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Metabolic Rate, Temperature Regulation, and the Energetic Implications of Roost Nests in the Bananaquit (*Coereba flaveola*)

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Many factors can influence avian metabolic rates, including ambient temperature (T_a), time of day, season, climate, and phylogenetic relationships (e.g. Lasiewski and Dawson 1967, Zar 1968, Ligon 1969, Aschoff and Pohl 1970a, b, Kendeigh and Blem 1974, Kendeigh et al. 1977, Weathers 1979, Bennett 1988). Of all the various parameters asso-

ciated with basal levels of energy expenditure, perhaps the most important is body size. This relationship has been the subject of extensive research, resulting in the production of standard allometric equations that predict avian basal metabolic rate based on body mass (Brody and Proctor 1932, King and Farner 1961, Aschoff and Pohl 1970a, b, Kendeigh et al. 1977, Bennett and Harvey 1987). Most avian physiological studies, however, including those that provided the data for the allometric equations, have concentrated on birds from the temperate zone (e.g. Lasiewski and Dawson 1967,

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Aschoff and Pohl 1970a, b, Kendeigh et al. 1977), inviting the question of whether these equations accurately reflect the relationship between metabolic rate and body size in the tropics, where most avian species occur. To obtain a more comprehensive and accurate picture of avian metabolic patterns, additional data from tropical birds are required (Vleck and Vleck 1979, Hails 1983, McNab 1988).

Here, I describe the energetics of the Bananaquit (*Coereba flaveola*), a small passerine common throughout much of the New World tropics, ranging from southern Mexico to Northern Argentina, and inhabiting most of the islands of the Caribbean (Leck 1983). Bananaquits build distinctive globular, semipendant nests of grasses and plant fibers. Nests are used for care of young and also for nighttime roosts. In addition to measures of metabolic rate and body temperature (T_b), I evaluate the potential energetic significance of the Bananaquit's unusual roosting behavior.

Methods.—Adult Bananaquits were captured from 1 October to 17 December 1994 in the Luquillo Experimental Forest, a rain forest located on the northwest slope of the Luquillo Mountains in northeastern Puerto Rico (18°19′N, 65°45′W). All birds were captured with mist nets between 1500 and 1730; sunset was at approximately 1720.

I estimated metabolic rates by measuring oxygen consumption ($\dot{V}O_2$) in a portable open-flow respirometry system. Immediately after capture, birds were weighed to the nearest 0.1 g on a portable balance (Acculab 333) and placed inside a 946-mL (1 quart) new paint can with a pressure-seal lid and ports for air flow through the chamber; the interior of the can was painted flat black. The chamber was submerged into a constant-temperature water bath (Techne ESRB-7, accurate to ±1°C) set at 25°C, and the birds were held at this temperature for at least 4 h to ensure that they were in a post-absorptive state. The rate of $\dot{V}O_2$ was monitored during this period to confirm that it had stabilized prior to beginning the measurements. Complete darkness was maintained in the chamber for the duration of the acclimation and test periods.

A mass flow controller (MKS Instruments, accurate to ±5 mL) positioned upstream from the metabolic chamber maintained the flow of air into the metabolic chamber at 150 mL/min. I used a simple air manometer fashioned from an inverted graduated cylinder filled with water to calibrate the flow controller by measuring the volume of water displaced over time; all measures were corrected to STPD. Air was passed through tubes of Ascarite and Drierite to remove carbon dioxide and water, respectively, both before the flowmeter and upon exiting the metabolic chamber. Oxygen concentrations were measured on the dry, CO_2-free air exiting the metabolic chamber to the nearest 0.1% using a paramagnetic oxygen analyzer (Servomex 570A, cali-brated per manufacturer's instructions) and recorded on a portable computer every 60 s by use of DATACAN V data acquisition and analysis software (Sable Systems). $\dot{V}O_2$ was determined from the rate of air flow into the chamber and the difference between the concentration of oxygen in the incurrent and excurrent air based on Hill (1972: equation 2).

Chamber temperature was monitored constantly using a copper-constantan thermocouple and a microprocessor thermometer (Omega HH23, accurate to ±0.1°C). Following the initial 4-h acclimation period at 25°C, $\dot{V}O_2$ was recorded at that temperature for 30 min. The chamber temperature was then changed to a new test temperature, and the bird was held at the new temperature for a minimum of 1 h or until $\dot{V}O_2$ had again stabilized, followed by another 30-min measurement period. This procedure was then repeated at the next test temperature. Test temperatures were increased or decreased sequentially from 25°C in increments of 5° over the range of temperatures from 15 to 40°C. $\dot{V}O_2$ for each test temperature was considered to be the average of the lowest consecutive 10 min of readings within the 30-min measurement period. Birds were tested at one to four different temperatures during the course of a night. $\dot{V}O_2$ measurements ended at various times in the early morning (prior to 0400), but began no earlier than 1930; all measures can therefore be considered to be in the rest phase (sensu Aschoff and Pohl 1970a, b). Birds were again weighed following removal from the chamber. No bird was used for more than one night. Measurements were discarded if the bird was obviously active during the measurement period, as evidenced by repeated spikes in the $\dot{V}O_2$ recording or by hearing the bird moving inside the chamber. The number of birds tested at each temperature ranged from 6 to 10, but it was not possible to obtain complete data over the full range of T_as tested for any single individual.

Active-phase T_bs were measured within 30 s of removing the bird from the net following capture. A thin (36 gauge) copper-constantan thermocouple probe was inserted approximately 1 cm into the cloaca, or until a slight withdrawal effected no change in the reading. T_b was determined to the nearest 0.1°C from a microprocessor thermometer (Omega HH23). Rest-phase T_bs were obtained at the end of the $\dot{V}O_2$ trials. The T_b corresponding to the final test temperature was measured immediately upon removing the bird from the metabolic chamber, following the procedure for active-phase T_b described above. All birds were therefore exposed to the test T_a for 1.5 h prior to measurement of T_b. Measurements were discarded if not accomplished within 30 s of removing the bird from the chamber. The final test temperatures were varied in order to obtain T_bs over the range of T_as tested. Test birds were held in a cage until daylight, at which time they were released at the point of original capture.
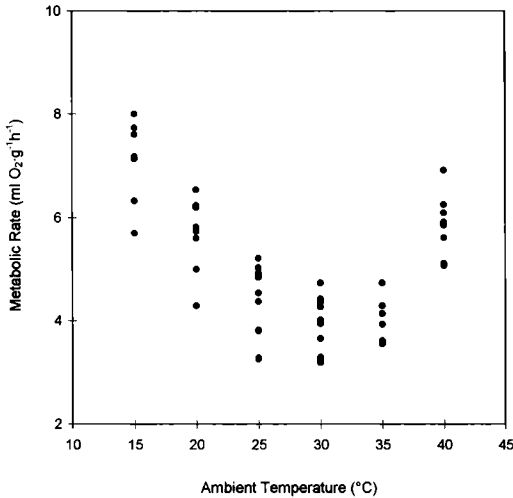
FIG. 1. Metabolic rate of Bananaquits as a function of ambient temperature. Each point at an ambient temperature represents a different bird. See text for estimate of basal metabolic rate.
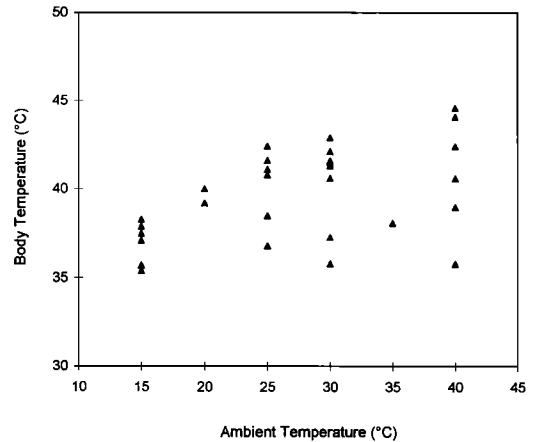

FIG. 2. Rest-phase body temperature of Bananaquits as a function of ambient temperature. Bananaquits became hypothermic at an ambient test temperature of 15°C but otherwise remained homeothermic (see text).

Ten Bananaquit nests observed in use as roost nests at the study site were collected to determine an index of nest insulation. The insulative value of the nests was estimated by comparing the cooling constants of models made from balloons filled with 10 g of water and heated to about 40°C to approximate the size and T_b of a Bananaquit. A copper-constantan thermocouple probe was inserted into the center of each model and the model was clamped shut. Two models were used simultaneously in each trial: a "nest" model placed inside a Bananaquit nest, and a "control" model exposed to ambient conditions. The control model was positioned next to the nest containing the nest model on a cardboard tray, and the tray was placed in an environmental chamber maintained at 26°C. The internal temperatures of the two models were recorded simultaneously every 60 s over a period of 10 min by use of a microprocessor thermometer. Each nest and its associated models were tested simultaneously three times, and the results averaged for greater accuracy.

Cooling constants (k) for the nest and control models were calculated following the method of Toolson (1987). To determine k from the logistic cooling curve, I plotted the natural logarithm of $(T_t - T_c)/(T_0 - T_c)$ against time, where T_t is the temperature of the model at any time t, T_c is the environmental chamber temperature (assumed to be constant), and T_0 is the starting temperature of the model. The slope of the resulting regression is an estimate of the cooling constant, k, in units °C/°C per min, or more simply, min^{-1}.

Results.—$\dot{V}O_2$ rates were measured on a total of 29 adult Bananaquits (mean body mass = 10.0 ± SD of

0.8 g). A curve of thermogenesis was created by plotting $\dot{V}O_2$ versus ambient test temperature (Fig. 1). Although $\dot{V}O_2$ appeared similar over the range of T_as from 25 to 35°C, significant differences occurred among the individuals tested at each of these T_as (paired t-tests; mean difference = 0.243 ± 0.21 for individuals tested at both 25 and 30°C, $n = 6$, $P = 0.04$; mean difference = 0.28 ± 0.09 for individuals tested at both 30 and 35°C, $n = 6$, $P < 0.0005$). $\dot{V}O_2$ was minimal for all individuals at $T_a = 30$°C. Because the birds were post-absorptive, at rest, and in the rest phase of their daily cycle at the time of measurement, I considered the mean $\dot{V}O_2$ rate at 30°C to represent basal metabolic rate (BMR) as defined by Bligh and Johnson (1973). The BMR of the Bananaquit is therefore estimated to be 3.85 ± 0.17 mL O_2 g^{-1} h^{-1} ($n = 11$). The T_as of 25 and 35°C appear to be below and above the bounds of the thermoneutral zone, respectively, but the degree of resolution used here does not permit a more precise definition of the lower (LCT) and upper critical temperatures.

The average active-phase T_b was 40.7 ± 1.6°C ($n = 26$). Measures of rest-phase T_b showed that Bananaquits remained homeothermic over the range of temperatures from 20 to 40°C ($T_b = 40.6 ± 2.2$, $n = 24$) but became slightly hypothermic at $T_a = 15$°C ($T_b = 37.0 ± 0.5$, $n = 6$; see Fig. 2, Table 1). Hypothermia is defined here as a T_b more than one SD below rest-phase T_b in a thermoneutral environment (Bligh and Johnson 1973).

The tests of nest insulation showed that the cooling constant for the model inside the nest ($k_n = 0.047$ min^{-1}, $n = 10$) was significantly lower than that of the exposed control model ($k_c = 0.068$ min^{-1}, $n = 10$; ANCOVA, $P < 0.001$). Using this difference as an in-

TABLE 1.   Metabolic rate (mL O_2 g^{-1} h^{-1}) and rest-phase body temperature (°C) of Bananaquits over the range of ambient temperatures tested. Values are $\bar{x}$ ± SD, with range in parentheses.

Temperature	Metabolic rate	n	Body temperature	n
15°C	7.09 ± 0.31 (5.70 to 8.00)	7	37.0 ± 0.5 (35.4 to 38.3)	6
20°C	5.69 ± 0.23 (4.29 to 6.53)	9	39.6 ± 0.4 (39.2 to 40.0)	2
25°C	4.36 ± 0.21 (3.26 to 5.21)	11	40.3 ± 0.7 (36.8 to 42.4)	7
30°C	3.85 ± 0.17 (3.19 to 4.73)	11	40.6 ± 0.8 (35.8 to 42.9)	9
35°C	3.97 ± 0.11 (3.55 to 4.73)	14	38.1 ± 0.0 (38.1 to 38.1)	1
40°C	5.85 ± 0.21 (5.07 to 6.90)	8	42.1 ± 1.1 (39.0 to 44.6)	5

dex of the nest's insulative value, I estimated that the roost nest reduces the rate of heat loss from the model by 31%.

Discussion.—Tropical birds are commonly reported to have lower BMRs than predicted on the basis of their body mass (Enger 1957, Ricklefs 1970, Weathers 1979, Hails 1983, Bryant et al. 1984, Ellis 1984; but see Vleck and Vleck 1979, Bryant and Hails 1983). This pattern is commonly cited in reviews of avian metabolic rates as an adaptive response to high temperatures and humidity levels in the tropics (e.g. Whittow 1986, Bennett and Harvey 1987, Daan et al. 1990). I found no evidence, however, that the BMR of the Bananaquit is any lower than would be expected for its size. On the basis of body mass, the observed BMR of the Bananaquit is 10% higher than predicted by the allometric equation of Aschoff and Pohl (1970b). This result corresponds with those of other researchers who have reported wide variation in metabolic rates of tropical birds, with some species showing basal rates equal to or greater than expected from allometric predictions (e.g. Vleck and Vleck 1979, Bryant and Hails 1983).

In addition, the BMR of Bananaquits reported here is lower than that reported in an earlier study. Wunderle et al. (1987) reported the average $\dot{V}O_2$ of five Bananaquits, measured at an T_a of 24 ± 1°C, to be 29.4 J/min. My measurements at an T_a of 25°C averaged 15.3 J/min (converted for comparative purposes from 4.56 ml O_2 g^{-1} h^{-1} using the standard 20.1 kJ/L O_2 and mean body mass of 10.0 g). Procedural differences most likely explain this discrepancy. The birds used in Wunderle et al.'s study may not have been post-absorptive (Cade et al. 1965, Calder and King 1974, Whittow 1986) because they were acclimated for only 1.5 h before measurements were taken (I found that many individuals required at least 4 h for $\dot{V}O_2$ rates to stabilize). Wunderle et al. (1987) did not report the time of day at which the measurements were recorded; however, they stated that indirect light was provided to the birds. If their measurements were recorded during the day (active phase), then the metabolic rates they reported are expected to be from 20 to 25% higher than if the birds were measured during their rest phase (Aschoff and Pohl 1970a, b); indirect light also would result in elevated metabolic rates (Aschoff and Pohl 1970b).

The active-phase T_b of Bananaquits is typical of that for passerines (McNab 1966, Calder and King 1974, Prinzinger et al. 1991), and regulation of T_b at 40 to 41°C over a range of moderate T_as also is typical for passerines (Kendeigh 1961). Bananaquits exhibited hypothermia at the lowest T_a tested (15°C), with T_b decreasing up to 5°C in some individuals (Table 1). Hypothermia at low T_as is a common phenomenon in birds (Cheke 1971, Chaplin 1976, Reinertsen 1983, Reinertsen and Haftorn 1986) and may represent an energy-conservation strategy (Ohmart and Lasiewski 1971, Calder and King 1974, Kendeigh et al. 1977, Reinertsen 1983, 1988, Phillips et al. 1985). Bananaquits, however, probably do not use hypothermia as an energy-saving mechanism under normal conditions. Although T_b dropped when tested at 15°C, these birds experience temperatures this low only infrequently in nature. The record low temperature on Puerto Rico is 4.5°C (Calvesbert 1974), but the average minimum temperature at my study site remains above 20°C year-round (Odum et al. 1970), a temperature at which Bananaquits maintained normal T_bs during the trials but that is below the presumed LCT. Bananaquits gain protection from exposure to low temperatures at night by the use of roost nests.

The use of favorable microclimates is a common behavior employed by birds to ameliorate the high energetic costs of thermoregulation at low environmental temperatures (Ricklefs 1974, Mayer et al. 1982, Walsberg 1985, 1986, Reinertsen 1988). Many birds use existing cavities or other structures, and a few construct their own nocturnal shelters (Kendeigh 1961, Skutch 1961, 1989, Kilham 1971, Buttemer et al. 1987, Farley 1993). Roosting in sheltered microclimates such as tree cavities or covered nests can result in substantial energy savings by shielding the bird from the wind, preventing heat loss through radiation to the night sky, and by warming of the surrounding air, thus reducing the gradient between T_b and T_a. Although intuitively it might seem that cavity roosting would be most common in species that encounter cold conditions in temperate regions, such behavior actually appears to be more widespread in small tropical species (Collias and Collias 1964, Skutch 1989). Because small birds lose endogenous heat rapidly over a relatively high surface area and

use more energy per unit body mass, it should be adaptive for them to employ a variety of physiological and behavioral strategies to conserve energy, even in the relatively warm climates of the tropics.

For the Bananaquit, the use of nocturnal roost nests may represent just such a behavioral strategy because the average minimum temperatures experienced are below the presumed LCT of the bird. Assuming T_a is below the LCT of an endothermic animal, any decrease in the rate of heat loss translates into an energy savings by reducing the metabolic requirements to an equal degree (Scholander et al. 1950). The Bananaquit's roost nest provides such a decrease in the rate of heat loss. The index of nest insulation calculated here shows that by using a roost nest, a Bananaquit may have to expend only about two-thirds of the energy that would be required to maintain homeothermy in the open. This value probably underestimates the potential energy savings to the Bananaquit because the test conditions did not include the effects of convection or radiation to the open night sky, or of exposure to precipitation, all of which may further increase the rate of heat loss (Kendeigh 1961, Phillips et al. 1985, Walsberg 1985, 1986, Reinertsen 1988).

By sleeping in roost nests, Bananaquits may also gain protection from a mode of heat loss that largely has been ignored in studies of avian thermoregulation, namely convection via precipitation (Walsberg 1985). The Bananaquits I studied reside in a rain forest where rainfall averages 3,000 mm annually (Recher 1970). Exposure to precipitation increases the rate of heat loss from birds (Gessaman 1972, Kendeigh et al. 1977), and wetting the plumage of passerines results in a dramatic increase in lower critical temperature (Lustick and Adams 1977). Although the use of nocturnal roost nests by tropical birds is considered "more a luxury than a necessity" (Skutch 1989:151) and may have originated as a means of gaining protection from predators (Collias and Collias 1964, Skutch 1989), the use of such shelters clearly confers significant energetic advantages. A principal benefit for the Bananaquit and other small tropical birds from sleeping in covered roost nests may be protection from frequent tropical rains and the associated high potential energy costs.

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Assortative Mating and Sexual Size Dimorphism in Western and Semipalmated Sandpipers

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Sexual dimorphism in body size is widespread among animals, and most explanations for the evolution of dimorphism can be grouped into two categories: (1) sexual selection, and (2) intraspecific niche differentiation (Jehl and Murray 1986, Shine 1989). Sexual selection clearly has been important in shorebirds (suborder Charadrii), because the direction and magnitude of size dimorphism are related to both mating system and the duration of parental care (Jönsson and Alerstam 1990, Reynolds and Székely 1997). Typically, the sex that competes for mating opportunities is larger, and this is true for most polygynous shorebirds (males larger) and species with sex-role reversal where females are larger (Jehl and Murray 1986, Jönsson and Alerstam 1990). It is more difficult to explain, however, why females are the larger sex in many shorebirds that mate monogamously (Jehl and Murray 1986, Olsen and Cockburn 1993).

Female-biased sexual size dimorphism could evolve if the sexes become adapted to different ecological conditions (Shine 1989). Alternatively, female-biased dimorphism may result if sexual selection acts such that fitness covaries positively with body size for females but negatively for males. Energy storage capacity increases with structural size, and large-bodied female sandpipers may have an advantage if they are able carry resources that allow them to breed earlier or lay larger eggs (Erckmann 1981, Jehl and Murray 1986, Jönsson 1987). On the other hand, energy efficiency decreases with increasing body size (Jönsson and Alerstam 1990). Male calidrine sandpipers often give complex display flights during courtship (Miller 1979), and small body size may allow for increased agility in these aerial displays (Jehl and Murray 1986, Blomqvist et al. 1997). Negative assortative mating could further increase selection on body size if birds pair with respect to morphology. Examples of negative assortative mating are rare in birds, and they usually are based on color-morph preferences (Partridge 1983, Houtman

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