

NOCTURNAL HYPOTHERMIA AND OXYGEN CONSUMPTION IN MANAKINS

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ABSTRACT.—Red-capped Manakins (*Pipra mentalis*) and Golden-collared Manakins (*Manacus vitellinus*), two species of small, frugivorous, tropical passerines, showed facultative hypothermia and reduced oxygen consumption at night. The lowest body temperature measured in *M. vitellinus* (30.5°C, when the ambient temperature was 19.5°C) represents a reduction of more than 40% in the difference between body temperature and ambient temperature. Under these circumstances, a reduction of more than 40% in the rate of oxygen consumption would also occur during the period of regulated hypothermia. Even moderate hypothermia at ambient temperatures typical of the lowland tropics substantially reduces the energy expenditure of a resting bird.

Hypothermia (lowered body temperature) has been regarded as an adaptive response by an organism to varying combinations of environmental and internal conditions that cause energy shortages either on a daily or a seasonal basis. Such factors include (1) small size because of the high mass-specific metabolism associated with it and the inability of small organisms to carry large energy reserves either as fat or in the gut, (2) insectivory or nectarivory and associated extreme fluctuations in the availability of food and/or rapid passage of food through the gut, (3) low ambient temperature (T_a), and (4) types of inclement weather that prohibit foraging and/or increase heat loss (see Bartholomew 1972, Hainsworth and Wolf 1978).

Degrees of hypothermia have been documented in at least eight avian orders. In the Caprimulgiformes and in the Apodiformes (Trochilidae), body temperature (T_b) may drop below 20°C and sometimes approach ambient temperature (even T_a 's as low as 7°C). More moderate nightly drops in T_b to between 20 and 30°C have been reported in the Coliiformes, Columbiformes, Apodiformes (Apodidae), and Passeriformes (Nectarinidae). Diurnal cycles in normothermic T_b are well known, however, and it is not yet possible to distinguish clearly between these cycles and the varying degrees of nocturnal hypothermia (T_b 's as low as 30°C) reported in Cuculiformes, Falconiformes, Strigiformes, and the passerine families Nectariniidae, Hirundinidae, Paridae, Ploceidae, and Fringillidae. (See Dawson and Hudson [1970], Calder and King [1974], Chaplin [1976], and Biebach [1977].)

In lowland tropical environments, ambient air temperatures rarely drop more than

15–20°C below the T_b of normothermic birds. Since the rate of heat production in endotherms is proportional to the difference between T_b and T_a , a decrease of 8–10°C in regulated T_b would decrease this difference by half and would yield an energy savings of about 50% during the period of hypothermia. Such fluctuations in T_b have been reported in the Smooth-billed Ani (*Crotophaga ani*) in Panama (Warren 1960) and several Brazilian hummingbirds (Morrison 1962).

We document here similar low nocturnal T_b 's in two species of small, tropical passerines, the Red-capped Manakin (*Pipra mentalis*) and the Golden-collared Manakin (*Manacus vitellinus*). These birds are common in the understory of second-growth forests in Panama and are almost entirely frugivorous. Because food passes through their gut very rapidly (in about 18 min), their feeding bouts are brief but frequent throughout the day (Worthington, in press). Thus, manakins are vulnerable to daily and seasonal food shortages (Foster 1977; Worthington, in press). Vleck and Vleck (1979) suggested that manakins may reduce their resting metabolic rate to ameliorate the effects of such energy shortages. Our study was undertaken to examine this possibility, and our data demonstrating hypothermia and associated low metabolic rates support their suggestion.

MATERIALS AND METHODS

Birds were mist-netted on Barro Colorado Island, Panama (9°N, 80°W). Three individuals (1 ♂ and 1 ♀ *P. mentalis*, 1 ♀ *M. vitellinus*) were maintained in captivity for at least one week before we measured their rates of oxygen consumption ($\dot{V}O_2$). On some occasions an individual was fasted from noon until

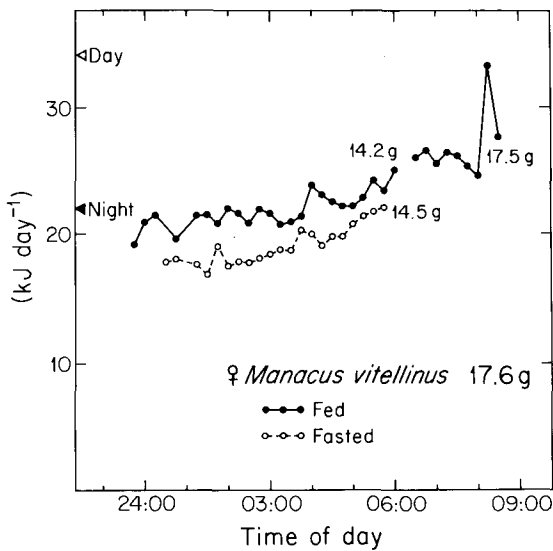


FIGURE 1. Metabolic rate of a resting *M. vitellinus* at $T_a = 26 \pm 1^\circ\text{C}$. Arrowheads on the ordinate indicate predicted levels of metabolism based on the bird's mean mass during experiments performed at night and during the day. The number to the right of the species name is the maximum mass recorded for the bird. Other values in the figure are the mean masses of the bird during each particular experiment.

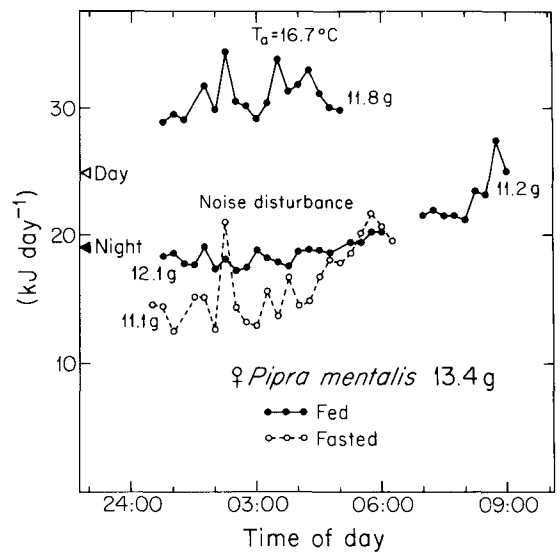


FIGURE 2. Metabolic rate of a resting *P. mentalis* at $T_a = 26 \pm 1^\circ\text{C}$ (lower traces) and at $T_a = 16.7^\circ\text{C}$ (upper trace). Symbols as in Figure 1. The time when an unintentional, loud disturbance occurred in the laboratory is noted.

the beginning of nighttime measurements of $\dot{V}O_2$. To determine $\dot{V}O_2$'s we put the birds in a plexiglass respirometer covered by a dark cloth and insulated by a styrofoam box. Dry, CO_2 -free air was drawn into the chamber, and CO_2 and H_2O vapor were absorbed from air leaving the chamber with Ascarite and Drierite, respectively. Flow rates from 90 to 215 ml min^{-1} were used. Fractional oxygen concentration was determined from air sampled continuously downstream from the flowmeter and passed through an Applied Electrochemistry S3A Oxygen Analyzer. The system was analogous to that described by Withers (1977), and we calculated $\dot{V}O_2$ using his equation 4a.

Before and after each experiment, birds were weighed using a Pesola scale, and T_b was taken cloacally with a thermocouple probe and a Bailey Bat-8 digital thermometer. T_a in the respirometer was measured by a thermocouple thermometer. The chamber within its styrofoam container was in an air-conditioned room, and chamber temperature was determined by room temperature except for one occasion when the chamber was placed in an ice bath and T_a stabilized at approximately 17°C .

T_b and body mass of these three and of other caged and mist-netted individuals were measured on several occasions during the day and in the middle of the night. In order to avoid any possible effects of long-term captivity, we

once netted six individuals (three of each species) at noon and kept them in captivity without food for the remainder of that day and night. We measured T_b and body mass at midnight and at dawn the following day in these freshly-caught and fasted individuals.

RESULTS AND DISCUSSION

At T_a of $26 \pm 1^\circ\text{C}$ minimal nighttime $\dot{V}O_2$ was 77.5–95.0% (*Manacus*, Fig. 1) and 53.5–89.6% (*Pipra*, Figs. 2 and 3) of nighttime rates predicted by the allometric equation of Aschoff and Pohl (1970) for passerine birds within thermal neutrality. Our lowest values were similar to the lowest values reported by Vleck and Vleck (1979) for *M. vitellinus* at $T_a = 30^\circ\text{C}$. However, on the average our values were lower than theirs, probably because our experiments were done in a completely quiet laboratory, whereas birds studied by Vleck and Vleck (1979) may have been subject to some disturbance. Even slight disturbance usually caused an immediate, but transient increase in the $\dot{V}O_2$ (Fig. 2). In three individuals, $\dot{V}O_2$ was measured both when the birds had had access to food all day and when they had been fasted from noon until the experiment began in late afternoon or during the night. In each case the lowest $\dot{V}O_2$'s occurred after the birds had been fasted. We cannot say whether this was a direct response to the fasting or was related to reduced energy stores associated with fasting. It is noteworthy that in the fasted and non-fasted manakins, $\dot{V}O_2$ spontaneously increased to similar

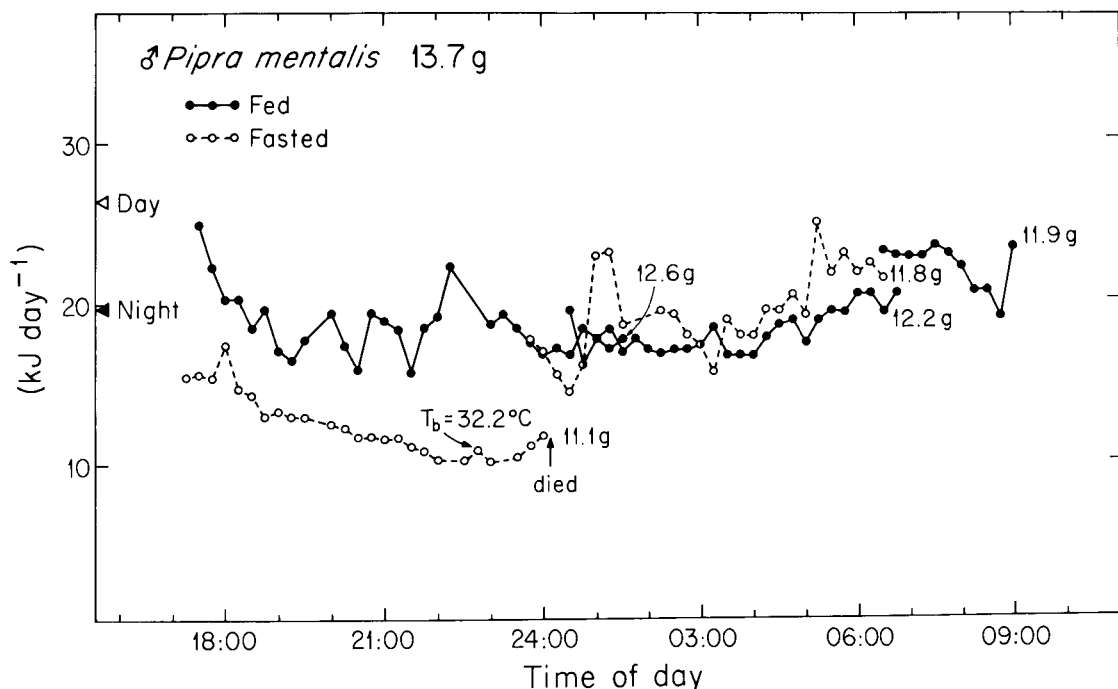


FIGURE 3. Metabolic rate of a resting *P. mentalis* at $T_a = 26 \pm 1^\circ\text{C}$. Symbols as in Figure 1.

daytime levels as dawn approached. In one *Pipra* a lower T_a (16.7°C instead of 26°C) resulted in an increased $\dot{V}O_2$ (Fig. 2), a response typical of homeothermic endotherms. T_b was 37.5°C at the end of this experiment. If this T_b was constant throughout the experiment, the difference between T_b and T_a was increased by about 80%. If one assumes that both 26°C and 16.7°C are below thermal neutrality, then an increase of 80% in $\dot{V}O_2$ would be expected and, in fact, was measured.

The $\dot{V}O_2$ of the one *Pipra* male was measured on two occasions after the individual had been fasted and was substantially lower when the weight of the bird was lower. The individual maintained a low (58% of predicted) but constant $\dot{V}O_2$ for over $3\frac{1}{2}$ h and then it abruptly died (Fig. 3). The bird's immediately recruitable energy reserves may have been depleted; its fat content was a third of that normally found in this species (Worthington, unpubl. data). During the experiment, the manakin was removed from the chamber, a T_b of 32.2°C was recorded and the bird was returned to the chamber. Its eyes were closed, its feet clenched, feathers fluffed, and it was not normally responsive. However, a T_b of 32°C is not necessarily lethal since two other individuals had similar T_b 's at midnight and were normally active the next morning (see Table 1).

Recorded daytime T_b 's ranged from 38.2 to 43.5°C in *Manacus* and from 39.4 to 44.0°C

in *Pipra*. At midnight, T_b 's were quite variable in both species (Table 1). The data are not appropriate for statistical analysis owing to the small sample size and the narrow range of T_a 's at which most measurements of T_b were taken. However, T_a and either the relative weight or the feeding history, or both, appear to affect the T_b that a manakin maintains at night. In both species, T_b was sometimes substantially reduced at night either in birds that were fasted, were exposed to low T_a 's, had a relatively low body mass, or experienced any combination of these factors.

The conditions that appeared to elicit hypothermia in our birds occur naturally and are ecologically realistic. Associated with tropical frugivory in these species are many of the environmental conditions and physiological traits that may result in daily and/or seasonal shortages of food. During the last half of the rainy season in central Panama (Aug.–Dec.), fruit production is low and the foraging effectiveness of manakins drops because the birds are feeding on widely dispersed understory plants with small individual fruit crops. On Barro Colorado Island, most heavy storms, lasting 4 h or more, occur in the afternoons. Manakins do not feed when it rains. The absence of male lek behavior and of females with begging young during this time of year suggests that it is a period of limited food availability (Worthington, in press). Furthermore,

TABLE 1. Body temperature, ambient temperature and body mass of individuals whose midnight T_b was recorded.²

	Maximum measured body mass (g)	Midnight			Morning		
		T_b	T_a (°C)	Mass (g)	T_b	T_a (°C)	Mass (g)
<i>Manacus vitellinus</i>							
♀	15.3	38.6	26.0	14.7	42.2	25.4	14.0
		37.7	26.5	—	—	—	—
♀	16.5	38.0	26.0	15.3	43.2	25.0	14.6
♀ ¹	18.1	38.0	25.5	15.8	40.2	25.5	15.2
♀	17.4	37.8	28.0	—	43.0	29.3	—
		36.5	27.4	—	—	—	—
		30.5	19.5	12.7	—	—	12.3
♀ ¹	17.3	37.2	25.5	15.1	41.8	25.5	14.8
♀ ¹	17.0	36.7	22.5	15.5	40.4	23.7	14.7
<i>Pipra mentalis</i>							
♀	13.8	40.0	26.6	13.3	—	—	—
		37.0	26.0	12.6	—	—	11.5
♀	13.4	38.0	28.0	—	—	—	—
		37.2	26.5	11.5	—	—	11.5
		29.0	16.4	12.4	—	—	—
♀ ¹	14.2	38.0	25.5	12.3	42.8	25.5	—
♂	13.7	37.8	28.0	—	42.2	29.3	—
		32.2	25.0	11.1	died	—	—
♀ ¹	13.1	35.7	25.5	11.3	40.1	25.5	11.3
♀ ¹	13.0	33.4	25.5	11.7	39.4	25.5	11.3
♀	14.1	32.2	21.5	—	—	—	12.4

¹ Individuals caught at noon one day, fasted and released the following morning. Other individuals usually were kept in captivity for several days.

² Morning T_b was measured between 06:00 and 07:00. Individuals for which there are no morning values were normally active except for one individual that died.

on Barro Colorado Island air temperature may drop to or below 15°C at night (Croat 1979).

Under environmental conditions such as these, several traits of manakins increase the likelihood that they may experience energy shortages. These include (1) their relatively small size (Table 2) and associated high mass-specific metabolism and inability to store substantial amounts of fat, (2) the short time required for food to pass through their gut (associated with frugivory) and their inability to store substantial amounts of food in the gut, and (3) the possibility of plumage wetting and concomitant increased rates of heat loss.

Thus, fat storage and food storage, two major mechanisms for energy storage and/or conservation used by birds faced with daily or seasonal restrictions in the availability of food,

TABLE 2. Body mass (g) of wild manakins mist-netted from August 1978 through December 1980. There are no statistically significant seasonal trends in mass.

	Average ^a	Maximum	Minimum
<i>Pipra mentalis</i>			
♂♂ and ♀♀	14.2 ± 1.3 (126)	16.5	12.0
<i>Manacus vitellinus</i>			
♂♂	18.6 ± 1.3 (57)	23.7	16.7
♀♀	16.9 ± 1.7 (78)	20.5	14.7

^a ±SD (n).

are not feasible for manakins. This leaves hypothermia as a possible mechanism for energy conservation in these birds. In free-living hummingbirds, hypothermia has been correlated with reduced feeding opportunity (Calder and Booser 1973). Fasting has been shown to induce nocturnal hypothermia in captive birds of several orders: Coliiformes, Columbiformes, and Caprimulgiformes (MacMillen and Trost 1967, Bartholomew and Trost 1970, Peiponen 1970). African sunbirds exposed to low nocturnal temperatures showed large drops (5–17°C) in T_b at night (Cheke 1971). Therefore, it is not surprising to find similar responses to similar stresses in manakins.

The most salient aspect of hypothermia in manakins is its occurrence in tropical passerine species at T_a 's that are less extreme than those in most other reported instances of avian hypothermia. We emphasize that even at these T_a 's, lowering T_b by the magnitude seen would result in a substantial energy savings for a resting bird. As more physiological studies are done on tropical species, moderate nocturnal hypothermia may prove to occur more commonly than is currently realized.

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