1992

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Recommended Citation

Powers, Donald R., "Effect of Temperature and Humidity on Evaporative Water Loss in Anna's Hummingbird (Calypte anna)" (1992). *Faculty Publications - Department of Biology and Chemistry.* Paper 13.
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Effect of temperature and humidity on evaporative water loss in Anna's hummingbird *(Calypte anna)*

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Summary. Evaporative water loss (EWL), oxygen consumption ($\dot{V}_{O_2}$), and body temperature (T_b) of Anna's Hummingbirds (*Calypte anna;* ca. 4.5 g) were measured at combinations of ambient temperature (T_a) and water vapor density (ϱ_{va}) ranging from 20 to 37 °C and 2 to 27 $g \cdot m^{-3}$, respectively. The EWL decreased linearly with increasing ϱ_{va} at all temperatures. The slopes of least squares regression lines relating EWL to ϱ_{va} at different temperatures were not significantly different and averaged -0.50 mg $H_2O \cdot m^{-3} \cdot g^{-2} \cdot h^{-1}$ (range: -0.39 to -0.61). Increased ϱ_{va} restricted EWL in *C. anna* more than has been reported for other endotherms in dry air. The percent of metabolic heat production dissipated by evaporation ($\dot{H}_e/\dot{H}_m$) was lower than that of other birds in dry air, but higher than that for other birds at high humidity when $T_a < 33$ °C. When $T_a > 33$ °C the effect of humidity on $\dot{H}_e/\dot{H}_m$ was similar to that in other birds. *Calypte anna* might become slightly hyperthermic at $T_a > 37$ °C, which could augment heat transfer by increasing the $T_b - T_a$ gradient. Body temperature for *C. anna* in this study was 43 °C (intramuscular) at T_as between 25 and 35 °C, which is above average for birds. It is estimated that field EWL is less than 30% of daily water loss in *C. anna* under mild temperature conditions (< 35 °C).

Key words: Thermoregulation – Water regulation – Endothermy – Climatic adaption – Trochilidae

Introduction

The rate at which body heat is dissipated by evaporation is partially dependent upon the difference in temperature and ϱ_{va} between the animal's surface and the surrounding air (Monteith 1973; Campbell 1977). The effect of temperature on EWL in endotherms is well documented and has been reviewed elsewhere (Chew 1965; Calder and King 1974; Skadhauge 1981; Dawson 1982). Less information is available on the effect of humidity, however, because of the difficulty in conducting EWL experiments in the laboratory under conditions of controlled ϱ_{va} (Lasiewski et al. 1966b; Bernstein et al. 1977; Welch 1980).

Most studies of EWL have not been concerned with the effect of humidity on EWL and have relied on measurements taken in dry air (e.g., Bartholomew and Dawson 1953; Chew 1955; Bernstein 1971; Lee and Schmidt-Nielsen 1972). Because air in the natural environment is not dry, measurements of EWL in dry air conditions may not reflect an animal's actual thermoregulatory ability during heat stress. In a few studies, measurements of EWL have been made under various humidity conditions (e.g., Lasiewski et al. 1966b; Proctor and Studier 1970; Richards 1976; Edwards and Haines 1978; Welch 1980; Webster and King 1987). These studies show that when ϱ_{va} is high, EWL is low in both mammals and birds at all temperatures. In pigeons *(Columba livia)*, for example, EWL at high humidity ($\varrho_{va} = 25$ $g \cdot m^{-3}$) is less than 50% of that at low humidity ($\varrho_{va} < 5$ $g \cdot m^{-3}$) (Webster and King 1987). Similarly, deer mice *(Peromyscus maniculatus)* measured at 30 °C show a four-fold decrease in EWL over the same range of humidities (Edwards and Haines 1978). These data suggest that understanding the effect of humidity on EWL is important for accurate assessment of water use and thermoregulation by free-living animals.

The relative impact of high humidity on thermoregulation and water regulation in homeotherms of different body size is uncertain. Measurements have been made on mammals ranging in size from ca. 7.5 g [little brown bat, *Myotis lucifugus;* Proctor and Studier (1970)] to ca. 1.1 kg [prairie dog, *Cynomys ludovicianus;* Welch (1980)]. No measurements are available for birds smaller than 42 g [painted quail, *Excalfactoria chinensis;* Lasiewski et al. (1966a)]. With the exception of the little brown bat, measurements of the effect of humidity on EWL in

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Abbreviations: BMR basal metabolic rate; EWL evaporative water loss; $\dot{H}_e$ evaporative heat loss; $\dot{H}_m$ metabolic heat production; $\dot{H}_e/\dot{H}_m$ percent of metabolic heat production dissipated by evaporation; ϱ_{va} ambient water vapor density; ϱ_{vs} body surface water vapor density; RMR resting metabolic rate; T_a ambient-temperature; T_b body temperature; T_d dew-point temperature; TNZ thermoneutral zone; T_s body surface temperature; $\dot{V}_{CO_2}$ carbon dioxide production; $\dot{V}_{O_2}$ oxygen consumption mammals have concentrated on larger species, presumably because of the ease with which they can be studied. However, the effect of humidity on smaller homeotherms may be more pronounced, because of their high levels of metabolic heat production and the rapid rate at which they gain heat from the environment at high temperatures.

Although the high surface-to-volume ratio of small homeotherms results in high rates of mass-specific EWL, there is some uncertainty as to whether EWL can dissipate enough heat for maintenance of body temperature when other avenues of heat loss (e.g., conduction and convection) become ineffective, such as when $T_a \geq T_b$ (Calder and King 1974). Costa's hummingbirds *(Calypte costa)*, for example, can dissipate only 62% of their metabolic heat production at 39.5 °C in dry air (Lasiewski 1964), which is less than the percent heat dissipated by many other birds under similar temperature conditions (Calder and King 1974). Because most hummingbirds live at least part of the year in the tropics, where temperature and humidity can be high (e.g., Evans 1939; Janzen 1976), a significant reduction in EWL due to high humidity could make thermoregulation difficult even under moderate temperature conditions.

This study examined the effect of temperature and humidity on EWL in Anna's hummingbird (*Calypte anna;* ca. 4.5 g). *Calypte anna* inhabit many regions of the southwestern United States where T_a can exceed 40 °C during the summer months. Although regions inhabited by *C. Anna* during the summer are generally not characterized by high humidity, the results of this study will provide useful information on the limits of thermoregulatory ability, and behavioral and metabolic adaptations of tiny endotherms to thermal stress. *Calypte anna* was chosen for this study because of its abundance and because much information on their physiology and ecology is already available (e.g., Pearson 1950, 1954; Bartholomew et al. 1957; Stiles 1971, 1973, 1982; Bartholomew and Lighton 1986; Powers 1987; Powers and Nagy 1988).

Materials and methods

Animals. Using mist nets, 10 male *C. anna* were captured at the Tucker Wildlife Sanctuary, Orange County, California in December 1987 (California Fish and Game permit no. 2135). The birds were transported to the University of California, Davis, and housed individually in 1.0 × 0.5 × 0.5 m cages at a controlled temperature (23 ± 1 °C) and photoperiod (12L: 12D) for at least 2 months prior to measurement. Birds were fed a purified liquid diet containing 19.9% carbohydrate, 0.9% protein, 0.9% fat, and 2.1% essential vitamins and minerals ad libitum (Brice and Grau 1989). All birds maintained mass over the course of the study.

Metabolism measurements. Protocol. Measurements of $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, and T_d were made with an open-circuit, positive-pressure respirometry system. Body mass was measured to the nearest 0.01 g before and after the respirometry trials with an electronic balance (Fisher model 7204A). The birds were fasted for a least 2 h prior to metabolic measurements and were placed in the metabolism chambers 1 h before data collection. Two birds were monitored simultaneously in separate metabolism chambers. During each run the birds typically spent 2.5–3.0 h in the metabolism chambers. Temperature and humidity conditions for a given metabolic trial were chosen randomly. At least six birds were measured under each set of temperature and humidity conditions. Individual birds were given at least 2 days of rest between metabolism trials. Birds were not run if their mass was more than 10% below their initial capture mass. Metabolic trials in which birds did not achieve a stable $\dot{V}_{O_2}$ or EWL for 30 min, or entered deep torpor, were discarded.

System design. Glass jars (2.5 l) were used as metabolism chambers and teflon tubing was used throughout the metabolism system to avoid errors due to water absorption through materials such as Plexiglas (Bernstein 1971; Welch 1980). The hummingbirds perched on a wooden dowel, at rest and in the dark, above a layer of mineral oil used to trap excreta. The T_a inside the chamber was monitored with a 24-gauge Cu-Cn thermocouple and recorded to the nearest 0.1 °C with a Sensortek Bat-12. Thermocouples were calibrated against a National Bureau of Standards certified thermometer.

Flow of CO_2-free air was regulated at a controlled humidity through the metabolism chamber at 500 ml · min^{-1} (STP) by placing a Brooks model 5815 mass flow controller, previously calibrated with a bubble meter (Levy 1964), upstream from the chamber. Because the flow controller was calibrated with dry air, air flow rates were corrected for humidity by subtracting the flow rate of water vapor from the total flow rate. Correcting for the water vapor content of the air stream is necessary because water vapor contributes to the total air flow through the chamber, thus reducing the amount of oxygen in the air stream. The water content of air both upstream and downstream from the metabolism chamber was determined by dew-point hygrometry. Outlet air passed through an infrared CO_2 analyzer (Beckman model 864 equipped with an optical filter to eliminate interference due to water vapor), through a dew-point hygrometer (General Eastern model 1100DP) to measure the water content, then through U-tubes containing soda lime and Drierite to remove CO_2 and water vapor, and finally to an oxygen analyzer (Applied Electrochemistry model S-3A). Prior to each run, the CO_2 analyzer was calibrated with certified gas standards (Matheson Gas Products, Inc. Secaucus, New Jersey, USA) and the oxygen analyzer with dry CO_2-free room air assuming an oxygen content of 20.95%. Accuracy of the hygrometer was verified gravimetrically using the methods of Bernstein et al. (1977). Data recording and analysis were done using BBC Acorn and Zenith MS-DOS microcomputers as described by Lighton (1985). Output from the analyzers was sampled at 3-s intervals. The fractional concentration of O_2 and CO_2 of inlet and outlet air was measured to the nearest 0.005%. Oxygen consumption was calculated from Eq. 2 of Hill (1972) and CO_2 production from the equation in Weathers et al. (1980). Heat production was calculated from $\dot{V}_{O_2}$ assuming $1\ l\ O_2 = 20.1$ kJ and $1\ l\ O_2 \cdot h^{-1} = 5.5824$ W. The T_d of inlet and outlet air was measured to the nearest 0.1 °C. The value of ϱ_{va} for a given T_d was determined from hygrometric tables (List 1951). Evaporative water loss was calculated using Eq. 1 and 6 of Bernstein et al. (1977). Heat loss by evaporation was calculated assuming $1\ g\ H_2O = 2.428$ kJ and $1\ g\ H_2O \cdot h^{-1} = 0.67454$ W. Because T_d is defined at a constant pressure, a water manometer was connected to the respirometry system to monitor changes in system pressure and a mercury barometer used to measure atmospheric pressure during each metabolic trail. All measurements of T_d, $\dot{V}_{O_2}$, and $\dot{V}_{CO_2}$ were corrected to STPD.

Body temperature. Body temperature (T_b) was measured intramuscularly with an Omega hypodermic Cu-Cn thermocouple probe (30-gauge) inserted into the pectoralis muscle. Measurements were considered valid only if they were made within 60 s after opening the door to the temperature control cabinet, and if the bird did not flap its wings. Because repeated measurements of T_b in this manner is potentially damaging to the birds, T_b was measured only under dry air conditions.

Statistics. The effect of varying humidity at different temperatures was analyzed with linear least-squares regression. Regressions were calculated from pooled data for all birds used in the study. Although pooling data in this manner is not ideal, it is necessitated by limitations in the number of animals that can be used in this type of study. Error is minimized by the fact that each bird contributed equally to each regression. Slopes and intercepts of regressions calculated for different conditions were compared using analysis of covariance (Zar 1974). Two-sample Student's *t*-tests were used to compare means. Results of statistical tests were considered significant at $P<0.05$. Data are given as mean ±1 SD.

Results

Body temperature and metabolic rate

Body temperature remained fairly constant between 25 and 37 °C, averaging 42.9±0.75 °C (Fig. 1). Mean T_b was slightly elevated to 44.3±0.60 °C at $T_a=40$ °C, although the increase was not statistically significant. At $T_a=20$ °C, T_b was highly variable, averaging 42.0±2.0 °C (Fig. 1). Median T_b was similar at all temperatures between 20 and 37 °C (range 42.0–43.1 °C), but was highest at 40 °C (44.7 °C) (Fig. 1).

Under dry conditions, the TNZ is narrow and appears to be located between about 33 and 37 °C during the active phase of the daily cycle (Fig. 1). The active phase metabolic rate in the TNZ is about 35 $W \cdot kg^{-1}$. Metabolic rate increases steadily with decreasing temperature below 33 °C, except at 20 °C where a slight decrease in metabolic rate was observed. Average metabolic rate at 40 °C was about 43 $W \cdot kg^{-1}$, but individual measurements were highly variable (Fig. 1). Metabolic rate under humid conditions did not differ significantly from that observed in dry air.

Mean mass for birds used in this study was about 4.5 g, ranging from a minimum of 3.89 g to a maximum of 5.30 g.

Evaporation and latent heat loss

The EWL (milligrams per gram per hour) decreased linearly with increasing ϱ_{va} at all temperatures (Fig. 2). Correlations for the relationship between EWL and ϱ_{va} were statistically significant at all temperatures (Table 1). Slopes of the regression lines (milligrams of water per cubic metre per grams squared per hour) ranged from −0.39 to −0.61 (Table 1). All slopes differed significantly from 0, but were not significantly different from each other. The simultaneous effects of temperature and ϱ_{va} on EWL are described by the multiple regression equation $EWL=2.314-0.490\ \varrho_{va}+0.427\ T_a$ ($S_{zyx}=2/72$, $r^2=0.63$, $P<0.05$). The behavior of this model over the range of temperature and ϱ_{va} used in this study is illustrated by the three-dimensional surface plot in Fig. 3.

Similarly, $\dot{H}_e/\dot{H}_m$ decreased linearly with increasing ϱ_{va} (Fig. 4). Correlations for the relationship between $\dot{H}_e/\dot{H}_m$ and ϱ_{va} were statistically significant at all temperatures (Table 2). Slopes of the regression lines ranged from −0.49 to −0.93 $m^3 \cdot g^{-1}$ (Table 2) and were significantly different from each other ($F=4.02$; $df=5165$; $P<0.05$), leading to rejection of the null hypothesis that the lines were parallel. Rejection of the null hypothesis appears to have resulted from a change in slope between 30 and

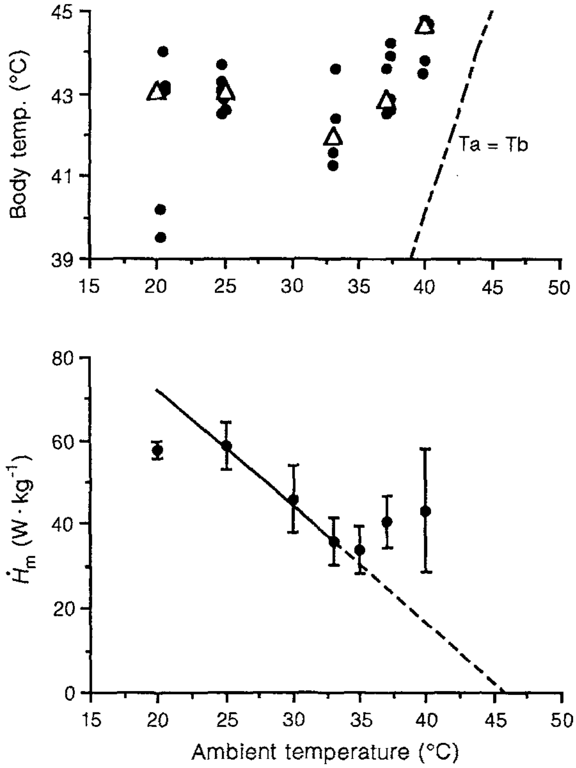

Fig. 1. Relation of T_b and metabolic rate (not determined concurrently) to T_a in dry air conditions. For T_b each *point* represents a measurement from a single bird. *Open triangles* represent median T_b. For metabolic rate each *point* represents the mean value ±1 standard deviation for all birds ($n=6$) measured at a given temperature. The line in the lower graph is the linear least-squares regression $\dot{H}_m$ as a function of temperature below the TNZ *(solid line)* and its extrapolation to T_b at $\dot{H}_m=0$ *(dashed line)*

Table 1. Least-squares linear regressions ($y=a+bx$) of evaporative water loss ($mg \cdot g^{-1} \cdot h^{-1}$) on vapor density ($g \cdot m^{-3}$) for *Calypte anna*

T_a (°C)	Y-Intercept *a*	Slope *b*	SE Estimate S_{yx}	SE Slope S_b	r^2
20	10.03	−0.39	1.82	0.08	0.53[a]
25	15.03	−0.59	3.10	0.12	0.51[a]
30	13.43	−0.42	1.97	0.06	0.62[a]
33	16.71	−0.53	2.61	0.06	0.69[a]
35	15.07	−0.45	2.20	0.05	0.79[a]
37	21.86	−0.61	2.99	0.08	0.70[a]

[a] Coefficient of determination is significant ($P<0.05$)

Table 2. Least-squares linear regressions ($y=a+bx$) of $\dot{H}_e/\dot{H}_m$ (%) on vapor density ($g \cdot m^{-3}$) for *Calypte anna*

T_a (°C)	Y-Intercept *a*	Slope *b*	SE Estimate S_{yx}	SE Slope S_b	r^2
20	11.78	−0.51	2.32	0.10	0.54[a]
25	16.55	−0.57	3.37	0.13	0.45[a]
30	19.16	−0.48	2.93	0.09	0.49[a]
33	30.68	−0.98	5.03	0.11	0.68[a]
35	30.27	−0.87	4.56	0.10	0.77[a]
37	37.62	−0.93	3.74	0.10	0.78[a]

[a] Coefficient of determination is significant ($P<0.05$)

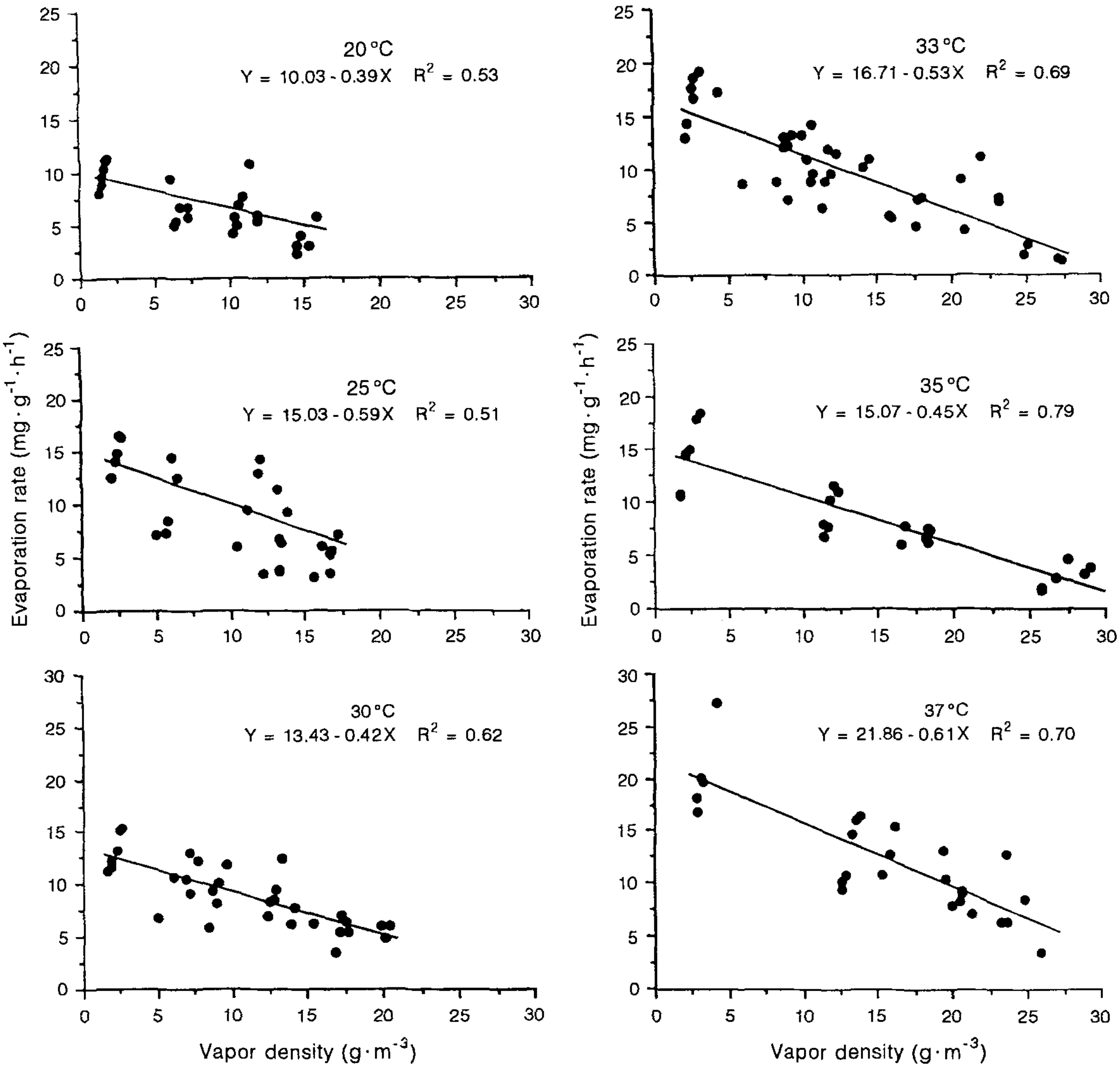

Fig. 2. Evaporative water loss as a function of water vapor density at various temperatures. Ten birds were used; each *point* represents a single measurement. Least-squares linear regression produced the lines and equations

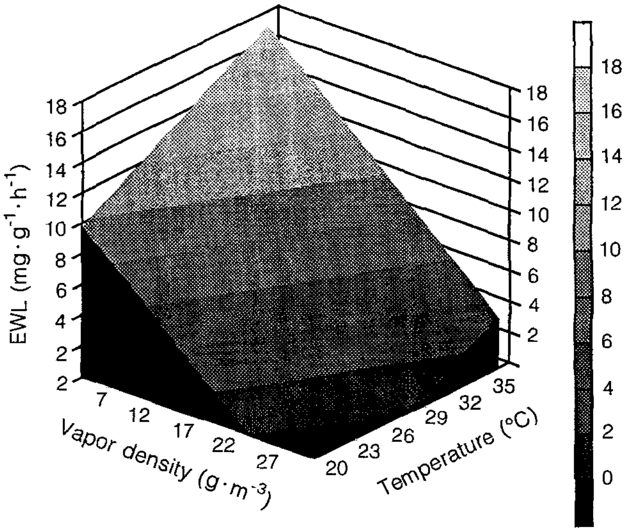

Fig. 3. Three-dimensional surface plot describing the affect of temperature and water vapor density ($g \cdot m^{-3}$) on EWL ($mg \cdot g^{-1} \cdot h^{-1}$)

33 °C. No statistical difference exists between the slopes of regression lines calculated for data at 20, 25, and 30 °C, or for regression lines calculated for data at 33, 35, and 37 °C. The mean slope of regressions between 20 and 30 °C was -0.52 ± 0.05. The mean slope of regressions between 33 and 37 °C was -0.91 ± 0.03. All slopes differed significantly from 0. The simultaneous effects of temperature and ϱ_{va} on $\dot{H}_e/\dot{H}_m$ are described by the multiple regression equation $\dot{H}_e/\dot{H}_m = T_a(0.026\ T_a - 0.025\ \varrho_{va})$ ($S_{zyx} = 4.05$, $r^2 = 0.95$, $P < 0.05$). The behavior of this model over the range of temperature and ϱ_{va} used in this study is illustrated by the three-dimensional surface plot in Fig. 5.

Discussion

Effect of temperature. Mass-specific EWL rates of heat-stressed *C. anna* are the highest measured for any endothermic vertebrate. In dry air, mean EWL for *C. anna*

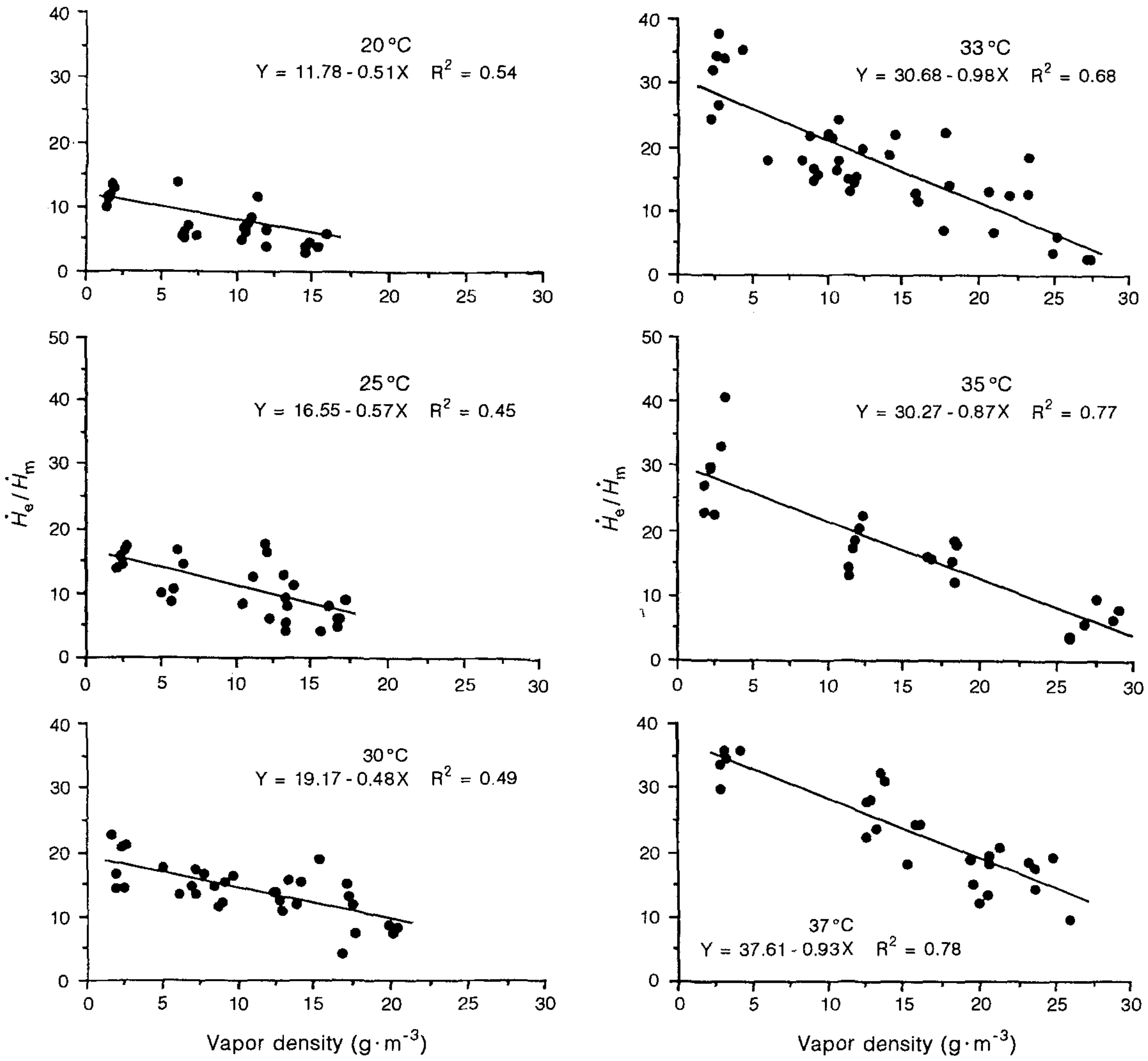

Fig. 4. The percent of metabolic heat production dissipated by evaporation ($\dot{H}_e/\dot{H}_m$) as a function of water vapor density for T_as ranging from 20 to 37 °C. Symbols and lines as in Fig. 2

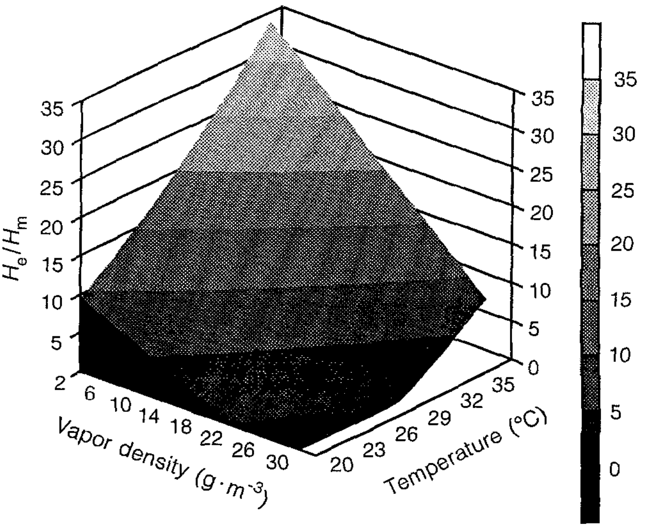

Fig. 5. Three-dimensional surface plot describing the affect of temperature and water vapor density (g · m^{-3}) on the percent of metabolic heat production dissipated by evaporation ($\dot{H}_e/\dot{H}_m$)

is 37.1 ± 11.7 mg $H_2O \cdot g^{-1} \cdot h^{-1}$ at 40 °C. This is 9.3% higher than that measured for 3.5-g Costa's hummingbirds [*Calypte costae;* Lasiewski (1964)] and 30% higher than that measured for the 9.5-g dusky munia [*Lonchura fuscans,* Weathers (1977)] and 28-g Cassin's finch [*Carpodacus cassinii;* Weathers et al. (1980)], which have the highest EWL recorded for endothermic vertebrates other than hummingbirds.

Area-specific EWL can be estimated from mass-specific EWL by allometry [external surface area 8.11 $cm^2 \cdot g^{0.67}$; Walsberg and King (1978) Eq. 2]. Area-specific EWL for *C. anna* is estimated to be 7.51 mg · $cm^{-2} \cdot h^{-1}$ at 40 °C. This is 17% greater than the 6.27 mg · $cm^{-2} \cdot h^{-1}$ estimated for *C. costae* and 10% greater than the 6.73 mg · $cm^{-2} \cdot h^{-1}$ estimated for *L. fuscans,* but 28% lower than the 9.62 mg · $cm^{-2} \cdot h^{-1}$ estimated for *C. cassinii.* These values show no clear relationship between area-specific EWL and body mass. However, the method used above to calculate area-specific EWL is sensitive to errors in the estimation of

Table 3. Slopes of regression lines relating evaporative water loss ($mg \cdot g^{-1} \cdot h^{-1}$) to ambient water vapor density ($g \cdot m^{-3}$) in various species of birds and mammals

Species	Mass (g)	Mean slope	Minimum[a] slope	Maximum[a] slope	Temperatures[b] (°C)	Source
Birds						
Calypte anna	4.5	−0.50	−0.39	−0.61	20–37	This study
Excalfactoria chinensis	42.7	−0.08	−0.07	−0.08	25–32	Lasiewski et al. (1966b)
Columba livia	472.9	−0.12	−0.09	−0.14	20–30	Webster and King (1987)
Gallus domesticus	2040.0	−0.10	−0.09	−0.11	20–35	Richards (1976)
Mammals						
Peromyscus maniculatus	16.0	−0.24	−0.15	−0.35	20–35	Edwards and Haines (1978)
Gerbillurus paeba	27.0	−0.20	–	–	23	Christian (1978)
Mus musculus	32.0	−0.11	−0.11	−0.12	23–35	Edwards and Haines (1978)
Rhabdomys pumilo	49.0	−0.21	–	–	23	Christian (1978)
Desmodillus auricularis	64.0	−0.11	–	–	23	Christian (1978)
Cynomys ludovicianus	1060.0	−0.03	−0.01	−0.07	10–40	Welch (1980)

[a] Minimum and maximum refer to the highest and lowest values calculated for the slopes of regression lines relating evaporative water loss with water vapor densitiy without regard to temperature

[b] Minimum and maximum temperature at which the relation of EWL to water vapor density was measured

surface area, and thus should be considered only a gross approximation.

Although *C. anna* has a high rate of EWL, its ability to thermoregulate by evaporation appears to be limited compared with that of other endotherms. The $\dot{H}_m$ for *C. anna* is also high (Fig. 1), twice that predicted from body mass [Aschoff and Pohl (1970), equation for active phase]. The high $\dot{H}_m$ exceeds $\dot{H}_e$ even at 40 °C. At 40 °C, *C. anna* was able to dissipate only 58.6% of its $\dot{H}_m$ via EWL. This is significantly less than the $\dot{H}_e/\dot{H}_m$ ratio predicted [72.8%; Calder and King (1974); Fig. 16] ($t=2.33$, $df=16$, $P<0.05$). The similiarity of $\dot{H}_e/\dot{H}_m$ for *C. anna* and that measured for Costa's hummingbird (Lasiewski 1964) suggests that evaporative heat loss might not be as effective in hummingbirds as it is in other birds.

Because of their low $\dot{H}_e/\dot{H}_m$ ratio, hummingbirds need other means of dissipating metabolic heat if they are to control T_b at high T_a. *Calypte anna* could solve this problem by simply maintaining a higher T_b, which would enhance dry heat transfer (i.e., convection, conduction, and radiation). Hyperthermia in response to elevated T_a is common in birds, and it often begins within the TNZ (Weathers 1981). The relationship between T_a and T_b for *C. anna* is difficult to analyze, because the sample sizes in this study are small ($n=4$–6). However, T_b in *C. anna* appears to follows a pattern similar to that observed in other birds; T_b was about 43 °C when T_a was between 25 and 37 °C, and increased to about 44 °C when T_a was 40 °C (Fig. 1). Thus, if T_b measurements in this study are accurate (see below), then *C. anna* maintained a favorable gradient between T_b and T_a even at $T_a=40$ °C.

At 20° C, mean T_b was lower than at higher T_a, but values for individual birds were highly variable (Fig. 1). Although measurements of T_b were not made simultaneously with measurements of metabolic rate, the lower mean T_b corresponds with the low metabolic rate exhibited by *C. anna* at 20 °C. Metabolic rate of *C. anna* at 20 °C was 57.8 $W \cdot kg^{-1}$, whereas the predicted metabolic rate, based on a thermal conductance of 2.795 $W \cdot kg^{-1} \cdot {}^{\circ}C^{-1}$ [predicted by the equation of Aschoff (1981)] and a daytime RMR within the TNZ of 36 $W \cdot kg^{-1}$, is 72.3 $W \cdot kg^{-1}$, a difference of 20.1% (Fig. 1). The metabolic rate measured at 20 °C may indicate the use of hypothermia. Assuming a Q_{10} of 4.1 (Lasiewski 1963) and a normal T_b of 43 °C, the observed metabolic rate at 20 °C would result from a reduction of less than 2 °C in T_b. The resting night-time metabolic rate of normothermic rufous hummingbirds *(Selasphorus rufus)* at 20 °C is about 59 $W \cdot kg^{-1}$ (Hiebert 1990), similar to the metabolic rate measured for *C. anna* in this study. This is much higher than the approximate value of 8.4 $W \cdot kg^{-1}$ exhibited by *S. rufus* in deep torpor (Hiebert 1990). However, because Hiebert (1990) did not measure T_b in normothermic birds, and because T_b measurements in this study are questionable, the possible use of limited hypothermia by *C. anna* at 20 °C cannot be discarded. During this study, deep torpor was observed only three times in *C. anna* run at 20 °C.

Effect of humidity. The EWL in *C. anna* decreases with increasing humidity (Fig. 2). Although the effects of humidity on animal EWL are not well studied, the available data suggests that EWL in *C. anna* is more sensitive to humidity than is the case for other species. The slope of the relationship between EWL and ϱ_{va} for *C. anna* is 2.1–16.7 times greater than that observed for other endotherms (Table 3). The larger slope is strictly a function of ϱ_{va} because slopes of the regression lines describing the effect of ϱ_{va} on EWL did not differ between temperature conditions (Fig. 2). This indicates that the effects of ϱ_{va} on the slope of the regression lines are independent of T_a.

The physical properties that determine EWL are the water vapor density gradient between the evaporating surface (i.e., skin or lungs) and the air ($\varrho_{vs}-\varrho_{va}$), the bird's resistance to water vapor diffusion, and ventilation

Table 4. Slopes of regression lines relating the ratio of evaporative heat dissipated to metabolic heat produced ($\dot{H}_e/\dot{H}_m$) to ambient water vapor density ($g \cdot m^{-3}$) in various species of birds and mammals

Species	Mass (g)	Mean slope	Minimum[a] slope	Maximum[a] slope	Temperatures[b] (°C)	Source
Birds						
Calypte anna	4.5	−0.52	−0.48	−0.57	20–30	This study
Calypte anna	4.5	−0.91	−0.87	−0.93	33–37	This study
Excalfactoria chinensis	42.7	−1.30	−0.88	−1.72	40–42.5	Lasiewski et al. (1966a)
Columba livia	472.9	−1.25	−0.95	−1.54	20–30	Webster and King (1987)
Mammals						
Peromyscus maniculatus	16.0	−0.67	−0.57	−0.75	20–35	Edwards and Haines (1978)
Mus musculus	32.0	−0.47	−0.34	−0.54	20–35	Edwards and Haines (1978)

[a] Minimum and maximum refer to the highest and lowest values calculated for the slopes without regard for temperature and humidity conditions

[b] Minimum and maximum temperature at which the relation between $\dot{H}_e/\dot{H}_m$ and water vapor density was measured

rate (Monteith 1973; Campbell 1977; Webster et al. 1985). The term $\varrho_{vs}-\varrho_{va}$ is a function of ambient humidity and T_s. It has been postulated that some birds have the ability to alter their skin resistance to cutaneous evaporation through structural changes in the epidermis, changes in blood flow to the skin, or changes in the level of hydration of the keratin layer of the skin (Webster et al. 1985). A bird that has shown some ability to alter cutaneous resistance to water vapor diffusion is the pigeon [*Columbia livia;* Webster et al. (1985)]. At high temperatures, a few *C. anna* in this study spread their retrices and exposed a bare patch of skin around the cloaca. If this area is highly vascularized it might serve as a means of reducing resistance to water vapor diffusion.

Changes in ventilation rate and resistance to water vapor diffusion at different ϱ_{va} in *C. anna* can be determined by plotting EWL as a function of $\varrho_{vs}-\varrho_{va}$. The contribution of these factors to EWL is reflected in the value of the slope, or vapor transport coefficient $\left(\frac{d\,\mathrm{EWL}}{d(\varrho_{vs}-\varrho_{va})}\right)$, as calculated by least-squares linear regression. The general form of the equation is $\mathrm{EWL}=C\cdot(\varrho_{vs}-\varrho_{va})$, where C is the vapor transport coefficient. Since T_b is stable in *C. anna* between 20 and 37 °C, ϱ_{vs} is constant at all temperatures measured in this study, assuming T_s is also constant. Thus, if T_s does not change significantly over the temperature range used then $\left(\frac{d\,\mathrm{EWL}}{d(\varrho_{vs}-\varrho_{va})}\right)=\frac{d\,\mathrm{EWL}}{d\varrho_{va}}$, and C is equal to the slope of the regression lines relating EWL to ϱ_{va} in Table 1. Some birds are believed to alter T_s by changing blood flow patterns as described above.

The thermoregulatory effectiveness of EWL is determined not by the evaporation rate alone, but also by the rate of metabolic heat production (Calder and King 1974). Although humidity has a greater effect on the rate of EWL in *C. anna* than in other endotherms, humidity appears to have a smaller influence on $\dot{H}_e/\dot{H}_m$ at lower temperatures (<33 °C) than has been measured in other birds (Table 4). The slope of the regression relating $\dot{H}_e/\dot{H}_m$ to ϱ_{va} for *C. anna* at T_a below 33 °C is less than half that calculated for the painted quail, *Excalfactoria chinensis* [applying least-squares regression to data from Fig. 2 in Lasiewski et al. (1966a)], and the pigeon, *Columba livia* [using data from Table 2 in Webster and King (1987); $\dot{V}_{O_2}$ and EWL were converted to heat assuming $1\ l\ O_2 \cdot h^{-1} = 5.5824$ W and $1\ g\ H_2O \cdot h^{-1} = 0.67454$ W, respectively]. The shallower slope observed for *C. anna* probably results from high levels of metabolic heat production that keeps the $\dot{H}_e/\dot{H}_m$ ratio small at low humidities when EWL is not severely restricted by ϱ_{va}. At T_a above 33 °C the slope of the relationships between $\dot{H}_e/\dot{H}_m$ and ϱ_{va} did not differ significantly from those of the other birds listed in Table 4. Since the vapor transfer coefficient did not vary between temperature conditions (see above), this change in slope suggests an increase in the effect of temperature on EWL in *C. anna* at T_as above 33 °C.

The $\dot{H}_e/\dot{H}_m$ ratios at various humidities are available for two mammals [deer mouse, *Peromyscus maniculatis* and house mouse, *Mus musculus;* Edwards and Haines (1978)] for T_a ranging from 20 to 35 °C. The ϱ_{va} dependence in the mammals is similar to that measured for *C. anna* below 33 °C. No values are available for heat-stressed mammals.

Water loss. Water turnover in free-living *C. anna* averaged 1.64 ml $H_2O \cdot g^{-1} \cdot day^{-1}$ for birds experiencing a mean daytime temperature of 24 °C (Powers and Nagy 1988). This value is high compared with that of other birds [see Nagy and Peterson (1988) for review], and presumably reflects their liquid diet. To determine the contribution of EWL to water turnover, the fraction of total daily water loss due to evaporation was calculated from the equations in Table 1. In addition, changes in this fraction over temperatures ranging from 25 to 40 °C were approximated by using the appropriate equation from Table 1 and by making adjustments to total daily

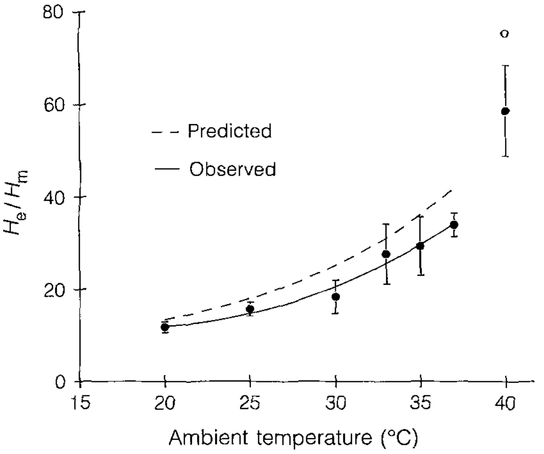

Fig. 6. The percent of metabolic heat production dissipated by evaporation ($\dot{H}_e/\dot{H}_m$) as a function of temperature in dry air. *Points* represent mean values; *error bars* represent ± 1 SD. The *dotted line* is the predicted relationship based on Calder and King (1974, eq. 56). The *solid line* is based on the equation $\dot{H}_e/\dot{H}_m = 3.24 + 2.73\, e^{-2T_a}$ calculated from the observed data at T_a from 20 to 37 °C

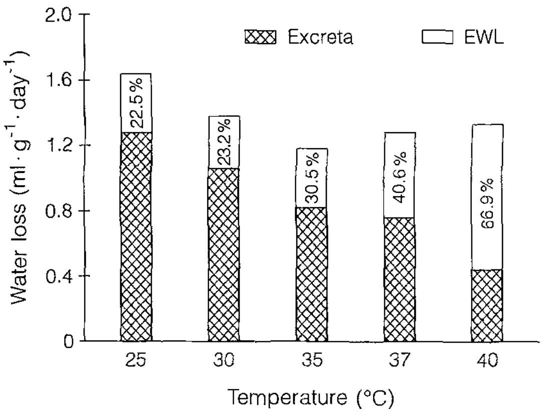

Fig. 7. Relation between estimated daily water loss, the fraction of water loss due to evaporation, and ambient temperature. Evaporative water loss values taken from the present study are for fasted birds at rest during the day

water turnover based on changes in energy intake expected to occur over this temperature range. The calculations are as follows.

Since hummingbirds drink little free water, total water intake is directly related to energy expenditure if the birds are in energy balance. Field metabolic rate of free-living *C. anna* when daytime temperature averages 24 °C is 83 W · kg^{-1} (Powers and Nagy 1988). Thus, daily water consumption is equal to 1.64 ml · g^{-1} · day^{-1}/83 W · kg^{-1}, or 0.02 ml · g^{-1} · day^{-1} for each watt per kilogram. It is assumed that daytime RMR is 36 W · kg^{-1} (the average metabolic rate of birds between 33 and 37 °C in Fig. 1), and nighttime RMR is 0.75 × 36 W · kg^{-1}, or 27 W · kg^{-1} [nighttime RMR is approximately 25% lower than daytime RMR; Aschoff and Pohl (1970)]. The photoperiod during the measurement of field metabolic rate was 12L:12D (Powers and Nagy 1988); thus mean 24-h RMR is (36 W · kg^{-1} + 27 W · kg^{-1})/2, or 31.5 W · kg^{-1}. Although thermal conductance has been shown to differ between the active and resting phase of the daily cycle (Aschoff 1981), it was assumed to be constant at 2.78 W · kg^{-1} · °C^{-1} (Fig. 1) for the purpose of these calculations. Assuming that the lower critical temperature for *C. anna* is 33 °C (Fig. 1), the daily thermostatic cost at 24 °C is 2.78 W · kg^{-1} · C^{-1} × (33 °C − 24 °C), or 25 W · kg^{-1}. Therefore, the total daily maintenance cost for *C. anna* at 24 °C is 31.5 W · kg^{-1} + 25 W · kg^{-1}, or 56.5 W · kg^{-1}. The total cost of activity for free- living *C. anna* (field metabolic rate − maintenance) is 83 − 56.5 W · kg^{-1}, or 26.5 W · kg^{-1}.

Assuming that calculated activity costs do not vary with temperature, water consumption will change in proportion to thermostatic costs. For example, at 25 °C the estimated thermostatic cost of *C. anna* is about 2.78 W · kg^{-1} · °C^{-1} × (33 °C − 25 °C), or 22 W · kg^{-1}. Field metabolic rate for *C. anna* at 25 °C would thus be 22 + 31.5 + 25.5 W · kg^{-1}, or 80 W · kg^{-1}, and daily water intake would be 80 W · kg^{-1} × 0.02 ml · g^{-1} · day^{-1} per W · kg^{-1}, or 1.60 ml · g^{-1} · day^{-1}. Assuming *C. anna* exhibits the maximum possible EWL rate 25 °C ($\varrho_{va} = 0$), water loss by evaporation is 0.36 ml · g^{-1} · day^{-1}, only 22.5% of the total daily water turnover. Similar calculations have been made for T_a equal to 30, 35, 37 and 40 °C (Fig. 7).

Evaporative water loss in many species of birds is 50% or more of total daily water turnover (Bernstein 1971; Skadhauge 1981; Dawson 1982). For *C. anna*, EWL represents a relatively small portion of the total daily water turnover at low to moderate temperatures, even though the rate of EWL is high compared with that of other birds and mammals (see above). Estimated field EWL in *C. anna* did not exceed 50% of the total daily water flux until T_a reached 40 °C (Fig. 7). Although daytime temperatures experienced by hummingbirds can be high, mean T_a experienced over a 24-h period is typically below 25 °C (e.g., Powers and Nagy 1988; Powers 1989).

The largest fraction of daily water loss in hummingbirds occurs in the excreta, and offers a plausible explanation of why hummingbirds have osmoregulatory systems adapted to produce dilute urines (Calder and Hiebert 1983). These data support the hypothesis that hummingbirds are not water stressed under moderate temperature conditions [$T_a \leq 35$ °C; Calder (1979)].

Birds in hot-humid climates. Free-living animals do not live in completely dry environments, yet the effects of humidity on thermoregulation and water regulation are not well understood. In most temperate environments that support significant numbers of hummingbirds, the effects of humidity may not be a critical issue because humidity is generally low (e.g., Powers 1989). However,

Table 5. Basal metabolic rates and body temperatures for tropical and non-tropical hummingbird species

Species	Mass (g)	BMR[c] ($W \cdot kg^{-1}$)	% of Predicted[d] (°C)	T_b[e]	Source
Tropical species					
Amazilia tzacatl	4.3	32.4[a]	168	42.0	Schuchmann and Schmidt-Marloh (1979a)
Trochilus scitulus	4.9	36.8[a]	198	42.5	Schuchmann and Schmidt-Marloh (1979b)
Trochilus polyptmus	6.3	27.4[a]	157	43.0	Schuchmann and Schmidt-Marloh (1979b)
Colibri delphinae	7.1	27.4[a]	162	43.0	Schuchmann and Schmidt-Marloh (1979a)
Eulampis jugularis	8.5	17.3	137	42.0	Hainsworth and Wolf (1970)
Mean			164 ± 22.1	42.5	
Non-tropical species					
Patagona gigas	19.1	15.1	148	–	Lasiewski et al. (1967)
Archilochus alexandri	2.7	18.4[b]	107	–	Lasiewski (1963)
Stellula calliope	2.8	22.3[b]	131	–	Lasiewski (1963)
Selasphorus sasin	3.1	17.3[b]	128	–	Lasiewski (1963)
Archilochus colubris	3.2	24.0[b]	146	–	Lasiewski (1963)
Calypte costae	3.2	17.9[b]	109	–	Lasiewski (1963)
Selasphorus rufus	3.6	19.0[b]	119	–	Lasiewski (1963)
Calypte anna	4.5	35.2[a]	184	43.0	This study
Calypte anna	5.4	21.2[b]	152	–	Lasiewski (1963)
Eugenes fulgens	6.6	15.1	111	–	Lasiewski and Lasiewski (1967)
Lampornis clemenciae	7.9	12.8	99	–	Lasiewski and Lasiewski (1967)
Mean			130 ± 25.3	–	

[a] Measured during the active phase of the daily cycle

[b] Represents minimum metabolic rate and may be lower than the actual BMR

[c] Within the thermal neutral zone

[d] Calculated as the observed divided by the predicted × 100. Predicted values calculated from the resting phase equation for non-passerine in Aschoff and Pohl (1970)

[e] Body temperature measured at 37° C

for animals that live in the humid tropics, humidity might have important effects on physiological responses to heat.

Water vapor density in the humid tropics can exceed $25 \, g \cdot m^{-3}$ in some locations (e.g., Evans 1939; Janzen 1976), which can reduce hummingbird EWL by 50–70% (Fig. 2). Since the humid tropics are characterized by high T_as (> 30 °C during the day), a reduction in EWL might impose thermoregulatory difficulties. Some tropical birds might have evolved lower basal metabolic rates to compensate for the lower $\dot{H}_e/\dot{H}_m$ ratios expected in a humid environment (Weathers 1977). Evidence for this is most pronounced in species that forage in the sun (Weathers 1979). Basal metabolic rates of birds that forage in the sun are on average 24% lower than predicted from body mass [using the equations of Aschoff and Pohl (1970)] for 13 species of birds ranging in mass from 6.1 to 55 g (Weathers 1979; Bartholomew et al. 1983; Weathers 1986). Tropical birds that forage in the shade may have basal metabolic rates closer to allometrically predicted values (Weathers 1979).

Although some hummingbirds forage in the sun (e. g., Stiles and Wolf 1970; Powers 1987), metabolic rates of many hummingbird species do not follow the pattern described above. Basal metabolic rated of six species of tropical hummingbirds were on average 64% higher than predicted allometrically (Table 5). Non-tropical hummingbirds also exhibit high basal metabolic rates, but on average they are only 30% higher than predicted allometrically. This difference is statistically significant ($t = 2.58$, $df = 14$, $P < 0.05$), suggesting that tropical hummingbirds might have higher basal metabolic rates than non-tropical hummingbirds. If tropical hummingbirds living in humid environments do indeed face thermoregulatory difficulties because of restricted EWL, then it seems that a high basal metabolic rate would only make thermoregulation more difficult. Thus, the adaptive value of a higher basal metabolic rate in tropical hummingbirds is unclear.

In addition to hummingbirds having high levels of heat production, is the daytime T_b of hummingbirds high compared with birds in general? In five species of tropical hummingbirds, mean T_b is 42.5 °C (Hainsworth and Wolf 1970; Schuchmann and Schmidt-Marloh 1979a, b). Limited hyperthermia would augment both evaporative and non-evaporative heat loss, and it is possible that hummingbirds allow their T_b to increase slightly for this reason. Weathers (1981) has reported high T_b for several small birds during heat stress, and suggested that hyperthermia may be a common means of conserving both water and energy.

The only T_b data for non-tropical hummingbirds measured during the active phase are those for *C. anna* measured in this study, for which T_b was 43 °C, a single *C. anna* by Bartholomew et al. (1957) for which T_b was 41.9 °C, five species measured by Wetmore (1921, reported in Morrison 1962) for which T_b ranged from 38.2 to 41.4 °C, and four species by Lasiewski (1964) for which T_b ranged from 39 to 41 °C. Body temperature in the last two studies was lower than that measured for tropical species. However, Lasiewski's measurements were made only at low T_as (< 30 °C).

Another complication is that the methods used to measure T_b vary greatly. This limits the usefulness of these data for comparison. For example, Morrison (1962) measured T_b in three species of Brazilian hummingbirds and reported a range of 38.4–39.3 °C. These values are probably low because Morrison's measurements are based on axillary temperature rather than core temperature. Other methods include measurement of deep esophageal temperature (e.g., Bartholomew et al. 1957), pectoralis muscle temperature with a surgical implant (e.g., Lasiewski 1964) or hypodermic probe (this study), and cloacal temperature (Carpenter 1974). Together with the limited amount of hummingbird T_b data available, the variability that is undoubtedly produced by these various methodologies makes it difficult to identify patterns or draw general conclusions with regard to T_b in hummingbirds.

This study shows that *C. anna* have the highest mass-specific EWL of any endothermic vertebrate. Although EWL in *C. anna* is high, $\dot{H}_e/\dot{H}_m$ is relatively low, suggesting that EWL is not as effective as dissipating $\dot{H}_m$ in hummingbirds as it is in most other birds. In *C. anna* EWL decreased rapidly with increasing ϱ_{va}. The slope of the relationship between EWL and ϱ_{va} was much greater than that observed for other birds. If EWL in other hummingbirds respond to changes in temperature and humidity in a manner similar to *C. anna,* then hummingbirds on hot-humid tropics might have trouble handling heat stress, or have evolved mechanisms to enhance EWL when $\varrho_{vs} - \varrho_{va}$ is low. Data currently available hint at the possibility that hummingbirds might become hyperthermic, which would enhance dry heat transfer, but more data are needed before this hypothesis can be accurately evaluated.

Acknowledgements. I wish to thank Wesley W. Weathers, Kyaw Tha Paw U, James R. Millam, Marcus D. Webster, Sara Hiebert and an anonymous reviewer for comments on earlier drafts. Anne Kjemtrup, Tom Greek, and Ray Munson provided valuable technical assistance. My thanks to California State University, Fullerton, for use of the facilities at the Tucker Wildlife Sanctuary. This project was supported by NSF grants PCM 76-18314 and BSR 85-05490 to WWW and funds from the California Agricultural Experiment Station.

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