Low Metabolism and Inactive Lifestyle of a Tropical Rain Forest Bird Investigated via Heart-Rate Telemetry

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ABSTRACT

Birds in the lowland tropical rain forest are expected to have low energy turnover. Here, we used heart rate telemetry to estimate nighttime resting metabolic rate (RMR), daily energy expenditure (DEE), and locomotor activity of a small, long-lived tropical rain forest–understory bird, the spotted antbird (*Hylophylax naevioides*). Heart rate was linearly related to oxygen consumption in respirometry measurements that encompassed 96% of heart rates measured in wild birds. Heart rates in the wild ranged from 260 beats/min at night to 824 beats/min during the day, with a mean of 492 beats/min. Compared with temperate-forest birds of similar body mass, wild spotted antbirds had a low DEE, only 51% of the expected value. Such low metabolism was achieved mainly by being locomotively inactive for 35% of the daytime (i.e., 0 hops or flights/min). On average, spotted antbirds exhibited 1.6 hops or short flights/min during the daytime. In addition, they decreased nighttime RMR in the wild (at ambient temperatures below their thermoneutral zone [TNZ]) to levels equivalent to nighttime RMR in the laboratory at temperatures within their TNZ. This suggests that wild birds reduce their body temperature every night. Our data confirm and extend previous studies showing that tropical passerines have low metabolic rates.

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Introduction

Nighttime resting metabolic rate (RMR) is generally lower in tropical birds than in comparable temperate-zone or arctic birds (e.g., Vleck and Vleck 1979; Hails 1983; Klaassen 1995; Lindstrom and Klaassen 2003; Tieleman et al. 2006; Wiersma et al. 2007). Metabolic rates are even lower in tropical populations within the same species when birds are raised under similar captive conditions, suggesting intrinsic differences in energy metabolism between birds living in different habitats/latitudes (Klaassen 1995; Furness 2003; Wikelski et al. 2003; Tieleman 2007). In addition, there is laboratory evidence that tropical birds may use facultative and regulated hypothermia and torpor to save energy (e.g., Bartholomew et al. 1983; Merola-Zwartjes and Ligon 2000). Some authors have also suggested that tropical birds lead a much more "leisurely" lifestyle than other birds (Hamilton 1966; Ricklefs 1991; Wikelski et al. 2003) and exhibit lower activity rates (Weathers and Stiles 1989; Martin 1996; Wikelski and Ricklefs 2001), consistent with low rates of energy expenditure.

In this study, we used heart rate to estimate the nighttime RMR, daily energy expenditure (DEE), and locomotor activity of a small, long-lived, rain forest suboscine passerine, the spotted antbird (*Hylophylax naevioides*; family Thamnophilidae; del Hoyo et al. 2003). These small (~17-g) insectivorous birds are characterized by life spans longer than 15 yr and high annual survival rates of up to 81% (Willis 1972, 1983; Brawn et al. 1995; Hau et al. 2000). Spotted antbirds are members of mixed bird aggregations that often follow army ant swarms to catch insects flushed by the ants (Willis 1972). On average, about 50% of their food is taken at ant swarms (Willis 1972). Spotted antbirds generally remain in the undergrowth of the tropical rain forest (below 2 m height), where they hop from perch to perch and rarely fly more than 20 m at a time (Willis 1972). This niche is adopted by only 2%–3% of the forest songbirds at any one site and only about 10% of the family (Ridgely and Gwynne 1989). Spotted antbirds exhibit an unusually sedentary lifestyle that makes them likely to be among the more inactive species in a community. Thus, we hypothesized that Neotropical spotted antbirds show reduced rates of energy turnover and low activity in the wild. Combined measurements of nighttime RMR and DEE of, for example, small free-living tropical songbirds are rare (Ricklefs et al. 1996; Tieleman et al. 2006).

Several studies have shown that heart rate is a useful indicator of energy expenditure in free-ranging animals and perhaps as accurate as the doubly labeled water (DLW) method (Nolet et al. 1992; Bevan et al. 1995; Shaffer et al. 2001; Butler et al.

2004; Cooke et al. 2004; Cochran and Wikelski 2005; Bowlin and Wikelski 2008). Heart rate allows for the prediction of oxygen consumption and thus energy expenditure via Fick's equation (Bevan et al. 1994; Green et al. 2001; Butler et al. 2004). However, calibration experiments are needed to determine the exact relationship between the two variables. Heart rate studies have generally been conducted on large vertebrates because of the previous lack of techniques to monitor heart rate in small animals (Bevan et al. 1995; Shaffer et al. 2001; Green et al. 2002; Cooke et al. 2004).

Our study had three main aims: (i) to test whether captive spotted antbirds are able to reduce body temperature to save energy, (ii) to estimate the nighttime RMR and DEE of free-living spotted antbirds via heart rate telemetry, and (iii) to compare the estimated values of energy expenditure in the wild with general predictions of nighttime RMR and DEE in temperate-zone and arctic birds of similar size.

Material and Methods

Animals and Study Site

Twenty male spotted antbirds were captured in mist nets on Barro Colorado Island, Panama (9°N, 79°W), from March 24 to April 7, 2002, September 18 to October 17, 2002, and March 24 to April 7, 2003. On Barro Colorado Island, the average annual temperature is 27°C (with a diurnal temperature range of 9°C; Dietrich et al. 1982). Birds were attracted to nets with song playbacks broadcast using a tape recorder and loudspeakers (Wikelski et al. 1999). Birds were carried to the laboratory in cloth bags and weighed to the nearest 0.2 g with spring balances. We believe that we monitored only nonbreeding birds, for the following reasons. First, we never observed any courtship feeding or copulation. Second, we never recorded any nest-building behavior. Third, we never monitored incubating birds. Fourth, we never saw any fledglings close to the observed birds.

Respirometry

We measured rates of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) in an open-flow, push-through respirometry system. External, naturally humid air (85%–95% humidity, ~25°C) was pumped through a mass flow controller (TR-FCI, Sable Systems, Las Vegas, NV) and a multiplexer (V2-0, Sable Systems) into the metabolic and reference chambers. Flow rate was 1,000 mL/min, and the flow controller was calibrated before use via a bubble meter. A factory calibration after use indicated that flow rate errors were less then 1.2%. Air leaving the chambers was dehumidified using a Peltier-Effect Condenser (PC-1; Sable Systems), and CO_2 concentration was measured from a subsample of the outlet flow (CA-1B, Sable Systems). Before $\dot{V}_{O_2}$ was determined (FC-1B, Sable Systems), Drierite was used to scrub potential remaining water from the air. The respirometry system was tested for leaks. No loss of air was observed.

We estimated instantaneous oxygen consumption from the equation of Bartholomew et al. (1981):

$$FE_{O_2}(eq) = FE_{O_2}(t-1) + \left[\frac{FE_{O_2}(t) - FE_{O_2}(t-1)}{1 - e^{(-\dot{V}/V)\Delta t}}\right],$$

where FE_{O_2} is the oxygen concentration in the excurrent air, $FE_{O_2}(eq)$ is the equilibrium value, V is the volume of the system including tubing, $\dot{V}$ is the flow rate through the system, and Δt is the interval between measurements at times t and $t-1$. We determined the denominator of this equation (the so-called Z value) empirically using Datacan (Sable Systems). We then calculated the rate of oxygen consumption with equation (3b) of Withers (1977):

$$\dot{V}_{O_2} = \dot{V}\left[\frac{(FI_{O_2} - FE_{O_2}) - \dot{V}_{CO_2} \times FI_{O_2}}{1 - FI_{O_2}}\right],$$

where FI_{O_2} is the incurrent oxygen concentration. We also determined the respiratory quotient (RQ)—the ratio of CO_2 produced to O_2 consumed—and used it to calculate thermal equivalents and metabolic rate (in kJ/d, following Walsberg and Hoffman 2005).

Influence of Ambient Temperature on Oxygen Consumption and Body Temperature

To determine the relationship between ambient temperature, metabolic rate, and body temperature, we measured the oxygen consumption of eight males in 1-L chambers for 4 h after 2100 hours (i.e., starting 3 h after sunset) between March 24 and April 7, 2002. Birds were fed ad lib. during the day. At sunset (~1800 hours), the food was removed from the cage. Thermocouples in the respirometry chamber and thermocouples inserted deep (~1 cm) into the birds' cloacae and superglued to cloacal feathers (Ricklefs and Williams 2003) allowed for continuous readings of ambient and body temperatures, respectively. We used the "up-down" and "down-up" temperature protocol developed by Ricklefs and Williams (2003). In short, birds were introduced into the chamber at an ambient temperature of 29°C and allowed to settle for 1 h. Then we determined the lowest 3-min average $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ during the following 30 min. Subsequently, we either slowly decreased (down to 14°C) or increased (up to 36°C) the ambient temperature in random sequence. Each up-down or down-up temperature protocol lasted for 3 h. During this protocol, we averaged values of oxygen consumption for windows of 3 min whenever ambient temperatures in the chambers had changed by 2°C (Fig. 1).

Calibration of Heart Rate versus Oxygen Consumption

The relationships between energy expenditure and heart rate were determined between March 24 and April 9, 2003, in six males. Birds with heart rate transmitters (for attachment of heart rate
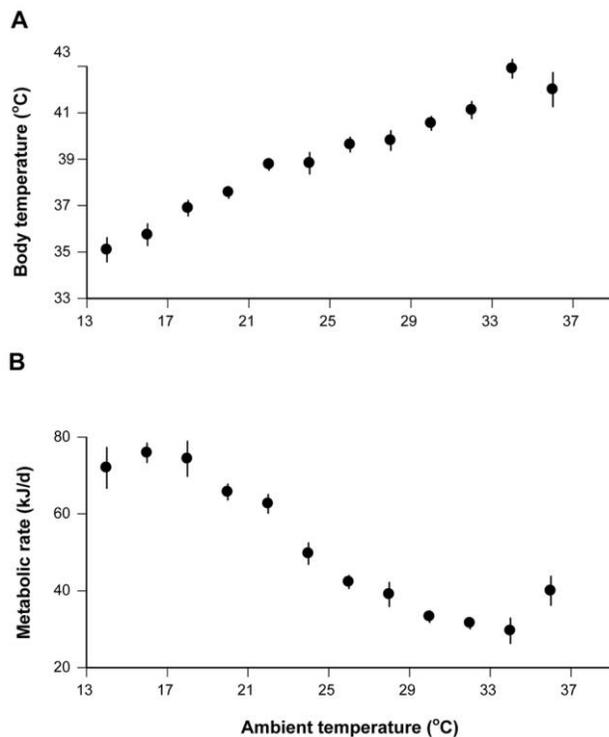
Figure 1. Relationship between ambient temperature and body temperature (*A*) and metabolic rate (*B*) as determined in laboratory respirometry trials. Data show means $\pm$ SE for eight male spotted antbirds. Note that body temperature decreases linearly with ambient temperature even within the ambient temperature range where energy expenditure is minimal (30°–34°C).

transmitters, see below) were placed in 7-L plastic metabolic chambers, and heart rate, $\dot{V}O_2$, and $\dot{V}CO_2$ were measured continuously for a period of 38.8 ± 5.6 h (mean $\pm$ SE) at an ambient temperature of $25.5° \pm 2°C$ (mean $\pm$ SD). Birds could move and hop freely and had mealworms and water ad lib. In order not to add unnecessary stress during these measurements, we did not use a smaller metabolic chamber and a higher flow rate (M. Wikelski, unpublished data). To account for the washout time for the chamber and for analyzer responses, instantaneous oxygen consumption was calculated as described above after adjusting flow rate for the amount of water due to humidity (LabAnalyst X, Riverside, CA; Withers 2001).

Heart rate was recorded as a sound file in a laptop computer. After measurements, the transmitters were removed and birds were weighed and then released at their original capture sites. $\dot{V}O_2$ and heart rate data were obtained from each bird for nine random time points, when $\dot{V}CO_2$ was stable (± 1 mL/h) for on average 121 ± 69 s (mean $\pm$ SD; range: 37–375 s). For one spotted antbird we obtained only four time points. Instantaneous oxygen consumption and heart rate were averaged over these periods.

Heart Rate Transmitter and Attachment

We used newly developed ~1-g heart rate transmitters (0.2 cm × 0.7 cm × 0.3 cm; SP2000 HR, Sparrow Systems, Fisher,

IL) that emitted a continuous signal amplitude (AM) that was frequency modulated by heart muscle potentials (FM; for detailed technical information, see Cochran and Wikelski 2005). Transmitters had a 9-cm flexible wire antenna that was 0.2 mm in diameter. Transmitters had a reception range of at least 100 m even in dense tropical forest. In short, birds were anesthetized with a mixture of Isoflurane (Abbott Laboratories, North Chicago, IL) and air. A patch of approximately 2 cm^2 of back body plumage close to the birds' center of gravity was cut to the feather stumps (following Raim 1978). The heart rate transmitter was glued to a <2-cm^2 cloth. The cloth was then glued onto the feather stumps on the back of the bird with eyelash adhesive. Two wire electrodes were placed under the skin (for a detailed description of the attachment procedure, see Cochran and Wikelski 2005). Birds were released within 1 h, and we could not detect an apparent change in the behavior of radio-tagged birds: they foraged, defended their territory, and continued to interact socially after their release.

We are aware that despite their small size, the heart rate transmitters are somewhat heavy (~5% body mass) for spotted antbirds. To quantitatively assess potential behavioral differences in birds fitted with transmitters, we observed the prey capture rate in each of six spotted antbirds with and without regular transmitters at an army ant swarm for a total of 2 h each. We observed the focal bird (with transmitter) for 2 min continuously and then immediately switched observations to a nonmanipulated conspecific for the same amount of time, treating these observations statistically as a matched pair. We could not detect differences in the number of prey items captured (Wilcoxon test, $N = 6$, $P = 0.4$) or in the total number of moves (Wilcoxon test, $N = 6$, $P = 0.65$). Note, however, that the transmitters could potentially also affect flight dynamics. Furthermore, feather clipping for transmitter attachment may affect conductance, but at present we are unable to quantify these effects in the wild.

Heart Rate Telemetry and Analysis of Field Energy Expenditure

The heart rates of six free-ranging birds were recorded for at least 24 h continuously during fieldwork conducted between September 18 and October 19, 2002. Average ambient temperature during day and night was $27.2° \pm 0.11°C$ (minimum: 23°C; maximum: 32.4°C) and $24.4° \pm 0.04°C$ (minimum: 22.3°C; maximum: 26.6°C), respectively. A receiver (AR8200, AOR, Tokyo) was used to recover the continuous transmitter signal. The transmitted acoustic signal was recorded on a minidisc (MZ-S1, Sony) and later transferred to a computer and analyzed with Cool Edit 2000 software (Syntrillium Software, Phoenix, AZ; as described in Cochran and Wikelski 2005). Every 5 min throughout 24 h we determined instantaneous heart rate from an average of 10 beats. We obtained, on average, 243 ± 13 measurements per day per bird in a 24-h period (of 288 possible; Table 1). In addition, for one bird, every heartbeat was counted throughout 24 h, and these values were averaged per minute. These results were only 1.94% different from the 5-min average values of the same bird.

Table 1: Identification number (ID), mass, number of counted 5-min blocks, mean heart rates (day, night, 24-h period), and estimated daily energy expenditure (DEE) with 95% confidence intervals (CI) obtained for six male spotted antbirds on Barro Colorado Island, Panama

ID	Mass (g)	5-min Block (N)	Heart Rate (beats/min ± SE)			DEE (kJ/d)		
			Day	Night	24-h Period	Estimate	Lower 95% CI	Upper 95% CI
1	18.25	277	515.7 ± 8.5	322.0 ± 4.0	418.8 ± 7.5	28.34	23.73	32.99
2	18.10	196	642.3 ± 6.6	367.8 ± 4.9	488.3 ± 10.5	35.16	30.52	39.80
3	16.50	233	571.9 ± 7.9	423.8 ± 4.6	489.3 ± 6.5	41.25	36.62	45.88
4	17.50	253	614.1 ± 4.8	380.1 ± 5.8	496.7 ± 8.3	38.16	32.17	42.78
5	18.25	219	579.0 ± 5.1	395.4 ± 5.6	512.8 ± 7.1	36.80	32.16	41.44
6	17.00	277	685.4 ± 6.3	416.0 ± 5.6	545.4 ± 9.1	44.42	39.80	49.05
Mean	17.60	242.5	601.4 ± 24.2	384.2 ± 15.1	491.9 ± 11.6	37.36	32.73	41.98

We observed locomotor activity continuously, either directly, when the bird was in sight, or indirectly, via a clearly audible sudden increase of heart rate that occurred only when a flight or hop was performed. We visually confirmed that locomotor movements and sudden increases in heart rate always coincided in time. Minor locomotor movements were not analyzed (e.g., preening, bathing, posture changes related to stationary foraging). One-minute periods were analyzed to quantify locomotor activity.

We used heart rate data to estimate each bird's metabolic rate by applying a multiple-regression equation (including mass) derived from the calibration procedure. The lowest heart rate value measured per night was used to estimate RMR in the field. RMR results were compared with values predicted by Aschoff and Pohl (1970), Bennett and Harvey (1987), Reynolds and Lee (1996), and McKechnie and Wolf (2004). Note that Bennett and Harvey (1987) and McKechnie and Wolf (2004) included only data that met the criteria for basal metabolic rate. We estimated DEE by calculating energy expenditure from instantaneous heart rate measurements and averaged those values over 24 h. DEE results were compared with values predicted for small birds (Nagy et al. 1999).

Statistical Analysis

It should be noted that, as for the DLW method, large individual errors might arise when the heart rate method is used (Butler et al. 2004). Thus, averaging larger sample sizes will be more informative, and that is a procedure we follow here. Data were analyzed with SPSS (ver. 14.0, SPSS, Chicago). Two-tailed tests were used, and results are presented as means ± 1 SE, unless otherwise stated. We used least squares regressions to determine the relationship between heart rate and metabolic rate and ANCOVA to test whether slopes and intercepts were significantly different between individuals. Slopes were not different, but intercepts were; thus, we included the intercept as a random effect (Green et al. 2001) in a linear mixed model. For the final model, we included mass as a covariate. We separated daytime from nighttime as the period between the first locomotor activity in the morning and the last locomotor activity in the evening.

Ethical Note

This study was approved by the Princeton Institutional Animal Care and Use Committee (protocol 1428). The treatment of the animals adheres to the American Ornithologists' Union recommendations for the use of wild animals in research.

Results

Relationship among Ambient Temperature, Metabolic Rate, and Body Temperature

Birds in the respirometry chambers had high body temperatures (~40°C) at ambient temperatures of 30°C (Fig. 1). Although individuals increased their metabolic rate at decreasing ambient temperatures below 30°C, their body temperatures steadily decreased, suggesting that spotted antbirds have limited ability to cope physiologically with cold. The decrease in body temperature and increase in metabolic rate at low temperatures may also indicate poor insulation in spotted antbirds. A similar pattern has been observed in the tropical variable seedeater (*Sporophila aurita*; Weathers 1997). Below an ambient temperature of ~18°C, birds did not increase energy expenditure any longer; thus, trials were stopped at ambient temperatures of ~14°C. Birds also increased body temperatures when warmed toward higher ambient temperatures. Above an ambient temperature of ~34°C, individuals increased energy expenditure again, which appeared to stabilize body temperature at ~42°C. Ambient temperature was not increased beyond 36°C to avoid undue stress on the birds. It appears that the spotted antbirds had only a very narrow thermoneutral zone (TNZ) where energy expenditure was stable at changing temperatures (ambient temperature range from approximately 30° to 34°C).

Relationship between Metabolic Rate and Heart Rate

The mean mass of birds used for calibration was 16.6 ± 0.6 g before and 16.0 ± 0.3 g after calibration (Table 2; $t = 1.0$, $P = 0.3$). The mean mass of birds used for heart rate telemetry was 17.6 ± 0.3 g. On average, the RQ was 0.69 ± 0.01. Note that although the RQ usually is expected to be between 0.7 and 1, there is evidence for values beyond that range in several bird

Table 2: Individual regression equation variables for metabolic rates against heart rate for six male spotted antbirds from Barro Colorado Island, Panama

ID[a]	Mass (g)	N[b]	a[c]	b[d]	r^2	P
			Variable			
1	14.75	4	−29.18	.26	.80	.106
2	17.00	9	6.62	.15	.65	.009
3	18.25	9	−13.48	.19	.76	.002
4	17.00	9	.45	.14	.54	.025
5	17.50	9	−28.54	.22	.78	.002
6	15.25	9	−19.67	.28	.81	<.001

[a] Bird identification number.
[b] Data points in each group.
[c] Intercept.
[d] Slope.

species (Nolet et al. 1992; Walsberg and Wolf 1995; Hawkins et al. 2000). The maximum values for heart rate and $\dot{V}o_2$ were 695 beats/min and 125 mL/h, respectively. A significant linear relationship between heart rate and metabolic rate was found for every bird ($0.54 < r^2 < 0.81$; Fig. 2; Table 2). The regression slopes were not significantly different among birds, but the intercepts were (ANCOVA: $F_{5, 42} = 7.7$, $P < 0.001$). Thus, following Green et al. (2001), we adopted a random-effect model and included the intercept as a random factor and the slope as a fixed effect. We derived the following equation:

$$\text{MR} = 0.09f_{\text{H}} - 4.04,$$

where MR is metabolic rate in kJ/d and f_{H} is heart rate in beats per minute. After mass was included, we obtained the following relationship:

$$\text{MR} = 59.07 + 0.09f_{\text{H}} - 3.749m,$$

where m is mass in grams. Using equation (11) from Green et al. (2001), we calculated the SE of the estimated MR (Table 1). The error associated with the variation between spotted antbirds (d^2) was 13.25; the error associated with the scatter around the regression lines (e^2) was 35.22.

Heart Rates of Free-Living Birds

During the day, heart rate was 36% higher and was also more variable than nocturnal heart rate (Fig. 3). A sharp increase in heart rate was detected from 0500 to 0700 hours, and a sharp decrease in heart rate was detected from 1700 to 1800 hours (Fig. 3). Heart rate started to increase in the early morning before the birds started to be active. The average nocturnal heart rate was 384.2 ± 15.1 beats/min, and the average diurnal heart rate was 601.4 ± 24 beats/min (Table 1). The mean daily heart rate (24 h) was 491.9 ± 11.6 beats/min. The maximum recorded heart rate, recorded during the day, was 824 beats/min, which was 3.2 times as high as the lowest observed value, recorded at night, of 260 beats/min. Notably, 96.2% of the heart

rates monitored in free-living spotted antbirds were within the range of heart rates measured during calibration. The heart rate frequency distribution was bimodal, with peaks occurring at 650 beats/min and at 400 beats/min; day ($N = 730$) and night values ($N = 725$) partially overlapped (Fig. 4A).

Locomotor Activity

Locomotor activity started, on average, 16.3 ± 2.3 min before official sunrise (which was at 0542–0550 hours) and ended 9.3 ± 5.7 min after official sunset (which was at 1748–1757 hours). When active, spotted antbirds mostly hopped and never flew for more than ca. 20 m at any one time, thus, flying and hopping were combined into one measure of locomotor activity (moves/min). Note that the average movement rate is an average of the locomotor activity of only the active period (from ~0550 until ~1750 hours; see above). Locomotor activity was not normally distributed but highly skewed (Fig. 4B). During approximately 35% of the day, spotted antbirds were not locomotively active (no moves per minute; Fig. 4B). Diurnal locomotor activity was consistently low and stable throughout the day. On average, spotted antbirds moved 1.6 ± 0.04 times/min throughout the day.

Oxygen Consumption and Metabolic Rate of Wild Birds

The calculated nighttime RMR for all six free-living birds was 20.1 ± 1.9 kJ/d. Compared with the nighttime RMR predicted by Aschoff and Pohl (1970) and Reynolds and Lee (1996), our value for wild spotted antbirds was 21.3% (Fig. 5A; $t = 2.9$, $P < 0.05$) and 22.9% (Fig. 5A; $t = 3.16$, $P = 0.01$) lower than expected, respectively. However, compared with values predicted by Bennett and Harvey (1987) and McKechnie and Wolf (2004), observed RMRs for wild spotted antbirds were 30.2% (Fig. 5A; $t = -2.5$, $P < 0.05$) and 27.2% (Fig. 5A; $t = -2.3$, $P < 0.05$) higher, respectively. Note that these studies predicted metabolic rate for captive, postabsorptive animals in a thermoneutral environment, whereas our wild study birds most
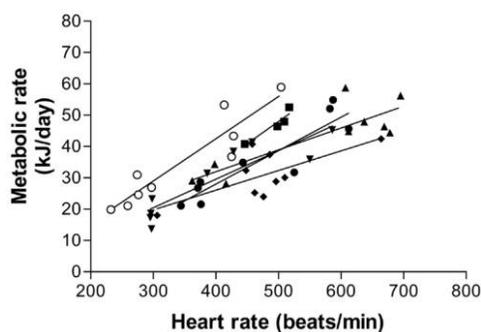

Figure 2. Linear relationships between heart rate (beats/min) and metabolic rate (kJ/d) for six male spotted antbirds (SPAN) from Barro Colorado Island, Panama: SPAN 1 (*squares*), SPAN 2 (*triangles*), SPAN 3 (*inverted triangles*), SPAN 4 (*diamonds*), SPAN 5 (*filled circles*) and SPAN 6 (*open circles*). The slopes are not significantly different, but the intercepts are.
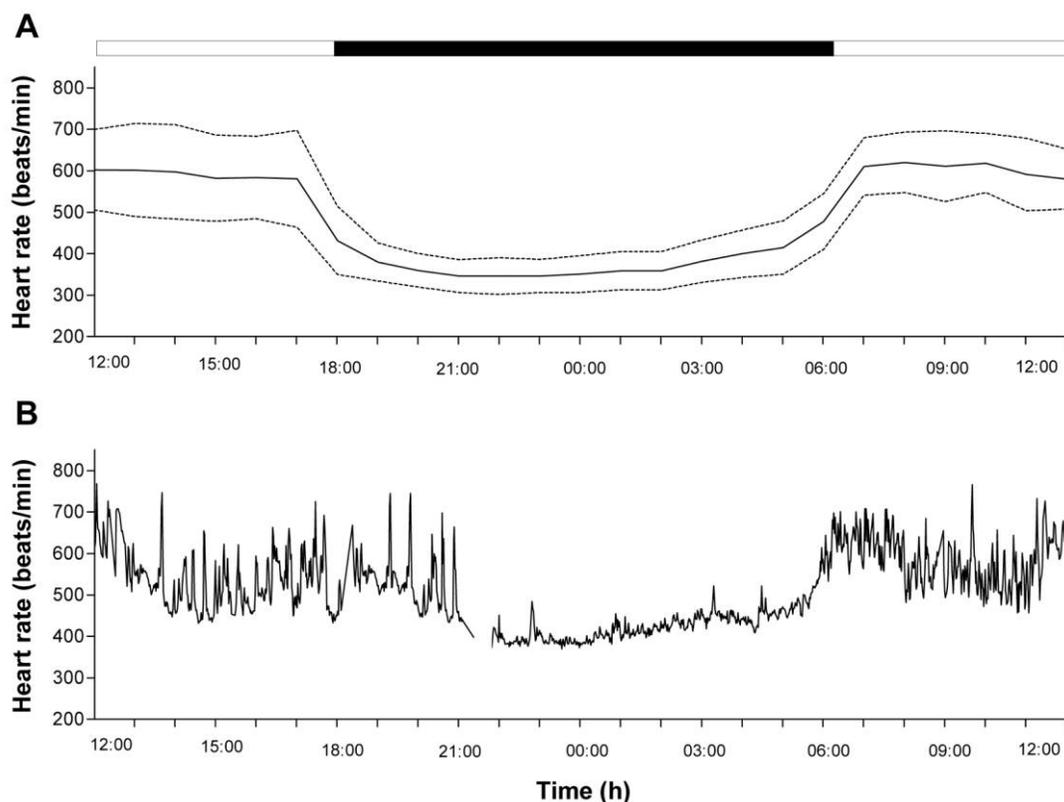
Figure 3. Daily heart rate patterns (beats/min). The black bar at the top indicates nighttime (inactive period), and the white bars indicate daytime. *A*, Mean hourly heart rates of six spotted antbirds. The solid line represents the hourly mean and the dashed lines ± 1 SD. *B*, Second-by-second heart rate analysis conducted for spotted antbird 3. Heart rate was measured every second, and measurements were averaged every minute ($N = 1,317$).

likely did not experience thermoneutral conditions. Moreover, the birds in the wild may have been feeding. Thus, our values might be an overestimate of nighttime RMR, and therefore it is not surprising that our nighttime RMR values are higher than values predicted by Bennett and Harvey (1987) and McKechnie and Wolf (2004). DEE was 37.36 ± 2.3 kJ/d. When we compared our estimate of DEE with Nagy's allometric equation (Nagy et al. 1999) for temperate-forest/small birds, spotted antbirds exhibited only 51% of the expected value (Fig. 5*B*; $t = 15.1$; $P < 0.001$).

Discussion

Using heart rate telemetry, we measured both the nighttime RMR and the DEE of a small tropical passerine living in the rain forest understory. Before this study, the DEE of free-living tropical rain forest passerines had not been measured, perhaps because of the difficulty of recapturing such birds after a 24-h period, making DLW measurements hard to conduct in the rain forest (Speakman 1998).

Our data show that the DEE is low in the wild compared with expected values for birds of this size. Low overall energy expenditure was mainly achieved in two ways. First, spotted antbirds had a very low locomotor activity during the day, compared with temperate-zone birds (M. Wikelski, K. S. Shel-

don, and R. E. Ricklefs, unpublished manuscript). On average, spotted antbirds moved only 1.6 times/min and either hopped or flew only short distances. We cannot exclude that we missed some long flights (>20 m). However, our observation that spotted antbirds mostly hopped and never flew for more than 20 m at any one time is consistent with a previous study (Willis 1972). Spotted antbirds are facultative ant followers and take only ~50% of their food at ant swarms (Willis 1972; M. Wikelski, behavioral observation). Thus, they exhibit short flights even if they are not roosting right over the bivouacs. Flight has been suggested to be one of the most expensive avian activities (Butler 1991); therefore, a low locomotor activity could be a way to save large amounts of energy. Measures of locomotor activity of free-living birds have not been standardized yet; thus, it is difficult to directly compare our estimate with those from other studies.

Second, spotted antbirds sleeping in the wild at ~25°C (~5°–9°C below the TNZ) kept their nocturnal energy expenditure at levels similar to that of birds in the laboratory measured under thermoneutral conditions (~30°–34°C ambient temperature). How is this achieved? As inferred from laboratory respirometry trials, rest-phase thermoregulation in spotted antbirds was not consistent with typical avian patterns, that is, the maintenance of an approximately constant body temperature
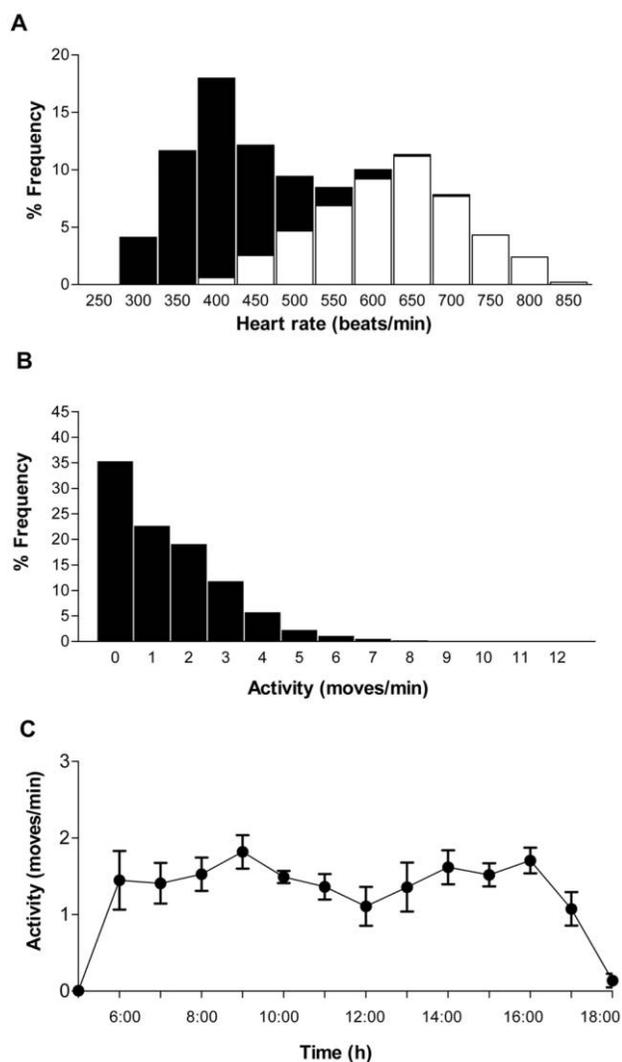
of bird species, such as the 6-g Puerto Rican tody (Merola-Zwartjes and Ligon 2000), pigeons (Schleucher 2001), nightjars and nighthawks (McNab and Bonaccorso 1995), mousebirds (McKechnie et al. 2004), and white-throated sparrows (Dolby et al. 2004). However, while most studies only infer lowered metabolic activity from body temperature data, here we estimate it via Fick's equation from heart rate. Because the nutritional state of a bird is inversely correlated with the depth of nocturnal hypothermia (Reinertsen and Haftorn 1984), it is important to note that the captive experimental birds in this study were fed ad lib. and thus that the decrease of body tem-
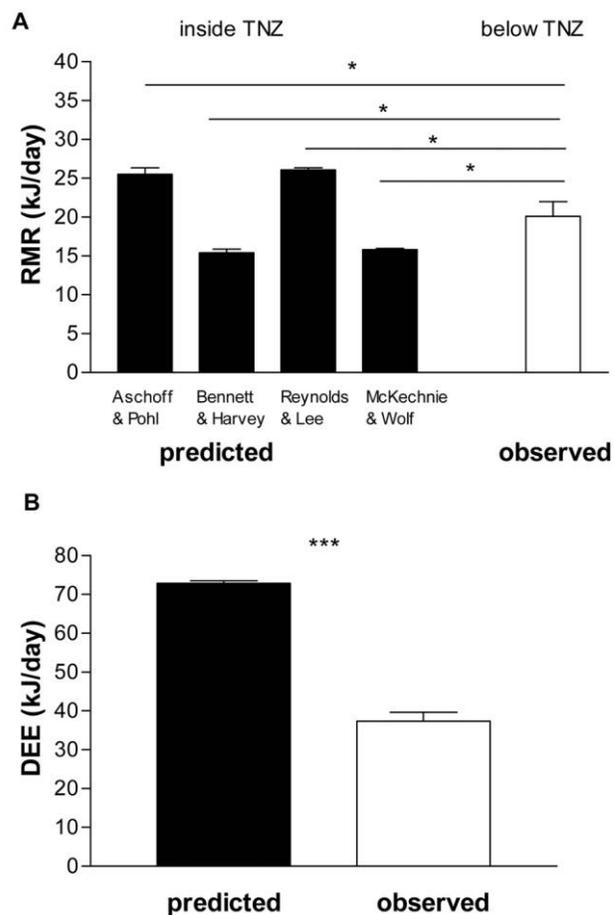

Figure 4. *A*, Bimodal frequency distribution of heart rate (beats/min) for six male spotted antbirds from Barro Colorado Island, Panama. Black bars represent heart rates measured at night ($N = 725$), and white bars indicate heart rate measured during the day ($N = 730$). Heart rate peaks occur at 400 and 650 beats/min. *B*, Frequency distribution of locomotor activity (hops and flights termed "moves") during the day (moves/min) for six male spotted antbirds from Barro Colorado Island. Data are highly right skewed, indicating generally low activity rates of wild spotted antbirds. *C*, Daily locomotor activity pattern (moves/min) for six male spotted antbirds from Barro Colorado Island. Data are hourly means $\pm$ 1 SE.

over a wide range of ambient temperatures (Blem 2000). Instead, spotted antbirds were able to markedly decrease their body temperature (Fig. 1). A decrease in body temperature reduces the difference between ambient temperature and body temperature and thus decreases the rate of heat loss. Hence, the demand for metabolic heat production decreases (Merola-Zwartjes and Ligon 2000). We suggest that spotted antbirds use this strategy to lower metabolic rate at night. Similar instances of low body temperature (Bartholomew et al. 1983) or even torpor (sensu Geiser and Ruf 1995) have been found in a variety

Figure 5. Predicted (*black bars*) and observed (via heart rate telemetry, *white bars*) resting metabolic rate (nighttime RMR, in kJ/d) $\pm$ 1 SE (*A*) and daily energy expenditure (DEE, in kJ/d) $\pm$ 1 SE (*B*) for six male spotted antbirds. *A*, Predicted nighttime RMR values are from (i) the equation of Aschoff and Pohl (1970) for rest-phase passerines: $\log \text{BMR (kcal/h)} = \log 0.0317 + 0.726 \log m$, where m = mass in grams; (ii) the equation of Bennett and Harvey (1987): $\log \text{RMR (kcal/d)} = 0.67 \log m - 0.25$; (iii) the phylogenetically corrected least squares regression of Reynolds and Lee (1996): $\log \text{BMR (W)} = -1.311 + 0.635 \log m$; and (iv) the equation of McKechnie and Wolf (2004): $\log \text{BMR (W)} = -1.461 + 0.669 \log m$. Horizontal bars represent pairwise comparisons between predicted and observed values; asterisk indicates $P < 0.05$. *B*, Predicted DEE values are from the equation of Nagy et al. (1999) for small/temperate- forest birds: DEE $(\text{kJ/d}) = 15.94 m^{0.53}$, where m = mass in grams. Three asterisks indicate $P < 0.001$.

perature was not caused by limited food supply. Therefore, as mentioned above, we hypothesize that the reduction of body temperature in spotted antbirds reflects a metabolic strategy for nocturnal energy saving. Two nonexclusive alternative explanations could account for the fact that estimated nighttime RMR in the field was below that measured for birds in a respirometer and within their TNZ. First, stress is expected to increase metabolic rates (Wingfield and Farner 1993). Thus, it is conceivable that birds in the laboratory did not completely settle in the respirometer. Second, measurement noise in the calibration (linear regression) between the metabolic rate and heart rate could have contributed to this result.

We conducted calibration experiments to determine the exact relationship between heart rate and oxygen consumption at a single ambient temperature. However, it has been shown that body temperature can affect the intercept of the relationship between oxygen consumption and heart rate (Butler et al. 2002). For example, in marine iguanas *Amblyrhynchus cristatus*, oxygen consumption was higher for a given level of heart rate as body temperature declined (Butler et al. 2002). Because the body temperature of free-living spotted antbirds may not have been constant, it is possible that the same effect may have occurred here. Because we did not measure heart rate in the birds for which we determined the relationship between ambient temperature, metabolic rate, and body temperature (Fig. 1), we were not able to adjust for this effect. Thus, we cannot exclude that RMR and DEE may have been underestimated. Ideally, the calibration of heart rate versus oxygen consumption should have been repeated at different ambient temperatures.

Nevertheless, spotted antbirds have life-history traits indicative of a slow pace of life (e.g., relatively long life spans, high annual survival rates, production of few offspring, slow development of offspring), similar to what has been observed in birds of paradise and other tropical bird groups (see Willis 1972, 1983; Brawn et al. 1995; Hau et al. 2000; Stutchbury and Morton 2001). Consistent with their slow pace of life, the metabolic rates—both nighttime RMR and DEE—of spotted antbirds are low. Because the decline in DEE is much higher than the decline in nighttime RMR, our data suggest that the low energy expenditure is predominantly caused by the decline in activity. Our data support and extend previous studies suggesting that life-history traits covary with the rate of energy expenditure. Future studies could investigate whether the low activity rates and low DEE are characteristic of this South American lineage of birds (antbirds; family Thamnophilidae).

Acknowledgments

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