962; Lasiewski, 1962*b*, 1963, 1964; Lasiewski *et al.*, 1965). Although hummingbirds range in size from approximately 2 to 20 g, the smaller, North American species were used in most of these studies. Little is known about the physiological characteristics of intermediate or larger sized hummingbirds and how they compare with those of the smaller species. This study presents data on some physiological responses of the two largest (6.5 to 9 g) species of hummingbirds found in the United States, the Blue-throated Hummingbird, *Lampornis clemenciae*, and Rivoli's Hummingbird, *Eugenes fulgens*.

Materials and Methods

The hummingbirds were captured in southeastern Arizona during July and August, 1965. The techniques for the maintenance of hummingbirds (Lasiewski, 1962*a*), measurement of oxygen consumption (Lasiewski, 1963), measurement of heart and breathing rate and core body temperatures (Lasiewski, 1964), and measurement of evaporative water loss by direct weighing (Lasiewski *et al.*, 1966) have been presented earlier and need not be discussed here. Air flow rates of 300–350 cc/minute were used in open flow determinations of oxygen consumption.

Wing beat frequencies were determined with a stroboscopic tachometer (Strobotac, General Radio) while the hummingbirds hovered in a cage which was 20 × 20 × 40 inches.

Body temperatures during entry into and arousal from torpor were obtained by placing the hummingbird in a one-quarter inch mesh cloth restraining jacket. A 40 gauge copper-constantan thermocouple was sewn through the deep pectoral musculature, and ambient and body temperatures were recorded continually with a Honeywell Electronik 16 potentiometric thermocouple recorder. Ambient temperature was maintained at 20° C during studies of rates of entry into and arousal from torpor.

All gas volumes are corrected for standard temperature and pressure, and all temperatures are given in degrees Centigrade.

Results

In all, 14 adult Rivoli's and Blue-throated hummingbirds were used. Their weights (in grams) upon capture were: Rivoli's males, 8.5, 7.8, 7.5, 7.3, 8.0, 8.5; Rivoli's female, 7.0; Blue-throated males, 8.5, 8.5, 8.6, 8.6, 8.2; Blue-throated females, 6.5, 6.9. The males of both species weighed

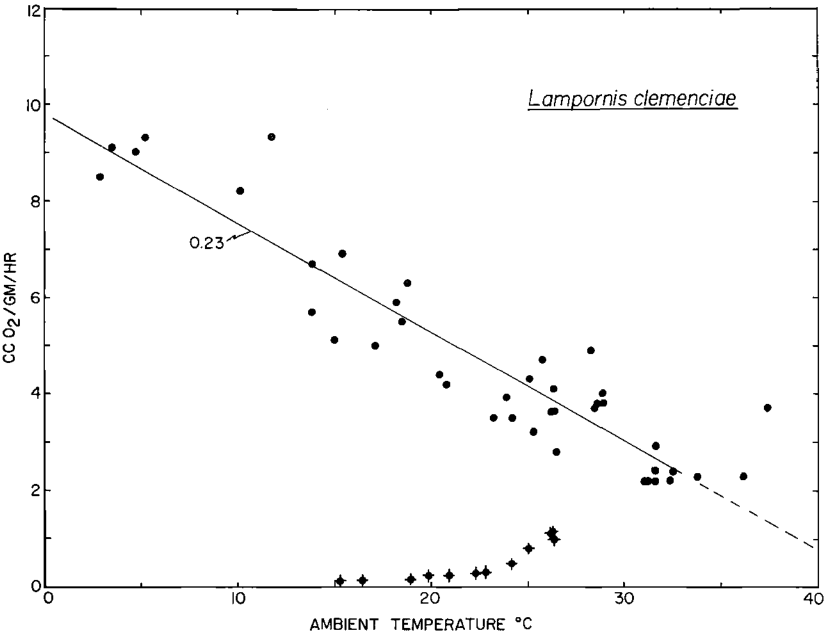

Figure 1. Relationship between oxygen consumption and ambient temperature in homeothermic and torpid *Lampornis clemenciae*. The regression line fitted through homeothermic values below thermoneutrality was fitted by method of least squares, and is taken as an estimate of thermal conductance. Torpid birds are indicated by a +.

more than the females, and Blue-throated males were slightly heavier ($\overline{X}$ [i.e., mean] = 8.5) than Rivoli's males ($\overline{X}$ = 8.0) when caught.

The relationships between ambient temperature and metabolic rates of both torpid and postabsorptive hummingbirds resting in the dark are similar in both species (Figures 1 and 2). The mean weight of Blue-throated hummingbirds when used in metabolic measurements was 7.9 g, while their metabolic rate in the thermoneutral zone averaged 2.3 cc O_2/g/hr. At ambient temperatures of approximately 31° and below, the metabolic rate of *Lampornis clemenciae* in an homeothermic state increased with decreasing environmental temperatures, at the rate of 0.23 cc O_2/g/hr/°C. A line fitted by the method of least squares to those data below the zone of thermoneutrality extrapolates to zero metabolism at a temperature of 43.5°. The slope of this line is representative of thermal conductance, and values for thermal conductance are inversely related to the effectiveness of insulation.

Comparable values for the homeothermic species *Eugenes fulgens* are: $\overline{X}$ weight when used in metabolism studies, 6.6 g; standard metabolic

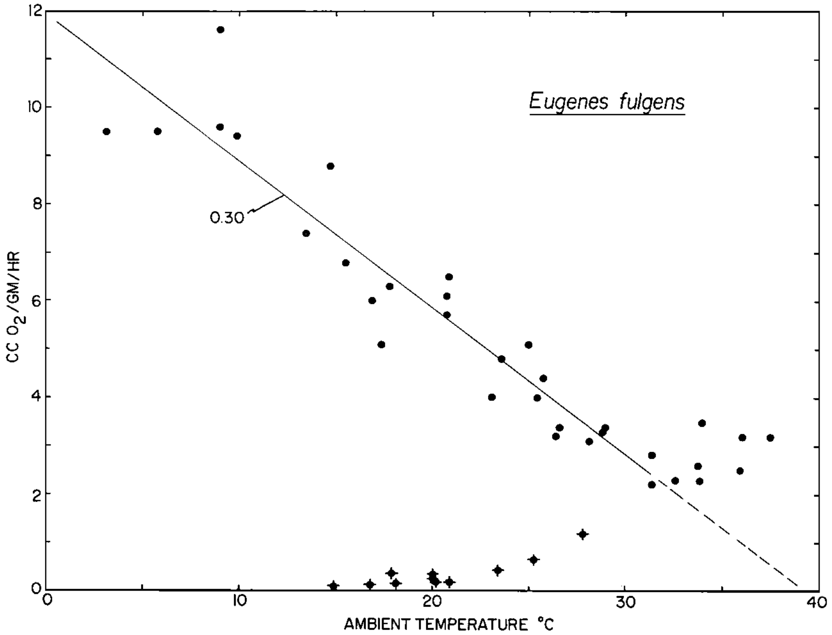

Figure 2. Relationship between oxygen consumption and ambient temperature in homeothermic and torpid *Eugenes fulgens*. Torpid birds are indicated by a +.

rate in zone of thermoneutrality, 2.7 cc O_2/g/hr; thermal conductance 0.30 cc O_2/g/hr/°C; least squares line through values below zone of thermoneutrality extrapolates to zero metabolism at a temperature of 39°.

The metabolic rates of torpid *L. clemenciae* and *E. fulgens* increase with increasing ambient temperature, and are plotted below the homeothermic values in Figures 1 and 2. The torpid metabolism values are similar for both species, ranging from 0.10 cc O_2/g/hr at 14.9° to 1.18 cc O_2/g/hr at 26.9° C. The Q_{10}* of torpid metabolism of Blue-throated and Rivoli's hummingbirds is 4.3 between 14.9° and 22.3°, which is similar to Q_{10} values found for smaller hummingbirds that were torpid (Lasiewski, 1963).

The lowest homeothermic heart rates recorded in these intermediate-sized hummingbirds were 480–510 beats/min at 35° for *L. clemenciae,* and 420 beats/min at 34° for *E. fulgens* (Table 1). Maximum recorded

* Q_{10} or temperature coefficient is the ratio of the rate of some process at a given temperature to the rate at a temperature 10° C lower. If data are gathered at temperature intervals other than 10° C, the temperature coefficient may be calculated by the following equation:

$$\log Q_{10} = \frac{10}{t_1 - t_2} \log \frac{k_1}{k_2}$$

where k_1 is the rate at temperature t_1, and k_2 is the rate at t_2.

TABLE 1

HEART RATES RECORDED FROM BLUE-THROATED AND RIVOLI'S HUMMINGBIRDS

Species	*Heart rate (beats/min)*	*Ambient temperature (°C)*
	Lampornis clemenciae	
Homeothermic		
Minimum	480–510	35
Maximum	1200–1260	35
Torpid	140	24
Torpid	36	15
	Eugenes fulgens	
Homeothermic		
Minimum	420	34
Maximum	1200	34
Torpid	120	22.6
Torpid	107	20.5
Torpid	55	15

heart rates for both species were 20–21/sec. Heart rates during torpor decreased in both species with decreasing temperatures (Table 1).

Evaporative water loss of postabsorptive homeothermic *L. clemenciae* and *E. fulgens* at water vapor pressures of 6.0–7.3 mm Hg increases with increasing ambient temperature (Figure 3), with recorded values ranging from 6.7 to 12.5 mg H_2O/g/hr at 15° and 34.8° C, respectively. Torpid hummingbirds of both species show a marked decrease in evaporative water loss below homeothermic levels at 15° and 25° C.

Wing-beat frequencies during hovering flight generally increase with decreasing body weight, in the four species of hummingbirds which we have studied in this respect. Wing-beat rate is inversely related to the wing length of hummingbirds (Figure 4) in the Black-chinned Hummingbird, *Archilochus alexandri,* the Violet-crowned Hummingbird, *Amazilia verticalis* (R. C. Lasiewski, unpublished observations), and Blue-throated and Rivoli's hummingbirds.

Core body temperatures were recorded while birds, maintained in the dark at 20°, entered into and aroused from torpor. Body temperature during entry into torpor dropped rapidly initially, then more slowly as the gradient between body and environmental temperatures decreased (Figure 5). According to Newton's law of cooling, the rate of change of body heat (dH/dt) is proportional to the temperature gradient between the body and the environment (T_B–T_A). When the logarithm of the temperature gradient is plotted against time, the data approximate a straight line in a Newtonian cooling curve, as shown in Figure 5 for a male Blue-throated Hummingbird. The slope of this straight line is related to the thermal conductance of the bird, with steeper slopes indicating higher values of conductance (less effective insulation).

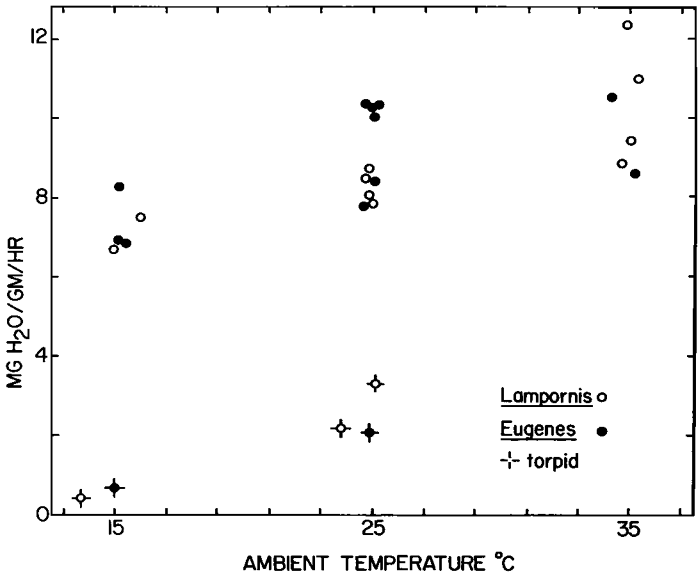

Figure 3. Relationship between evaporative water loss and ambient temperature (water vapor pressure 6.0–7.3 mm Hg) in homeothermic and torpid *Lampornis clemenciae* and *Eugenes fulgens.*

An inverse relationship exists between the rate of entry into torpor and the body weight of the bird studied, in the Black-chinned, Rivoli's, and Blue-throated hummingbirds, and Poor-will, *Phalaenoptilus nuttallii* (Figure 6), and all four species cooled in a manner predicted by Newton's law of cooling. Arousal from torpor was more rapid than entry, and the rate of arousal is inversely related to the body weight of the species studied (Figure 7).

DISCUSSION

The body weights we recorded upon capture of Blue-throated and Rivoli's hummingbirds are similar to the few values (given below in grams) published for these two species: *Lampornis clemenciae,* males, 7.4, 8.0, female, 7.9, nestlings (20–29 days), 9.5, 9.2, 8.9, 8.4, 9.9 (Wagner, 1952); *L. clemenciae,* males, 8.2, 8.1, 7.7, female, 6.9, *Eugenes fulgens,* male, 7.9 (Miller, 1955). All other species of hummingbirds occurring naturally in the United States weigh less than Blue-throated and Rivoli's hummingbirds.

The males of many large and intermediate-sized hummingbirds weigh more than the females, as in the cases of *L. clemenciae* and *E. fulgens.* In most of the smaller hummingbirds, the females weigh more than the males, as illustrated by data of Hartman (1954, 1961) and R. C. Lasiewski

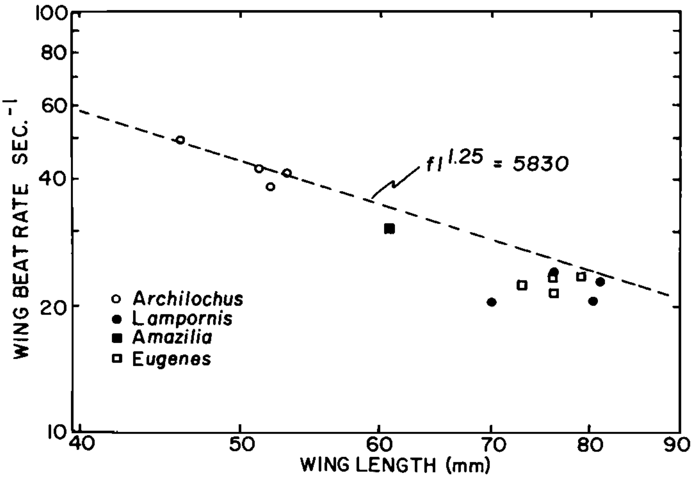

Figure 4. The relation between wing-beat frequency during hovering flight and wing length in *Archilochus alexandri, Lampornis clemenciae, Amazilia verticalis,* and *Eugenes fulgens.* Dashed line drawn from equation of Greenewalt (1962), where f is wing-beat frequency/sec, and l is wing length in mm.

(unpublished observations). Female hummingbirds almost invariably build the nest, incubate the eggs and young, and feed the young, unassisted by the male. A selective advantage, related to rearing of young, may be conferred upon the smaller species by the greater relative size of the females. Smaller birds have a higher weight-specific metabolic expenditure and produce heavier eggs per unit body weight (Brody, 1945). Perhaps the body weight attained by the males of the smaller species (as little as 1.7–2.5 g in some males of the Calliope Hummingbird, *Stellula calliope,* Amethyst Hummingbird, *Calliphlox amethystina,* and the Bee Hummingbird, *Calypte helenae*) are below the optimal size required for egg production and rearing of the young.

The relationship between standard metabolic rate and body weight in birds has been the subject of some controversy. Brody and Proctor (1932) published the following equation relating the standard metabolic rates and body weights in birds:

$$\log \text{Metabolism (kcal/day)} = \log 89 + 0.64 \log \text{Weight (kg)}$$

This equation differs markedly from the comparable accepted equations for mammals. King and Farner (1961), using many more data, provided the following equation for birds weighing more than 125 g:

$$\log \text{Metabolism (kcal/day)} = \log 74.3 + 0.744 \log \text{Weight (kg)}$$

This latter equation, not including small birds, is similar to Kleiber's (1947) equation for mammals ranging in weight from 0.02 to 600 kg. Lasiewski and Dawson (1967) re-analyzed the relation between the

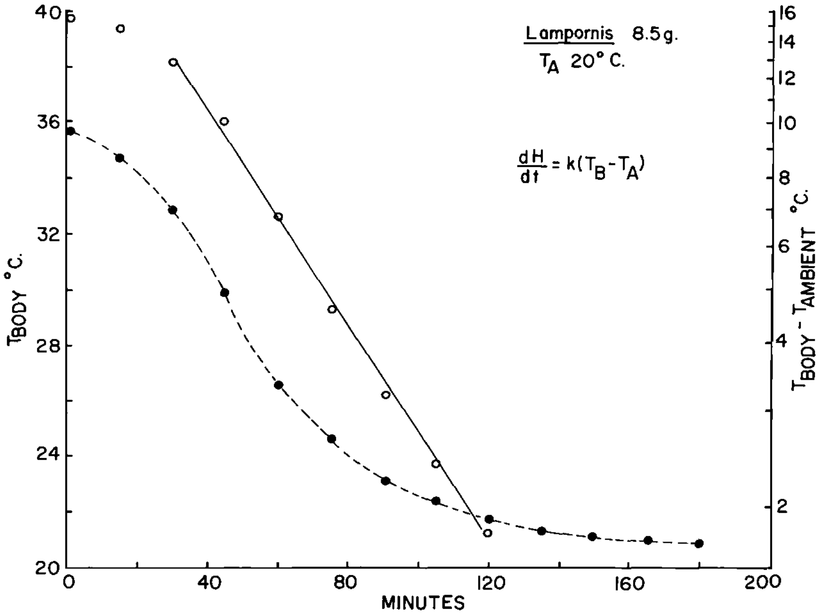

Figure 5. Body temperatures of a *Lampornis clemenciae* during entry into torpor at ambient temperature of 20° C. Shaded circles indicate body temperatures recorded, while unshaded circles represent the log of the temperature gradient between the body and the environment (T_B–T_A).

standard metabolism and body weight in birds, and found that passerines have a higher metabolism per unit weight than do nonpasserines. They presented an equation for nonpasserine birds, ranging in size from hummingbirds to the ostrich (*Struthio camelus*):

$$\log \text{Metabolism (kcal/day)} = \log 78.3 + 0.723 \log \text{Weight (kg)}$$

This equation is statistically indistinguishable from the comparable equations for mammals. For nonpasserine birds, it predicts standard metabolic rates of 2.08 and 2.36 kcal/day for 6.6 and 7.9 g birds, respectively. Our data reveal that the Rivoli's Hummingbird ($\overline{X}$ wt = 6.6 g) has a standard metabolism of 2.08 kcal/day, while that of the Blue-throated Hummingbird ($\overline{X}$ wt = 7.9 g) equals 2.09 kcal/day, assuming that 1 liter of O_2 consumed equals 4.8 kcal. Both of these intermediate-sized hummingbirds, as well as the six species of smaller hummingbirds studied by Lasiewski (1963) have standard metabolic rates which are similar to those predicted by this equation based on the size-metabolism relationships of larger nonpasserine birds.

An inverse relationship exists between thermal conductance, expressed as cc O_2/g/hr/°C, and body weight in small birds and mammals (Lasiew-

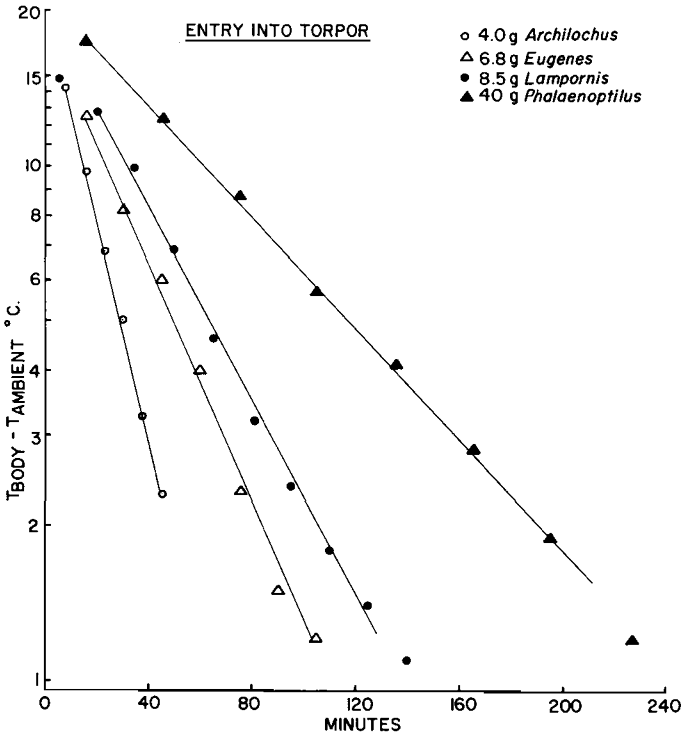

Figure 6. Rates of entry into torpor at ambient temperature of 20° C in *Archilochus alexandri, Eugenes fulgens, Lampornis clemenciae*, and *Phalaenoptilus nuttallii*. Values for *P. nuttallii* are from unpublished data collected by Bartholomew and Lasiewski.

ski, 1963). The relatively high values of thermal conductance for the Blue-throated and Rivoli's hummingbirds are consistent with the generalization that smaller homeotherms have less effective insulation (higher conductance) than do larger ones.

Torpid metabolism of the Blue-throated and Rivoli's hummingbirds at ambient temperatures below 24°, is slightly lower than that reported by Lasiewski (1963) for four species of smaller hummingbirds. Because of higher homeothermic metabolism and higher thermal conductance in smaller birds, the amount of energy per unit weight conserved by entering torpor increases markedly as the body weight decreases, particularly at lower ambient temperatures (Table 2). Torpid metabolism at 15° represents 7.5 per cent of the homeothermic level in a 75 g Common Nighthawk, *Chordeiles minor* (Lasiewski and Dawson, 1964), and only 1.7 per cent of the homeothermic metabolism at that temperature in a 3.2 g Costa's Hummingbird, *Calypte costae*.

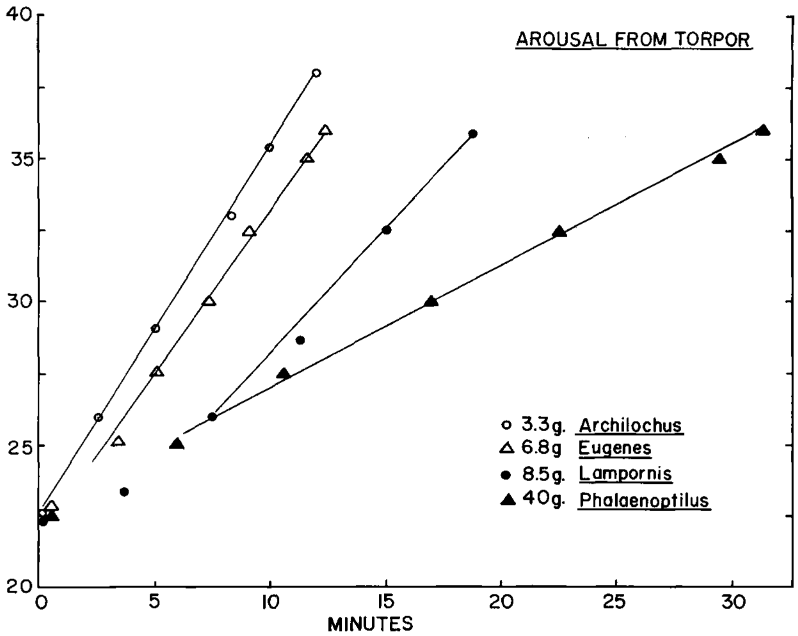

Figure 7. Rates of arousal from torpor at ambient temperature of 20° C in Black-chinned, Rivoli's, and Blue-throated hummingbirds, and the Poor-will. Values for the Poor-will are from unpublished data collected by Bartholomew and Lasiewski.

The minimal homeothermic heart rates recorded for *L. clemenciae* (480/min) and *E. fulgens* (420/min) are similar to, or slightly lower than, those recorded for the smaller Costa's Hummingbird, *Calypte costae*, Anna's Hummingbird, *C. anna*, and Ruby-throated Hummingbird, *Archilochus colubris* (Lasiewski, 1964). There is a marked decrease in the heart rate during torpor in the Blue-throated and Rivoli's hummingbirds (Table 1), reflecting lowered energy expenditures. The maximal recorded heart rates of 1200–1260/min for both *L. clemenciae* and *E. fulgens* are as high as those recorded in the small shrew, *Sorex cinereus* (Morrison *et al.*, 1959), the 6.1 g Black-rumped Waxbill, *Estrilda troglodytes* (Lasiewski *et al.*, 1964), and smaller hummingbirds (Odum, 1941; Lasiewski, 1964). This high heart rate of 20–21/sec may represent the physiological upper limit of avian cardiac function, as suggested by Yapp (1962). If so, other aspects of cardiac performance, such as stroke volume, or the amount of oxygen removed from the blood, must compensate for the almost ten-fold increase over resting levels in metabolic expenditures during flight.

The amount of water lost through evaporation by the Blue-throated and Rivoli's hummingbirds is similar to the amounts lost by other small birds

TABLE 2

DIFFERENCE BETWEEN TORPID METABOLISM AND METABOLISM OF BIRDS RESTING IN THE DARK AT 15–16° C

Species	*Body weight (g)*	*Metabolism (cc O_2/g/hr)*		*Metabolism ratio (torpid/resting)*	*Reference*
		Torpid	*Resting*		
Calypte costae	3.2	0.17	10.1	1:59	Lasiewski, 1963
Calypte anna	4.8	0.17	9.8	1:58	Lasiewski, 1963
Eugenes fulgens	6.6	0.12	7.0	1:58	Present study
Lampornis clemenciae	7.9	0.12	6.5	1:54	Present study
Phalaenoptilus nuttallii	40	0.15*	2.7	1:18	Bartholomew *et al.*, 1957
Chordeiles minor	75	0.18	2.4	1:13	Lasiewski and Dawson, 1964

* Estimated.

(Table 3) at similar temperatures and water vapor pressures. Values for evaporative water loss for *L. clemenciae* and *E. fulgens* at 25° and 6.3 mm Hg water vapor pressure are lower per unit weight than those expected for birds of this size from the inverse relationship between water loss and body weight described by Bartholomew and Dawson (1953). In fact, values for evaporative water loss for all hummingbirds studied to date are lower than expected on the basis of the data presented by Bartholomew and Dawson, although the reasons for this apparent discrepancy are unclear at present. Further data on water loss of very small and very large birds and on the effects of ambient water vapor pressure on water loss are needed before the relationship between size and evaporative water loss can be established more firmly.

Torpidity markedly decreases evaporative water loss in hummingbirds, as might be expected from the decreased breathing rates and metabolic expenditures during this period of abandonment of homeothermy. Since very small homeotherms are characterized by high rates of water turnover, as well as high energy expenditures, torpidity should be considered as a means of both water and energy conservation.

Greenewalt (1962) compiled and analyzed data on the dimensional relationships of flying animals, including many measurements of frequencies of the wing beats of different species of hummingbirds. He demonstrated that hummingbirds differ from other flying organisms in several characteristics, and fitted the following equation to available data on wing-beat frequency and wing length in hummingbirds:

$$fl^{1.25} = 5830$$

where f is the wing-beat rate per sec and l is the wing length in mm. This equation predicts wing-beat frequencies of 25/sec for *L. clemenciae* ($l = 79$), 26.3/sec for *E. fulgens* ($l = 76$), 34.6/sec for *Amazilia verticalis*

TABLE 3

EVAPORATIVE WATER LOSS IN SEVERAL SPECIES OF SMALL BIRDS AT AMBIENT TEMPERATURE OF 25° C

Species	*Body weight (g)*	*Evaporative water loss (mg/g/hr)*	*Water vapor pressure (mm Hg)*	*Reference*
Calypte costae	3.2	13	6.0	Lasiewski, 1964
Calypte anna	5.2	10	6.2	Lasiewski, 1964
Eugenes fulgens	6.6	9.5	6.3	Present study
Lampornis clemenciae	7.9	8	6.3	Present study
Estrilda troglodytes	6.5	12	3.4	Cade *et al.*, 1965
	6.1	8	4.6	Lasiewski *et al.*, 1964
Troglodytes aedon	10.7	15	18.4	Kendeigh, 1939
Taeniopygia castanotis	11.5	9	4.5	Cade *et al.*, 1965
	11.5	7.5	3.4	Calder, 1964

($l = 61$), and 42.5/sec for *Archilochus alexandri* ($l = 51$). The wing-beat frequencies we recorded stroboscopically for *A. alexandri* are the same as those predicted by Greenewalt's equation, while those for the Blue-throated, Rivoli's, and the Violet-crowned hummingbirds are slightly lower than predicted by the equation (Figure 4), but well within the scatter of Greenewalt's data.

Rates of entry into and arousal from torpor are inversely related to the body weight of the four species of hummingbirds so far studied. The lowering of body temperature during entry into torpor approximates a Newtonian cooling curve, suggesting that once entry into torpor is initiated, the rate of entry is determined by physical phenomena. Smaller birds enter torpor more quickly than do larger ones due to their smaller body mass, larger relative surface area, and less effective insulative capacities.

The rates of arousal from torpor presented in Figure 7 are comparable to those presented by Bartholomew *et al.* (1957) for the Anna's Hummingbird, the White-throated Swift (*Aeronautes saxatalis*), and the Poor-will. They noted that the smaller birds aroused more quickly than did the larger ones. Small birds are capable of raising their body temperatures faster than their larger counterparts, probably because of their higher metabolic output per unit weight coupled with the lower energy expenditure required to warm a smaller mass of body tissue. Assuming a specific heat for flesh of 0.95 Cal/kg/°C (Pearson, 1960), a 4 g Black-chinned Hummingbird could warm its body from 22.5° to 37.5° by expending 0.057 Cal, while the 40 g Poor-will would require 0.57 Cal to warm its body 15°. The higher heat producing capacities of the tissues of smaller birds are probably related to increased enzyme activity, such as the high levels of succinic dehydrogenase activity described in the pectoral muscles of hummingbirds by Lasiewski *et al.* (1965).

Pearson (1960) and Morrison (1960) have discussed size-related aspects of hibernation in homeotherms. Pearson suggested that "large birds or large mammals could not afford the time necessary to enter and emerge from torpidity each day in the manner of hummingbirds and bats." Our data demonstrate that the total time required simply to enter and arouse from torpor increases markedly with the size of the bird. At an ambient temperature of 20°, entry and arousal requires approximately 75 minutes for a 4 g *A. alexandri*, 126 minutes for the 6.8 g *E. fulgens*, 160 minutes for the 8.5 g *L. clemenciae*, and over 285 minutes for a 40 g *Phalaenoptilus nuttallii*. On the basis of these few data, it appears that a bird of 80 to 100 g would require a total of 12 hours merely to lower its body temperature to 20° and then to arouse to homeothermic levels by physiological means. The rates of arousal would be speeded up somewhat if the torpid bird oriented itself to the rays of the sun, thus augmenting physiological heat production, as reported by Marshall (1955) for the Lesser Nighthawk (*Chordeiles acutipennis*) and by Lasiewski and Thompson (1966) for Violet-green Swallows (*Tachycineta thalassina*). Body size obviously limits the ability of a species to engage in torpor each day, and the largest bird for which there is good evidence of daily torpor is the Poor-will (Marshall, 1955; Howell and Bartholomew, 1959; Lasiewski and Bartholomew, unpublished observations).

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We dedicate this paper to our mother, Stephanie Lasiewski, and our late father, Constanti S. Lasiewski, who made it possible.

SUMMARY

A variety of physiological responses were studied in the two largest species of hummingbirds found in the United States, the Blue-throated Hummingbird, *Lampornis clemenciae*, and the Rivoli's Hummingbird, *Eugenes fulgens*. The males of both species are heavier than the females.

Levels of standard metabolism for both species of hummingbirds are similar to those predicted by the weight-metabolism relationships of larger birds. Oxygen consumption of *L. clemenciae* (mean wt. = 7.9 g) was 2.3 cc O_2/g/hr in the thermoneutral zone and increased at the rate of 0.23 cc O_2/g/hr/°C below the zone of thermoneutrality. Standard metabolism of *E. fulgens* (mean wt. = 6.6 g) was 2.7 cc O_2/g/hr, with a thermal conductance of 0.30 cc O_2/g/hr/°C. Oxygen consumption dur-

ing torpor was markedly lower than at homeothermic levels, ranging from 0.10 to 1.18 cc O_2/g/hr at 14.9° and 26.9°, respectively.

Minimal homeothermic heart rates of 480 and 420 beats/min were recorded for *L. clemenciae* and *E. fulgens*, respectively, while maximal recorded values were 20–21 beats/sec for both species. Torpid heart rates were considerably lower than homeothermic levels, and decreased with decreasing temperature.

Evaporative water loss was similar in both species, ranging from 6.7 to 12.5 mg H_2O/g/hr at 15° and 34.8°, respectively, when the birds were homeothermic, and decreased markedly during torpidity. Torpidity in hummingbirds is important in terms of both water and energy conservation.

Wing-beat frequencies recorded stroboscopically from hovering hummingbirds are inversely related to the length of the wings, and similar to values predicted by Greenewalt's equation derived from data on many species of hummingbirds.

Rates of entry into and emergence from torpor are inversely related to the body weight of the four birds for which this has been studied: the Black-chinned, Rivoli's, and Blue-throated hummingbirds, and the Poor-will. The lowering of the body temperature during entry into torpor approximates a Newtonian cooling curve. On the basis of data relating the amount of time required to enter and arouse from torpor at an ambient temperature of 20°, it appears that a bird weighing approximately 80 to 100 g would require 12 hours merely to lower its body temperature to 20° and then to arouse again to homeothermic levels.

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