

GROWTH AND ENERGETICS OF CHICKS OF THE SOOTY TERN (*STERNA FUSCATA*) AND COMMON TERN (*S. HIRUNDO*)

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ABSTRACT.—We measured the energy budgets of chicks of the Common Tern (*Sterna hirundo*) on Great Gull Island, New York and of the Sooty Tern (*S. fuscata*) on the Dry Tortugas, Florida. The respiratory energy requirement was determined by measuring oxygen consumption in a closed system. We calculated the growth energy requirement from the lipid and protein contents of a series of chicks spanning the range between hatching and fledging. Young Common Terns grow about twice as rapidly as young Sooty Terns. In most respects, their development follows a similar course, but energy budgets calculated for the two species differed in several ways. (1) Maintenance metabolism was lower in the Sooty Tern owing to its warm environment. (2) Sooty Terns allocated more of their energy intake to lipid accumulation from an earlier age. (3) In the Sooty Tern, the allocation of energy to growth initially was high, but its absolute amount decreased steadily throughout the growth period. In the Common Tern, both growth and maintenance energy allocations increased rapidly during the first half of the development period. (4) In Sooty Tern chicks energy metabolism approached its maximum rate (135 kJ/day) by the end of the first third of the development period, after which it leveled off. In the Common Tern, energy metabolism increased from about one-quarter of its maximum during the first 5 days after hatching to its maximum of 200 kJ/day during the third week of the postnatal development period.

Although these observations support the hypothesis that slow growth in pelagic seabirds is selected to reduce the energy requirement of the chick, our energy budgets also suggest that a doubling of the growth rate by the Sooty Tern would increase the maximum energy requirement of the chick by only 20% and the total feeding requirement of the adult by only 5%. Moreover, the levels of water in muscles suggest that the Sooty Tern develops mature function earlier than does the Common Tern, which in itself might be sufficient to account for the slower growth of the first species. *Received 4 March 1980, accepted 16 December 1980.*

MANY seabirds grow more slowly than one would expect on the basis of adult size and pattern of development (Lack 1968; Ricklefs 1968, 1973). These slowly growing species include most of the Procellariiformes (albatrosses, shearwaters, petrels), all the Phaethontidae (tropicbirds) and Fregatidae (frigatebirds), as well as many of the Sulidae (boobies), Laridae (gulls and terns), and Alcidae (auks). Although these species are alike in laying only one egg per clutch, they vary in geographical distribution, mode of development, and feeding ecology.

In this study, we compare the growth and energetics of the chicks of two closely related species of terns (genus *Sterna*). One, the Common Tern (*S. hirundo*), is a north-temperate species that rears two or three rapidly growing young. The other, the Sooty Tern (*S. fuscata*), is a tropical species that feeds pelagically and rears a single, slowly growing chick. The fledging periods (hatching to flight) of the two species are approximately 30 and 60 days, respectively. Our objectives were to describe physiological differences associated with differences in growth rate and to determine how these differences might bear upon the evolution of slow growth in pelagic seabirds.

METHODS

We studied Sooty Terns on Bush Key, Dry Tortugas, Florida between 4 and 15 June 1972. The colony has been described by Watson (1908), Sprunt (1948), Robertson (1964), and Dinsmore (1972). We studied

Common Terns on Great Gull Island, New York between 1 and 9 July 1972. Aspects of Common Tern biology on Great Gull Island have been described by Cooper et al. (1970), Hays (1970), Collins and LeCroy (1972), and LeCroy and LeCroy (1974).

We estimated ambient temperatures and solar radiation in several microhabitats by measuring the temperature of water in vials either wrapped in aluminum foil or painted with a flat black paint (Ricklefs and Hainsworth 1968). We used a Gossen "Super Pilot" CdS light meter to measure incident light in each microhabitat.

We weighed chicks to 0.1 g on an Ohaus triple-beam balance placed in a box to reduce the effects of wind. We measured feathers and appendages with flexible plastic rulers and body temperatures with a Yellow Springs Instruments thermistor inserted into the proventriculus.

To determine the size and composition of body parts, we collected a series of 26 chicks, varying between 1 and about 50 days of age, and 4 adults of the Sooty Tern, and 22 chicks, 1 to 28 days of age, and 2 adults of the Common Tern. The birds were frozen and analyzed in Philadelphia within 1 month after collection. We dissected the specimens into 10 body components: integument (skin and feathers), head, legs, wings, pectoral muscle, heart, liver, stomach (contents removed), intestines (contents not removed), and the remainder (body). Each component was analyzed separately for water, lipid, and nonlipid dry matter content (Ricklefs 1975, 1979a). All components having bone and some components comprised of soft tissues were combusted in a muffle furnace at 550°C to determine ash content. To calculate the energy content of individual birds, we used energy equivalents of 38 kJ/g lipid and 20 kJ/g nonlipid dry matter (assumes 13% ash) (Ricklefs 1974).

We measured oxygen consumption in a closed circuit apparatus consisting in series of a chamber for the bird, a small chamber fitted with a thermometer and oxygen probe, tubes containing silica gel to remove water, and tubes containing potassium hydroxide to remove carbon dioxide (Ricklefs et al. 1980). Air was circulated through the system with a Dynapump. Oxygen concentration was measured with a Beckman Fieldlab oxygen analyzer. We used four different chambers, depending on the size of the bird. The total volumes of the systems, measured by filling the chambers and tubes with water, were 878, 1,801, and 3,735 cc for measurements of Common Terns, and 1,184, 1,728, 2,653, and 3,813 cc for measurements of Sooty Terns. After a bird was placed in a chamber, we allowed the system to equilibrate for about a minute before we began readings. We kept the bird in the chamber until the oxygen concentration had been reduced from 21 to 18 or 19%, which usually required 5–15 min. In calculating the rate of oxygen consumption, we corrected the volume of the system for the volume of the bird by subtracting its weight. We also corrected all values to sea level pressure (760 mm Hg) and 0°C. The energy equivalent of oxygen consumption is 20.1 kJ/l O₂. Most determinations were obtained at ambient temperatures.

We obtained samples of food from Sooty Terns by forcing chicks to regurgitate and from Common Terns by picking up fish that had been dropped by adults at the colony. The food samples were analyzed for amounts of water, lipid, nonlipid dry material, and ash. We determined rates of defecation and respiratory water loss by placing chicks in plastic boxes, lined with aluminum foil and having false bottoms of wire mesh, for periods of 6 h (Common Terns) or 12 h (Sooty Terns). The excreta were scraped off the foil, dried, and weighed. Total water loss was estimated as the loss of mass of the chick.

RESULTS

Aging criteria.—We knew the true chronological ages of all Common Terns from records of the dates of hatching provided by Helen Hays. But in order to minimize the variation among individuals, we used an index to developmental age obtained by comparing the wing length of each chick to the relationship between age and wing length for Common Terns on Great Gull Island during 1968 (Collins and LeCroy 1972).

The growth of Sooty Terns on Bush Key has not been reported, but increments of increase in wing length over the interval between 4–6 June and 14 June 1972 indicated that wing growth on Bush Key closely paralleled that of Sooty Terns on Manana Island, Oahu, Hawaii (Burckhalter unpubl. obs., Ricklefs and White 1975, White et al. 1976). We therefore used the wing length growth curve from Manana Island as an aging criterion for chicks on Bush Key, except for those that hatched during our study period.

TABLE 1. Constants of growth equations fitted to weights of Common and Sooty tern chicks.

Species and locality	Number of chicks	Asymptote (g)	Growth rate (days ⁻¹) ^a	Inflection (days)	t_{10-90} ^b (days)	Source
Common Tern						
England	9	130	0.300	8.3	14.7	Pearson (1968)
England B/1 ^c		125	0.254	8.6	17.3	Langham (1972)
England B/2		122	0.249	9.5	17.5	Langham (1972)
Great Gull Island, New York (1968)	15	110	0.265	8.2	16.6	Collins and LeCroy (1972)
Sooty Tern						
Manana Island, Hawaii	12 ^d	205	0.073	10.8	42.1	Burckhalter (pers. comm.)
Manana Island, Hawaii	22 ^e	190	0.086	8.8	36.0	Brown (1976)

^a Value of K for the logistic equation (Common Tern) or Gompertz equation (Sooty Tern).

^b For the logistic equation $t_{10-90} = 4.4/K$; for the Gompertz equation $t_{10-90} = 3.09/K$ (see Ricklefs 1967).

^c Brood size.

^d 1968.

^e 1972.

The growth curve.—We fitted equations to curves of growth in body mass using the graphical method of Ricklefs (1967). Masses of Common Tern chicks were reasonably described by the logistic equation

$$M(t) = A / \{1 + \exp[-K(t - t_i)]\},$$

where $M(t)$ is the mass at age t , t_i is the inflection point of the growth curve, A is the asymptote of the growth curve, and K is a growth rate constant. Increase in the mass of Sooty Terns was described better by the Gompertz equation

$$M(t) = A \exp\{-\exp[-K(t - t_i)]\}$$

(see Ricklefs 1967, 1968).

Constants of equations fitted to growth curves are presented in Table 1. Because the growth curve of each species was fitted by a different equation, the growth rate constants (K) cannot be compared directly. In such cases, one may calculate the time required to grow from 10% to 90% of asymptotic weight (t_{10-90}) as an index to the length of the development period. The value of t_{10-90} for the Sooty Tern on Manana Island (average 39 days) is about 2.3 times that of the Common Tern on Great Gull Island (17 days).

Because Sooty chicks fledge at about the same age on Manana Island and on Bush Key, rate constants (K) for the two populations probably are similar. For comparisons of developmental changes between species, we doubled the age of Common Tern chicks to bring the growth curves of the two species into general agreement and more or less equalize the length of the nestling period. The shapes of the growth curves do differ markedly, however, and we shall return to this point below.

The hatchlings.—Body proportions and composition of newly hatched Sooty and Common terns are presented in Table 2. The masses of 13 Common Tern neonates on Great Gull Island varied between 12.0 and 17.7 g (average 14.8 g, or 12.8% of adult weight) (Collins and LeCroy 1972). Four Sooty Tern neonates collected by us on Bush Key weighed between 20.0 and 22.4 g (average 21.1 g, 12.1% of adult mass). If these masses are representative, neonates of the two species are about the same proportion of adult mass.

The levels of water and nonlipid dry matter in the chicks and adults of the two species are similar. Adult Sooty Terns have a somewhat heavier integument than

TABLE 2. Characteristics of newly hatched chicks and of adults of the Sooty Tern and the Common Tern.

	Chick		Adult	
	Sooty Tern	Common Tern	Sooty Tern	Common Tern
Number of individuals	4	1	2	2
Mass ^a	20.5	14.9	176.7	111.5
Percentage water	75.2	78.7	61.2	59.9
Percentage nonlipid dry material	20.8	19.4	33.9	34.1
Percentage lipid	4.0	1.9	7.1	6.0
Water index ^b of				
whole bird	3.58	4.06	1.74	1.76
integument	1.95	2.42	0.93	0.67
stomach	3.44	3.84	2.56	2.64
leg	3.47	3.80	1.74	1.82
pectoral muscle	4.55	7.05	2.75	2.91
head	5.13	5.75	2.33	2.60
Percentage of nonlipid wet mass				
integument	15.0	13.5	22.2	19.6
body	30.5	29.5	25.7	24.6
intestine	2.6	5.9	2.7	4.7
heart	1.4	1.3	1.7	1.6
liver	4.3	4.8	6.0	6.3
head	20.8	20.0	9.4	10.2
pectoral muscle	1.3	1.3	15.3	16.3
legs	17.1	15.8	4.3	4.5
wings	3.4	3.7	10.3	10.1
stomach	3.7	4.4	2.4	2.3
total	100.1	100.2	100.0	100.2

^a Sum of all components, therefore slightly less than the preprocessing mass.

^b Water/nonlipid dry matter.

adult Common Terns, but their proportions are otherwise nearly identical. Compared to Common Tern neonates, Sooty Tern neonates appear to have higher levels of lipids and slightly lower levels of water at hatching.

Developmental changes.—Several indices of development, including lengths of appendages and proportions and composition of tissues, are graphed in Figs. 1 through 3. Conspicuous differences between the species include the early elongation of the scapular feathers of the Sooty Tern, which shade the chick's back from the sun (Dinsmore 1972), and lower proportions of water in some of the tissues of the Sooty Tern during the first half of the development period.

Ambient and body temperature.—We recorded ambient temperatures and incident solar radiation in three microhabitats on Bush Key: (a) exposed sand, where vials were set vertically on corks to avoid conduction of heat from the sand itself; (b) base of a bush, hung 7 cm above the ground, typical of the microhabitat that Sooty Tern chicks seek during the heat of the day; and (c) 1 m inside a large bush, about 1 m off the ground in a well-shaded position; this was the coolest microhabitat in the area, but it was unavailable to Sooty chicks.

We made similar measurements in three microhabitats on Great Gull Island: (a) exposed ground; (b) ground level in deep grass, a microhabitat within which young Common Tern chicks spent most of their day; and (c) approximately 1.5 m above the ground, exposed to the sky. We measured the temperature of the water in the vials hourly throughout one sunny day in each location (5 June and 4 July) and made occasional readings on other days and at night. Although incident light levels were similar in the two localities and solar radiation elevated the temperature of the

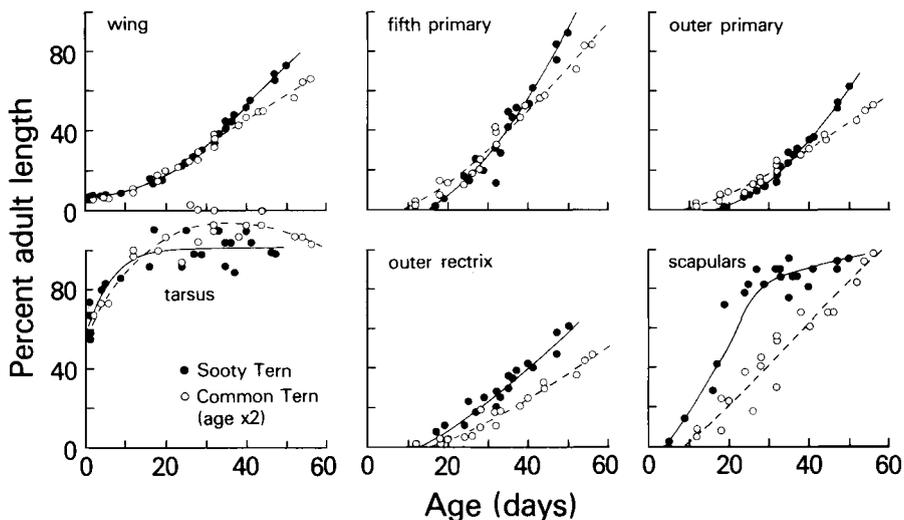


Fig. 1. Increase in the length of appendages and feathers of Common Terns (open symbols, dashed lines) and Sooty Terns (solid symbols, solid lines) as a function of age. For the Common Tern, the age scale has been expanded two-fold in order to make the development periods of the two species more nearly coincide. Measurements are expressed as percentages of adult values ($n = 2$ and 4, respectively). All measurements were obtained from specimens collected for analysis of body components.

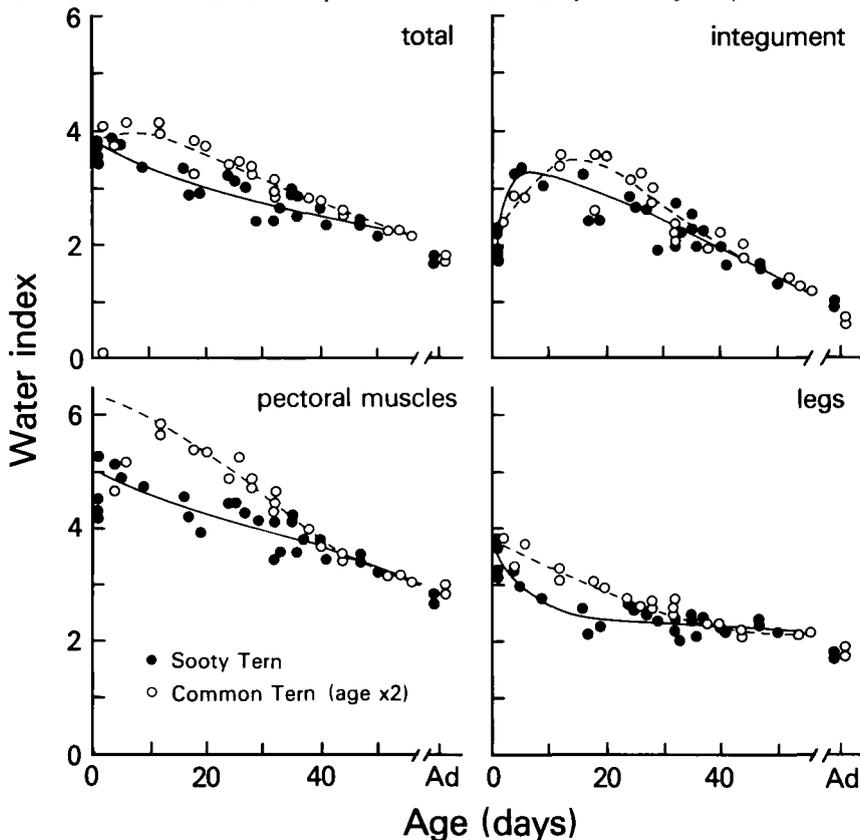


Fig. 2. Water index (water/nonlipid dry mass) of individuals, their integuments, pectoral muscles, and legs, of Common and Sooty terns. Symbols and age scale as in Fig. 1.

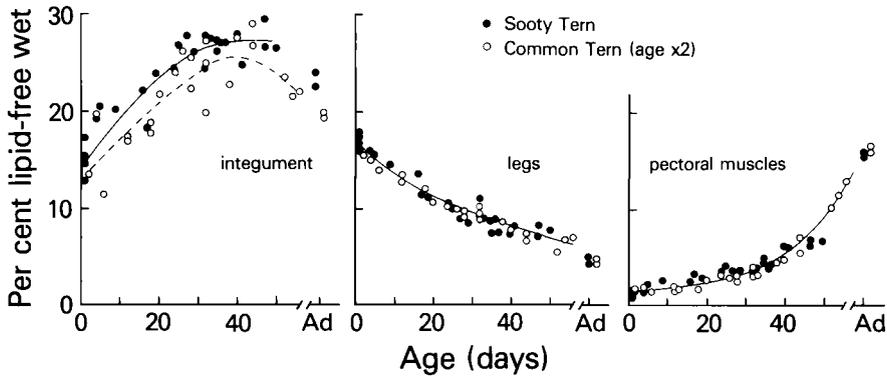


Fig. 3. Lipid-free wet mass of the integument, legs, and pectoral muscle, expressed as a percentage of the total, of Common and Sooty terns. Symbols and age scale as in Fig. 1.

water in the black vials a similar amount, ambient temperatures on Great Gull Island were 10°C lower than on Bush Key both during the day (25°C versus 35°C) and during the night (17°C and 27°C) (Fig. 4).

We recorded the body temperatures of numerous tern chicks at different times of the day and night (Fig. 5). Sooty Tern chicks in these samples were at least 2 weeks old, and Common Tern chicks were at least 1 week old. The body temperatures of both species were elevated during midday compared to early morning and evening. On one clear day (5 June), most Sooty Tern chicks had temperatures of between 41 and 43°C during the period from 1200 to 1800. The temperatures of Common Terns varied between 40 and 42°C during the early afternoon. On one heavily overcast day (12 June), body temperatures of Sooty Tern chicks were between 39 and 41°C at 1600.

At night, the average body temperature of Sooty Tern chicks decreased, and the range of temperature appeared to increase. Some individuals cooled to as low as 37–38°C. The temperatures of birds captured at night (10 June) that regurgitated food were about a degree higher [$40.5 (\pm 0.36 \text{ SD})$ °C, $n = 4$] than those that did not regurgitate and presumably had not been fed recently [$39.6 (\pm 0.51 \text{ SD})$ °C, $n = 9$]. We did not record the temperatures of Common Terns at night under natural conditions. Birds kept overnight in cages did not become hypothermic.

Oxygen consumption.—We obtained 82 measurements of oxygen consumption from Sooty Tern chicks and adults taken directly from the field. Measurements were paired, i.e. we repeated the first determination after opening the system to the outside air but not removing the subject from its chamber. In most cases, differences between successive determinations were less than $0.2 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ and few exceeded $0.5 \text{ ml O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. Paired measurements were averaged and treated as single values. Metabolic rate, expressed on a mass-specific basis, reached a peak of $2.18 (\pm 0.34 \text{ SE}) \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ between 11 and 20 days and decreased to about $1.4 (\pm 0.1 \text{ SE}) \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ thereafter (Table 3). The rate of oxygen consumption by four adults between 2300 and 0200 also was about $1.4 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, except for one underweight (150-g) individual (2.6 and $2.8 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) whose body temperature was elevated (42.2°C) at the end of the determination, apparently owing to activity in the metabolism chamber. Determinations on two birds 1 and 2 days old were

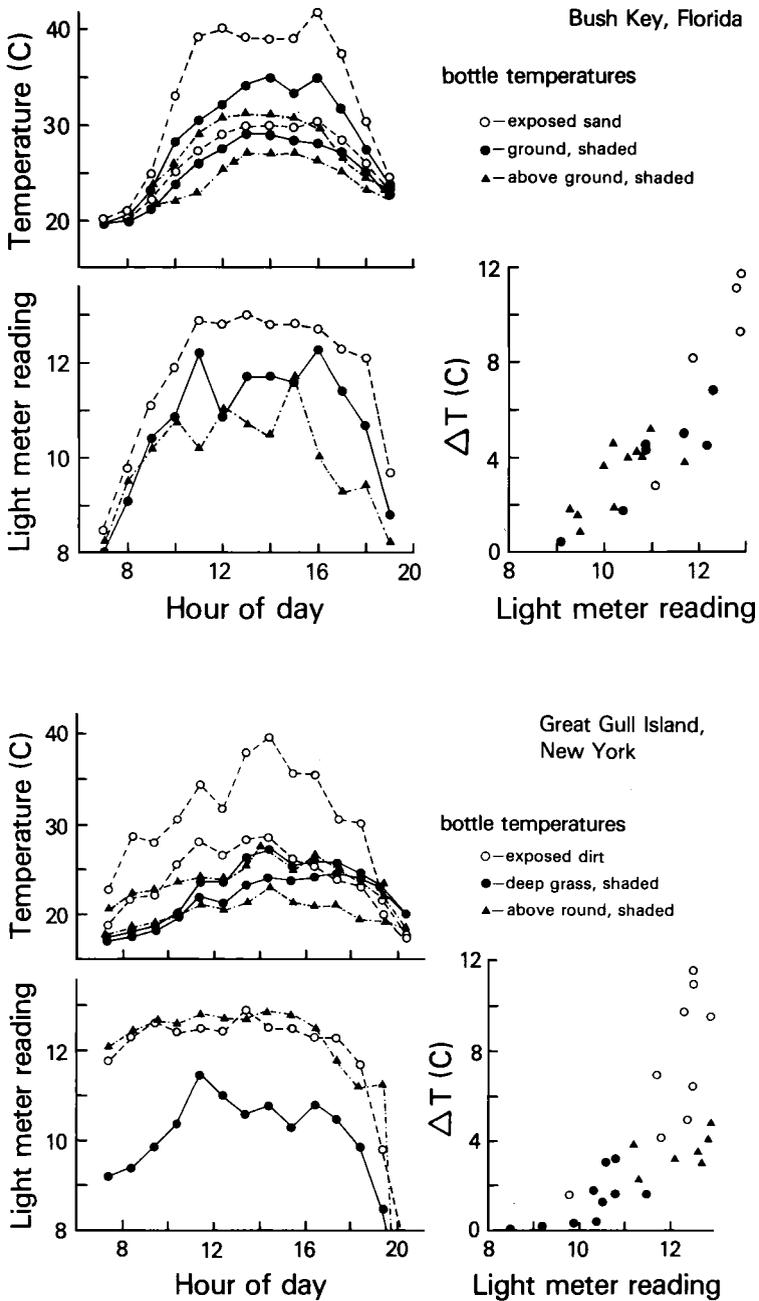


Fig. 4. Diurnal course of temperature in black and foil-covered vials (top left) and solar radiation (bottom left) in three microhabitats on Bush Key, Dry Tortugas, and Great Gull Island, New York. Graphs at right depict difference in temperature between black and foil-covered vials (see text) as a function of solar radiation.

TABLE 3. Oxygen consumption of Sooty Tern chicks and adults at ambient temperatures of 26–38°C.

	Estimated age (days)				
	1–10	11–20	21–30	31–43	Adult
Total					
<i>n</i>	5	7	12	13	4
\bar{x}	86.2	158.4	185.5	221.8	298.2
SD	46.2	53.3	40.3	64.2	75.1
SE	20.7	20.1	11.6	17.8	37.5
Mass-specific					
<i>n</i>	5	7	12	13	4
\bar{x}	1.75	2.18	1.46	1.35	1.75
SD	0.57	0.89	0.30	0.35	0.64
SE	0.25	0.34	0.09	0.10	0.32

1.05 and 2.46 cc O₂·g⁻¹·h⁻¹, respectively. The younger of these birds had just hatched and weighed only 21 g. The older bird with the higher metabolic rate weighed 30 g.

Our measurements of oxygen consumption were evenly distributed throughout the day and night, but no diel pattern in metabolism was evident. Furthermore, between 26 and 38°C, oxygen consumption was not related to temperature, suggesting that Sooty Tern chicks are within their thermoneutral zone throughout this range.

We obtained 69 values for oxygen consumption from Common Terns. We repeated trials on most individuals within an hour, after several other subjects had been run. We measured metabolism at prevailing air temperatures (18–34°C) and obtained ambient temperatures between 30 and 38°C in a box heated by an electric light. This range exceeded the temperatures normally experienced by the chicks. We conducted the trials between 0600 and 1800, except for one series between 0000 and 0100.

The metabolic rate of the Common Tern increased at lower temperatures, nearly doubling between 30 and 20°C (Fig. 6). Metabolism appeared to vary little with age, although the metabolic rates of birds 1–5 days old were slightly lower than the average and those of birds 6–10 days old were frequently higher than the average.

Metabolism appeared to decrease at night by about 1.0 cc O₂·g⁻¹·h⁻¹. Among nestlings 11 days of age and older, at ambient temperatures between 18 and 22°C, oxygen consumption averaged 3.26 (±0.12 SE) cc O₂·g⁻¹·h⁻¹ between 0500 and 0900 and 2.31 (±0.25 SE) cc O₂·g⁻¹·h⁻¹ between 0000 and 0100. Adults consumed less oxygen than chicks when tested at an ambient temperature of 20°C between 0700 and 0900 [2.54 (±0.25 SE), 1.84–3.12, *n* = 5) cc O₂·g⁻¹·h⁻¹].

Water loss.—We used loss of mass to estimate water loss in a group of chicks maintained at prevailing ambient temperatures. Because each gram of lipid metabolized results in the formation of 0.96 g of water, the net change in mass resulting from gas exchange is negligible, and loss of mass provides a reasonable index to water loss. We kept 10 Sooty Tern Chicks in small cages in the shade for periods of up to 4 days without food or water. To calculate the percentage loss of mass per day, we used the expression: percentage mass loss = 2 × (W₁ - W₂)(W₁ + W₂)⁻¹ × 100, where W₁ and W₂ are masses recorded at an interval of 24 h. Loss of mass averaged 12.1% (±0.9 SE)/day or 5.0 (±0.4 SE) mg·g⁻¹·h⁻¹ in 25 trials. Dry matter in feces, which was excreted at an average rate of 5 mg·g⁻¹·day⁻¹ (see

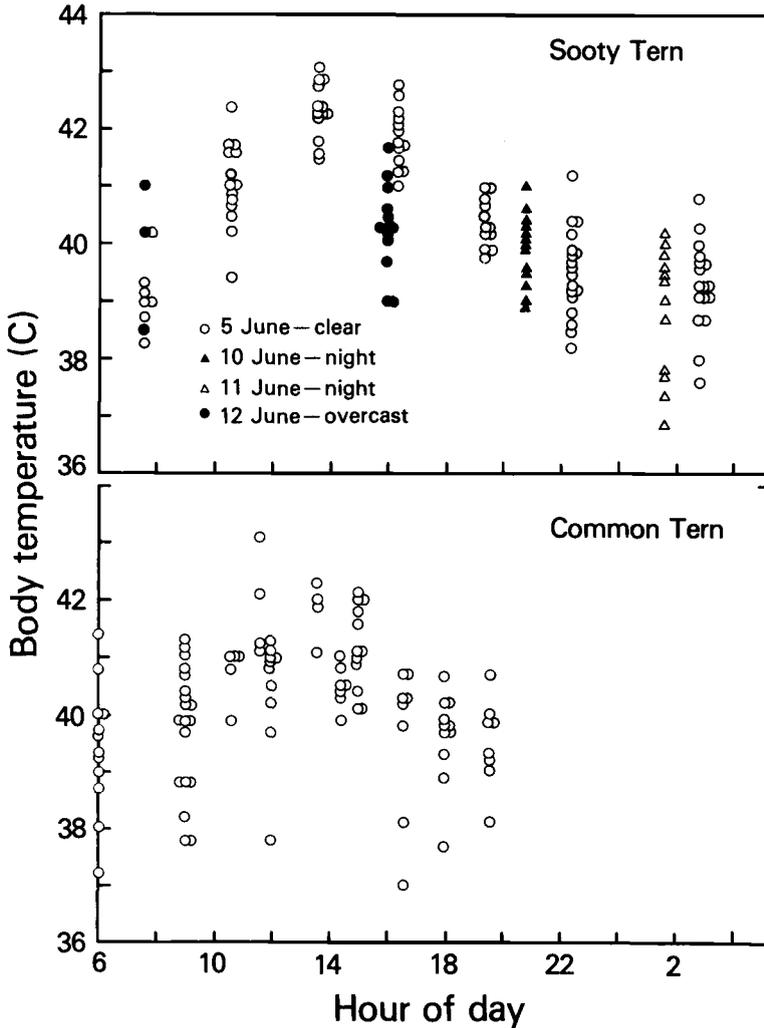


Fig. 5. Body temperatures of Sooty Terns (top) and Common Terns (bottom) throughout the course of a day.

below), was negligible in comparison. Twenty-two similar determinations on Common Tern chicks, lasting between 6 and 10 h, revealed loss of mass at a rate of 41.5% (± 3.4 SE)/day, or 17.3 (± 1.4 SE) $\text{mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. Dry matter in feces accounted for about 4% of the loss.

Food and excreta.—Sooty Terns feed their young small fish and squids (Watson 1908, Ashmole and Ashmole 1967, Potthoff and Richards 1970, Dinsmore 1972, Brown 1976). The meal is usually regurgitated by the adult in large quantity, and the condition of the contents varies from fairly fresh to partially digested. Common Terns bring one or a few fish carried in their bills to their young.

We collected nine samples of food regurgitated from Sooty Tern chicks and adults. Water contents of the samples varied between 75 and 80%; of the dry matter, 6–14% was lipid and 12–22% was ash. Two samples of fresh fish collected from

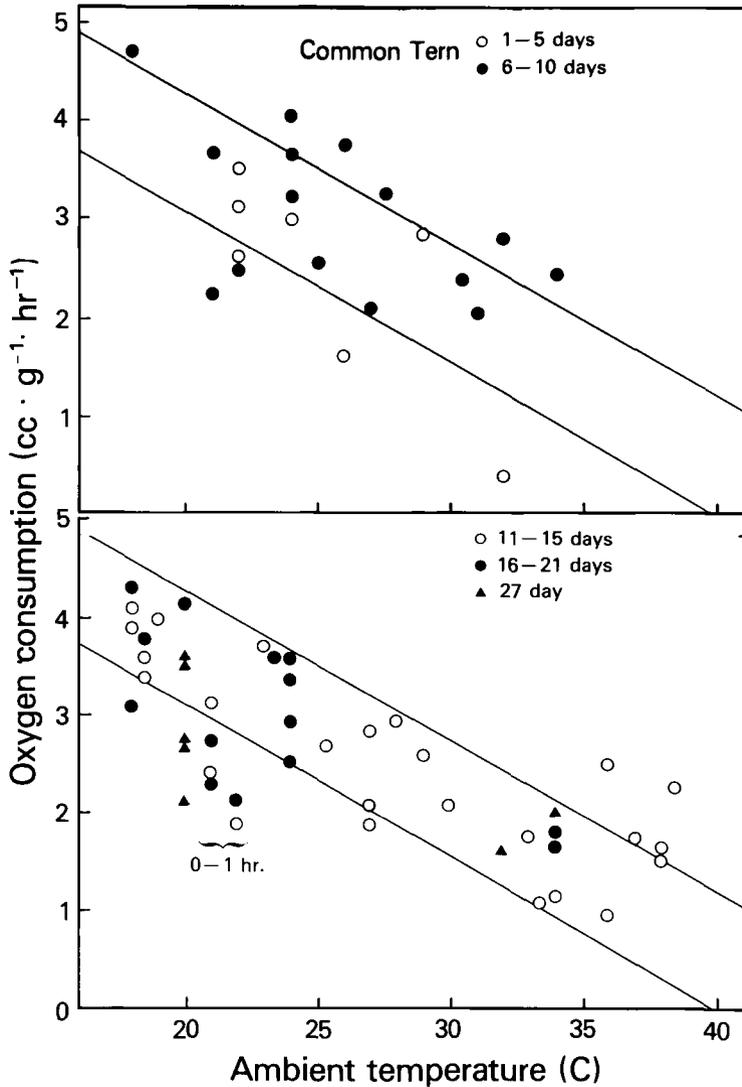


Fig. 6. Oxygen consumption per gram of body mass of Common Tern chicks as a function of ambient (chamber) temperature. The parallel lines on both graphs enclose most of the data for 11-21-day-old chicks.

Common Terns were 64 and 74% water; the dry matter contained 11 and 23% lipid, and 13 and 15% ash.

Rate of defecation (milligrams of dry matter per gram body weight per day) did not appear to vary with age or between day and night periods. The mean defecation rate of the Common Tern ($n = 27$) was $17.4 (\pm 2.3 \text{ SE}) \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$, and of the Sooty Tern, ($n = 25$) $4.6 (\pm 1.2 \text{ SE}) \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$.

DISCUSSION

Energetics of development.—We have calculated tentative energy budgets for tern chicks during the nestling period, assuming that the total metabolized energy is the

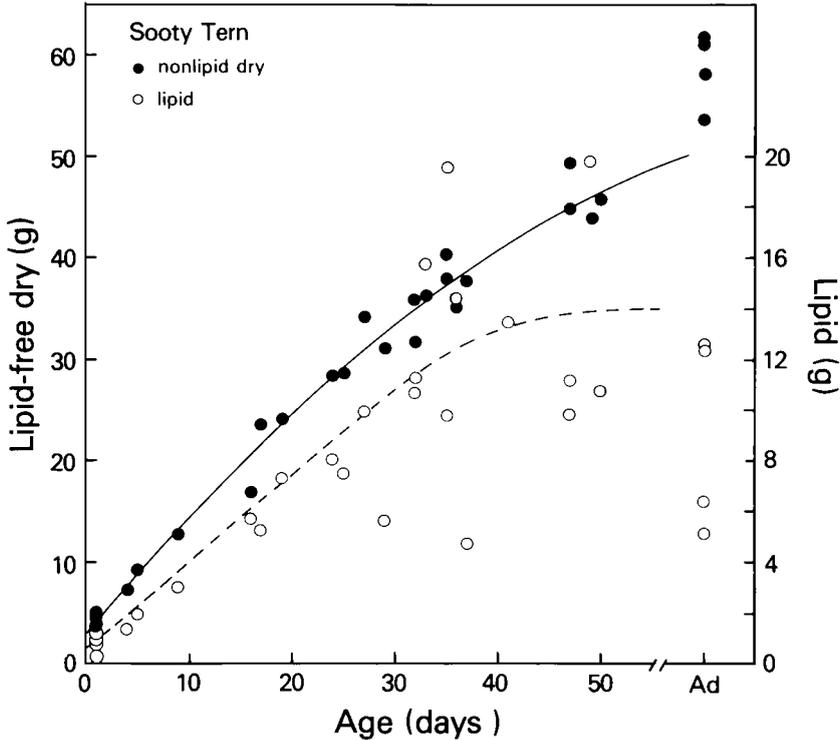


Fig. 7. Increase in mass of lipid and nonlipid dry components of Sooty Tern chicks. Curves were drawn by eye to indicate the trends.

sum of energy respired and that accumulated in biomass per unit time. We were not able to measure energy expended in activity, which has been estimated to be 30–80% of basal metabolic rate in several species (see Dunn 1973, 1980).

The rate of oxygen consumption by Sooty Tern chicks is taken from Table 3. The rate of oxygen consumption by Common Tern chicks was estimated from data in Fig. 6. We assumed that the tendency of metabolism to decrease at night due to inactivity was balanced by the increased cost of temperature regulation. For example, among chicks 11–21 days old, metabolism between 0000 and 0100 at 21–22°C averaged $2.10 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$; during daylight periods at 27–30°C, metabolism averaged $2.09 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ (6 measurements in each group). The difference in temperature between these groups of observations was about equal to the typical day-night differential. In our calculations, we assumed a typical daytime temperature of 22°C (see Fig. 4) and an average rate of oxygen consumption of $3.0 \text{ cc O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ for all age classes. We estimated average body mass for each age group of Common Terns from the data of Collins and LeCroy (1972) for chicks in 1968.

We estimated the accumulation of lipid and nonlipid dry components from curves relating each of these components to age (Fig. 7 and 8). We assumed that the accumulation of energy in tissue required an expenditure for biosynthesis equal to one-third of the energy accumulated (Ricklefs 1974). Energy budget calculations are summarized in Table 4.

The energy budgets of Sooty and Common Tern chicks are compared in Fig. 9. In the Common Tern, the rate of accumulation of energy in lipid (Table 4, column

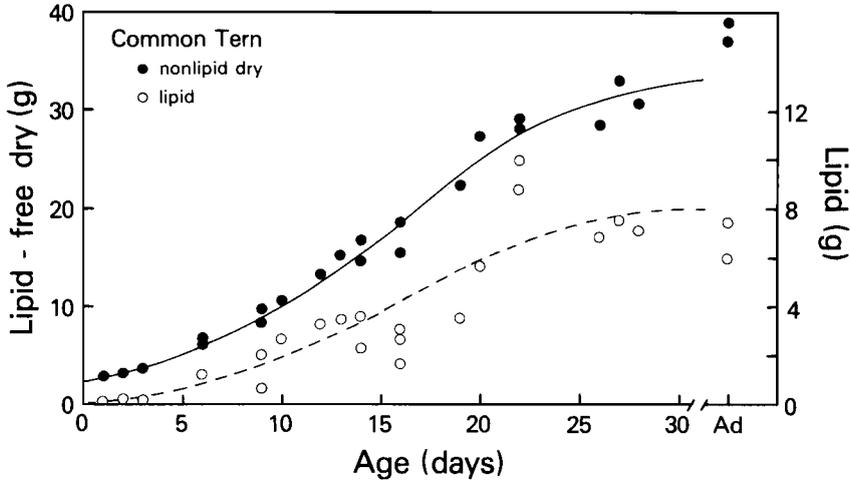


Fig. 8. Increase in mass of lipid and nonlipid dry components of Common Tern chicks. Curves were drawn by eye to indicate the trends.

4) is about 50% that of the accumulation of energy in nonlipid dry matter (column 5) throughout the growth period. In the Sooty Tern, the rate of accumulation of energy in lipid increases from about 60% of that in nonlipid dry matter during the 1st week to almost 75% at the end of the 4th week. Although lipid accumulation drops to near zero by 7 weeks in our table, this drop may be an artefact of sampling, or it may have resulted from poor feeding conditions for terns near the end of our study (White et al. 1976).

The allocation of energy between growth and maintenance differs strikingly in the two terns. In the Common Tern, the growth energy requirement initially is low, rises to a peak at between 15 and 20 days, and then declines (Fig. 9). Maintenance costs increase throughout the growth period as the young become larger. Total metabolized energy, the sum of growth and maintenance, increases steadily until 15–20 days, when it levels off at 175–200 $\text{kJ} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$.

Sooty Tern chicks grow more rapidly than Common Tern chicks during their first week of life, but growth rate does not increase with age. The allocation of energy to growth decreases slowly during the first 30 days of growth and more rapidly thereafter. The total energy requirement increases to within 80% of its highest value (135 kJ/day) within 20 days after hatching.

Lipid reserves of the chicks.—The energy accumulated as lipid by Sooty Tern chicks represents about 11–17% of the metabolized energy during the first 30 days of posthatching life (Table 4). In the Common Tern, lipid reserves accumulate more slowly and do not reach such high levels as in the Sooty Tern, although about 10% of metabolized energy is allocated to lipid storage during the first 2 weeks.

Lipid reserves would be expressed more meaningfully in terms of the metabolic rate of the chick than as mass if the purpose of lipid storage were to provide energy insurance against poor feeding conditions. A 20-day-old Sooty Tern chick carries an average of 7.5 g of lipid and has a maintenance energy requirement of about 75 kJ/day . Assuming 38 kJ/g lipid, stored lipid could maintain the bird for $7.5 \times 38/75 =$

TABLE 4. Calculations of the energy budgets of chicks of the Common Tern and Sooty Tern.^a

Age interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Common Tern											
0-5	76	0.12	0.58	4.6	11.6	16.2	36.7	21.5	31.4	52.9	31
5-10	152	0.26	0.96	9.9	19.2	29.1	73.3	38.8	63.7	102.5	28
10-15	253	0.36	1.36	13.7	27.2	40.9	122.1	54.5	108.6	163.1	25
15-20	310	0.44	1.64	16.7	32.8	49.5	149.5	65.8	133.2	199.0	25
20-25	327	0.50	1.10	11.4	22.0	33.4	157.7	44.4	146.7	191.1	17
25-30	330	0.12	0.50	4.6	10.0	14.6	159.2	19.4	154.4	173.8	8
Sooty Tern											
0-10	86	0.35	1.12	13.3	22.4	35.7	41.5	47.5	29.7	77.2	46
10-20	158	0.35	1.01	13.3	20.2	33.5	76.2	44.6	65.2	109.8	31
20-30	186	0.35	0.90	13.3	18.0	31.3	89.7	41.6	79.4	121.0	26
30-40	222	0.24	0.72	9.1	14.4	23.5	107.1	31.3	99.4	130.7	18
40-50	250	0.08	0.56	3.0	11.2	14.2	120.6	18.9	115.9	134.8	11

^a Explanation of columns:

- (1) Oxygen consumption (cc O₂/h) from Table 2 and Fig. 6.
- (2) Rate of accumulation of lipid (g/day) from Figs. 7 and 8.
- (3) Rate of accumulation of nonlipid dry matter (g/day) from Figs. 7 and 8.
- (4) Energy equivalent of lipid accumulation (kJ/day) = (2) × 38 kJ/g lipid.
- (5) Energy equivalent of accumulation of nonlipid dry matter (kJ/day) = (3) × 20 kJ/g.
- (6) Energy equivalent of tissue accumulation (kJ/day) = (4) + (5).
- (7) Energy equivalent of oxygen consumption (kJ/day) = (1) × 24 h/day × 20.1 kJ/l O₂ + 1,000 ml/l.
- (8) Total energy requirement for growth (kJ/day), assuming production efficiency of 75% = (6) × 1.33.
- (9) Total energy expenditure for maintenance (kJ/day) = (7) - 0.33 × (6).
- (10) Total energy expenditure for growth and maintenance (kJ/day) = (8) + (9).
- (11) Energetic efficiency of tissue accumulation (growth efficiency, %) = (6) ÷ (10) × 100.

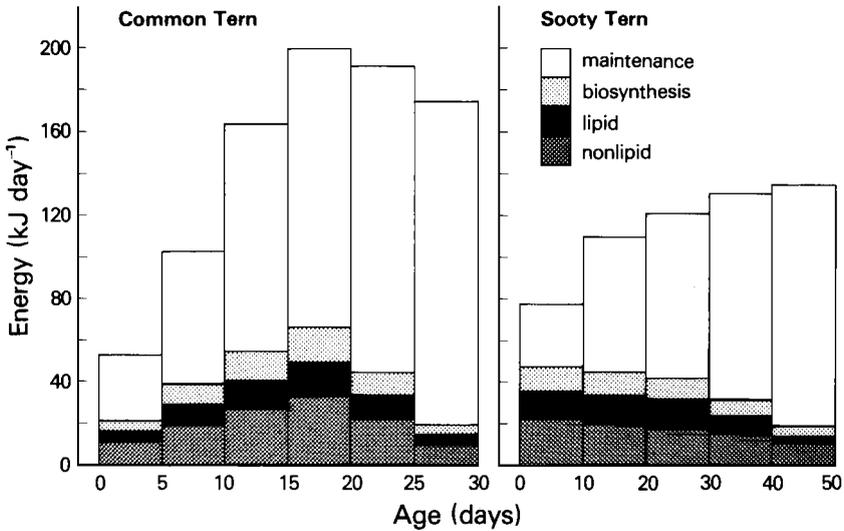


Fig. 9. Energy budgets of Common and Sooty tern chicks as a function of age. Values are from Table 4.

3.8 days. A similar calculation for a 10-day-old Common Tern gives a value of about 1 day ($2.0 \times 38/75$). For 40-day-old Sooty Tern chicks and 20-day-old Common Tern chicks, comparable values are 4.8 days and 1.4 days; for 5-day-old and 2.5-day-old chicks, they are 2.9 and 0.4 days. These calculations assume that all lipid can be metabolized, that there is no energetic cost of growth during periods of starvation, and that activity is negligible. Even accounting for these assumptions, the chicks of Sooty Terns would appear to be able to withstand longer periods of food deprivation than those of Common Terns.

Water balance of the chicks.—Tern chicks obtain all their water from food. This supply must replace water lost through excretion and respiration. Water is obtainable as free water in the food and as that formed during the oxidative metabolism of protein and lipids. The total supply of water is approximately equal to the total mass of the prey consumed minus the mass of tissue accumulated by the chick. To calculate the amount of food consumed by the chick, we divided the metabolic requirement for energy by the energy equivalent of the food. Assuming the typical meal of a tern to be 70% water, 3.5% lipids, 22% metabolizable protein, and 4.5% ash and undigestible remains, its energy content is $0.035 \times 38 + 0.22 \times 23 = 6.4$ kJ/g. This value is similar to that (5.9) reported for commercially harvested species of fish (see Ricklefs 1974).

Focusing on the 20-day-old Sooty Tern chick once more for a sample calculation, we note that the total water intake, including potential metabolically produced water, is the total metabolizable energy (about $115 \text{ kJ} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$) divided by 6.4 kcal/g, or $18 \text{ g water} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$. From this we must subtract an average growth rate of 4 g/day, giving a net water intake of $14 \text{ g} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$. We conservatively estimate respiratory and fecal water loss to be $5 \text{ mg H}_2\text{O} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ (see above). For a 106-g chick, this amounts to $12.7 \text{ g H}_2\text{O} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$. At 40 days the same calculations indicate that chicks assimilate 18.5 g and lose $19.7 \text{ g H}_2\text{O} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$.

Comparable values for Common Terns, assuming water is lost at a rate of $17.3 \text{ mg H}_2\text{O} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, are 11.8 g/day intake and 20.8 g/day loss on day 10, and 26.3 g/day intake and 44.4 g/day loss on day 20. Our estimates of water intake and loss by Sooty Tern chicks are approximately balanced and indicate that water flux is on the order of $5 \text{ mg H}_2\text{O} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. Our estimate of water loss by Common Tern chicks exceeds that for water intake by 50% or more, perhaps because short-term measurements during daylight hours overestimate the average rate of weight loss. We nonetheless conclude that water flux per gram of mass in the Common Tern chick is 2 to 3 times that of the Sooty Tern chick. But we cannot determine whether or not the chicks of either species live close to the point of water stress. Sooty Tern chicks do have conspicuous morphological and behavioral adaptations to reduce insolation. It is conceivable that lipid storage, which increases water intake by elevating metabolized energy 10–20% and which provides a reserve of metabolic water, is in fact an adaptation to increase tolerance of short-term heat stress.

Energetic benefits of slow growth.—The growth rate and the shape of the growth curve of the Sooty Tern are adjusted so as to make the energy requirement of the chick relatively uniform throughout most of the development period. This pattern utilizes most efficiently the ability of the parents to gather food, which presumably is independent of the age of the chick. Because the energy requirement of the chick during the first 20 days after hatching increases from about 55% to over 80% of the maximum rate, parent birds ought to be able to forage less and devote more time to brooding and shading their chicks during this early period. In 369 h of observing chicks less than 2 weeks old, Dinsmore (1972) noted that females spent 42.5% and males 35.8% of the time with their chicks. After the end of the 3rd week, adults spent little time at the nest.

The energy budget of the Sooty Tern chick is such that any increase in growth rate during the entire nestling period would increase the maximum energy requirement of the young. If the rate of growth between 20 and 30 days of age were doubled, the energy requirement for growth would increase from 41.6 to 83.2 kJ/day, and the total energy requirement from 121 to 163 kJ/day, about 20% above the maximum level of 135 kJ/day (ignoring expenditures for activity). If the growth rate were increased 50%, the energy requirement for growth would increase to 62.4 kJ/day and the total requirement to 142 kJ/day, about 5% above the maximum level.

Growth rate during the first 2 weeks presumably could be increased greatly without increasing the maximum energy requirement of the chick. Indeed, during the first 4 days after hatching, the relative growth rate of the Sooty Tern chick (20%/day) is similar to that of the Common Tern chick (18%/day).

The energy budget of the Common Tern indicates that, during the period of most rapid growth (0–20 days), the potential feeding capabilities of the adults are not well-utilized. The chicks are rarely attended after the first 4 days. Between 5 and 10 days of age, the chicks metabolize only half their maximum level of 199 kJ/day. If the growth rate of Common Tern chicks were reduced uniformly by half over the entire growth period, the maximum energy requirement would be reduced by 12% to 169 kJ/day.

The energy budget of the family unit.—The energy required by the single, slowly growing chick of the Sooty Tern presumably increases the parents' foraging rate, over and above what they must themselves consume, less than the energy required by two or three rapidly growing chicks increases the foraging rate of adult Common

Terns. In order to calculate the energy budget of the family unit, we have made some assumptions about the energy needed for various activities. First, we estimated that one Sooty Tern chick requires a maximum of 135 kJ/day and that three Common Tern Chicks require a maximum of 600 kJ/day. We assumed that resting adult Sooty Terns require energy at a rate of 1.5 times basal metabolisms (about 3.6 kJ/h; Aschoff and Pohl 1970, Utter and Le Febvre 1973, King 1974). Over a 24-h period, this sums to 130 kJ/bird, or 260 kJ/pair. To rear their single chick, adult Sooty Terns must therefore increase their foraging time by about 50%, assuming that food is gathered in direct proportion to foraging time. Similarly, to rear a brood of three, adult Common Terns each must increase their foraging time by more than 200%.

Over and above the energy requirement of the young, one must account for the traveling time of the adult between the nesting and feeding areas. This time is much longer for Sooty Terns, which may feed up to 160 km, and commonly up to 80 km from Bush Key, than it is for Common Terns, which often feed within sight of the colony on Great Gull Island. Sooty Terns make few trips, usually one per day, and regurgitate large quantities of food to the young, whereas Common Terns make many trips carrying a single fish in their bill. If the mass of fish brought averaged 2–3 g and had an energy content of 13–20 kJ, each adult would have to make 10–15 trips to satisfy the needs of three fully-grown chicks. It may be reasonable to assume, therefore, that time spent traveling between feeding and breeding areas is of the same order of magnitude in both species of terns.

Slow growth in pelagic seabirds.—Among seabirds, prolonged development is found almost exclusively among pelagic species, of which the Sooty Tern is typical. Slow growth may (1) reduce the energy requirement of the chick, (2) bring the requirement for scarce, essential nutrients into line with their concentration in the diet, and (3) result from selection for increased precocity of the chick.

The energy budget of the Sooty Tern chick does not allow us to distinguish among these hypotheses. Growth rate could be increased by 33% without raising the maximum energy requirement; doubling growth rate would increase the maximum by only 20%, not even taking into account the energy requirement of activity. These calculations argue against energy limitation. But the shape of the growth curve of the Sooty Tern is adjusted so that development is energetically more efficient, from the standpoint of the parents' ability to provide food, than is the growth curve of the Common Tern. In the first, growth slows more rapidly with age, and the maximum energy requirement is reached at an earlier age. This form of growth curve is common among pelagic seabirds (Ricklefs 1968).

A consequence of reducing the rate of growth is to reduce the requirement for nutrients that are essential for building tissues, relative to the requirement for metabolizable energy. In this case, the benefits vary in direct proportion to the change in growth rate. Prolonging the development period by 50% makes 50% more nutrients available over the entire development period. But terns feed their chicks a high quality diet similar to that which supports rapid growth in such birds as cormorants and herons, and so there are no clearly supportive data for the nutrient-limitation hypothesis at present. We need to know more about supplies and requirements of essential nutrients.

In broad comparisons among species, rate of growth is inversely related to precocity of development of locomotion and temperature regulation (Ricklefs 1973, 1979a, b). Early maturation of skeletal muscle and other tissue is accompanied by

decreasing water levels as contractile proteins and other functional elements are accumulated in tissues. Sooty Tern neonates have lower proportions of water in their tissues than do Common Tern neonates (Table 2), suggesting that the first have acquired more mature function at hatching than the second. The difference in water content between the two species is accentuated during the first one-third of the postnatal development period, during which the water indices of the legs and pectoral muscles of the Sooty Tern drop well below those of the Common Tern (Fig. 2). These differences disappear before fledging.

The water contents of the legs of the two species of terns differ most about 15% of the way through the nestling period (10 and 5 days), when the water indices are about 2.5 and 3.0 (71 and 75% water) in the Sooty Tern and Common Tern, respectively. Comparisons between species and between different-aged chicks of the same species have shown that a 4% difference in water content at this level is equivalent to a two-fold difference in the growth rate of the legs (Ricklefs 1979b). Ricklefs (1973, 1979a, b) has argued that in most precocial species with late acquisition of flight (i.e. Charadriiformes, Anseriformes), the growth rate of the legs sets the overall pace of development. The legs are the primary source of mobility and of heat for temperature regulation, the two functions that distinguish precocial and altricial species. If this hypothesis were confirmed, the earlier maturation of the Sooty Tern would be sufficient to account for its slower development compared to the Common Tern. It is possible that the extremely crowded conditions and intense activity within colonies of Sooty Terns have selected earlier development of mobility in chicks than in those of the Common Tern, which spend much of the day resting quietly under cover of vegetation. Alternatively, the level of precocity may be adjusted to match the growth rate, itself determined by limits imposed by energy or nutrients.

Although anecdotal evidence could be cited to support each of the hypotheses concerning slow growth in pelagic seabirds, the problem will not be fully resolved until detailed comparative studies have more fully investigated the many facets of seabird biology touched upon in this paper.

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