ENERGETICS AND THERMOREGULATION BY SMALL PASSERINES OF THE HUMID, LOWLAND TROPICS

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ABSTRACT.—Birds of the open, humid lowland tropics encounter challenging thermal conditions—high temperatures, high humidity, and intense solar radiation. I examined how one such species, the Variable Seedeater (*Sporophila aurita*, Emberizidae), responds to temperature by measuring its body temperature (T_b), metabolic heat production ($\dot{H}_m$, calculated from oxygen consumption), and evaporative heat loss ($\dot{H}_e$, calculated from evaporative water loss) at stable air temperatures (T_a) between 14 and 46°C. I also measured basal metabolic rate (BMR) and T_b of the Variable Seedeater's diminutive (7.5 g) congener, the Ruddy-breasted Seedeater (*S. minuta*). All measurements utilized fasted, active-phase birds that were resting in the dark. BMR was lower than expected allometrically in both species, averaging 76% of predicted (or 0.718 kJ/h) in the 9.8-g Variable Seedeater ($n = 11$) and 67% of predicted (or 0.525 kJ/h) in the Ruddy-breasted Seedeater ($n = 3$). The Variable Seedeater's thermoneutral zone (TNZ) was relatively high (28.9 to 39.2°C). Below the TNZ, $\dot{H}_m$ was linearly related to T_a as follows: $\dot{H}_m$ (kJ/h) = 2.22 − 0.052 T_a. Thermal conductance, as indicated by the slope of this relation, was 12% lower than predicted allometrically. Data for 14 tropical bird species show BMR and thermal conductance to be linked; species with relatively high thermal conductance have a high BMR and vice versa. Evaporative cooling is relatively ineffective in the humid tropics, and compared with most birds Variable Seedeaters have a blunted evaporative response to heat. They dissipate evaporatively a maximum of 127% of their metabolic heat production at high T_a, even when measured in air only half as humid as that of their native habitat. Consequently, Variable Seedeaters employ hyperthermia (elevated T_b) to cope with heat. They are more tolerant of hyperthermia than most bird species and survive T_bs that are among the highest recorded for birds (46.8 to 47.0°C). Tolerance of hyperthermia is advantageous because it allows Variable Seedeaters to maintain an unusually large T_b-T_a gradient in hot environments (0.8 to 1.4°C at T_a = 43°C), and thereby to dissipate heat passively. Variable Seedeaters are able to circumvent partially the well-known temperature dependency of chemical reactions (i.e. the Arrhenius-van't Hoff effect). This enables them to become progressively hyperthermic at T_as above 35°C with relatively little increase in metabolic heat production, their $\dot{H}_m$ increasing at only 52% of the allometrically predicted rate above the TNZ. Variable Seedeaters possess several traits that enhance their tolerance of high T_a, yet because of their small size and limited thermal inertia their principal response to heat stress in the field is to avoid it behaviorally rather than to overcome it physiologically. *Received 20 June 1996, accepted 8 January 1997.*

BETWEEN THE TROPICS OF CAPRICORN AND CANCER one finds deserts, savannas, montane coniferous forests, rain forests, and even glaciers (Hastenrath 1985:376). Birds from these diverse habitats face very different thermoregulatory challenges, and although it is geographically correct to refer to them as tropical, it is ecologically misleading. The most important characteristics of the tropics from a physiological perspective are heat and humidity. Hot-humid conditions occur seasonally or sporadically in many regions of the earth, but they persist only in the lowland tropics (Young 1964, Ayoade 1983, Hastenrath 1985). Regardless of habitat, tropical species encounter relatively uniform thermal conditions year-round, unlike their temperate relatives. The specific conditions encountered vary widely, however, depending upon local circumstances and the extent of exposure to the sun. Tropical species that live beneath the canopy of humid, lowland forests seldom encounter temperatures above 35°C (Young 1964, Coen 1983, Windsor 1990) and are unlikely to have special physiological adaptations for coping with heat. In contrast, when exposed to full sunlight in the lowland tropics, small finches with dark plumage encounter operative temperatures that exceed

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50°C (Weathers 1986). Such high temperatures coupled with high humidity create conditions that seem thermally untenable for small birds, yet many species of small birds occur in the open lowland tropics. How they respond physiologically to high temperatures, and whether they possess special adaptations for coping with heat, are unclear because only two studies (Weathers 1977, 1986) have examined the responses of lowland tropical birds to high temperatures since the pioneering work of Scholander et al. (1950a,b). This study examines a third such species, the Variable Seedeater (*Sporophila aurita*), and compares its responses with those of tropical species from a variety of microhabitats.

Variable Seedeaters range from northern Oaxaca, southern Veracruz, and Tabasco in Mexico southward through Central America to western Colombia, western Ecuador, and northwestern Peru (AOU 1983). They prefer grassy and shrubby areas of open, humid lowland and foothill forest (Ridgely 1976, AOU 1983) and often are exposed to full sunlight while foraging on grass seeds. At such times they may encounter high operative temperatures. For example, operative temperature of seedeaters measured with taxidermic mounts on the ground averaged 49.6 ± SD of 3.3°C (range 44.4 to 54.6°C, $n = 16$; Weathers unpubl. obs.) between 1110 and 1255 on 28 June 1984 near Gamboa, Panama. As this study will show, Variable Seedeaters have limited capacity to cope physiologically with extreme heat and humidity because of their small size; thus, their main coping mechanisms are necessarily behavioral.

METHODS

I measured rates of oxygen consumption and colonic body temperature of 13 Variable Seedeaters and 3 Ruddy-breasted Seedeaters (*Sporophila minuta*) between 29 June and 30 July 1984 at the Smithsonian Tropical Research Institute (STRI), Ancon, Panama. High ambient humidity in the STRI laboratory interfered with measurements of evaporative water loss (EWL) using the gravimetric technique available there, and eight *S. aurita* subsequently had their EWL measured at the University of California between 7 December 1984 and 7 February 1985.

Animals.—I captured 16 adult *S. aurita* (8 of each sex) and 3 adult *S. minuta* (sex unknown) between 16 June and 30 July 1984 with mist nets near the former Canal Zone town of Gamboa and at the Chiva Chiva

antenna field. Birds were immediately color-banded and weighed to the nearest 0.05 g with a K-Tron electronic balance. Male and female *S. aurita* did not differ in capture mass ($t = 0.70$, df = 14, $P = 0.51$), and averaged 10.93 ± SD of 0.72 g. The three *S. minuta* ranged in mass from 6.9 to 8.4 g and averaged 7.51 ± 0.76 g. Birds were maintained in roofed, outdoor cages at STRI on a diet of mixed-finch seeds and grit. Metabolic measurements began within two days of capture. Most individual *S. aurita* did well in captivity, but all initially lost some mass before stabilizing at a mass that was 9.3 ± 4.0% below their mass at capture. Fourteen of the 16 *S. aurita* were used for metabolic measurements, 13 of them in Panama.

Following the measurements in Panama, eight *S. aurita* were flown to the United States for further study. They were moved to the University of California after spending a month in quarantine and were placed in individual 30-cm square cages housed within a controlled temperature room (26 ± 2°C) on a 12:12 LD photoperiod. They were provided mixed-finch seed and grit *ad libitum* and were periodically given fresh spinach and lettuce leaves. Respirometry measurements began three months after the birds' transfer to the University of California. All birds remained healthy and active throughout the study. Six of the eight birds had been measured in Panama and four were female.

Physiological measurements in Panama.—Daytime rates of oxygen consumption ($\dot{V}O_2$) were determined by open-circuit respirometry on birds that had been fasting at least 3 h. For these measurements, individuals rested inside a dark 3.7-L metal metabolism chamber with flat-black interior walls to maximize radiative heat transfer (Porter 1969). The chamber was equipped with a hardware-cloth floor above a mineral-oil trap for excreta. Chamber temperature was measured with a 24-gauge Cu-Cn thermocouple (calibrated against a National Bureau of Standards certified Hg thermometer) and controlled by submersion in a controlled temperature water bath (± 0.2°C). *Sporophila aurita* were exposed to the following stable temperatures for 1 h before measuring $\dot{V}O_2$: 14, 20, 25, 30, 35, 37.5, 40, 43, 45°C. Not every bird was run at all nine temperatures, however. Usually birds were tested only once per day with at least two days between tests. Some *S. aurita* were measured more than once per day. These birds were allowed to equilibrate at the new test temperature for 1 h before the next measurement was made. The three *S. minuta* were measured only once at about 35°C (range 34.7 to 35.2°C).

Dry, CO_2-free air was pumped through the metabolism chamber at 0.30 to 0.67 L/min (higher flows at higher temperatures). Airflow rate upstream of the chamber (corrected to STPD) was measured with a rotometer and calibrated against a bubble meter (Levy 1964). The fractional concentration of O_2 in inlet and outlet chamber air (both dry and CO_2-free)

was determined with an Applied Electrochemistry S3-A O_2 analyzer, which was calibrated using known gases. $\dot{V}O_2$ was calculated using equation (2) of Hill (1972). Rates of metabolic heat production were calculated from oxygen consumption assuming a heat equivalent of 20.1 kJ/L of oxygen consumed by the fasted birds (Schmidt-Nielsen 1975:210).

Body temperature (T_b) was measured at the end of the $\dot{V}O_2$ determination using a Yellow Springs Instrument model 511 Telethermometer (0.6-mm diameter probe) that was calibrated against a certified Hg thermometer. To measure T_b, the bird was quickly removed from the metabolism chamber (<30 s) and the probe inserted through the cloaca into the colon to a sufficient depth such that the indicated temperature did not decrease when the probe was withdrawn slightly.

Rates of EWL were determined gravimetrically during initial $\dot{V}O_2$ measurements in Panama. However, tests of the system without a bird present yielded values of "EWL" as high as 55 mg/h, which is twice the birds' EWL at low temperatures (based on California measurements). The source of the exogenous water probably was the metabolism chamber walls (hygroscopically bound water) and the Tygon tubing used to plumb the system. Attempts to measure EWL in Panama were abandoned because the rate of entry of exogenous water was variable and could not be corrected.

Physiological measurements in California.—The protocol and apparatus used to measure $\dot{V}O_2$ and T_b of birds in California were similar to those employed in Panama, except that a 0.93-L glass metabolism chamber was used instead of a 3.7-L metal chamber, and the system was plumbed with hydrophobic Teflon® tubing (fluorocarbon plastic) rather than tygon tubing. EWL was determined with a gravimetrically calibrated (Bernstein et al. 1977) EG&G model 992 Dew Point Hygrometer. Agreement between measured and known water contents of air over a range of dew points (−8.8 to 14.5°C) was excellent (mean agreement = 100.1 ± 3.3%, n = 8). The rate of air flow through the metabolism chamber ranged from 0.39 L/min at low temperatures to 0.60 L/min at higher temperatures. Rates of evaporative heat loss were calculated from EWL assuming a heat equivalent of 2.43 kJ/g of water evaporated (Schmidt-Nielsen 1975:313).

Statistics.—Characterizing a species' metabolic response to temperature requires many individual measurements. Multiple measurements per individual are normal because fewer animals are typically available than is required if each measurement is to be independent. A total of 83 metabolic measurements was made in Panama on 13 *S. aurita*, each bird being measured an average of 6.2 ± 2.1 times (range 2 to 9 times). In California, 70 measurements were made on 8 individuals, each bird being measured an average of 8.8 ± 0.7 times (range 7 to 9 times). To
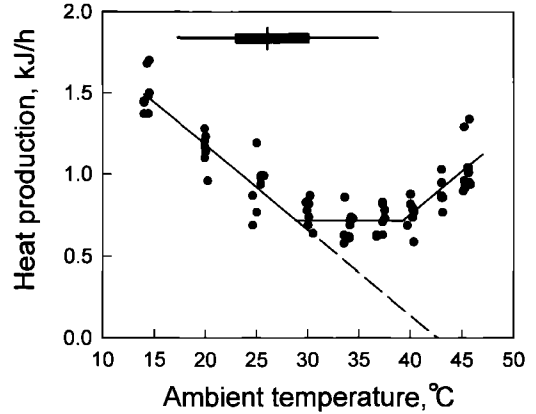

FIG. 1. Relation of metabolic heat production to ambient temperature (T_a) in Variable Seedeaters. Heat production was calculated from the oxygen consumption of postabsorptive birds that were resting in the dark during their active phase. See text equations 1 and 3 for regression statistics. Horizontal bar presents T_a data (1907 to 1965) for Balboa Heights, Panama (Panama Canal Company, Meteorology and Hydrology Branch). The thin horizontal line represents the absolute T_a range recorded for the 58 years of record; the thick horizontal bar connects the mean minimum and maximum daily T_a; and the vertical line denotes the average T_a.

accommodate this pseudoreplication (Hurlbert 1984), I used repeated-measures analysis of covariance (SAS 1992) to compare California and Panama regression equations. The sample size given for regression equations in the text is the number of measurements, not the number of individuals. When means are reported, the sample size is the number of individuals. Means are reported ± 1 SD throughout the text.

RESULTS

Metabolic heat production.—The heat production ($\dot{H}_m$) of fasted Variable Seedeaters resting in the dark during the day conforms with the model of endotherm energetics proposed by Scholander et al. (1950b). Measurements in Panama and California exhibited similar patterns, and for simplicity only the Panama data are presented (Fig. 1).

The three principal segments in Figure 1 were determined using an iterative dual-regression technique to establish the join-points (Pinshow et al. 1976, Nickerson et al. 1989, Yeager and Ultsch 1989) and by comparing mean $\dot{H}_m$ values for the five T_a intervals from 25

TABLE 1. Daytime basal metabolic rate (BMR) and body mass of Variable Seedeaters measured in Panama (n = 11) and California (n = 8). Values are $\bar{x} \pm$ SD; df = 17 for t-test.

Parameter	Panama	California	t	P
Body mass (g)[a]	9.82 ± 0.20	10.46 ± 0.17	2.87	0.01
Observed BMR (J·g^{-1}·h^{-1})	74.5 ± 9.0	79.8 ± 7.2	1.31	0.21
Observed BMR (kJ/h)[b]	0.718 ± 0.071	0.834 ± 0.076	2.34	0.03
Predicted BMR (kJ/h)[b]	0.948	0.991	—	—
% of predicted BMR	76	84	—	—

[a] Mean mass of birds during measurements.
[b] Predicted for passerines of this mass (Aschoff and Pohl 1970).

to 40°C. Heat production was significantly higher at 25°C, indicating that these measurements fall outside the TNZ (Kruskal-Wallis test, H = 12.37, df = 3, P = 0.006). Within the TNZ (28.9–39.2°C), daytime basal metabolic rate averaged 0.718 ± 0.071 kJ/h (Table 1). At ambient temperatures below the TNZ, heat production varied linearly with T_a as follows (Panama measurements):

$$\dot{H}_m \text{ (kJ/h)} = 2.22 - 0.052\, T_a \qquad (1)$$

(r^2 = 0.711, s_{yx} = 0.132, s_b = 0.006, n = 24). The comparable equation for birds measured in California is:

$$\dot{H}_m \text{ (kJ/h)} = 2.95 - 0.060\, T_a \qquad (2)$$

(r^2 = 0.845, s_{yx} = 0.194, s_b = 0.004, n = 40). The y intercepts of equations 1 and 2 differ significantly (ANCOVA, F = 18.84, df = 1 and 43, P
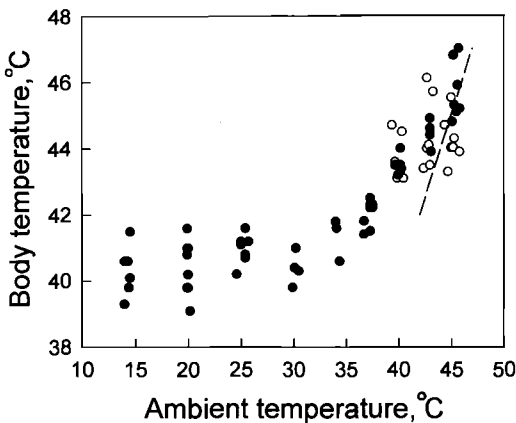

FIG. 2. Relation of body temperature measured at the end of metabolic determinations to ambient temperature. Shaded circles denote birds measured in Panama, unshaded circles denote birds measured in California. Dashed line depicts temperature equality.

= 0.0001), but not the slopes (F = 1.91, df = 1 and 43, P = 0.17).

The line relating $\dot{H}_m$ to T_a at low temperatures extrapolates to zero at 42.7°C (Fig. 1), which exceeds the mean T_b measured below the TNZ (40.5 ± 0.70°C). Thus thermal conductance, C, was not constant below the T_{lc} and can be evaluated alternatively as the mean of individual measurements, rather than as the slope of the line relating $\dot{H}_m$ to T_a below the TNZ (McNab 1980). The mean C for measurements below the TNZ does not differ from that predicted allometrically (0.058 vs. 0.059 kJ/h·°C; Aschoff 1981). However, Aschoff's equation is based mainly on slopes, not on calculated C as discussed below. The slope for Panama measurements is 12% lower than predicted allometrically (Aschoff 1981). Heat production of birds measured in California extrapolates to zero at 49.1°C. Assuming T_b of California birds also was 40.5°C below the T_{lc}, then the mean conductance in California calculated from individual measurements is 0.099 kJ/h·°C.

Heat production increased linearly with temperature above the upper critical temperature (39.2°C) as follows (Panama measurements):

$$\dot{H}_m \text{ (kJ/h)} = -1.32 + 0.052\, T_a \qquad (3)$$

(r^2 = 0.526, s_{yx} = 0.119, s_b = 0.0105, n = 24). The comparable equation for birds measured in California did not differ from the above either in slope (ANCOVA, F = 0.64, df = 1 and 30, P = 0.43) or y intercept (ANCOVA, F = 0.26, df = 1 and 30, P = 0.61). Individuals differed in heat production for measurements below the TNZ (ANCOVA, F = 1.96, df = 1 and 43, P = 0.04), but not for those above (F= 1.78, df = 1 and 30, P = 0.08).

Body temperature.—The relation between Variable Seedeater T_b and T_a appears to be curvilinear (Fig. 2) but can be adequately described
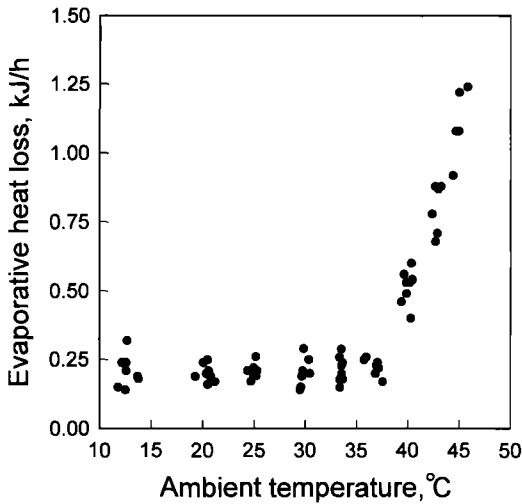
FIG. 3. Relation of evaporative heat loss to ambient temperature for Variable Seedeaters. Evaporative heat loss was calculated from the evaporative water loss of postabsorptive birds that were resting in the dark during their active phase.
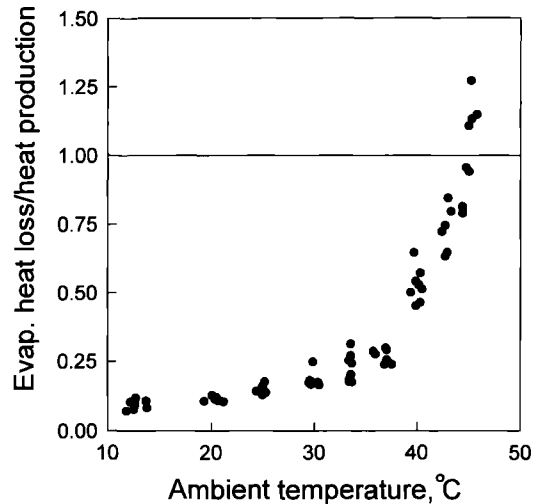
FIG. 4. Relation of the ratio of evaporative heat loss to metabolic heat production to ambient temperature for Variable Seedeaters measured in California.

by two linear equations, one for T_a < 35.1°C (the dual regression join-point) and another for values above 35.1°C. Below T_a = 35.1°C,

$$T_b = 39.67 + 0.041 \, T_a \qquad (4)$$

(r^2 = 0.211, s_{yx} = 0.601, s_b = 0.012, n = 42). Above T_a = 35.1°C,

$$T_b = 25.55 + 0.443 \, T_a \qquad (5)$$

(r^2 = 0.908, s_{yx} = 0.510, s_b = 0.029, n = 27). Body temperatures were only determined at T_as higher than 40°C during California measurements (Fig. 2; unshaded circles). They were more variable than T_bs of birds measured in Panama but were statistically indistinguishable (ANCOVA, F = 0.99, df = 1 and 30, P = 0.32 for slopes; F = 0.76, df = 1 and 30, P = 0.39 for y intercepts).

Evaporative heat loss.—A bird's ability to dissipate heat evaporatively at high air temperatures can be compromised if the airflow rate through the metabolism chamber is too low. In general, the higher the airflow rate the drier the chamber air and the higher the rate of EWL (Lasiewski et al. 1966, Welch 1980). Airflow rates used in this study were sufficiently high that evaporation should not have been impeded. Chamber relative humidity averaged 14.0 ± 5.8% (maximum = 26.7%) and water vapor density 7.6 ± 4.6 g/m³ (maximum = 17.7 g/m³)

when chamber air temperature was between 33–45°C. Chamber humidities would have been lower and rates of EWL undoubtedly would have been higher had higher flow rates been employed. However, humidities at the highest T_as in this study were comparable to those of other studies (Weathers 1977, 1981, 1986) and were much lower than those encountered by seedeaters in the field.

Evaporative heat loss ($\dot{H}_e$) of Variable Seedeaters measured in California was independent of T_a between 11.8 and 37.6°C (r = 0.115, df = 46, P = 0.43) and averaged 0.21 ± 0.04 kJ/h (Fig. 3). Above 37.6°C, $\dot{H}_e$ increased exponentially with T_a as follows:

$$\log \dot{H}_e = -1.850 + 0.074 \, T_a \qquad (6)$$

(r^2 = 0.895, $\log s_{yx}$ = 0.057, s_b = 0.006, n = 22).

The ratio of evaporative heat loss to metabolic heat production ($\dot{H}_e/\dot{H}_m$) increased exponentially with T_a (Fig. 4). Calder and King (1974:328) fit a single exponential relation to a similar plot that summarized data for birds in general, but their equation's usefulness is limited because it does not include data at T_as > 38°C. There are at least two ways to describe the entire data range mathematically. One is to use a double exponential relation, which for the Figure 4 data is:

$$\dot{H}_e/\dot{H}_m = 1.145 - 0.911 \; e^{0.012 \; Ta}$$
$$+ \; 0.016 \; e^{0.100 \; Ta}, \qquad (7)$$

where $e = 2.7182$ (base of natural logarithms). The first exponential term in equation 7 describes the relationship between $\dot{H}_e/\dot{H}_m$ and T_a at low temperatures; the second term describes the data at higher T_as. Alternatively, two linear relations often are obtained if one plots the logarithm of $\dot{H}_e/\dot{H}_m$ versus T_a (Weathers 1981). Linear equations are easier to fit than double exponential equations. Log-transformation of the data in Figure 4 yields:

$$\log \dot{H}_e/\dot{H}_m = -1.302 + 0.019 \; T_a \qquad (8)$$

below $T_a = 33.6°C$ (the dual-regression join-point; $r^2 = 0.818$, $\log s_{yx} = 0.056$, $s_b = 0.001$, $n = 35$), and

$$\log \dot{H}_e/\dot{H}_m = -2.585 + 0.057 \; T_a \qquad (9)$$

above $T_a = 33.6°C$ ($r^2 = 0.907$, $\log s_{yx} = 0.077$, $s_b = 0.003$, $n = 35$). Log-transformation of $\dot{H}_e/\dot{H}_m$ data facilitates interspecific comparisons because the entire data set is included (not just the data below $T_a = 38°C$ as in Calder and King [1974]), and the slopes and intercepts of the two equations are easily compared among species.

Ruddy-breasted Seedeaters.—The $\dot{H}_m$ of fasted Ruddy-breasted Seedeaters resting in the dark and measured at 35°C during the day averaged 0.525 ± 0.038 kJ/h ($n = 3$). Body temperature of the three Ruddy-breasted Seedeaters averaged $40.2 \pm 0.32°C$.

DISCUSSION

The Variable Seedeater's physiological response to temperature can be characterized by combining metabolic heat production ($\dot{H}_m$) and body temperature (T_b) data of birds measured in Panama with evaporative heat loss ($\dot{H}_e$) data of birds measured in California. The composite pattern should be reasonably accurate, especially at higher temperatures, because $\dot{H}_m$ and T_b of the two groups were not significantly different at temperatures above the thermoneutral zone, nor was BMR different when expressed in mass-specific units (Table 1). Heat production at low temperatures was significantly higher in California than in Panama (cf. equations 1 and 2), indicating lower insulation in the California birds. The birds gradually lost feathers during the study due to repeated handling, and their plumage was visibly less dense

in California than in Panama. This feather loss largely accounts for the California birds' higher $\dot{H}_m$ at low T_as.

Rates of evaporative heat loss ($\dot{H}_e$) measured in California should be similar to rates in Panama at T_as above the lower critical temperature, but may have been slightly higher at lower T_as, because of the California birds' sparser plumage. Relatively little evaporation occurs at low T_as, however, and the absolute difference in $\dot{H}_e$ between the two groups likely would be small.

Metabolic heat production.—The Variable Seedeater's metabolic profile conforms with the typical endotherm pattern (Fig. 1), but with some differences from what would be predicted allometrically. Basal metabolic rate, for example, is 24% lower than predicted (Table 1). Reduced BMRs are common among small tropical birds that forage in the sun (Weathers 1979, 1986, Marschall and Prinzinger 1991) and should extend the time that foraging birds can be exposed to the sun. In contrast, the BMRs of most tropical species that occupy shaded habitats are not reduced, although those of some species are (Weathers 1979; Table 2). Low BMR in manakins native to shaded forests, for example, is thought to be an adaptation to predictable, seasonal food shortage (Vleck and Vleck 1979, Bartholomew et al. 1983). It is impossible to say whether low BMR in Variable Seedeaters is an adaptation to heat stress (i.e. an evolved response) because low BMR can result from a variety of selective forces. Nevertheless, a low BMR has obvious thermal advantages for birds living in hot environments (Bartholomew et al. 1962).

Scholander et al. (1950a,b) focused on the responses of birds and mammals to low T_a and suggested that tropical species would frequently be cold stressed despite their warm environment because of their poor insulation. Long-term temperature records for Balboa Heights, Panama suggest that Variable Seedeaters seldom incur added thermoregulatory costs due to cold. The Variable Seedeater's rest-phase T_{lc} was not determined, but the allometrically predicted value (22.9°C; Weathers and van Riper 1982) is 6°C below their active-phase T_{lc} and is identical to the long-term mean minimum T_a at Balboa Heights (Fig. 1). The mean annual shade temperature at Balboa Heights, 26.0°C, is 3°C below the active-phase T_{lc} determined for fasted birds. Variable Seedeaters normally feed

TABLE 2. Body mass (g), basal metabolic rate (kJ/h), and thermal conductance ($cm^3O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$) of tropical bird species from various habitats. Values for BMR and conductance are presented both in the preceding units (Obs.) and as % of value predicted allometrically (% pred.) by the equations of Aschoff and Pohl (1970) and Aschoff (1981), respectively.

Species	Mass	Phase[a]	Basal metabolic rate		Conductance		Reference
			Obs.	% pred.	Obs.	% pred.	
Open, often humid lowlands							
Estrilda troglodytes[b]	6.2	1	0.46	67	0.388	106	Cade et al. 1964, Lasiewski et al. 1964
Estrilda melpoda[b]	7.5	2	0.47	82	0.308	135	Marschall and Prinzinger 1991
Volatinia jacarina	8.6	1	0.56	65	0.323	102	Weathers 1986
Lonchura fuscans[b]	9.5	2	0.35	51	0.218	107	Weathers 1977
Sporophila aurita	9.9	1	0.72	76	0.260	88	This study
Taeniopygia guttata[b]	11.5	1	0.86	81	0.286	103	Cade et al. 1964
Taeniopygia guttata[b]	12.1	2	0.73	90	0.274	150	Calder 1964, Marschall and Prinzinger 1991
Chloebia gouldiae[b]	15.5	2	0.78	80	0.209	128	Marschall and Prinzinger 1991
Amadina fasciata[b]	17.2	2	0.77	74	0.199	128	Marschall and Prinzinger 1991
Padda oryzivora[b]	25.4	2	1.11	80	0.169	130	Marschall and Prinzinger 1991
Merops viridis	33.8	2	1.07	100	0.075	62	Bryant et al. 1984
Colius striatus	50.0	1	1.21	68	0.104	73	Bartholomew and Trost 1970
Colius striatus	50.0	2	0.97	68	0.087	90	Bartholomew and Trost 1970
Humid lowland forest							
Pipra mentalis	12.3	2	0.70	85	0.315	174	Bartholomew et al. 1983
Manacus vitellinus	15.5	2	0.84	86	0.230	141	Bartholomew et al. 1983
Trogon rufus	53.0	2	1.54	104	0.180	192	Yarbrough 1971
Podargus ocellatus	145.0	2	2.04	66	0.066	127	Lasiewski et al. 1970
Foothill and/or montane forest edge							
Ocreatus underwoodii	2.7	1	—	—	0.860	159	Schuchmann 1979
Amazilia tzacatl	4.3	1	—	—	0.890	204	Schuchmann et al. 1979
Panterpe insignis	5.0	1	—	—	0.370	91	Wolf and Hainsworth 1972
Colibri delphinae	7.0	1	—	—	0.535	154	Schuchmann et al. 1979
Eulampis jugularis	8.3	1	—	—	0.325	101	Hainsworth and Wolf 1970

[a] Phase of the circadian rhythm during which measurements were made. 1 = active, 2 = rest.

[b] Family Estrildidae.

during the day, and their daytime T_{lc} in the field would be lower than that of fasted birds in the laboratory. Consequently, thermoregulatory costs due to cold seem unlikely during the day. Metabolic heat production would be elevated at the lowest T_a recorded at Balboa Heights (17.2°C), but such low air temperatures occur only rarely. Wind and rain might increase a bird's heat loss, but their overall effect is difficult to judge.

Thermal conductance.—Thermal conductance (C), the reciprocal of insulation, traditionally has been calculated as the slope of the line relating oxygen consumption to T_a below thermoneutrality (expressed as a positive value). The slope represents an animal's functional insulation and may differ from the mean thermal conductance calculated for individual measurements below thermoneutrality (McNab 1980). The slope is the appropriate basis for comparisons with allometric predictions, however, because allometric equations are derived largely from slopes, not mean conductances (Lasiewski et al. 1967, Aschoff 1981).

Scholander et al. (1950a,b) found tropical birds (n = 3 species) to be less well insulated than arctic birds (i.e. to have steeper slopes). Calder (1964) extended this observation to nontropical birds from hot environments and pointed out that reduced insulation aids heat loss when T_a is less than T_b. Reduced insulation increases heat gain when T_a exceeds T_b, however, and could be maladaptive in hot climates. Interestingly, three species of small tropical finches have average or better than average insulation (Weathers 1977, 1986, this study); the opposite of Scholander et al.'s original finding. All three of these species are routinely exposed to the sun and would experience excessive heat gain were they poorly insulated. I investigated the link between heat load and insulation in tropical species by summarizing thermal conductance and BMR data of birds that occur between the tropics of Capricorn and Cancer (Table 2). Species were assigned to one of three groups: (1) those that occupy fairly open (i.e. sunny), often humid, lowland habitats; (2) those that are restricted to shaded, humid lowland forests; and (3) those from foothill or montane habitats. The latter group consists of five hummingbird species that mostly occur between about 1,000 to 2,500 m elevation. These species are included in Table 2 for completeness

but were excluded from the analyses because they encounter a subtropical or temperate climate, rather than a tropical one (Holdridge 1947), and they lack BMR data.

Thermal conductance is relatively high in several tropical species (Table 2), but it is uniformly high only in species from shaded, humid lowland forests. Conductance among species from open (sunny) habitats is higher than expected only in the family Estrildidae; C averages 123 ± 12% of predicted values in estrildids versus 83 ± 17% of predicted values in open-habitat birds belonging to other families (t = 4.69, df = 9, P = 0.001). Phylogeny thus appears to be important, but accounting for its influence on C using modern comparative methods (e.g. Harvey and Pagel 1991) is problematic given (1) the small sample sizes within habitat types, (2) the differences between active-phase and rest-phase conductances in *P. guttata* and *C. striatus,* and (3) the variation in C determined in different laboratories (Table 2).

Marschall and Prinzinger (1991) noted a positive correlation between C and BMR in five estrildid species, those with a lower-than-expected BMR having a lower-than-expected conductance and vice versa. Presumably, species with lower rates of heat production require better insulation if T_b is to be maintained at normal levels. A positive trend between C and BMR appears to hold for tropical species generally, with the notable exception of the Blue-throated Bee-eater (*Merops viridis*; Fig. 5, Table 2). BMR and C are strongly positively correlated if the bee-eater data are excluded (r = 0.750, df = 12, P = 0.002; Fig. 5). Including the bee-eater data, the correlation is not significant (r = 0.361, df = 13, P = 0.18). The methods used to measure bee-eater oxygen consumption differed from those of other studies, and the bee-eater's BMR was somewhat ill-defined. Clearly, more data from tropical bee-eaters and representatives of other families are needed to test further the apparent correlation between C and BMR.

Heat strain and hyperthermia.—Hyperthermia ranks among the Variable Seedeater's principal physiological responses to high T_a. Hyperthermia enables Variable Seedeaters to maintain a positive thermal gradient between body and environmental temperatures at relatively high T_as and thus to dissipate heat non-evaporatively. Birds generally become hyperthermic at high T_as, but Variable Seedeaters seem es-
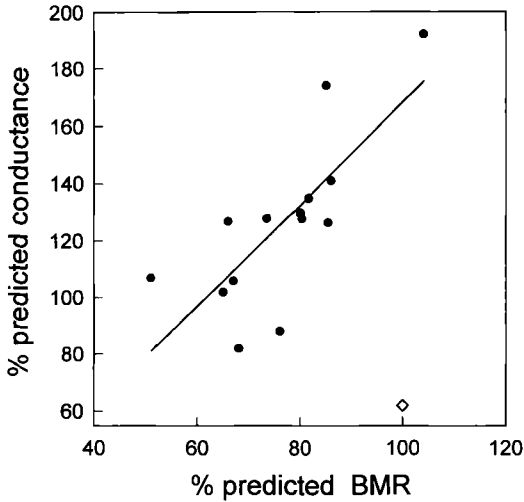
FIG. 5. Relation between thermal conductance as a percent of the value predicted allometrically to basal metabolic rate as a percent of that predicted allometrically for tropical bird species (see Table 2). The datum for *Merops viridis* (unshaded diamond) was not included in the least-squares regression, $y = 1.76x - 9$.

pecially adept at exploiting this mechanism. They allowed their T_b to rise to an average of 44.4°C ($n = 5$; range 43.9 to 44.4°C) at a T_a of 43.0 to 43.1°C, and by doing so they maintained a mean gradient of 1.4°C (range 0.8 to 1.9°C) between their core and T_a. In contrast, six nontropical species maintained a gradient of only 0.01 ± 0.64°C (range −0.96 to 0.77°C) at 43°C (Weathers 1981). The comparable values for two tropical species (calculated from data of Weathers 1977, 1981) are 0.4°C for the Dusky Munia (*Lonchura fuscans*) and 0.9°C in the Blueblack Grassquit (*Volatinia jacarina*). Variable Seedeaters thus exceed other birds, including tropical species, in their extent of hyperthermia. The highest seedeater T_bs measured in Panama were 46.8, 47.0, and 47.0°C. All three individuals survived these T_bs, which are near the upper limit for birds (Calder and King 1974).

The rate of increase in $\dot{H}_m$ above the upper critical temperature (T_{uc}) has been termed the coefficient of heat strain, h_s (Weathers 1981), and provides an integrated measure of the physiological response to heat stress. In Variable Seedeaters, h_s is only 52% of the value predicted allometrically (Weathers 1981). In two other species of small, dark-plumaged seedeat-

ers native to the humid lowland tropics, h_s also is much lower than expected, averaging 68% of predicted in Dusky Munias from Borneo (Weathers 1977) and 35% of predicted in Blueblack Grassquits from Panama (Weathers 1986). Much smaller than expected increases in $\dot{H}_m$ at high T_as in these three species result partly from their ability to uncouple increases in metabolism from increases in body temperature, a trait they share with some small desert passerines (Weathers 1981).

The Variable Seedeater's T_b increased by 3.2°C within the TNZ (Fig. 2), yet its $\dot{H}_m$ was unchanged ($r = 0.202$, df $= 19$, $P = 0.32$). The Q_{10} for metabolic heat production within the TNZ is therefore 1.0 (see Prosser [1973:363] for an explanation of Q_{10} and the Arrhenius-van't Hoff effect). The Variable Seedeater's T_b increased by 3.0°C above the TNZ (equation 5), while $\dot{H}_m$ increased from 0.718 to 1.072 kJ/h (equation 3), yielding an apparent Q_{10} of 1.8. Part of the increase in $\dot{H}_m$ above the upper critical temperature is attributable to the effort involved in panting, however, and the actual Q_{10} therefore is less than 1.8. How much less is difficult to judge, in part because Variable Seedeaters presumably pant less vigorously at high temperatures than do typical birds. Nevertheless, Variable Seedeaters can circumvent the usual temperature dependency of chemical reactions, and this contributes to their relatively low coefficient of heat strain.

Evaporative water loss.—Ambient humidity in the Variable Seedeater's lowland, Panamanian habitat is uniformly high, with dew-point temperature (T_{dp}) at Balboa Heights varying by less than 2°C (either daily or seasonally) from a long-term average of 22.6°C (33-year record, Panama Canal Company pers. comm.). High humidity reduces the efficiency of evaporative cooling and mitigates against a solely physiological response to high temperature. Chamber T_{dp} during measurements of seedeater EWL at T_as between 40 and 45°C averaged 12.2 ± 5.4°C ($n = 18$), or about half that encountered by birds in the field. Nevertheless, Variable Seedeaters were only able to dissipate a maximum of 127% of their heat production evaporatively under these unusually dry conditions (Fig. 4). Even this modest level of cooling would not have been attained had humidity in the metabolism chamber been as high as that in the field. In theory, seedeaters might compensate for
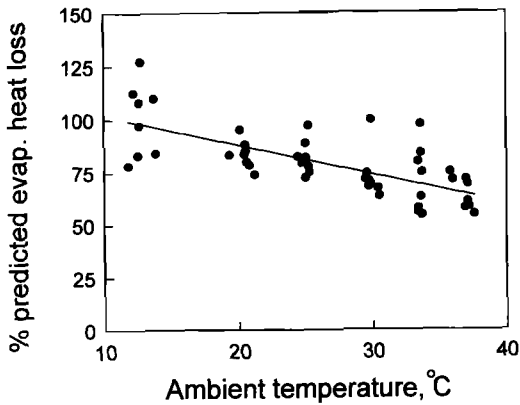
FIG. 6. Relation between the proportion of the metabolic heat production of Variable Seedeaters that is dissipated evaporatively (i.e. H_e/H_m) expressed as a percentage of that predicted for birds in general (Calder and King 1974:238) to ambient temperature. The least squares regression equation of the line is: $y = 116 - 1.39x$ ($r^2 = 0.509$, $P < 0.001$, $n = 48$).

high ambient humidity by increasing the ventilation of their evaporative surfaces at high T_as. But doing so would mean increasing the panting rate, which would increase their metabolic heat production and compound their thermoregulatory problems.

Variable Seedeaters exhibit a blunted evaporative response to heat even when measured at low humidities. Their H_e/H_m ratio is comparable to that of other species at low T_as, but as T_a increases, their H_e/H_m ratio becomes progressively smaller than predicted (Fig. 6). High ambient humidity in their native habitat reduces the effectiveness of evaporative cooling, and Variable Seedeaters apparently have lost the ability to increase EWL at high temperatures (even when measured at relatively low humidities) to the same extent as species native to less humid habitats. Variable Seedeaters dissipated 79 ± 16% of their heat production evaporatively over the temperature interval depicted in Figure 6, which is comparable to the value of 78 ± 21% ($n = 53$) found in Blue-black Grassquits (Weathers unpubl. data).

Overall, the ability of Variable Seedeaters to deal with heat stress physiologically seems only modestly better than that of other small birds. Behavioral observations of seedeaters in an open grassland in central Panama reveal that both Variable Seedeaters and Blue-black

Grassquits cease foraging and retreat to the shade when operative temperatures (measured with taxidermic mounts) exceed their upper critical temperature (Weathers 1986). These species thus behaviorally avoid high T_es when foraging. If tropical seedeaters can avoid heat stress behaviorally, then why do some species have reduced BMRs? The answer may be that a reduced BMR extends the time that birds can be exposed to the sun (Weathers 1977). Blue-black Grassquits have a much lower BMR than Variable Seedeaters (Table 2). One selective pressure that might contribute to the grassquit's lower BMR is the male's unusual courtship display. Male grassquits tolerate T_es as high as 46.9°C when performing courtship displays in open, sunny sites. The fitness costs of not displaying at high temperatures probably outweigh those of not foraging, which could explain the grassquit's lower BMR.

Ruddy-breasted Seedeaters also have a relatively low BMR (67% of that predicted allometrically). Observations I made of Ruddy-breasted Seedeaters in Panama indicate that this species is even more heat tolerant than its bigger congener. A male Ruddy-breasted Seedeater maintained a territorial song post near the spot from which I observed the behavior of Variable Seedeaters and grassquits described in Weathers (1986). When the weather was hot, calm, and partly cloudy this male often was the only bird perched in the sun. On three occasions when sun T_e measured 1.2 m above ground with a grassquit taxidermic mount was between 43.0 and 44.5°C, only the male Ruddy-breasted Seedeater was visible. He sat in the sun "singing away with no signs of panting" (Weathers pers. obs.). Male Ruddy-breasted Seedeaters have lighter colored plumage than male Variable Seedeaters and male grassquits, and this might reduce their thermal load and effective T_e when exposed to the sun. Overall, Ruddy-breasted Seedeaters seem to be remarkably tolerant of high T_a for such a small bird, and this intriguing species deserves further study .

SYNOPSIS

The combination of shade air temperatures that are usually within or below the thermal neutral zone and high humidity creates conditions in the lowland tropics that favor a be-

havioral rather than a physiological response to heat in small birds. Nevertheless, some small tropical species differ from their temperate-zone relatives in ways that suggest adaptation to their thermal environment. Tropical species have high rates of evaporative water loss (Williams 1996) but limited capacity to augment evaporation at high temperatures, even at low humidity (Weathers 1977; Fig. 6). Many tropical species are less well insulated than temperate species (which aids heat loss at moderate temperature), but except for the family Estrildidae those from the sunny, humid lowlands are well insulated (Table 2). Among tropical species there is a positive correlation between thermal conductance and BMR (Fig. 5). Tropical species that occupy shaded forest sites generally have average BMRs, whereas those from open, sunny sites have reduced BMRs (Weathers 1977, 1979; Table 2). Because tropical species appear to be only slightly more tolerant of high body temperature than their temperate relatives, a low BMR would increase the time that a tropical bird can be exposed to direct sun when foraging (Weathers 1977) or when performing courtship displays (Weathers 1986). Whether low BMR in sun-foraging tropical species is an evolved trait is unclear, however, because a preponderance of sun-foraging species studied thus far belong to the family Estrildidae, and members of that group have reduced BMRs regardless of habitat of origin (Marschall and Prinzinger 1991). Clearly, more studies of birds from the humid, tropical lowlands are needed to establish the generality of the above pattern. It is equally clear that because most physiological ecologists work and reside at temperate latitudes, progress in this endeavor will continue to be slow.

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