

Basal Metabolic Rate in Tropical Seabirds

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There is evidence that the basal metabolic rates (BMR) of tropical birds are lower than those of birds in higher latitudes (Weathers 1979, Hails 1983). Some species of tropical seabirds appear to have relatively low BMRs, while others do not (MacMillen et al. 1977; Ellis et al. 1982a, b; Ellis 1984). The purpose of our study was to obtain additional data on tropical seabirds. The impetus came from the use of BMRs of tropical seabirds in the estimation of the energy requirements of tropical seabird populations, in which a small error in the BMR of an individual is magnified considerably when multiplied by the number of birds comprising the population (Pettit et al. 1984).

A small field laboratory was established on Tern Island, French Frigate Shoals (23°52'N, 165°18'W) in the Northwestern Hawaiian Islands. The 8 species studied (see Table 1) nest on Tern Island and are present throughout much of the year. Experiments were conducted during August and September 1981 and January, February, and July 1982.

The BMR was determined from the oxygen consumption of resting birds in a darkened metabolic chamber, during the day, at the air temperature prevailing on Tern Island. Birds were captured by hand, encouraged to regurgitate their stomach contents, and held overnight (15–20 h) to achieve a fasting condition.

Oxygen consumption (\dot{V}_{O_2}) was measured by two techniques. In the open-flow technique, ambient air was drawn through a metabolic chamber (volume 38 l or 11 l depending on the size of the bird) with a diaphragm pump. Constant flow rates ranged from 0.9 to 3.0 l/min, as determined with a calibrated Brooks rotometer flow meter, the level of flow depending on the size of the chamber. After the bird was placed in the chamber, the first gas sample was obtained following a 60-min equilibration period. Gas samples, collected in glass syringes lubricated with mineral oil, were analyzed in duplicate by a Scholander micro-gas analyzer. All gas values were converted to STPD. For petrels, an 8-l closed system was employed. Oxygen consumption was measured manometrically after a 45-min equilibration period. Carbon dioxide absorbant (sodasorb) and water-vapor absorbant (silica gel) were placed in the chamber, and a measured volume of oxygen was introduced to maintain the pressure within the chamber at atmospheric pressure. A compensating thermobarometer chamber was not used.

Body temperatures were measured with a telethermometer (Yellow Springs Instruments Co., Model 46TUC) before and after each determination of oxygen consumption by inserting a YSI probe (#402 or #403) into the proventriculus. For small species the body temperature was measured with a Schultheis thermometer inserted 2–3 cm into the cloaca. The average of the two temperatures is reported to reflect the body temperature during the experiment. Body temperatures of birds in the field were measured with the same techniques, within 60 s of capture. The YSI telethermometer and probes were calibrated against a mercury thermometer in a water bath; the Schultheis thermometer agreed with the probes within 0.2°C. The mass of each bird was determined before each measurement of \dot{V}_{O_2} using an Ohaus Dial-O-Gram balance.

The mean O_2 consumption (\dot{V}_{O_2} ; $cm^3 O_2 \cdot g^{-1} \cdot h^{-1}$) for each species is presented in Table 1. The respiratory quotient (RQ) ranged from 0.69 to 0.76 and air temperatures from 28.4°C to 29.5°C. In general, the body temperatures of birds in the laboratory were higher than those measured in the field (Table 2), and the body temperatures of procellariiform birds were the lowest.

It is presumed that the air temperatures at which the measurements were made were within the thermoneutral zone, a necessary condition for the measurement of the BMR. This is a safe assumption for the larger species and, as shivering was not observed to occur in the smaller species, it may provisionally be taken to be true for all the species studied. The respiratory quotient suggested that fat was the principal metabolic substrate. For this reason, the values for oxygen consumption were converted to heat units using a factor of 19.79 kJ/l O_2 (Table 1). Because the activity patterns of the birds were not known with any certainty, we compared the measured values with the predictions of Lasiewski and Dawson (1967) for nonpasserine birds, rather than those of Aschoff and Pohl (1970).

The BMR of 6 of the 8 species included in Table 1 was lower than predicted. However, the measured values of only 4 species (Bonin Petrel, Bulwer's Petrel, Gray-backed Tern, and Red-tailed Tropicbird) were outside the limits set by Lasiewski and Dawson's (1967) equation:

$$\log \text{BMR} = \log 78.3 + 0.723 \log M \pm 0.068,$$

where M = body mass. It has been reported elsewhere, that 4 other tropical seabirds [Magnificent Frigatebird (*Fregata magnificens*), Sooty Tern (*Sterna fuscata*), Brown Noddy (*Anous stolidus*), and Laysan

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TABLE 1. Body mass (M), oxygen consumption (\dot{V}_{O_2}), air temperature (T_a), and basal metabolic rates (BMR) of Hawaiian seabirds. The values are means \pm 1 SD; numbers of birds are in parentheses.

Species	M (g)	T_a ($^{\circ}$ C)	\dot{V}_{O_2} ($\text{cm}^3 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$)	Measured (kJ/day)	Predicted ^a (kJ/day)
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	337.8 \pm 4.0 (4)	28.9 \pm 0.1	0.80 \pm 0.01	128.4	149.4
Christmas Shearwater (<i>P. nativitatis</i>)	307.6 \pm 4.1 (6)	28.4 \pm 0.1	0.87 \pm 0.02	127.2	139.7
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	167.4 \pm 15.3 (7)	24.7 \pm 0.7	0.91 \pm 0.11	72.4	90.0
Bulwer's Petrel (<i>Bulweria bulwerii</i>)	87.0 \pm 7.8 (6)	28.7 \pm 0.2	1.06 \pm 0.04	43.9	56.1
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	593.2 \pm 7.5 (5)	29.5 \pm 0.1	1.02 \pm 0.03	287.4	224.7
Gray-backed Tern (<i>Sterna lunata</i>)	131.7 \pm 1.4 (2)	29.1 \pm 0.4	0.97 \pm 0.06	60.7	75.7
White Tern (<i>Gygis alba</i>)	98.1 \pm 1.0 (6)	29.1 \pm 0.1	1.51 \pm 0.04	70.3	61.1
Black Noddy (<i>Anous minutus</i>)	90.2 \pm 1.3 (4)	28.8 \pm 0.3	1.28 \pm 0.02	54.8	57.7

^a Lasiewski and Dawson (1967).

Albatross (*Diomedea immutabilis*) have relatively low basal metabolic rates (Enger 1957, MacMillen et al. 1977, Ellis et al. 1982a, Grant and Whittow 1983). The metabolic rates of Sooty Terns studied by Ricklefs and White (1981) were higher than the predicted values, but it is possible that the conditions in their determinations did not meet the prerequisite of measuring basal metabolic rate. In the Red-tailed Tropicbird (Table 1), the Red-footed Booby (*Sula sula*, Ellis et al. 1982b), and the Masked Booby (*Sula dactylatra*, Ellis 1984), all members of the Pelecaniformes, the BMR is higher than predicted values.

Among the tropical terns and noddies, only the

White Tern had a higher BMR than predictions based on body mass. This species also had the highest body temperature (Table 2). The BMR of the Bonin Petrel, as determined in the present study, was lower than that reported elsewhere (Grant and Whittow 1983). In the earlier study (Grant and Whittow 1983) the air temperature was somewhat lower (19–24 $^{\circ}$ C as opposed to 24.7 \pm 0.7 $^{\circ}$ SD), and it is possible that at the lower air temperatures the birds were not within their thermoneutral zone.

When more exact information is available on the activity and rest phases of tropical seabirds, it will be possible to make a more extensive comparison of measured and predicted values. The data obtained in this investigation lead to the tentative conclusion that some tropical seabirds, e.g. petrels and at least one tern, do have relatively low basal metabolic rates. The advantages of a low BMR are clear: from a thermoregulatory perspective a bird with a low BMR is less likely to be heat stressed. From an energetic perspective, a seabird with a low BMR requires less energy and food from the oceans, which are relatively impoverished in the tropics (Lack 1968). Nevertheless, it is evident that not all tropical seabirds have low basal metabolic rates and that in some, e.g. the Red-tailed Tropicbird, the BMR may be relatively high. It is likely that factors other than the low productivity of tropical oceans and the high air temperatures in the tropics have played a part in shaping the BMR of tropical seabirds.

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TABLE 2. Daytime body temperatures^a of Hawaiian seabirds.

Species	Laboratory	Field ^b
Wedge-tailed Shearwater	38.8 \pm 0.2 (4)	39.0 ^c
Christmas Shearwater	40.2 \pm 0.2 (6)	38.1 ^d
Bonin Petrel	38.7 \pm 0.3 (7)	38.5 ^d
Bulwer's Petrel	38.3 \pm 0.8 (6)	37.2 \pm 0.1 (2)
Red-tailed Tropicbird	40.6 \pm 0.1 (5)	39.0 ^e
Gray-backed Tern	40.8 \pm 0.1 (2)	—
White Tern	41.5 \pm 0.1 (6)	40.4 \pm 0.1 (8)
Black Noddy	40.5 \pm 0.1 (4)	40.0 \pm 0.1 (6)

^a Data presented as mean \pm SD, number of birds in parentheses.

^b All field data collected during this study except as noted.

^c Udvardy (1963).

^d Howell and Bartholomew (1961).

^e Howell and Bartholomew (1962).

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Winter Range Expansion of the Long-billed Curlew (*Numenius americanus*) to South America

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On 7 February 1984, a Long-billed Curlew (*Numenius americanus*) was sighted and photographed on a mud flat of the Chacopata Lagoon (10°41'N, 63°46'W) on the north side of the Araya Peninsula, State of Sucre, in northeastern Venezuela. Another sighting, presumably of the same bird, was obtained at the same location on 20 February. One individual of this species also was seen in this area by Rosauro Navarro in October 1982, and on several occasions between August 1983 and January 1984 Gedio Marin and the second author saw up to 5 individuals at a time.

The A.O.U. check-list (1983: 186) reports *N. americanus* as wintering from central California and the southern U.S. south to southern Mexico, and irregularly to Guatemala, Honduras, Costa Rica, and Panama (accidental). The species is not listed as occurring in Venezuela nor elsewhere in South America (Meyer de Schauensee 1970, Meyer de Schauensee and Phelps 1978). The Long-billed Curlew was reported for Tobago under the name of *N. longirostris* by James Kirk in 1883 (French 1973), but French be-