OXYGEN CONSUMPTION, EVAPORATIVE WATER LOSS, AND BODY TEMPERATURE IN THE SOOTY TERN

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ABSTRACT.—The oxygen consumption, total evaporative water loss, and deep-body temperatures of Sooty Terns were measured at air temperatures within the range 10–45°C. At air temperatures from 10°C to 30°C, the cloacal temperatures were relatively constant, the temperature of the fledglings tending to exceed that of the adults. At air temperatures of 35°C and higher, the birds became hyperthermic. The thermoneutral temperature was approximately 30°C. The heat production of the terns was lower than the predicted value for nonpasserine birds of their weight. Thermal polypnea was observed at the higher air temperatures, but at an air temperature of 44–45°C, only one bird was able to dissipate heat in excess of heat production by evaporative cooling. The calculated thermal conductance was constant at air temperatures of 10–30°C, but the conductance increased at higher temperatures. It was concluded that Sooty Terns are not especially proficient at evaporative cooling, in spite of the thermal demands of their tropical environment. They appear to rely also on a rather low level of heat production, air movement, and behavorial mechanisms of temperature regulation.—*Department of Population and Environmental Biology, University of California, Irvine, California 92650* (MacMillen, Christopher); and *Department of Physiology, School of Medicine, University of Hawaii, Honolulu, Hawaii 96822* (Whittow, Ebisu). *Christopher's present address: Department of Biology, Santa Rosa Junior College, Santa Rosa, California 95401.* Accepted 5 June 1975.

THE Sooty Tern (*Sterna fuscata*) is widely distributed throughout the tropical oceans, and it establishes nesting colonies on many of the islands within its range. The islands are typically of low latitude and low profile, and they are therefore exposed to maximal solar radiation during the day, imposing a potential heat load on ground-nesting birds, such as Sooty Terns. Howell and Bartholomew (1962, Ibis 104: 98) conducted a field study of temperature regulation in the Sooty Tern on Midway Island in the Leeward Chain of the Hawaiian Islands. Their study demonstrated the importance of behavior in thermoregulation, but necessarily was only implicit concerning the role of physiological regulation.

We had an opportunity to investigate some of the physiological aspects of temperature regulation in adult and immature fledgling Sooty Terns from a nesting colony on Manana Island, off the southeastern coast of Oahu, Hawaii. This report deals with the roles of energy metabolism and evaporative water loss in temperature regulation by the Sooty Tern.

MATERIALS AND METHODS

Experimental animals.—Sooty Terns collected on the nesting colony at Manana Island were maintained for 2 to 4 days in a cage, subject to natural photoperiod, at the Manoa campus of the University of Hawaii or at the University's Kewalo Marine Laboratory in Honolulu. While captive they were fed thawed, fresh-frozen squid or smelt, and they were provided with a shallow pan of seawater for bathing and drinking. With the exception of one bird that died during the study, all were released following their confinement.

Five adult birds, weighing an average of 155.9 ± SD 16.1 g, were captured and measured in August 1972. One fledgling immature bird was used in August 1972 and two others in August 1973. The average weight of the three fledglings, all capable of flight, was 138.6 ± SD 5.3 g. The average weight of all eight birds was 149.4 ± SD 15.4 g. Body temperatures were measured, under field conditions, on an additional 42 birds.

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Body temperatures.—Field measurements of body temperature were made by catching nonnesting birds resting on the ground in the colony with a long-handled net. Body temperatures were determined within 30 sec of capture by inserting a vinyl ensheathed small-animal thermistor probe, connected to a Y.S.I. Telethermometer, at least 5 cm into the cloaca.

Laboratory measurements of body temperature were made simultaneously with measurements of oxygen consumption, ambient temperature, and evaporative water loss, by inserting a vinyl ensheathed copper-constantan thermocouple at least 5 cm into the cloaca. The thermocouple was attached to a Speedomax recording potentiometer or to a Bailey amplifying thermometer. After insertion of the thermocouple into the cloaca the leads were attached firmly to the rectrices with surgical clips, to prevent withdrawal of the thermocouple.

Ambient temperature.—Field ambient temperatures were measured with a Y.S.I. Telethermometer using appropriate probes. Dry-bulb and wet-bulb temperatures were measured with a sling psychrometer. Black-bulb temperature was measured with a mercury thermometer enclosed in a black metal globe.

Laboratory ambient temperatures were monitored with copper-constantan thermocouples inserted into the respirometer chamber and attached either to the Speedomax recording potentiometer or the Bailey amplifying thermometer.

Oxygen consumption.—Oxygen consumption was measured in an open-airflow system with a Beckman Model E2 paramagnetic oxygen analyser. Air, dried by passage through indicating Drierite or magnesium perchlorate, and flowing at rates between 1,600 and 1,837 ml/min, was metered through a 9.75-liter respirometer chamber fashioned from a wide-mouthed jar. The chamber was equipped with ports for the introduction and removal of air, and for the introduction of thermocouples for measurements of ambient temperature (T_a), and body temperature (T_b); the bird rested on a hardware cloth platform, over mineral oil, which prevented evaporation from any excreta voided.

Each Sooty Tern was weighed immediately before being placed in the respirometer chamber and again upon removal from the chamber. Weights during periods of measurements of oxygen consumption were interpolated. The chamber bearing the bird was then placed in a Hotpack, dimly illuminated, constant temperature cabinet equipped with heating and refrigeration units and blowers. Temperature control within the respirometer chamber was ± 0.5°C. At air temperatures of 10, 20, 30, 35, and 40°C the birds were allowed to adjust to each temperature for a period of 1 h, following which the oxygen consumption was measured at that temperature for a period of 30 min. For measurements at T_a = 44 to 45°C, the air temperature was increased rapidly after measurements at T_a = 40°C; the bird was allowed a 15-min period of adjustment to T_a = 44 to 45°C, followed by a 20-min period of measurements. The rate of oxygen consumption was measured at 5-min intervals. For calculation of standard metabolism, the two lowest measurements recorded for each individual at each T_a, corrected to S.T.P., were used. All measurements were made between 1000 and 1730 h, and the birds were generally quiescent.

Evaporative water loss.—Evaporative water loss (EWL) was measured simultaneously with measurements of oxygen consumption. In August 1972 EWL was measured gravimetrically, with U-tubes filled with drierite attached to the airline downstream from the respirometer chamber; a second U-tube measured the amount of water vapor in the dried incurrent air. In August 1973, EWL was measured with a Hygrodynamics Model 15-3001 electric hygrometer with sensing units placed both upstream and downstream from the respirometer chamber. The two methods gave consistently equivalent results.

RESULTS

Body temperatures.—Body temperatures of Sooty Terns taken on the nesting colony of Manana Island on 24 August 1972 and 4 August 1973 are summarized in Table 1. The colony was at an elevation of about 8 m, on open sand, and about 25 m from the water's edge, quite exposed to ocean breezes from the south. On 24 August 1972 the breeze was very light, while on 4 August 1973 the breeze was noticeably stronger. Although the black-bulb temperature was lower on the earlier date, the body temperatures of the fledgings were significantly higher ($P < 0.05$); no adults were measured on the later date, as none could be captured. In addition, the mean body temperature of the four adults on 24 August 1972 ($\bar{x}$, T_b = 41.7°C) was significantly higher ($P < 0.05$) than that of the 26 fledglings ($\bar{x}$, T_b = 40.6°C) on the same day.

TABLE 1

Cloacal Temperatures (T_b) of Sooty Terns on Manana Island, Hawaii

	24 August 1972 (1230–1507 h)		4 August 1973 (1000–1108 h)
	Adults	Fledglings	Fledglings
No. of birds	4	26	12
T_b (± S.D.) (°C)	41.7 ± 0.1	40.6 ± 1.0	38.9 ± 0.6
T_a (°C)[1]	30.9		27–30
T_s (°C)[2]	> 50		36–47
T_g (°C)[3]	42.2		46.4
Rel. humidity (%)	62		65

[1] Air temperature in the shade.
[2] Substrate temperature.
[3] Black globe temperature.

Body temperatures of adult and fledgling Sooty Terns, measured under laboratory conditions with controlled T_a, are indicated in Fig. 1. Between T_a = 10 and 30°C, T_b was fairly constant; that of the fledglings (ca. 40°C) was typically higher than that of the adults (ca. 38.5°C). At T_a = 35°C and higher, T_b increased dramatically and similarly for both adults and fledglings. The mean T_b for the 5 adults and 2 fledglings, measured between T_a = 44 and 45°C, was 44.3°C, which did not differ significantly ($P = > 0.05$) from the mean T_a (44.6°C) at which they were measured. The highest T_b measured (46.0°C) was that of an adult at T_a = 44.7°C; this bird died on the night following this exposure.

Oxygen consumption.—The relationship between oxygen consumption and T_a is shown in Fig. 2, which reveals a curvilinear relationship for both adults and fledglings. Below T_a = 30°C, the fledglings appear to have rates of oxygen consumption lower than those of the adults, with the suggestion of a broader thermal neutral zone. Both adults and fledglings are in thermal neutrality at T_a = 30°C, with the former having a very narrow thermal neutral zone, at about that T_a. The standard metabolic rate (SMR) of four adults and two fledglings, measured at $T_a = 30 \pm 0.5$°C, was 0.98 ± SD, 0.11 ml O_2/g.h; the mean weight of the six birds

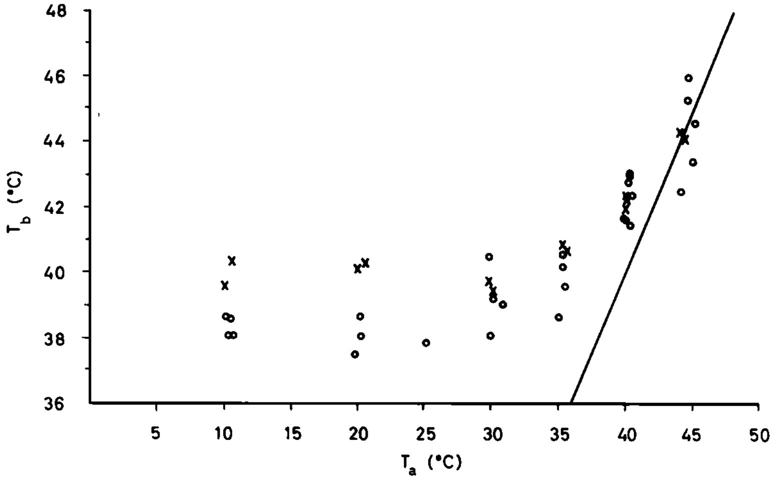

Fig. 1. The relationship between body temperature (T_b) and ambient temperature (T_a) in adult (O) and fledgling (X) Sooty Terns. The diagonal line indicates equality between T_b and T_a.

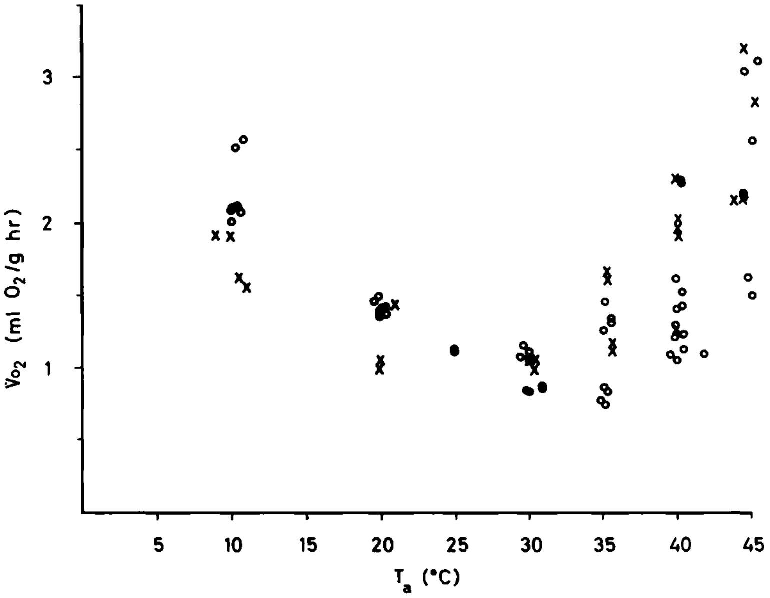

Fig. 2. The relationship between oxygen consumption ($\dot{V}_{O_2}$) and T_a in adult (O) and fledgling (X) Sooty Terns.

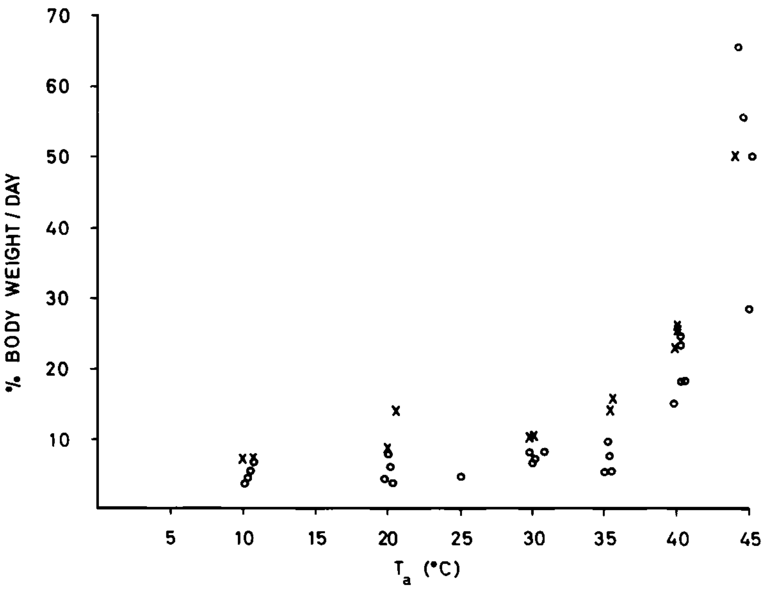

Fig. 3. Percentage of body weight lost by evaporation as a function of T_a in adult (O) and fledging (X) Sooty Terns.

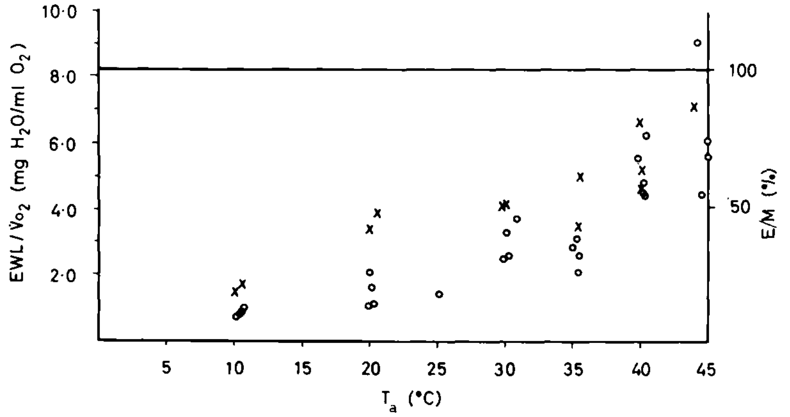

Fig. 4. The relationship between evaporative water loss (EWL), oxygen uptake ($\dot{V}_{O_2}$), heat production (M) and T_a in adult (O) and fledgling (X) Sooty Terns. The left-hand ordinate expresses the ratios between evaporative water loss (EWL) and oxygen consumption ($\dot{V}_{O_2}$), while the right-hand ordinate expresses the ratios between evaporative heat dissipation (E) and metabolic heat production (M). The horizontal line indicates equality between E and M.

at the time of measurement was 147.5 ± SD, 11.3 g (the SMR of the adults, with a mean weight of 150.4 ± SD, 13.0 g, was 0.97 ± SD, 0.14 ml O_2/g.h; that of the fledglings, weighing 141.7 ± SD, 2.2 g, was 1.02 ± SD, 0.03 ml O_2/g.h). Above $T_a = 30°C$ oxygen consumption increased rapidly, with that of the fledglings appearing to be higher than that of the adults.

Evaporative water loss.—Weight-relative rates of evaporative water loss in relation to T_a are shown in Fig 3. Both adult and fledgling Sooty Terns have rates of EWL that are directly related to T_a, with only slight increases from T_a = 10 to 35°C; above T_a = 35°C the increase in EWL is very marked. Between T_a = 10 and 40°C the rate of EWL of fledglings generally exceeds that of the adults.

Expressed as a function of oxygen consumption, EWL is also directly related to T_a (Fig. 4). Again, at the lower temperatures (T_a = 10–35°C), the EWL of fledglings exceeds that of adults, but at the higher temperatures (T_a = 40–45°C) there appear to be no differences between the two age groups. When the EWL values are converted into the relationship between heat produced by metabolism (M) and heat dissipated by evaporation (E), E is generally less than M, even at the highest ambient temperatures. Only one individual Sooty Tern (an adult) was able to dissipate, by evaporative cooling, more heat than was being produced by metabolism, at a T_a of 44–45°C.

Discussion

Simultaneous measurements of oxygen consumption, body temperature, and evaporative water loss afford values for the calculation of dry thermal conductance (C), according to the equation $C = (M - E)/T_b - T_a$, where M and E represent weight-specific heat production and heat dissipation, respectively (after Dawson and Bennett 1973, Comp. Biochem. Physiol. 44A: 249). In making these calculations it was assumed that consumption of 1 ml O_2 yields 4.8 cal, and evaporation of 1 mg H_2O dissipates 0.58 cal. Dry thermal conductances for adult and fledgling Sooty Terns are indicated in Fig. 5; the values are very stable for both age groups within and below thermal neutrality. At T_a = 10 and 20°C, the C of fledglings is conspicu-

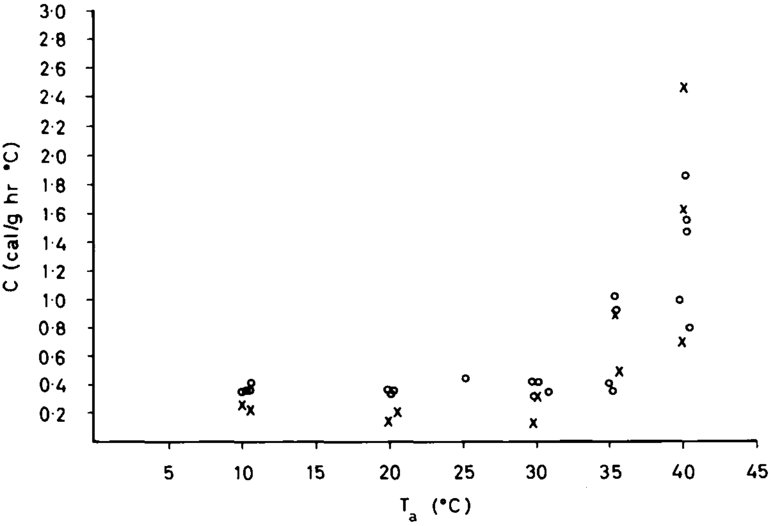

Fig. 5. Dry thermal conductance (C) as a function of T_a in adult (O) and fledgling (X) Sooty Terns. Calculated from the equation $C = (M - E)/(T_b - T_a)$. These calculations assume that 1.0 ml O_2 = 4.8 cal, and 1.0 mg H_2O = 0.58 cal.

ously lower than that of adults, which is consistent with the observation that fledglings have a higher T_b (Fig. 1) and lower oxygen consumption (Fig. 2) at those temperatures. Thus fledglings appear to be more economical, energetically, at the lower temperatures, by virtue of more effective insulative capacities (down or subcutaneous fat, or a combination of both). This increased efficiency could be particularly important when the fledglings are independent from the parents at night, yet they are not fully self-sufficient in feeding. Dry thermal conductance of both adults and fledglings increases markedly and similarly above thermal neutrality; but, at high air temperatures, errors in the computation of thermal conductance are relatively high because of the small difference between T_b and T_a and an accelerated rate of heat storage.

Passerine birds generally have higher standard metabolic rates than do nonpasserines of the same size (for recent review see Dawson and Hudson 1970, Birds. Pp. 223–310 *in* Comparative physiology of thermoregulation (G. C. Whittow, Ed.), New York, Academic Press). Further, Dawson and Hudson (ibid.) suggest the likelihood that within nonpasserine birds ordinal differences in size-related metabolism will be found, such as has recently been demonstrated for columbiform birds (Dawson and Bennett ibid.). Size-related standard metabolism in birds has been further elucidated by Aschoff and Pohl (1970, Fed. Proc. 29: 1541), who have shown that in both passerines and nonpasserines standard metabolism measured during the active phase of the 24-h period is predictably higher than that measured during the inactive phase. Very little information is available on the standard metabolism of charadriiform birds so that a detailed analysis of their size-related metabolism is premature at this time, but our data lend themselves to comparisons with other nonpasserine birds. The standard metabolic rate of six Sooty Terns (four adults, two fledglings) at $T_a = 30 \pm$ SD, 0.5°C, and weighing an average of 147.5 ± SD, 11.3 g was 0.98 ± SD, 0.11, ml O_2/g.h. This is equivalent to a standard metabolism of 16.65 kcal/24 h (assuming 1 ml O_2 = 4.8 cal). Using Aschoff and Pohl's (ibid.) equation

TABLE 2

EFFECTIVENESS OF EVAPORATIVE HEAT LOSS (E/M) IN SOOTY TERNS AT HIGH AMBIENT TEMPERATURES

				Humidity[4]	
Age of birds	T_b (°C)[1]	T_a (°C)[2]	E/M × 100[3]	RH (%)	WVP (mm Hg)
Adult	42.5	44.2	109.3	67.2	46.4
Adult	43.4	45.0	73.1	24.8	17.8
Adult	44.6	45.1	68.1	52.0	37.6
Adult	45.3	44.6	53.5	62.9	44.3
Fledgling	44.3	44.0	88.7	50.3	34.3

[1] Cloacal temperature.
[2] Air temperature.
[3] E = total evaporative heat loss, M = heat production.
[4] RH = relative humidity, WVP = water vapor pressure.

($M = 91.0\ W^{0.729}$, where M is standard metabolism in kcal/day, and W is body weight in kg) relating body size to standard metabolism in nonpasserine birds measured during the normal period of activity (daytime for diurnally active birds such as terns), the predicted M for birds the size of ours is 22.55 kcal/24 h. Thus the standard metabolic rate of our Sooty Terns is 74% of that predicted for a nonpasserine species.

A relatively low metabolism and concomitant low rate of heat production in both adult and fledgling Sooty Terns are probably valuable in ameliorating the total heat load on these ground-nesting birds. This in fact may be the primary physiological adaptation of Sooty Terns to excessive heat, for they seem to have only modest capacities for evaporative cooling. Simultaneous measurements of T_b, T_a, oxygen consumption, and EWL (Figs. 1 and 4) reveal that in four of seven birds tested at T_a = 44–45°C, T_b was less than T_a while in only one of these birds was E greater than M (see Table 2). The most likely explanation for this finding is that the four birds were storing heat and that their body temperature had not quite increased to that of the environment within the relatively short experimental time period. Another possibility is that the cloacal temperature was not the same as the mean body temperature. Still another individual was removed prematurely from the experimental procedure when its body temperature reached 46°C at T_a 44.7°C; this animal was dead on the following day, presumably from excessive heat exposure. During exposure to T_a = 44 to 45°C, no gular flutter was apparent in any of the birds, but they all panted vigorously and were quite restless. Panting rates of six adult Sooty Terns at T_a = 44–45°C averaged 174 ± SD, 8.0 respirations/min, which is considerably less than the reported rates of gular flutter in other birds (Dawson and Hudson ibid.).

Relative humidities (RH) and water vapor pressures in the respirometer chamber during heat exposure were calculated for each of the birds after the method of Lasiewski et al. (1966, Comp. Biochem. Physiol. 19: 445). These, as indicated in Table 2, were extremely variable and the average was rather high ($\bar{x}$, RH = 51.4 ± SD, 16.5%, $\bar{x}$ WVP = 36.1 ± SD, 11.3 mm Hg). This average value is at least 10% lower than the RH measured in the nesting colony but the WVP on Manana Island was lower (Table 1). It is possible that the humidities were sufficiently high to preclude effective evaporative cooling, but we doubt this because the single bird capable of dissipating more heat by evaporation than that produced by metabolism was also subjected to the highest humidity (Table 2). Therefore we must interpret the data to indicate that physiological mechanisms for the dissipation of heat by evaporation in the Sooty Tern are only moderately developed. Very likely this inefficiency in heat dissipation by the Sooty Tern is more related to the inability to control heat production while panting than to the inability to mobilize water for evaporation.

It is doubtful that Sooty Terns are often exposed to excessive heat loads, even in the direct sun on the nesting colonies. Howell and Bartholomew (ibid.) state that air temperatures on Midway Island rarely rise above 30°C and that thermoregulation in adult Sooty Terns is accomplished without unusually heavy panting or special behavior patterns. Our data obtained on Manana Island (Table 1) show the T_b of adults and fledglings to be comparable to those exposed in the respirometer chambers to a T_a of 35 to 40°C. The air temperature (27–30.9°C) on Manana is within the thermal neutral zone determined in the laboratory. Convective cooling is likely to be more important, under natural conditions, than in the respirometer chamber. Thus we feel that a propitious choice of the nesting site, close to the moderating influence of the sea and exposed to sea breezes, is sufficient to enable adults and fledglings to cope with the moderate heat load imposed by the environment without requiring specialized physiological mechanisms for heat dissipation. The combination of a depressed metabolism, a moderate capability for evaporative cooling, and behavioral adjustments such as standing with head upwind and with wings slightly drooped, appear to be adequate.

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