

are evident (Fig. 1). Miller (1940) reported on the absence of the dive-noise in the displays of sub-adults. Pitelka (pers. comm.) noted that the dive of young males is not totally silent for there is a rush of air, which is a noise. In molting birds, he noted a rush of air which might progress to a louder click noise as the feathers mature. Whereas the developing rectrices may contribute to the louder dive-noise, it could be that ontogeny of the voice parallels development of the rectrices. "Crystallization" of the (vocal) dive-noises may be complete when the rectrices are fully mature. If so, then the function of the specialized rectrices may be to provide added maneuverability during the complex dive display.

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## METABOLIC RATE IN FIVE TROPICAL BIRD SPECIES

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Metabolic rates are often predicted from allometric equations relating metabolism to body mass. Although the relationship between metabolic rate and body mass varies among taxa of birds (Lasiewski and Dawson 1967), and with time of day (Aschoff and Pohl 1970), it has not been shown to vary predictably with climate (Scholander et al. 1950). Few metabolic data are available on birds living in the lowland tropics where ambient temperatures are usually high. A few birds from hot climates have low metabolic rates (Hudson and Kimzey 1966, Weathers 1977). It is therefore of interest to determine if metabolic rates of tropical species are lower than those predicted from allometric equations based largely on temperate species. We report standard metabolic rates of four tropical passerines, all suboscines, and one tropical nonpasserine, a dove.

#### MATERIALS AND METHODS

Birds were mist-netted in August and September 1977 on several islands in Gatun Lake in central Panama, latitude 9°N. Rates of oxygen consumption were measured for at least two hours during the night after capture. We kept the birds in the dark without food for 3-8 h before testing. They were weighed to the nearest 0.5 g with a Pesola scale before and after testing. Cloacal temperatures were measured at the end of each experiment with a quick-registering

Schultheis thermometer or thermocouple probe and Bailey Bat-8 digital thermometer.

We measured oxygen consumption in an open flow respirometer analogous to the mask system described by Withers (1977). Birds were placed in a plastic or glass metabolic chamber within a darkened box maintained at  $30 \pm 1^\circ\text{C}$  and at ambient water vapor pressures which did not exceed 24 torr. Air flow through the metabolic chamber ranged from 120 to 645 cc/min. Carbon dioxide and water vapor were absorbed from air leaving the chamber by using Ascarite (sodium hydroxide asbestos) and Drierite (anhydrous calcium sulfate). Fractional concentration of oxygen was then determined with an Applied Electrochemistry S3A Oxygen Analyzer. Flow rates were measured downstream of the oxygen sensor with a Gilmont Flowmeter calibrated against a Brooks Thermal Mass Flowmeter. Oxygen consumption was calculated from equation 4a of Withers (1977). All gas volumes are reported at standard temperature ( $0^\circ\text{C}$ ) and pressure (760 torr, 1 torr = 0.133 kPa).

Birds sat in the chamber undisturbed for at least one hour before we began recording oxygen consumption. The lowest rate of oxygen consumption during the second hour of each experiment was assumed to be the standard metabolic rate at  $30^\circ\text{C}$ . Rate of oxygen consumption usually did not vary more than 5% throughout the last 30 min of an experiment. Oxygen consumption was converted to energy assuming a caloric equivalent of 4.8 kcal/l  $\text{O}_2$  (1 kcal = 4.184 kJ) (King and Farner 1961, Lasiewski and Dawson 1967).

#### RESULTS

Standard metabolic rates of the five species are shown in Table 1. Predicted metabolic rates in the resting phase of the daily activity cycle were calculated from the appropriate allometric equations of Aschoff and Pohl (1970). For nonpasserines:

TABLE 1. Nighttime resting metabolic rates at 30°C and body temperatures in five tropical bird species. Predicted metabolic rates are calculated from the appropriate equation in Aschoff and Pohl (1970). Percentage is (observed ÷ predicted) × 100.

Species	Sex	Sample size	Mass (g ± SD)	T <sub>b</sub> (°C ± SD)	Metabolic rate (kcal/day)		Percentage
					Observed ± SD	Predicted	
<i>Leptotila verreauxi</i> (White-tipped Dove)	♀	2	131 ± 20	38.6 ± 0.4	18.3 ± 2.12	16.53	111
<i>Pipra mentalis</i> (Red-capped Manakin)	♀/Juv. <sup>1</sup>	2	14.5 ± 0.7	39.5 ± 2.8	6.14 ± 0.94	5.31	116
<i>Manacus vitellinus</i> (Golden-collared Manakin)	♂	2	18.2 ± 1.1	38.5 ± 0.0	4.88 ± 1.27	6.26	78
	♀/Juv. <sup>1</sup>	9	15.0 ± 1.1	38.7 ± 0.7	5.91 ± 0.72	5.44	109
	(Total)	11	15.6 ± 1.7	38.7 ± 0.4	5.72 ± 0.87	5.60	102
<i>Xiphorhynchus guttatus</i> (Buff-throated Woodcreeper)	♀	2	45.2 ± 5.3	39.3 ± 0.6	9.21 ± 1.46	12.12	76
<i>Thamnophilus punctatus</i> (Slaty Antshrike)	♂	1	21.0	37.3	7.05	6.95	101

<sup>1</sup> We were not able to distinguish female from juvenile manakins.

$$MR = 73.5 M^{0.734}$$

and for passerines:

$$MR = 114.8 M^{0.726}$$

where MR is metabolic rate in kcal/day and M is body mass in kg. The White-fronted Dove (*Leptotila verreauxi*) had a metabolic rate slightly higher than predicted, as did the Red-capped Manakin (*Pipra mentalis*), Golden-collared Manakin (*Manacus vitellinus*), and Slaty Antshrike (*Thamnophilus punctatus*). The Buff-throated Woodcreeper (*Xiphorhynchus guttatus*) had a metabolic rate only 76% of the predicted rate. Birds rested quietly throughout an experiment, and none showed obvious signs of stress afterwards. Body temperatures ranged from 38.6°C in *Leptotila* to 39.5°C in *Pipra*.

## DISCUSSION

The climate in the lowlands of central Panama is always warm. Annual mean minimum and maximum air temperatures for the Canal Zone are 23.7°C and 30.1°C respectively. During the rainy season (May–December) humidities are high, often near saturation. Weathers (1977) has suggested that a low basal metabolic rate may be adaptive for endotherms living in a hot, humid, tropical climate because lower heat production might reduce heat stress. Some tropical birds, notably Caprimulgiformes, have low rates of metabolism which are associated with low body temperatures (Lasiewski et al. 1970). A few tropical passerines, for example the Dusky Munia (*Lonchura fuscans*; Weathers 1977), have relatively low basal metabolic rates at normal passerine body temperatures. The standard metabolic rate of *Xiphorhynchus guttatus* (9.21 kcal/day) lies below the 95% confidence interval of the predicted value (10.49–13.95 kcal/day). Our value for *Pipra mentalis* (6.14 kcal/day) is above the confidence interval of the prediction (4.63–6.08 kcal/day) for this species, although Scholander et al.'s (1950) previously reported value for *P. mentalis* is within the confidence interval (103% of predicted daytime rate). Body temperatures we measured were lower than those reported for active birds in the same order (Dawson and Hudson 1970), but within the

normal range for birds at rest (King and Farner 1961).

Oxygen consumption rates of *Manacus vitellinus* ranged widely from 1.83 to 4.30 cm<sup>3</sup>/g h (mean = 3.26 ± 0.71 cm<sup>3</sup>/g h) in the 11 individuals tested. We found no regular relationship between oxygen consumption and sex or body temperature. The two lowest values were only 55 and 74% of predicted. A check of the system revealed no reason to doubt the validity of these measurements. Manakins are small frugivorous birds which may face periods of decreased energy availability (Foster 1977). *Manacus* may ameliorate the effects of such energy shortages by reducing metabolic rates when resting as has been suggested for several other species (Steen 1958, Warren 1960, Lasiewski 1963, Chaplin 1974, 1976). Birds with low metabolic rates were not captured earlier in the day or treated differently from others. However, we do not know their history prior to capture. The birds with low metabolic rates did not have conspicuously low body temperatures, but it may not be possible for birds to become measurably hypothermic in two hours at 30°C.

Some birds from tropical climates, e.g. *Xiphorhynchus* (this study), *Lonchura* (Weathers 1977), Waxbills (*Estrilda*; Lasiewski et al. 1964) have metabolic rates below the passerine norm while other tropical species apparently do not. Time, energy, and water budget data are needed to assess the role of reduced levels of metabolism in adaptation to a hot and humid environment. Ricklefs (1971) suggested that the Mangrove Swallow (*Tachycineta albilinea*) of the tropics must reduce its activity in the middle of the day because of the difficulty of dissipating heat from flight metabolism. However, the available data are insufficient to evaluate the thermal importance of resting metabolic rates. Adaptations that involve physiological processes such as metabolic rates cannot be better understood until more work is done in the tropics.

Most passerines have a standard metabolic rate 50–60% higher than that of nonpasserines and a separate allometric equation is used for prediction of metabolic rate (Lasiewski and Dawson 1967). However, almost all the data used to determine the relationship in passerines have come from members of the oscine suborder Passeres. The suboscines,

comprising about one-fifth of the passerines, are considered by some workers to be more primitive than the oscines and by others to be of separate phyletic origin (Feduccia 1977). Except for *Xiphorhynchus*, the metabolic rates of the suboscines we measured fit the prediction based on Passeres quite well.

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#### EXPERIMENTAL EVIDENCE FOR FACILITATION OF PAIR FORMATION BY BRIGHT COLOR IN WEAVERBIRDS

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Experimental studies of the role of color in displays of male birds have generally emphasized responses of the male, rather than of the female. Smith (1972) painted the red epaulets black on male Red-winged

Blackbirds (*Agelaius phoeniceus*) who then often lost their territories, but were still able to attract females. However, no data were presented on relative numbers of females attracted by normal and painted males which retained territories.

The Village Weaverbird (*Ploceus cucullatus*) is a polygynous African species. In the course of pair formation the male hangs beneath the bottom entrance of the roofed nest he has woven and attempts to attract a female to enter his nest by a special display in which he vigorously flaps his wings, revealing their bright yellow linings. The upper surfaces of the wings are mostly dark. Our object was to see if this flashing display attracted a female to the nest more than it would if the yellow color were not present.

Birds were maintained at Los Angeles in three large outdoor aviaries (9.2 × 5.2 × 5.2 m, 7.9 × 6.1 × 4.0 m, and 9.2 × 4.6 × 4.0 m), in which they had bred each spring and summer for several years previously. Methods of maintaining the birds and details