

## SOME CONSIDERATIONS ON THE REPRODUCTIVE ENERGETICS OF PELAGIC SEABIRDS

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**ABSTRACT.**—I develop a model of the energetics of breeding seabirds that incorporates energy requirements at the nest site, rate of energy gathering at sea, and constraints on transporting energy between the feeding area and the breeding colony. Energy requirements are greatest during the period of chick brooding, but an upper limit to the volume or mass of food that parents can carry may ultimately limit brood size to one and preclude rapid growth in pelagic species. Meal sizes are typically 14–18% of adult mass. Feeding rate and energy density of the meal also influence rate of energy delivery to the chick. These considerations suggest that data on diet quality, meal size, and feeding frequency may provide a basis for comparing feeding ecology and corresponding breeding adaptations among species of pelagic seabirds.

Pelagic seabirds forage at great distances from their breeding colonies and return to feed their young at most once each day, and frequently less often. This definition applies to all species of Sphenisciformes (which are not considered here) and Procellariiformes, and many Pelecaniformes (boobies, frigatebirds, tropicbirds) and Charadriiformes (noddies, some terns, gulls, and auklets) nesting on remote islands at all latitudes. Most of these species share a set of reproductive characteristics (single-egg clutch, prolonged incubation period, and slow chick growth) that have suggested energy limitation (Lack 1968). This situation is thought of as arising from three sources: 1) patchy and sparse dispersion of food resources making prey difficult to locate and capture, 2) irregular and unpredictable fluctuations in food availability, requiring birds to adjust reproductive requirements to a minimum anticipated level, and 3) constraints on the ability of birds to transport food between the feeding and nesting site. Severe energy limitation is often regarded as limiting brood size in pelagic seabirds to a single chick. In most experiments in which brood size was increased from 1 to 2, parents did not rear the additional offspring (e.g., Rice and Kenyon 1962, Harris 1966). Slow postnatal development may be an additional means by which the energy demands of reproduction are reduced (Ricklefs, in press). Werschkul and Jackson (1979) have alternatively attributed slow growth rate in pelagic seabirds to the lack of sibling competition (but see Ricklefs 1982), in which case parents may benefit from the reduced daily energy requirement of a slowly growing chick. The accumulation of large quantities of fat by the chicks of some seabirds, especially petrels, has been viewed as an adaptation to a fluctuating and unpredictable food resource (e.g., Lack 1968).

Balancing this view of seabird reproduction

based on food limitation is the observation that pelagic seabirds are among the most long-lived of any group of animals of similar size (e.g., Ashmole 1971, Harris 1977). Hence, food shortages critical enough to threaten the lives of adult seabirds appear to be infrequent. One may argue that adults require less food when they are at sea during the nonbreeding period than they do when nesting, and that while at sea they may range widely in search of suitable feeding areas. If so, the low reproductive rates and long development periods of pelagic seabirds would appear to derive from the special circumstance of having to feed on the open ocean while tied by nesting to a particular locality. This circumstance may impose energy restriction in several ways. First, suitable feeding habitats close to nesting colonies may be less available than areas chosen from a broader area of the ocean. In particular, if local food resources fluctuate unpredictably, birds tied to a particular area must adjust their reproduction to the minimum expected resource level. Second, Ashmole (1963) suggested that the high concentration of seabirds around tropical nesting colonies may depress the local availability of food and thus affect reproduction through density-dependent feedback. Third, the limitation may be derived, not from the quality of the food resource itself, but rather from the problem of transporting food between the feeding area and the nest site.

In this paper, I develop a simple model of the reproductive energetics of pelagic seabirds, incorporating the problem of transporting energy. I then explore some of the implications of this model for reproductive adaptations. Although I have not proposed any new factors or circumstances to explain both the particular adaptations of pelagic seabirds as a group or variation in these adaptations among pelagic seabirds, I have treated energy requirement and food provisioning in a novel fashion that clarifies the problem of reproductive energetics in seabirds and suggests new avenues of investigation.

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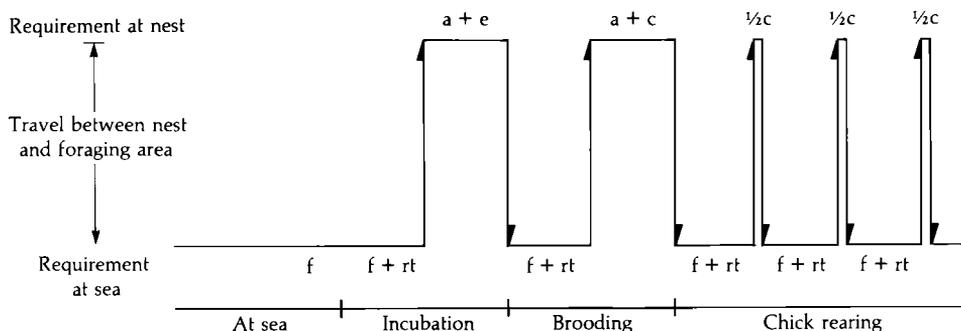


FIGURE 1. A model of the energetics of reproduction in pelagic seabirds based upon a species in which adults return to the colony either to exchange with their mates or feed their chicks after a 24-hour foraging cycle.  $f$  = energy required by adult during the foraging cycle,  $rt$  = energy required for one round-trip between the feeding area and the breeding colony,  $a$  = daily energy requirement (DER) of an adult at the nest,  $e$  = DER of the incubation cost of the egg,  $c$  = DER of the chick. The model could be modified for any length of foraging cycle.

### THE MODEL

The model distinguishes foraging at sea and activities associated with reproduction at the breeding colony (Fig. 1). These activities are connected by round trips between the two areas. While foraging at sea, birds maintain a positive energy balance. That is, food intake not only supplies the energy required to forage but also provides a surplus of energy available to support travel between the feeding area and the nesting colony combined with the energy demands of reproduction at the nest. In my model, I define the energy provided for reproduction by each foraging bout as the net energy return of foraging minus the energetic cost of a single round trip between the feeding area and the breeding colony.

During the nonreproductive period, the energy balance of adults is potentially most positive because they do not have to support reproduction or travel between feeding and breeding areas; molt imposes an unknown cost at this time, however, and food supplies may be lower or less available during the nonbreeding than the breeding season. For breeders, the daily energy (power) requirements of individuals (adults plus eggs or chicks) at the nest site vary with stage of reproduction. During the incubation period, each foraging bout (including feeding and traveling between the nest and the feeding area) must supply the requirements of the adults' incubation bout. In all pelagic seabirds, both members of the pair share incubation and chick rearing, and so time during the incubation period is split roughly half and half between foraging or resting and incubation. After hatching, the energy demands of reproduction increase dramatically. Between the day the chick hatches and the end of the chick-

brooding period, each day of foraging at sea must provide the adult with enough stored energy to supply a day's requirements of one brooding adult plus the chick. After the end of the brooding period, however, adults are no longer tied to the nest site, except briefly to feed the chick, and if need be they may devote all their time to foraging. During this period, until the chick leaves the nesting colony, each day's foraging need furnish only one-half the power requirements of the growing chick, the other half being supplied by the second member of the pair. As a result, during the rearing period, power requirements of reproductive activity at the nest are considerably reduced compared to those during the incubation and brooding stages.

The net energy available for reproduction could be increased by reducing the frequency of foraging trips between the feeding areas and the colonies, particularly if the distance were great. This option may be limited by restrictions on the amount of food that adults can carry per trip, as I shall discuss below. Before doing so, however, I shall provide some estimates for energy demands at the nest.

### POWER REQUIREMENTS OF REPRODUCTION

The energetics of reproduction have been determined for only a few species of pelagic seabirds, and the available studies must be considered as very preliminary (e.g., Dunn 1980, Drent and Daan 1980, Ricklefs et al. 1980, Ricklefs and White 1981). Patterns of energy requirement likely vary considerably from species to species, but here I report data on the Sooty Tern (*Sterna fuscata*) to illustrate the basic pattern. I assume that the power requirement of an incubating adult

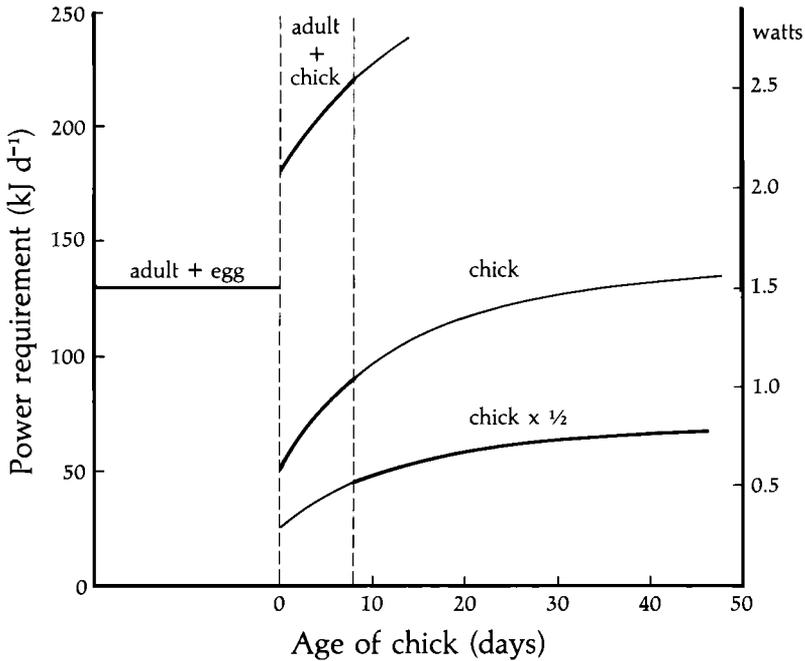


FIGURE 2. Power requirements for reproduction at the nest based on data for the Sooty Tern (after Ricklefs and White 1981).

Sooty Tern is approximately 1.5 times its standard metabolic rate, or SMR (see King 1974, Mugaas and King 1981). Using published allometric equations to estimate SMR (Aschoff and Pohl 1970) results in a value of about  $130 \text{ kJ d}^{-1}$  (1.50 W). Because Sooty Terns incubate a single egg in a warm climate, incubation probably requires little or no excess heat production by the adult. During the middle of the day, Sooty Terns spend more time shading their eggs than warming them by direct contact with the brood patch (Dinsmore 1972) and metabolism may be elevated over its thermoneutral level (MacMillen et al. 1977). The power requirement of the chick increases from approximately  $50 \text{ kJ d}^{-1}$  (0.58 W) at hatching to a maximum of  $135 \text{ kJ d}^{-1}$  (1.56 W) when the chick is fully grown (Ricklefs and White 1981). These estimates do not include activity by either the adult or the chick, but they probably accurately portray the relative power demands during different stages of the nest cycle (Fig. 2).

During the incubation period, the power requirement of the single adult is  $130 \text{ kJ d}^{-1}$  (1.50 W). During the chick brooding period, approximately eight days on the Dry Tortugas, Florida (Dinsmore 1972), the power requirements for brooding and of the growing chick sum to be-

tween 180 and  $220 \text{ kJ d}^{-1}$  (2.08 and 2.55 W). After the end of the brooding period, one-half the power requirement of the chick, which must be supplied each day by each parent, drops to about  $45 \text{ kJ d}^{-1}$  (0.50 W) initially and increases to almost  $70 \text{ kJ d}^{-1}$  (0.81 W) by the time the chick is fully grown. According to this model, the maximum power requirement during the chick-rearing period is approximately one-third the maximum during the brooding stage and about one-half the requirement of the adult during the incubation period.

If adults balanced their energy budgets during the incubation period and if the food supply did not vary over the nesting season, then we must conclude that during the chick-rearing period adults could usually gather much more food than the chicks require. Furthermore, if adults balanced their energy budgets during the chick-brooding stage—I know of no data concerning this point—the discrepancy between the amount of food adults can gather and what they have to provide for their chicks would be even greater. Under such circumstances, pelagic seabirds might be able to rear a second chick with little difficulty except, perhaps, during the brooding stage. The failure of twinning experiments (Palmer 1962, Rice and Kenyon 1962, Harris 1966) suggests,

however, that the ability of parents to supply the chick's requirements are constrained by factors other than their ability to gather food. Although the quality of the diet, meaning the relative proportions of certain essential nutrients, may bear upon the growth rate of the chick, diet quality cannot itself be responsible for the small brood size, unless chicks made up potential dietary limitations of essential nutrients at rapid rates of growth by consuming more food rather than reducing growth rate. Therefore, either birds are not energetically constrained during the chick-rearing period and brood size is limited by factors other than rate of energy supply at that time, or the amount of energy that can be delivered to the chick is limited by the ability of adults to transport food between feeding areas and the nest site. I shall elaborate below that constraints upon feed size have less bearing upon the power requirement of the adult bird at the nest site because this demand can be satisfied by stored fat carried at a high energy density.

#### FEED SIZES IN PELAGIC SEABIRDS

The size of the feed brought to the chick is known for a small number of seabirds. In a few species, food samples have been obtained by regurgitation from adults returning to the nest site, but it is difficult to know whether such samples represent the full amount carried by the adult. Studies reporting the masses of regurgitated food samples rarely have verified by dissection that complete feeds have been obtained. The simplest and most reliable way to measure the size of the feed is by the increment of mass of the chick upon feeding. This technique is most practical for species that feed their chicks no more than once each day; sizes of feeds may be determined by periodically weighing the chick throughout the feeding period. Because meals are assimilated and water is excreted quickly, chicks must be weighed frequently so as not to underestimate grossly the size of the feed (compare Harper 1976 and Richdale 1965). Most of the studies reported here were based upon weighings at 3-hour or 4-hour intervals. Ricklefs (unpubl. data) estimated that about 25% of the mass of meals of Christmas Shearwater and Phoenix Petrel chicks was lost during a 4-hour period following feedings. If feeds occur half-way between weighings, on average, meal size would be underestimated by about 15%.

Unless feeding is observed directly, the investigator must judge whether a chick has been fed by one or both parents during the interval between weighings. In some species, such as some diving petrels (Pelecanoididae), in which feeding rates are high and both parents visit the colony during the same brief period each night, the re-

corded mass increment usually is twice the average meal size delivered by each parent. For species that feed their chicks infrequently, mass increments are more often due to a single feeding, and it is often possible to distinguish unusually large mass increases as resulting from two feedings. Although this technique has limitations, it is beginning to produce data that reveal certain patterns in the foraging ecology of pelagic seabirds.

Feeding rate and feed size are summarized in Table 1. One must remember that these are representative values only and that meal size and, especially, feeding rate may vary widely over seasons, years, and localities. The average feed size in most of the species falls between 14 and 18% of adult body mass. Lower values were recorded for the Northern Gannet (*Morus bassanus*), which feeds primarily inshore and may make several trips per day to the nest site, particularly during the early part of the development period (Montevocchi and Porter 1980), and for the Brown Noddy (*Anous stolidus*). Values about 18% have been reported only for the diving petrels. The median mass of 27 complete stomach samples of adult Adelie Penguins (*Pygoscelis adeliae*) collected during the chick-rearing period at Cape Crozier, Antarctica, was 500–600 g, or 14–17% adult mass (Emison 1968). Meal size, expressed as % adult mass, and adult mass appear to be unrelated (Fig. 3; excluding the gannet by virtue of its being an inshore feeder). Although some meals are much larger than the average, the available data (Table 1) suggest that seabirds, as a group, have a characteristic feed size and that the rate of energy delivery to the chick may be limited by the amount that can be carried by the parent. In the Sooty Tern, average feed size is approximately 25 g and meals have an energy density of between 4 and 5 kJ g<sup>-1</sup> (estimated from compositional data in Ricklefs and White 1981). Hence feeds of between 100 and 125 kJ are provided to chicks at an average rate of 1.2 and 1.6 times per day in two studies; the total energy delivered (120–200 kJ d<sup>-1</sup>, excreted energy not discounted) is on the same order as the estimated power requirement of a single, fully grown chick (135 kJ d<sup>-1</sup>).

If feed size has an upper limit, it could be imposed either by 1) the maximum volume of the proventriculus, or other storage organ, 2) by the added energy required to transport additional food, or 3) by other aerodynamic considerations that prevent adults from lifting heavier meals. For the energetic cost of transporting additional food to impose an abrupt upper limit to feed size, cost of transport per gram of food carried would have to increase abruptly at large meal size.

TABLE 1  
CHARACTERISTICS OF MEALS FED TO SEABIRD CHICKS

Species	Adult mass (g)	Feeding rate <sup>a</sup> (d <sup>-1</sup> )	Feed mass (g)		Sample size (n)	CV <sup>c</sup> (%)	% of adult mass	Method <sup>d</sup>
			Range	Mean (SE)				
<b>Procellariidae</b>								
<i>Pachyptila turtur</i> (1) <sup>a</sup> Fairy Prion	111	ca. 1		16.6	57		15	I
<i>Puffinus nativitatis</i> (2) Christmas Shearwater	340	0.63	30-60	48.2 (2.4)	14	19	14	I (4)
<i>Pterodroma alba</i> (2) Phoenix Petrel	272	0.36	30-85	49.4 (7.6)	8	44	18	I (4)
<b>Hydrobatidae</b>								
<i>Oceanodroma leucorhoa</i> (3) Leach's Storm-Petrel	45	0.27		6.3 (3.6)	34	58	14	I (3)
<i>Oceanodroma furcata</i> (4) Fork-tailed Storm-Petrel	60			7.5		32	13	
<b>Pelecanoididae</b>								
<i>Pelecanoides georgicus</i> (5) Georgian Diving Petrel (6)	105	ca. 1		18.6	9		18	I (3)
<i>Pelecanoides urinatrix</i> (6) Common Diving Petrel	105	0.89	13.5-36	22.3 (0.3)	149	15	21	I (3)
	127	0.94	10-31	26.0 (0.4)	146	16	20	I (3)
<b>Phaethontidae</b>								
<i>Phaethon rubricauda</i> (7) Red-tailed Tropicbird	650	0.49	55-125	96.1 (4.6)	26	24	15	I (4)
<b>Sulidae</b>								
<i>Sula bassana</i> (8) Northern Gannet (9)	3000		150-500	c. 250			8	R
	3263	1+		359		7	11	R
<i>Sula sula</i> (10) Red-footed Booby (10)	1003			126			13	I (3)
	982	0.45		144			15	I
	900	0.74	65-200	142.0 (9.7)	23	33	16	I (4)
<b>Sternidae</b>								
<i>Sterna lunata</i> (7) Gray-backed Tern		1.0	8-19	13.1 (0.7)	28	27		I (4)
<i>Sterna fuscata</i> (11) Sooty Tern (7)	175	0.79	9-46	25.1 (2.5)	15	38	14	I (3)
	175	0.57	14-47	25.9 (2.4)	16	37	15	I (4)
<i>Anous stolidus</i> (11) Brown Noddy (7)	160	0.92		15.5			10	I (3)
	160	1.0	10-25	18.3 (1.4)	10	24	11	I (4)
<b>Alcidae</b>								
<i>Ptychoramphus aleuticus</i> (12) Cassin's Auklet	167	1.0	8.6-45.6	27.8 (2.1)	22	35	17	R

<sup>a</sup> (1) Harper 1976; (2) R. E. Ricklefs, unpubl. data from Christmas Island (Pacific Ocean); (3) R. E. Ricklefs, unpubl. data from Kent Island, New Brunswick; (4) Boersma et al. (1980); (5) Payne and Prince (1979); (6) D. D. Roby and R. E. Ricklefs, unpubl. data from Bird Island, South Georgia; (7) R. Shea and R. E. Ricklefs, unpubl. data from Midway Islands; (8) Nelson (1978a); (9) Montevecchi and Porter (1980); (10) Nelson (1978b); (11) Brown (1975); (12) Manuwal (1972).

<sup>b</sup> Feeding rates expressed per parent.

<sup>c</sup> Standard deviation of feed mass divided by the mean.

<sup>d</sup> R = meals obtained from adults by regurgitation; I (h) = meal size estimated from mass increments over periods of h hours.

The effect of meal size on the power requirements of transport may be estimated as follows. Pennycuik (1969, 1975) describes the power requirement of level flight as

$$P = \frac{W^2}{2pS_dV} + P_p + P_o$$

where  $P$  = total power (watts, W),  $W$  = weight of bird (newtons,  $N = \text{mass [kg]} \times 9.81$ ),  $p$  = air density ( $1.22 \text{ kg m}^{-3}$  at sea level),  $S_d$  = disk area

( $\text{m}^2$ ),  $V$  = forward speed ( $\text{m s}^{-1}$ ),  $P_p$  = parasite power required to overcome the drag of the body, and  $P_o$  = profile power required to overcome the drag of the wings as they are flapped. The first term of the sum is the induced power ( $P_i$ ) required to keep the bird aloft against the pull of gravity. It is the only one of the three power terms that contains body weight as a variable.

The total energy required for travel between the feeding ground and nest site is the power

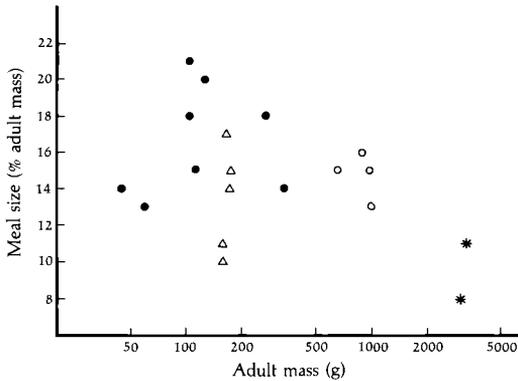


FIGURE 3. Relationship between relative meal size (% adult mass) and adult mass. Solid circles: Procellariiformes; open circles, Pelecaniformes (stars, Northern Gannet); open triangles: Charadriiformes. Data from Table 1.

requirement times time (s), or  $Pt$ . The right-hand terms ( $P_p$  and  $P_c$ ) in the equation for  $P$  are independent of body mass and may be considered as a constant ( $C$ ) in calculating the effect of meal size on transport cost. Assume the following for Sooty Terns: wing span = 0.86 m (Tuck and Heinzel 1978) (therefore  $S_d = 0.58 \text{ m}^2$ ), flight speed ( $V$ ) =  $11 \text{ m s}^{-1}$  (about 25 m.p.h.; guessed) and  $t = 14 \times 10^3 \text{ s}$  (about 4 hours; guessed). For a Sooty Tern of average adult mass (0.180 kg), level flight requires  $0.200 W + C$ , according to the equation for  $P$ . With a 0.025-kg meal, this cost increases to  $0.260 W + C$ . Adding another 0.025 kg would increase the flight cost to  $0.327 W + C$ , or approximately 0.06  $W$  per meal equivalent. During a 4-hour flight, this cost amounts to about 840 J, which is trivial compared to the approximately 112,500 J contained in the meal. I take this result to indicate that the cost of transporting food to the chick, deriving from the effect of meal weight on flight energetics, is so small as not to pose an upper limit to meal size. Alternatively, either volume constraints or limits to the weight that seabirds can lift off the water could set upper limits to meal size.

#### VARIATION IN MEAL SIZE

Some of the studies presented in Table 1 provided data for calculating the coefficient of variation (CV) in the size of the meal delivered by individual parents. The CV is an index to the variability of food provisioning. Excluding the Northern Gannet, CVs were lowest for the diving petrels and the Christmas Shearwater, and they were highest for storm-petrels, the Phoenix Petrel, and the Sooty Tern. In general, as the frequency of feeds decreases among species, the

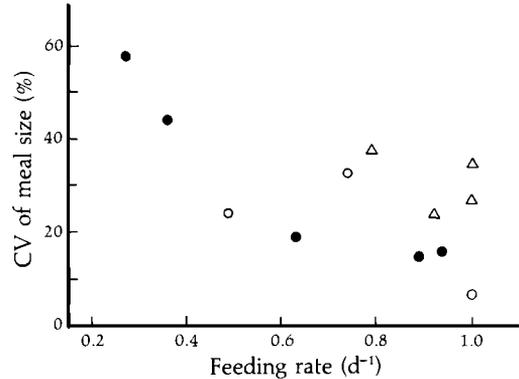


FIGURE 4. Coefficient of variation in meal size as a function of feeding rate per parent. Symbols as in Figure 3.

variability in feed size increases, suggesting that the most pelagically feeding species are faced with the most variable food supplies (Fig. 4). Among the petrels, variability in feed size could be influenced by variation in the degree to which meals are partially digested at sea and concentrated with respect to their lipid content. Also, because feed size could reflect variation in the timing of the feed within the interval between weighings or in the amount of food accepted by the chicks, which may not always equal the full amount brought by the parents to the nest (see Harper 1976). The data in Figure 4 suggest that as a group, terns have greater variation in meal size than do petrels. Other comparisons are worth following up with more detailed field work. For example, the Red-footed Booby appears to have more variable meal size than the Red-tailed Tropicbird, even though the latter has greater intervals between feedings. The Phoenix Petrel and Christmas Shearwater were studied in the same colony at the same time; the shearwater exhibited both a higher feeding rate and lower variation in feed size. Such results suggest that ecological differences between such species may be revealed through a study of their feeding rates. Further resolution of components of variation into seasonal, night-to-night, and between-individual components should provide an index to the variability in the food supply, against which patterns of lipid deposition might be compared.

#### METHOD OF ENERGY TRANSPORT

Energy can be carried from the feeding area to the breeding colony as 1) assimilated energy deposited as lipid stores in the adult, 2) undigested food, or 3) some combination of, or intermediate between, these extremes. Lipid deposits can be utilized only by the adult itself to cover the costs

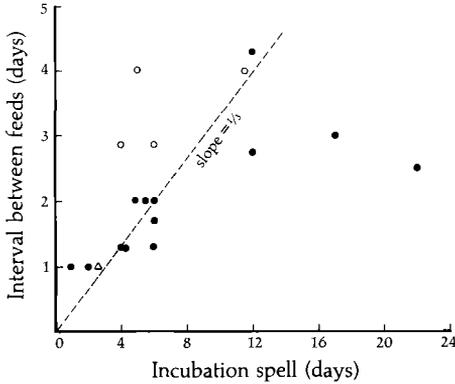


FIGURE 5. Relationship of interval between feeds to incubation spells in Procellariiformes. Data from Lack (1968), solid circles; Harris (1977), open circles; Roby and Ricklefs (1983), open triangle.

of incubation, brooding, and maintenance at the nest. Chicks consume regurgitated food, which may be fresh or partially digested. The manner in which energy is transported determines the amount that can be carried each trip. The energy equivalent of pure lipid is  $38 \text{ kJ g}^{-1}$ . A Sooty Tern with an incubation requirement of  $130 \text{ kJ}$  can satisfy that requirement by carrying less than  $4 \text{ g}$  of lipid from the feeding area to the nest site, i.e., less than one-sixth of the average meal size brought back to the chick. Meals of Sooty Terns were estimated to contain  $4\text{--}5 \text{ kJ g}^{-1}$  (Ricklefs and White 1981). The energy densities of fish average approximately  $6 \text{ kJ g}^{-1}$  (Watt and Merrill 1963), or about one-sixth of pure lipid. Species that consume prey having high concentrations of oil, particularly plankton-feeding seabirds at high latitudes, may have diets with considerably higher energy density. Petrels may further concentrate dietary energy by partial digestion of the meal and retention of lipids in the proventriculus, forming the familiar stomach oils (Ashmole and Ashmole 1967, Ashmole 1971, Clarke and Prince 1976, Warham et al. 1976).

One consequence of the higher energy density of lipid compared to fresh food is that adults may use fat deposits to sustain themselves for longer periods during incubation and the chick brooding stage than they could on an equivalent mass of food brought back undigested. Therefore, one might expect the length of the incubation spell, during which no food is transferred to the chick, to exceed the interval between feeds brought to the chick, where the amount of energy delivered is more severely limited by the size of the feed. In Figure 5, I have plotted the relationship between inter-feed interval and incu-

bation spell for several species of Procellariiformes. Many of these species are distributed close to a line that represents a feeding interval one-third the length of the incubation spell bearing out the expectation.

#### LENGTH OF THE BROODING PERIOD

The model of power requirement portrayed in Figure 1 suggests that the maximum demands upon parents occur during the brooding period. At this time, the parent must support not only itself but also the increasing power requirements of the chick. If at any time during the nest cycle parents must accept a negative energy position, it is during the brooding period (the long fasts of incubating polar penguins excluded). The demands of brooding may explain the rather curtailed chick-brooding periods and early development of endothermy of many pelagic seabirds. The chicks of storm-petrels, which are left alone after 2–4 days of brooding, often in very cold environments, may represent the extreme. Although the power requirements of these chicks might be reduced by extended brooding, the total energy demands upon the parent, including its own maintenance requirements at the nest, may be too much to sustain.

A simple model will illustrate the factors bearing on the length of the brooding period. Assume that the mass of lipid carried to support the parent during brooding spells is negligible compared to the mass of food required by the chick. Assume further that the parent must deliver all the food required by the chick for a day during the brooding period but only half the food required by the chick during the subsequent chick-rearing period. If, under these restrictions, parents additionally can deliver only one-half the maximum amount of food required by the full grown chick, then the brooding period should extend no further than the age at which the chick requires half of its maximum energy consumption when full grown. For the Sooty Tern (Fig. 2), this level is reached when the chick is only a couple of days old. In fact, when the chicks are finally left unbrooded during the day at eight days of age, the estimated power requirement of the chick ( $90 \text{ kJ d}^{-1}$ ) exceeds one-half of the maximum requirement of the full grown chick by about 30%. An energy budget calculated for Leach's Storm-Petrel (Ricklefs et al. 1980) indicates that chicks attain half their maximum power requirement shortly after hatching.

These considerations suggest that longer brooding periods should occur in species that hatch smaller chicks with lower power requirements, and in larger species. For the latter, the mass-specific metabolic rate is lower and a meal representing a given percentage of adult body

mass can supply the power requirements of the chick for a longer period. Among seabirds in general, longer brooding periods are found primarily in larger species, notably penguins, albatrosses, giant fulmars, and Pelecaniformes. The pattern of power requirement by chicks of the inshore-feeding Double-crested Cormorant illustrates the pattern for a large altricial species, and shows that the initial requirement of the small chick is low and that one-half of the maximum power requirement is not reached until after 15 days of age (Dunn 1980). In the Northern Gannet, that point is not reached until 3–4 weeks after hatching (Montevecchi et al. 1983). Prolonged brooding usually is associated with altricial development which, in turn, usually is associated with a low chick power requirement, particularly during the early development period. The energy requirement of the chick and length of brooding period may be mutually adjusted according to relationships that are beyond our ability to model at present.

#### FEEDING RATE

The net energy returned to the nest site conceivably could be increased by increasing the interval between feeds hence reducing costly travel between foraging areas and the nest. When meal size is limited, however, by the mass that the adults can carry, to reduce feeding rate is to bring about a corresponding reduction in the rate of energy delivered to the chick. To some degree, this could be compensated by concentrating lipid in the diet through selective digestion. It is thought that procellariiform birds do this in producing stomach oils that are then regurgitated to the chicks (Ashmole and Ashmole 1967, Ashmole 1971). For Leach's Storm-Petrel, the chick's power requirement of  $90 \text{ kJ d}^{-1}$  could be satisfied by an average meal size of 6.3 grams and a feeding rate of 0.27 feeds per parent per day only if the energy concentration of the diet were about  $26 \text{ kJ g}^{-1}$ , or 70% of the value of pure lipid. The ability of parents to deliver such an energy-concentrated diet may depend in large part on their ability to select prey with high lipid contents. Hence feeding far at sea, tied to long intervals between feeding visits, may be intimately connected with diet selectivity and may be possible only in regions where certain types of prey are available. When the biochemical composition of the diet cannot be altered substantially by selective digestion, prolonging the period between feedings will reduce the energy available to the chick and may require a reduction in growth rate to balance the energy budget. Among Pelecaniformes frequency of feeding and rate of growth are strongly and positively correlated (Harris 1977, Nelson 1977, 1978). This may be related

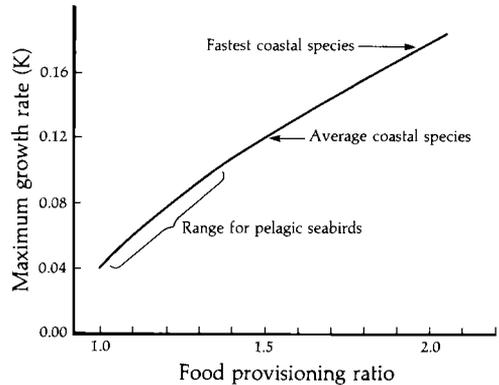


FIGURE 6. Relationship between maximum sustainable growth rate (rate constant of Gompertz equation) and food provisioning ratio (energy delivery rate per chick divided by power requirement of fully grown chick; from Ricklefs 1983a).

directly to the effects of foraging distance on food provisioning.

#### FEEDING RATE AND GROWTH RATE

I (Ricklefs, in press) have recently developed models describing how rapidly chicks can grow with different levels of food provisioning. These models are based upon sigmoid growth of Gompertz form (Ricklefs 1968) and the assumption that the maximum power requirement during the growth period cannot exceed the maximum potential level of food provisioning, which furthermore is assumed to be constant throughout development. I evaluated the model for a 1000-g seabird patterned after the Red-footed Booby. Maximum sustainable growth rate is related to the food delivery rate in Figure 6, where growth rate is expressed as the rate constant ( $\text{d}^{-1}$ ) of the Gompertz equation and rate of food delivery is expressed as the ratio of the delivery rate to the power requirement of a fully grown chick. When the food delivery rate equals this level, and the ratio is thus 1.0, the maximum sustainable growth rate is  $0.041 \text{ d}^{-1}$ . As the level of food provisioning increases above this level the maximum sustainable growth rate increases rapidly, approximately doubling between food provisioning ratios of 1 and 1.2. When the ratio reaches 2, a growth rate of approximately  $0.18 \text{ d}^{-1}$ , 4.5 times faster than that at a ratio of 1, can be supported. The models developed by Ricklefs (in press) indicate that at ratios much in excess of 2, parents should double brood size at the expense of greatly reducing the growth rate of the two chicks.

The maximum growth rate predicted for any seabird the size of the Red-footed Booby is on

the order of  $0.18 \text{ d}^{-1}$ , the minimum  $0.04 \text{ d}^{-1}$ . A survey of growth rates reveals that among 1000-gram species, the range of growth rates observed in pelagic seabirds rearing single chicks is approximately 0.04 to 0.10 (Ricklefs 1973, 1982), corresponding to food provisioning ratios of approximately 1 to 1.3 or 1.4. The average growth rate of inshore feeders rearing broods larger than 1 was approximately  $0.12 \text{ d}^{-1}$ , corresponding to a food provisioning ratio of 1.5 per chick, i.e., a total of 3 to 4.5 for most species. The highest observed growth rates were about that expected for a food provisioning ratio of 2 per chick, i.e., a total of 4 to 6.

If my model realistically assesses the relationship between growth and power requirement in birds, the observed growth rates of pelagic seabirds raise a number of issues. In particular, in no pelagic species does the food provisioning ratio appear to exceed about 1.4; we would expect to observe brood sizes of 1 among species with food provisioning ratios up to 2, or even more with high time-dependent chick mortality. Although pelagic seabirds may possibly be restricted to areas with uniformly low feeding conditions, the food provisioning ratio alternatively may be limited to below 1.4 by the amount of food that parents can carry. For a seabird the size of the Red-footed Booby, carrying 150 g meals at  $5 \text{ kJ g}^{-1}$  at a frequency of 0.45 meals per parent per day, the energy delivered ( $675 \text{ kJ d}^{-1}$ ) is 1.35 times the requirement of the fully grown chick ( $1.5 \times \text{SMR}$ ). At a feeding frequency of 0.74 meals per parent per day, the provisioning ratio is 2.22. For the Sooty Tern, similar calculations give ratios of 1.06 and 1.46 at the feeding frequencies reported in Table I (0.57 and 0.79). If observed feed sizes are close to upper limits, then these calculations lend force to the suggestion that the growth rate of pelagic seabirds is food-limited, directly so by the ability of the parents to carry food in species that feed their young frequently.

#### FUTURE WORK

Using the model presented in this paper to interpret aspects of seabird ecology depends in part upon its quantitative evaluation. Hence to increase the precision of the model is to increase our understanding of how seabirds interact with their environments. Current knowledge of seabird energetics and certain aspects of seabird reproduction is rudimentary, to the point of hindering substantial progress in the study of pelagic birds. In the context of the discussion presented in this paper, I believe that the following areas deserve close attention.

(1) Quantitative theory provides the appropriate context for field observation and experi-

mentation. With minor exceptions, there has been no progress in the development of explicit theory for seabirds in two decades, since the work of D. Lack and N. P. Ashmole during the 1960s. Even many of their ideas on the evolution of reproductive rate and the regulation of seabird populations were not expressed in terms of easily testable predictions. Although seabirds are attractive for many kinds of work, biologists have continually been frustrated by their inability to study the ecology of their subjects away from breeding colonies. Until the techniques of satellite telemetry and on-bird microprocessing of activity data become inexpensive and accessible, we shall have to rely on assessing foraging ecology by indirect means at the nesting colony. To be useful, theories must be expressed in such measurable terms, at least for the present.

The more explicit the theory, the more precise and detailed must be the measurements used to evaluate models. All the relationships discussed in this paper should be written in more complex expressions, reflecting the real complexities of seabird biology. Sensitivity analyses will tell us how precisely we must measure each variable in order to optimally balance research efforts to answer particular questions. Without considering such models in further detail here, it is still possible to indicate some areas that require further work.

(2) Clearly, much of the discussion in this paper has been based on considerations of the power requirements of adults and chicks. These are poorly known, in part because few seabird colonies are amenable to physiological work. That situation is changing with the opening or upgrading of research stations and the increasing portability of apparatus. Where possible, investigators should measure power output directly by the doubly-labelled water technique. It is particularly important to obtain data on incubating and brooding adults, and on chicks both at the end of the brooding period and at the age of maximum power requirement.

(3) A major part of the power requirement of the chick is the accumulation of energy in the tissues of the body. These requirements can be measured only by biochemical analysis of a series of chicks collected during the nesting period. Such specimens could also reveal information on the management of energy reserves by nestlings, particularly of Procellariiformes, which store large quantities of fat as chicks.

(4) The discussion in this paper assumed that adults balanced their energy income and expenditures during the nesting cycle. It is possible, however that they may accept energy deficits for short periods of high power requirements, particularly the chick-brooding period. Trends in

adult mass during the nesting cycle may indicate such periods and their potential effect on the energy budget.

(5) Meal size and feeding rate are particularly revealing of feeding ecology, and their study should be pursued vigorously. Because these measurements are likely to be extremely variable over seasons, years, and localities, their estimation will require a large effort. In many species, this effort might be considerably reduced by continuous recording of chick masses on the nest (e.g., Poole and Shoukimas 1982, Sibly and McCleery 1980), coupled with time lapse photographic records of parental feeding.

(6) Data on food delivery are only as useful as estimates of the energy and nutrient composition of meals are accurate. Recent biochemical work on seabird diets, especially of the food consumed by chicks, must be greatly expanded and incorporated routinely in studies of other aspects of breeding biology.

The model discussed in this paper distinguishes between the food delivered to chicks and the energy carried by parents to fulfill their power requirements at the nest. Direct measurements of the latter by biochemical analysis of adults at the beginning and end of incubation bouts are indicated.

(7) Finally, additional information on growth rate, development of endothermy, parental care of the eggs and chicks, and patterns of fat deposition and utilization will enrich the phenomenology of seabird adaptations and increase the statistical power of comparative and correlative analyses. Measurements of breeding success and adult survival, in experimental studies where practical, will tell us the demographic outcome of the interaction between adaptations of seabirds and their environments, and provide a basis for evolutionary interpretations of the great diversification of seabird biology.

#### SUMMARY

I developed a model that matches the energy requirements of reproduction (i.e., of the eggs, chicks, and adults at the nest site) to the ability of parents to transport energy from the feeding area to the breeding colony. The greatest energy requirement relative to the ability of the parents to provide food occurs during the chick brooding period. At this time, the energetic demands of the nestling are increasing with chick growth while adult foraging is still constrained by the requirement of one parent to remain at the nest site. The ratio of energy demand to supply is also high during the incubation period, when the adult must spend half its time at the nest. Relative energy demands are lowest for each parent during the chick-rearing period, but brood size and the

growth rate of the chick may be limited by the ability of the parents to carry sufficient unassimilated food between the feeding and nesting areas.

This view of reproductive energetics suggests that problems involved in transporting food over long distances, rather than the foraging ability of adults, may limit the reproductive output of seabirds. During the incubation and brooding stages, adults can carry energy needed to maintain themselves at the nest site in the form of stored fat which has a high energy density. Chicks, however, require regurgitated, relatively fresh food transported between the feeding and breeding areas at a low energy density. Measurements of feed sizes in a variety of pelagic seabirds indicate a characteristic feed size on the order of 14 to 18% of adult body mass. The product of the feed size and its energy density sets an upper bound to the amount of energy that can be provided to the chick, assuming one feed per parent per day. In species that feed their young at intervals of more than one day, rate of energy provisioning may be severely reduced. By partial digestion of meals and retention of lipids in the foregut, petrels may have been able to increase the energy density of their feeds, thereby permitting extended foraging bouts. This strategy may be available only to species having high-lipid diets. The models suggests that seabird biologists should pay attention to the size and biochemical composition of feeds, as well as to the energy requirements of reproduction, in order to interpret adaptations of seabirds to their marine environments.

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