

# FLIGHT ENERGETICS OF FREE-LIVING SOOTY TERNS

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**ABSTRACT.**—The CO<sub>2</sub> production of free-ranging Sooty Terns (*Sterna fuscata*) was measured using doubly labeled water (HTO-18). Metabolic rate during flight was determined to be 4.8 times standard metabolic rate (SMR). This value is much lower than estimates of flight metabolism predicted from previously published equations. Observations of these birds at sea indicate that flapping flight predominated at the windspeeds (0–5 m/s) that prevailed during our measurement periods, so factors other than gliding must account for the comparatively low flight metabolism we measured. Sooty Tern flight metabolism is similar to that of some other birds, such as swallows and swifts, that also have high aspect ratios and low wing loadings. Received 27 April 1983, accepted 12 October 1983.

THE reliability of estimates of energy flow through biotic communities depends upon the extent to which the model used conforms to reality and the accuracy of the input parameters. In a sensitivity analysis of 44 model-specific and species-specific parameters of his bioenergetic model of a seabird colony, Furness (1978) identified several inputs that had the greatest effect on the precision of the model. Among these for Arctic Terns (*Sterna paradisaea*) were the hours of activity per day, the intercept and exponent of Lasiewski and Dawson's (1967) SMR equation, and the energy requirements of flapping and gliding flight. For birds, such as terns, that spend a large proportion of their foraging time in flight, the accuracy of estimates of daily energy expenditure depends on knowing the total time spent in various flight activities (i.e. flapping, gliding, and hovering) and the metabolic cost of those activities.

One goal of this study was to determine the energetic cost of free, natural flight in a species of bird. A second goal was to assess the reliability of several models that may be used for predicting the total metabolic rate of birds during flight by comparing model estimates with empirical measurements. Doubly labeled water (HTO-18) was used to measure CO<sub>2</sub> production in free-ranging Sooty Terns (*Sterna fuscata*) in the northwestern Hawaiian Islands during the incubation stage of breeding. We estimated the metabolic rate of flying birds from time-budget and field metabolic-rate (FMR) results. Sooty Terns are particularly amenable to this type of

experiment, because they do not rest on the water (Gould 1974) and can be assumed to be in constant flight when not at the breeding colony. The flight behavior of Sooty Terns was observed at sea, and morphological measurements were made in order to compare the power input predicted by aerodynamic models and measurements of gull flight in wind tunnels with field measurements.

## MATERIALS AND METHODS

Incubating pairs of adult Sooty Terns were studied during April and May 1981 on Tern Island, French Frigate Shoals (approximately 24°N latitude and 166°W longitude). Pair members were captured with a dip net, marked with colored leg bands and dye, and observed for several days to determine the duration and frequency of their incubation-foraging cycle. Incubation spans at Tern Island commonly last 2–3 days. Birds that were just beginning or just ending their turn at incubation were captured, weighed, injected intramuscularly with 0.60 ml of water containing 0.15 millicurie tritium and 95 atom percent oxygen-18, and held for 1 h while the isotopes mixed thoroughly in body fluids (time previously determined in the laboratory). Then, a small blood sample (ca. 0.10 ml) was taken from a brachial vein, and the birds were released. Incubating birds were recaptured about 48 h later, just before their mates relieved them on the nest. Foraging birds were recaptured as soon as possible after their arrival (15–80 h after release). The amount of time foraging birds actually spent in flight was estimated by periodically (every 2–4 h) surveying the nesting area and recording the presence or absence of marked birds. We assumed that the birds flew continuously while away from the island. This procedure yielded flight times that were accurate to

within  $\pm 9\%$ . Sooty Terns with chicks or eggs do not "loaf" or form "clubs" and are virtually never seen on land except at or near the nest site. Watson and Lashley (1915) found that Sooty Terns do not have plumage suitable for swimming and become waterlogged after 10 min of contact with the ocean surface.

At recapture, a second blood sample was taken and body mass was recorded before the bird was released onto the nest. While adults were being handled, the nests were covered to prevent egg overheating and predation by Ruddy Turnstones (*Arenaria interpres*). Eighteen terns were injected, and all were recaptured. Four of these birds, however, had been away much longer than the others, and too much of the isotope given to them had been washed out before recapture to yield reliable metabolic rate data. A normal proportion of injected birds went on to fledge their chicks.

Blood samples were vacuum-distilled to obtain pure water, which was analyzed for tritium content by liquid scintillation spectrometry and for oxygen-18 content by proton activation analysis (Wood et al. 1975, Nagy and Costa 1980). Body-water volumes at the time of injection were determined from oxygen-18 dilution space (Nagy 1980). Water contents of recaptured birds were estimated from their body masses and their initial water contents, assuming fractional water contents remained constant. Rates of  $\text{CO}_2$  production were calculated by means of equation 2 in Nagy (1980). Field metabolic rates (FMRs) were converted from  $\text{CO}_2$  production values to units of energy (joules) by means of the factor  $24.7 \text{ J/ml CO}_2$ . This factor was based on diet analyses (53.5% by volume of squid, 46.5% fish) of Sooty Terns in the northwestern Hawaiian Chain (Harrison et al. 1983), along with measurements of the composition of fresh squid (80.2% water, 16.4% protein, 0.9% fat, 1.5% carbohydrate, and 1.0% ash; Watt and Merrill 1963) and fresh anchovy (72.7% water, 19.7% protein, 5.2% fat, <0.5% carbohydrate, 2.0% ash; Fishing Industry Research Unit, University of Cape Town, South Africa, Annual Report, 1980), and energy and  $\text{CO}_2$  yields of protein, fat, and carbohydrates (Schmidt-Nielsen 1975). The published standard metabolic rate of Sooty Terns was converted from oxygen consumption to joules by means of the factor  $19.7 \text{ J/ml O}_2$  consumed (fat metabolism).

We estimated flight metabolism of Sooty Terns with predictive equations using measurements of body mass, wing area and span, and flight velocity (see Results section for details). The behavior of flying Sooty Terns at sea between French Frigate Shoals and Pearl and Hermes Reef was observed from the 'R/V Ferese' over an 8-day period. The behavior of an individual bird was recorded continuously while it was in visual range of the vessel. The average duration of visual contact was 45 s per bird. Wind speeds at sea were also recorded. Wing area and span were measured from tracings of Sooty Tern wings. Live

Sooty Terns were restrained with their backs to paper and wings fully extended. Span and area measurements include body width. These were used to calculate aspect ratio and, along with body mass values, wing loading.

Results are reported as means  $\pm$  standard deviations. The regression line in Fig. 1 was calculated using the least squares method. Statistical comparisons were done using Student's *t*-test.

The increment of metabolic heat production by a flying bird above that of a resting animal is termed "cost of flight," and the total metabolic rate of a flying bird (including resting costs) is called "metabolic rate during flight" in this paper.

## RESULTS

**Body Mass.**—The mean body mass of nine incubating terns ( $188 \pm 17 \text{ g}$ ) was slightly greater than that of five foraging birds ( $184 \pm 11 \text{ g}$ ), but the difference was not significant ( $P > 0.2$ ). The overall mean body mass of the 14 terns was  $187 \pm 15 \text{ g}$ . Foraging birds gained body mass at a mean rate of  $2.6 \pm 3.5\%/ \text{day}$ , while incubating terns lost  $5.2 \pm 1.7\%$  of body mass/day ( $P < 0.01$ ).

**Energy Metabolism.**—Metabolic rates of the nine incubating ("on nest") birds averaged  $1.27 \pm 0.38 \text{ ml CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , which is equivalent to  $0.751 \pm 0.224 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ . The five "off nest" terns had significantly higher ( $P < 0.01$ ) FMRs, averaging  $2.98 \pm 0.79 \text{ ml CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ , or  $1.850 \pm 0.534 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ . The average FMR of "off nest" birds is not equivalent to energy expenditure while flying, because these terns spent some of the time actually flying and some of the time standing in the nesting area. To estimate the FMR of a flying Sooty Tern, we regressed FMRs against the number of hours per 24-h period off the nest that individual birds were actually flying (Fig. 1). The regression line is described by the equation:

$$\text{kJ} \cdot \text{g}^{-1} \cdot \text{day}^{-1} = 0.748 + 0.061 \text{ h flying/day}$$

( $r = 0.92$ ,  $F_{(1,12)} = 62.1$ ,  $P \ll 0.001$ , SE of slope =  $0.008$ , SE of predicted 24-h flying value =  $0.270$ ). The slope of the line has the units  $\text{kJ} \cdot \text{g}^{-1} \cdot (\text{h flying})^{-1}$ . Thus, an estimate of the incremental cost of flight for a Sooty Tern is  $0.061 \text{ kJ} \cdot \text{g}^{-1} \cdot (\text{h flying})^{-1}$ , which is equivalent to  $1.46 \text{ kJ} \cdot \text{g}^{-1} \cdot (\text{day flying})^{-1}$ . Adding a maintenance cost of  $0.748 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  (the intercept of the regression line) yields an estimate of the total metabolic intensity of a flying tern:  $2.21 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ . This procedure involves the assumption

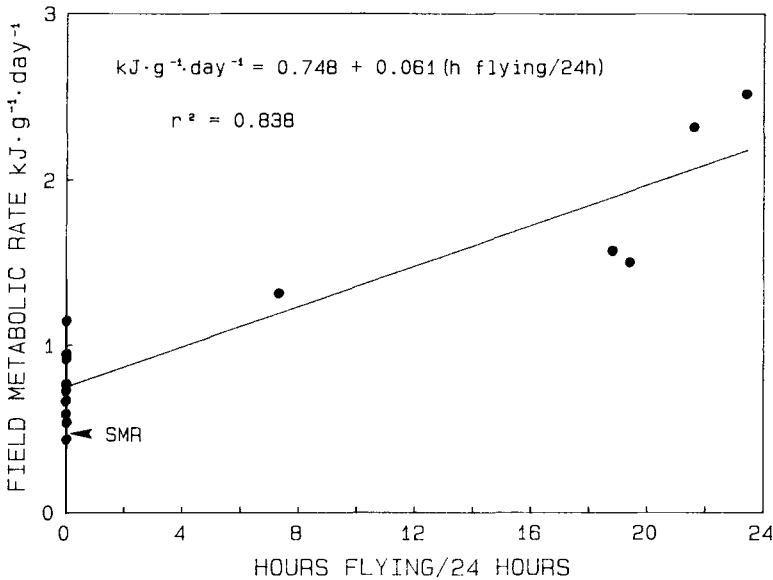


Fig. 1. Relationship between field metabolic rate of Sooty Terns and hours spent flying per 24-h period during the breeding season. The line is the least-squares regression, and the arrow indicates standard metabolic rate ( $0.463 \text{ kJ}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ ).

that flying terns had the same metabolic expenses for maintenance as did nonflying terns. Nonflight metabolism includes standard metabolism (energy expenditure of birds that are postabsorptive, thermally nonstressed, and completely at rest) plus costs of food digestion and assimilation, thermoregulation, alertness and muscle tension, comfort movements, and other activities of minor energetic cost. Because birds probably incur most of these energetic costs while flying as well as while incubating, we feel this assumption is reasonable.

Standard metabolic rate (SMR) of Sooty Terns is  $0.98 \text{ ml O}_2\cdot\text{g}^{-1}\cdot\text{h}^{-1}$  (MacMillen et al. 1977), which is equivalent to  $0.463 \text{ kJ}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ . Thus, nonflight metabolism (FMR of a nonflying tern, the intercept in Fig. 1) was  $1.62 \times \text{SMR}$ , and metabolic rate during flight was  $4.77 \times \text{SMR}$ . The cost of flight (above nonflight metabolism) was  $3.15 \times \text{SMR}$ .

*Flight behavior.*—Terns flying over water used a flapping mode of flight about 95% of the time in relatively calm air (Table 1). At higher wind speeds, the birds glided more often but still flapped about three-quarters of the time. These observations included terns that were apparently in transit between feeding and nesting areas, as well as birds that were foraging.

*Aerodynamic properties.*—The 11 terns used for morphological measurements had masses averaging  $194 \pm 15 \text{ g}$ , wing spans averaging  $0.84 \pm 0.023 \text{ m}$ , and a mean wing area of  $626 \pm 44.2 \text{ cm}^2$ . Wing loading, calculated from these measurements, was  $0.311 \pm 0.028 \text{ g/cm}^2$ . Aspect ratio [(wing span<sup>2</sup>/wing area) as defined by Pennycuik (1975: 33)] of the same birds averaged  $11.3 \pm 0.593$ .

*Predicted flight costs.*—Metabolic rate during flight was predicted using equations derived from aerodynamic theory for species whose flight costs have also been measured by doubly labeled water. These equations require an input of parameters such as flight speed, wing span, mass, and wing area.

Tucker's (1973) equation #49 was used to predict metabolic rate during level flapping flight. The necessary species-specific variables were mass ( $m$ , in kg), wing span ( $b$ , in m), flight speed ( $V$ , in m/s), and basal metabolic rate (BMR, in watts). For Sooty Terns the following values were used:  $m = 0.187$ ,  $b = 0.84$ ,  $V = 10.4$  (estimated from data of Schnell and Hellack, 1979), and  $\text{BMR} = 1.023$  (MacMillen et al. 1977). For House Martins (*Delichon urbica*)  $m = 0.019$  (Bryant and Westerterp 1980),  $b = 0.292$  (Magnan 1922),  $V = 11.18$  (Meinertzhagen 1955), and

$BMR = 0.258$  (Hails 1979); for Barn Swallows (*Hirundo rustica*)  $m = 0.018$  (Magnan 1922),  $b = 0.33$  (Magnan 1922),  $V = 7.598$  (Schnell 1965), and  $BMR = 0.305$  (Aschoff and Pohl 1970); for pigeons (*Columba livia*)  $m = 0.4$  (Pennycuick 1968),  $b = 0.66$  (Pennycuick 1968),  $V = 16.09$  (LeFebvre 1964), and  $BMR = 1.818$  (Aschoff and Pohl 1970).

Greenewalt's (1975) equation #23 for total power yields the power required to overcome induced drag and parasitic drag. Variables required for this equation are  $W$  (mass in g),  $S$  (projected wing area in  $\text{cm}^2$ ),  $b$  (wingspan in cm),  $V$  (velocity in km/h), and  $SMR$  ( $\text{J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ). In order to compare the results of this equation with those of Tucker's and with our doubly labeled water data, we multiplied the result by 4 to account for 25% muscular efficiency (Greenewalt 1975) and added nonflight metabolism. For Sooty Terns we measured nonflying or maintenance metabolism to be  $1.62 \times SMR$ . For pigeons we calculated it to be  $1.71 \times SMR$  (data from LeFebvre 1964). For House Martins and Barn Swallows we used the average of these two figures,  $1.66 \times SMR$ .

For Sooty Terns the following values were used in Greenewalt's (1975) equation:  $W = 187$ ,  $S = 625.5$ ,  $b = 83.99$ ,  $V = 37.44$  (from Schnell and Hellack 1979), and  $SMR = 19.3$  (MacMillen et al. 1977); for House Martins  $W = 18.8$  (Bryant and Westerterp 1980),  $S = 92$  (Magnan 1922),  $b = 29.2$  (Magnan 1922),  $V = 40.25$  (Meinertzhagen 1955), and  $SMR = 49.4$  (Hails 1979); for Barn Swallows  $W = 18.35$  (Magnan 1922),  $S = 135$  (Magnan 1922),  $b = 33$  (Magnan 1922),  $V = 27.35$  (Schnell 1965), and  $SMR = 59.8$  (Aschoff and Pohl 1970); for pigeons  $W = 400$  (Pennycuick 1968),  $S = 630$  (Pennycuick 1968),  $b = 66$  (Pennycuick 1968),  $V = 57.93$  (LeFebvre 1964), and  $SMR = 16.4$  (Aschoff and Pohl 1970).

Pennycuick's (1975) equation #25 yields total mechanical power required to fly horizontally as a function of forward speed. We corrected the value obtained from this equation for muscular efficiency (23%; Pennycuick 1975) to obtain total power input. Variables required for this equation are  $m$  (mass in kg),  $W$  (weight in newtons),  $b$  (wingspan in m),  $v$  (velocity in m/s), and  $SMR$  in watts.

For Sooty Terns we used  $m = 0.187$ ,  $W = 1.83$ ,  $b = 0.84$ ,  $v = 10.4$  (estimated from data of Schnell and Hellack 1979), and  $BMR = 1.023$  (MacMillen et al. 1977); for House Martins  $m = 0.019$  (Bryant and Westerterp 1980),  $W = 0.184$ ,

TABLE 1. Flight behavior of Sooty Terns at sea ( $n$  = number of birds observed).

	Percentage of total flying time	
	Wind velocity 0-5 m/s ( $n = 61$ )	Wind velocity 5-10 m/s ( $n = 6$ )
Flapping	94.3	75.4
Gliding	5.5	24.6
Hovering	0.2	0

$b = 0.292$  (Magnan 1922),  $v = 11.18$  (Meinertzhagen 1955), and  $BMR = 0.258$  (Hails 1979); for Barn Swallows we used  $m = 0.018$  (Magnan 1922),  $W = 0.180$ ,  $b = 0.33$  (Magnan 1922),  $v = 7.598$  (Schnell 1965), and  $BMR = 0.305$  (Aschoff and Pohl 1970); for pigeons  $m = 0.400$  (Pennycuick 1968),  $W = 3.92$ ,  $b = 0.66$  (Pennycuick 1968),  $v = 16.09$  (LeFebvre 1964), and  $BMR = 1.82$  (Aschoff and Pohl 1970). We used  $1.22 \text{ kg/m}^3$  to represent the density of air.

Estimates of total power in Greenewalt's equation #23 and power input in Tucker's equation #49 and Pennycuick's equation #25 were not calculated for the Purple Martin, because wingspan measurements ( $b$ ) were not available. Tucker (1973) provided an equation (derived from Greenewalt 1962) for estimating wingspan from mass, but, because aspect ratio may affect the cost of flight (see below), it would be counterproductive to use an "average" wingspan for a bird of a given mass.

## DISCUSSION

One approach to predicting the cost of flight has been the formulation of equations based on aerodynamic theory that require the input of measured parameters (Pennycuick 1969, 1975; Tucker 1973; Greenewalt 1975; Rayner 1979). Metabolic rates during flight, measured with isotopes for all four species considered here (Table 2), are generally lower than those predicted by Tucker's equation #49. Validation studies indicate that double labeled water measurements are accurate to within  $\pm 8\%$  in a variety of vertebrates (Nagy 1980). The 95% confidence interval for the slope of the regression in Fig. 1 (the incremental cost of flight for Sooty Terns) is  $\pm 28\%$  (0.044-0.078). All of the differences for Sooty Terns in Table 2 are much larger than 28%. Some portion of the differences shown in Table 2 may be attributed to the fact

TABLE 2. Comparison of doubly labeled water (DLW) method with three other methods for estimating total metabolic rates ( $J \cdot g^{-1} \cdot h^{-1}$ ) during free flight in birds.

Method	Sooty Tern (187 g)	House Martin (18.8 g)	Barn Swallow (18.35 g)	Purple Martin (50.5 g)	Pigeon (400 g)
Doubly labeled water					
$J \cdot g^{-1} \cdot h^{-1}$	92.1	167-239 <sup>a</sup>	247 <sup>a</sup>	289 <sup>b</sup>	230 <sup>c</sup>
Multiple of SMR	4.77	3.39-4.83	4.16	6.37	14.06
Tucker (1973)					
$J \cdot g^{-1} \cdot h^{-1}$	228	546	320	—	429
(% difference from DLW method)	(+147)	(+128-227)	(+30)	—	(+87)
Greenewalt (1975) <sup>d</sup>					
$J \cdot g^{-1} \cdot h^{-1}$	178	352	262	—	270
(% difference from DLW method)	(+93)	(+47-111)	(+6)	—	(+17)
Pennycuik (1975)					
$J \cdot g^{-1} \cdot h^{-1}$	175	304	197	—	410
(% difference from DLW method)	(+90)	(+27-82)	(-20)	—	(+78)
12 x SMR <sup>e</sup>					
$J \cdot g^{-1} \cdot h^{-1}$	232	593	718	545	196
(% difference from DLW method)	(+151)	(+148-255)	(+191)	(+89)	(-15)

<sup>a</sup> Hails (1979).

<sup>b</sup> Utter and LeFebvre (1970).

<sup>c</sup> LeFebvre (1964).

<sup>d</sup> Corrected to include nonflight metabolism (see text).

<sup>e</sup> Raveling and LeFebvre (1967); King (1974: 32).

that free-living birds have opportunities to take advantage of atmospheric movements to reduce the power requirements of flight. The failure to correct for the proportion of time spent gliding also contributes to the overestimate for the House Martin and Barn Swallow. House Martins in flight only flap 37.7% of the time (Bryant and Westerterp 1980).

Greenewalt's equation #23, modified for comparison, gives estimates of metabolic rate during flight that are higher than those measured using doubly labeled water (DLW) in the Sooty Tern and House Martin, but are relatively close to isotopic water results from the Barn Swallow and pigeon. The close agreement between Greenewalt's equation and LeFebvre's data for the pigeon may occur because Greenewalt used LeFebvre's data to estimate values for induced drag and parasitic drag. Agreement between DLW measurements and the results of equation #23 can be improved by using predicted flight velocities for minimum power output ( $V_{mp}$ ; Greenewalt 1975: 42), which are lower than the measured flight velocities we used to predict the values shown in Table 2. With  $V_{mp}$  values, the differences between equation #23 and DLW decline to between +13 and +51%. For purposes of estimating the bioen-

ergetics of birds in the field, we feel it is best to use measured values in predictive models whenever these measurements are available. In cases where flight velocities are unknown, however,  $V_{mp}$  may be a useful substitute. Greenewalt (pers. comm.) suggested that his equations are most useful on a comparative, rather than an absolute, basis.

It has become a standard procedure in the formulation of time-energy budgets of birds to adopt some multiple of basal metabolic rate as the cost of flight. This multiple is often an average value derived from empirical measurements made on a variety of species. Nisbet (1967) questioned the validity of this approach, stating that the cost of flight in birds depends on their aerodynamic properties. In his extensive treatment of flight in birds, Greenewalt (1975) found no basis for predicting a constant ratio of metabolic rate during flight to that at rest.

Metabolic rate during flight in Sooty Terns, estimated with isotopes of oxygen and hydrogen, is not closely predicted (1) by the commonly used multiples of SMR obtained from several species (Raveling and LeFebvre 1967, King 1974: 32) or (2) by the multiples of SMR obtained in wind-tunnel studies of members of

the same family. Using Tucker's (1972) factor of  $13 \times SMR$  for metabolic rate during flapping flight in the Laughing Gull (*Larus atricilla*) and  $3.1 \times SMR$  for gliding flight in Herring Gulls (*Larus argentatus*), derived from the measurements of Baudinette and Schmidt-Neilsen (1974) and measurements of *SMR* in Herring Gulls (Lustick et al. 1978), we calculated a rate of  $241.3 \text{ J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$  for Sooty Terns flying at low windspeeds (0–5 m/s). The isotopically measured value at those windspeeds ( $92.1 \text{ J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) was only 38% of this estimate.

The results of this study and Lyuleeva's (1970, cited in Hails 1979) estimate of flight costs in the Common Swift (*Apus apus*) do not support the suggestion made by Utter and LeFebvre (1970) that passerines may have some physiological advantage in flight proficiency over nonpasserines. Values for metabolism during flight relative to *SMR* of the Sooty Tern (a nonpasserine) fall in the same range (3.4–6.4) as those of martins and Barn Swallows (passerines) that have been measured (summarized by Hails 1979). Aerial feeding, low wingloading (values of 0.116–0.232), and high aspect ratio (values of 8.07–13.5) are characteristic of each of these groups. In contrast, pigeons exhibit wingloading values of 0.343–0.515 and aspect ratios of 6.30–8.19 (data summarized in Greenewalt 1962), and their metabolic rate during flight is  $14 \times SMR$ .

Sooty Terns are an extremely aerial species. During 3 yr of study of the distribution and behavior of Sooty Terns, the Pacific Ocean Biological Survey Program made 51,095 observations of bird behavior at sea. Only 0.16% of these were of birds sitting on the water (Gould 1974). At French Frigate Shoals, the terns are absent from the colony from September to January or February, presumably in continuous flight during this 4–5-month period. This would be a remarkable metabolic feat if flight costs for Sooty Terns were as high as, for example, pigeons ( $14 \times SMR$ ; Table 2). It appears that the morphology of Sooty Terns is largely responsible for their surprisingly low flight costs.

A standard multiple of *SMR* to estimate the cost of flight in all birds would greatly simplify making estimates of daily energy expenditure from time-activity budgets. There is no obvious reason, however, why birds of different habits and structure should have the same power requirements for flight, considering all the morphological compromises that might be made for

habitat type and terrestrial or aquatic locomotion. Our results indicate that behavior while aloft and the aerodynamic properties of different birds can have a large influence on their energetic costs of flight.

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