

Energy expenditure and food consumption by breeding Cape gannets *Morus capensis*

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ABSTRACT: Gannets (genus *Morus*) are piscivorous seabirds with a breeding distribution restricted to the cool to temperate waters of the mid latitudes. Field metabolic rates of breeding Cape gannets *M. capensis* and their chicks were measured using doubly labelled water. Energy expenditures of adults incubating or brooding chicks at the nest were 2090 kJ d⁻¹ (24.2 W, 2.9 × basal metabolic rate, BMR). Metabolic rates of adults at sea were 4670 kJ d⁻¹ (54.1 W, 6.5 × BMR). Overall field metabolic rates (FMRs), assuming birds spend half their time on land and half at sea, were 3380 kJ d⁻¹ (39.1 W, 4.7 × BMR). Relative FMRs of adult birds were high compared with those of most other volant seabirds and approach those of high latitude seabirds that use mainly flapping flight, including the closely related northern gannet *M. bassanus*. Such high values probably reflect the high energy cost of sustained flapping flight and the plunge-diving foraging of gannets while at sea. Food consumption rates, calculated on the basis of the chemical composition of Cape anchovy *Engraulis capensis* and energy expenditure determined from CO₂ production, averaged 691 g d⁻¹ for incubating or brooding adults and 521 g d⁻¹ for chicks. A pair of gannets successfully raising a chick would consume 246 kg of fish over the course of a breeding season. Total annual consumption of the gannet population in the southern Benguela upwelling system amounted to no more than 23 400 t. Of this 9000 t was accounted for by the commercially important anchovy. This probably represents no more than 1 % of the total adult spawner biomass of this fish in the region.

INTRODUCTION

Seabirds are conspicuous top predators in marine ecosystems. Their presumed importance as consumers has stimulated studies of their energy budgets and food consumption to assess their potential impact in such systems (Wiens & Scott 1975, Furness & Cooper 1982, Croxall 1987). The difficulty of observing these birds at sea, offset by their often easy accessibility at the nest during breeding, has made the doubly labelled water (DLW) technique a powerful tool in assessing energy costs and budgets of individual species (Nagy et al. 1984, Gabrielsen et al. 1987, Nagy 1987, Obst et al. 1987). Such studies have allowed refinement of population food consumption models previously based on extrapolations of laboratory measurements of metabolism.

Because many seabirds have long breeding seasons,

foraging costs of adults attending chicks are liable to form a significant portion of the annual energy budget (Furness & Cooper 1982). Field metabolic rates (FMRs) of seabirds, determined using the DLW technique, are closely correlated with body mass (Nagy 1987). However, flight behaviour and the aerodynamic properties of different species of seabirds may have a considerable influence on energy costs, in particular of foraging (see review by Birt-Friesen et al. 1989). For example, the very low relative energy costs of foraging by albatrosses (Adams et al. 1986, Costa & Prince 1987, Pettit et al. 1988) are consistent with their highly developed behavioural and morphological adaptations for economical flight. Although lower than calculated from published models (e.g. Tucker 1973), energy costs of foraging of the highly volant Wilson's storm-petrel *Oceanites oceanicus* (Obst et al. 1987), which engages in long periods of flapping flight, are considerably higher than albatrosses. The FMRs of least auklets *Aethia pusilla*, and common diving-petrels *Pelecanoides urinatrix* and South Georgia diving-petrels *P.*

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urinatrix, which combine flapping flight with pursuit diving, are similarly high (Roby & Ricklefs 1986). Gannets and boobies (Family: Sulidae) are large, active, volant foragers in temperate and tropical waters (Nelson 1978). Recent work on the northern gannet *Morus bassanus* indicates that its FMRs are the highest yet measured for seabirds (Birt-Friesen et al. 1989). We present here measurements of FMRs of breeding Cape gannets *Morus capensis* which, in contrast to northern gannets, breed and forage in an area characterized by high levels of insolation (Cooper & Siegfried 1976, Nelson 1978). Measurements of the FMRs of adults are combined with energy costs of chick maintenance and growth to estimate total food consumption during breeding.

Cape gannets are confined largely to the Benguela Upwelling system off the southwestern coast of southern Africa, an area that also supports a large purse-seine fishery. Both gannets and the fishery may take the same prey, particularly Cape anchovy *Engraulis capensis* and pilchard *Sardinops ocellatus* (Berruti 1987, Berruti & Colclough 1987) and such consumption estimates are a necessary step in assessing the degree of competition between these 2 consumer groups.

MATERIALS AND METHODS

Cape gannets resident at Bird Island, Lambert's Bay (32°05' S, 18°17' E), South Africa, were studied during the breeding season 1981–82. Metabolic rates (CO₂ production) and water-flux rates were measured using doubly labelled water (DLW; Lifson & McClintock 1966, Nagy 1980, Nagy & Costa 1980) in incubating adults (n = 11), adults attending large chicks (n = 10), and in the chicks themselves (n = 6). Adults were given intra-muscular injections of 0.50 ml water containing 45 atom-% ¹⁸O and 48 atom-% ²H. At least 2 h later, blood samples (ca 2 ml) were taken from a brachial vein, and birds weighed and returned to their nests. Chicks were injected with either 0.15 or 0.25 ml of DLW, depending on body mass. Some measurement intervals covered exclusively on- or off-nest periods. Birds sampled over off-nest periods were captured as they changed incubation or guard shifts, injected, and then held for the 2 h equilibration period before being bled and then released. Adult birds were recaptured on regular checks of study nests conducted throughout the day. Cape gannets are diurnally active, rarely returning to the nest after dusk. On recapture birds were bled and reweighed up to twice. Chicks (estimated age 19 to 45 d) remained at the nest and were bled 21 h to 40 h after initial equilibration and reweighed. An additional 8 birds not used for doubly labelled water measure-

ments were bled and the samples measured for background levels of heavy isotopes.

Isotope concentrations in water distilled from blood samples were measured by Global Geochemistry Corporation, Canoga Park, California, USA. For birds recaptured more than once we used only the initial and final blood sample to determine rates of CO₂ production and water flux. Using the CO₂ equilibration technique, ¹⁸O/¹⁶O ratios in the blood were assessed by isotope ratio-mass spectrometry, as were ²H:¹H ratios in H₂ gas generated from water samples using zinc catalyst. Rates of CO₂ production were calculated from Eq. (2) in Nagy (1980), and water-flux rates from Eq. (4) in Nagy & Costa (1980). Body-water volumes at the time of initial capture were estimated from the dilution space of ¹⁸O upon injection (Nagy 1980). Water volumes at recapture were calculated as initial fractional water content times body mass at recapture.

Time budget. Both male and female Cape gannets share incubation and brooding, one adult usually remaining in attendance at the nest (Nelson 1978). On regular checks of nest sites the activity of injected, breeding adults was recorded as incubating (on or off nest) or brooding (on or off nest).

Field metabolic rates and feeding rates. FMRs were calculated from CO₂ production, assuming an energy equivalent of 25.8 J ml⁻¹. This factor was calculated from the chemical composition of anchovies (72.7% water, 19.7% protein, 5.2% fat and < 0.5% carbohydrate) (South African Fishing Industry Research Institute 1980). Energy equivalents for fat and protein were taken from Schmidt-Nielsen (1979).

Rates of food consumption derived from metabolism measurements were calculated on the basis that anchovy dry mass contains 24.1 kJ g⁻¹ of which 72.2% was assumed metabolizable (Cooper 1978). Thus, the metabolizable energy of anchovy was 4.89 kJ g⁻¹ fresh mass. Rates of food consumption derived from water-influx rates were calculated on the basis that anchovy contains 72.7% H₂O. Metabolism of fish yields an additional 0.13 ml g⁻¹ fresh mass, giving a total of 0.86 ml H₂O g⁻¹ fresh mass.

Basal metabolic rates (BMRs). Five adult non-breeding Cape gannets were collected from Malgas Island (33°03' S, 17°55' E), some 100 km south of Lambert's Bay. Captive birds were fed daily at a rate at which they maintained capture mass (± 8%). Measurements were conducted on post-absorptive birds, at least 12 h since the previous feed, in the laboratory using an open flow respiratory system. Dry, CO₂-free air was pumped through a flow meter (Meterrate[®]) before entering an airtight metabolic chamber (75 l) containing the gannet. Dry, CO₂-free, outlet air was sampled off the main outlet pipe using an additional pump coupled to the sensor of an Ametek[®] S-3A/1 oxygen analyzer. The air

temperature experienced by the bird was measured using a thermocouple and a Fluke® thermometer. Temperatures in the metabolic chamber were maintained between 21 and 23°C by conducting measurements in a temperature-controlled room. Birds were allowed to acclimate in the metabolic chamber for 1½ h before readings commenced. Daytime measurements were conducted between 07:00 and 15:00 h, while nighttime measurements were conducted between 20:00 and 02:00 h.

Flow rates were maintained around 3 l min⁻¹ and calibrated against a bubble meter (Levy 1964), at the beginning and conclusion of every run. Readings of fractional proportion of oxygen in outlet air were taken every 15 min until the period of lowest stable metabolism could be identified. Oxygen consumption was calculated from the equation of Hill (1972) for dry, CO₂-free air converted to energy expenditure (assuming RQ = 0.8, 1 l O₂ = 20.087 kJ) (Gessaman 1987). Birds were within the thermoneutral zone predicted from the appropriate equation in Kendeigh et al. (1977). Accordingly, we assumed the measurements we describe were a good estimate of BMR.

Aerodynamic properties. We measured wing span and wing area of 7 birds in order to calculate aspect ratio (wing span²/wing area) and wing loading (mass in kg × 9.81 m s⁻¹/wing area in m²). Measurements were made from tracing of wing-outline obtained by restraining gannets with their backs to the paper and wings fully extended. Estimates of wing area included body area between wings.

Statistics. Means are quoted as ± 1 standard deviation. Two-tailed *t*-tests (homogeneous variances) and Mann-Whitney *U*-tests (heterogeneous variances) were used to assess significance of differences between means. FMRs and water influx rates of gannets while on and off their nests were estimated by least squares regression analysis, coupled with analysis of covariance to detect significant differences between correlations. Probability values for regressions were calculated using *F*-tests for significance of the regression.

RESULTS

Body mass, mass change and body water

The mean body mass of the 11 incubating adults (2690 ± 110 g) was significantly greater ($t = 3.70$, $df = 19$, $p < 0.005$) than that of the 10 brooding adults (2460 ± 170 g) we studied. Although incubating and brooding adults tended to lose body mass during the DLW measurement intervals (average mass losses of 1.3 and 2.9% of body mass d⁻¹, respectively, during average measurement periods of 2.17 and 1.93 d respectively),

these rates of body mass change were not significantly different from zero change (body mass maintenance), judging by the inclusion of zero within the 95% confidence limits of both mean values. Chicks (mean mass 1430 ± 540 g, $n = 6$) gained body mass at a statistically significant rate (9.3 ± 8.2% d⁻¹, 95% CI = 0.6 to 20.0) during the measurement period (1.04 ± 0.32 d).

Total body water, as a percent of body mass, was significantly lower in incubating adults (66.3 ± 2.1%, $n = 13$) than the brooding adults (71.0 ± 3.9%, $n = 6$) ($U = 66$, $df = 17$, $p < 0.01$). The water content of chicks (71.7 ± 2.1%, $n = 3$) was similar to that of brooding adults.

Field metabolic rate

Rates of CO₂ production were much lower when adult gannets were at the nest than when they were away at sea. Regressions of CO₂ production on percent of time off the nest for incubating adults and for brooding adults were statistically significant. However, analysis of covariance (ANCOVA) indicated that the separate regressions did not differ in either slope or intercept, so data were pooled and a single regression was calculated (Fig. 1). This relationship is highly sig-

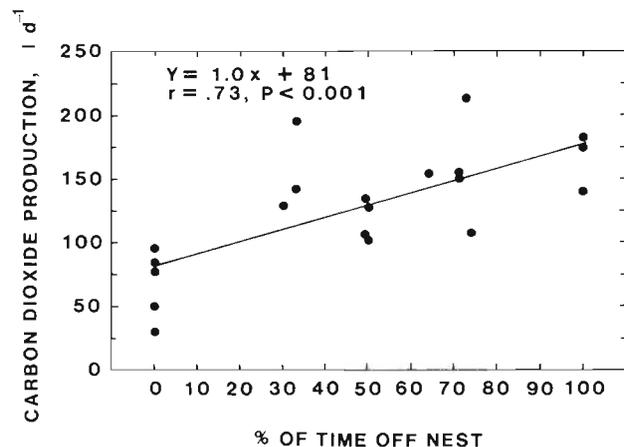


Fig. 1. *Morus capensis*. Carbon dioxide production rate of breeding Cape gannets as a function of the relative proportion of time off nest to the total sampling period

nificant ($F_{(1,19)} = 22.2$, $p < 0.001$), and is described by the equation: Litres CO₂ d⁻¹ = 1.0 (% time off nest) + 81 ($r = 0.73$, standard error of slope = 0.21, SE of *y*-intercept = 12).

The *y*-intercept (0% time off nest) of this regression should represent the rate of CO₂ production of gannets while on the nest. This value is 81 l CO₂ d⁻¹ (95% confidence interval of the prediction ± 74 l CO₂ d⁻¹), which is equivalent to an FMR of 2090 kJ d⁻¹ (24.2 W). A Cape gannet off the nest 100% of the time would be expected to produce 181 l CO₂ d⁻¹ (95% of the predic-

Table 1. *Morus capensis*. Energy expenditure of free ranging, breeding Cape gannets, and comparisons with basal metabolic rates and with energy expenditures of northern gannets *M. bassanus*

	FMR (kJ d ⁻¹)	BMR (kJ d ⁻¹)	Ratio FMR/BMR	Ratio At-sea FMR/ nest FMR	Predicted FMR ^a (kJ d ⁻¹)	Ratio Meas. FMR/ Pred. FMR ^a
Cape gannet (2.58 kg)						
Breeding adults						
On nest	2090	718	2.9			
Off nest	4670	718	6.5	2.2		
Overall	3380	718	4.7		2020	1.7
Northern gannet^b (3.21 kg)						
Breeding adults						
On nest	3452	742	4.7			
Off nest	6000	742	8.1	1.7		
Overall	4865	742	6.6		2356	2.1

^a From Nagy (1987), FMR = 8.01M^{0.704} (M = body mass in g)
^b From Table 1, Birt-Friesen et al. (1989)

tion ± 90 l CO₂ d⁻¹), which is equivalent to 4670 kJ d⁻¹ (54.1 W). Because the breeding adults we studied spent about half their time on the nest and half off the nest, we estimated their overall FMR as the predicted CO₂ production for 50% of the time off the nest: 131 l CO₂ d⁻¹ (95% CI of the prediction ± 72 l CO₂ d⁻¹). This is equivalent to 3380 kJ d⁻¹ (39.1 W) (Table 1).

Mass of chicks ranged from 850 to 2210 g. Correlation coefficients of regressions of log metabolism vs log body mass and log mass specific metabolism only approached significance ($0.1 > p > 0.05$). On average, chicks produced 49 ± 10 l CO₂ d⁻¹, which is equivalent to 1264 kJ d⁻¹ (14.6 W) or 933.1 kJ kg⁻¹ d⁻¹ (10.8 W kg⁻¹).

Water flux rate

Paired *t*-tests comparing water influx rates with water efflux rates of incubating and brooding gannets revealed no significant differences within either group as expected for animals maintaining water balance. As with CO₂ production, there were statistically significant correlations between water influx rates and % time off the nest for both incubating and brooding gannets. ANCOVA indicated no significant difference between the 2 regressions, so the data were pooled, and the overall regression was calculated. This regression (Fig. 2) is described by the equation: ml H₂O influx d⁻¹ = 4.5 (% time off nest) + 161 ($r = 0.75$, SE of slope = 0.9, SE of intercept = 55). The predicted water influx rate for 50% of time off the nest, as an estimate of overall water influx rate in breeding Cape gannets, is 336 ml d⁻¹ (95% CI of prediction = 312 ml d⁻¹). The water influx rates of chicks (average = 273 ± 98 ml d⁻¹) also did not differ significantly (paired *t*-test, $p > 0.05$) from their water efflux rates (average = 177 ± 137 ml d⁻¹).

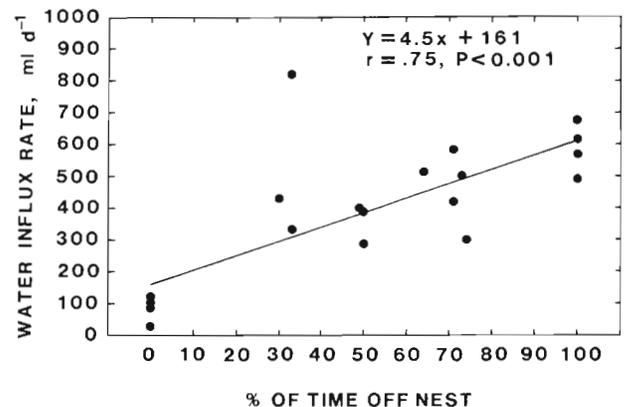


Fig. 2. *Morus capensis*. Water influx rate of breeding Cape gannets as a function of the relative proportion of time off nest to the total sampling period

Basal metabolic rates

BMRs of Cape gannets averaged 323 ± 15 kJ kg⁻¹ d⁻¹ ($n = 5$, mean mass = 2.66 ± 0.16 kg) or 856 ± 42 kJ d⁻¹ during the day, significantly different from the 278 ± 34 kJ kg⁻¹ d⁻¹ ($n = 5$, mean mass 2.62 ± 0.17 kg) or 731 ± 107 kJ d⁻¹ measured at night ($t = 2.68$, $df = 8$, $p < 0.05$).

Aerodynamic properties

Seven Cape gannets of average mass 2757 ± 169 g had a wing span of 173 ± 8 cm and a wing area, including body area between wings, of 2429 ± 169 cm². Calculated wing loading and aspect ratios averaged 111 N m⁻² and 12.5, respectively.

DISCUSSION

Metabolic rates

Absolute at-sea metabolic rates of Cape gannets are high compared to measurements for most other seabirds, being 143% and 34% higher than those predicted for seabirds using mainly gliding ($n = 5$) and non-gliding flight ($n = 10$), respectively (values predicted from equations in Table 4 of Birt-Friesen et al. 1989). In contrast, mass-specific at-sea metabolic rates of Cape gannets were only 3% lower than those of congeneric northern gannets (20% heavier than *Morus capensis*). Compared on BMR standard basis, at-sea metabolic rates of Cape and northern gannets were 6.5 and $8.1 \times$ BMR, respectively. The particularly high value for the latter species reflects their relatively low basal metabolic rates but high at-sea metabolism compared to Cape gannets.

Pennyquick (1989) has demonstrated that power requirements for actual flight in birds scale at a slope steeper than basal metabolism and, consequently, interspecific comparisons of potential flight costs based on multiples of BMR are inappropriate. However, this is not the case for the slope of the regression of at-sea FMR to body mass of seabirds (cf. Ellis 1984, Birt-Friesen et al. 1989). That the relationships between power requirements for flight and BMR and between FMR and BMR are different may be a consequence of FMR being an integrated value of actual flight costs and other activities at sea and of the fact that, in general, large bird species make less use of flapping flight than small species.

Aspect ratios of Cape and northern gannets are similar to those of albatrosses, reflecting their almost indistinguishable wing shapes (Pennyquick 1987a, this study). However, wing loading values of gannets are higher than similarly sized albatrosses. This coupled with the propensity of gannets to make relatively less use of dynamic soaring and more use of flap-gliding than albatrosses (Pennyquick 1987b) may account for their relatively high at-sea metabolic rates. Such costs may be further increased by plunge-dive foraging. This technique involves incipient underwater flapping of wings (Nelson 1978, Pennyquick 1987a) and, in addition, requires gannets to get airborne from the sea-surface with prey loads that for Cape gannets, at least, average 13% but may be up to 25% of total body mass (N. J. Adams unpubl. data).

Birt-Friesen et al. (1989) demonstrated that the FMR of northern gannets increased with increased flying time. Therefore, the absence of significant differences in the slope and intercept of regressions of CO_2 production on percent of time off nest for incubating and brooding adults suggests Cape gannets attending

chicks were not flying for an appreciably greater proportion of time at sea than those birds attending eggs. This was in spite of the need to collect additional food to feed chicks. However, in the absence of activity data such a conclusion must remain tentative.

Obst et al. (1987) argued that brooding was more costly than incubation. We were unable to distinguish any differences in the energy costs of these 2 activities. Cost of nest attendance by Cape gannets was 44% that of FMR at sea ($2.9 \times$ BMR), 14% lower than the 58% determined for northern gannets ($4.65 \times$ BMR). The relatively high cost of nest attendance of northern gannets was attributed to the high thermoregulatory costs in the cold, windy and wet environment off Newfoundland, Canada and very aggressive nest defence (Birt-Friesen et al. 1989). Cape gannets also breed in densely packed colonies characterized by high levels of intra-specific aggression, but at latitudes and in the season with high levels of insolation. However, at least some additional thermoregulatory costs are likely to be incurred by Cape gannets attempting to reduce heat loads during the frequent sunny days and the reason for the large difference between metabolic rates at nest sites is not readily apparent.

Overall metabolic rates of Cape gannets, assuming birds spent half their time at the nest and half away at sea, were estimated at 3380 kJ d^{-1} , 67% higher than predicted from the general equation for seabirds (Nagy 1987) but within 3% of that predicted for high latitude seabirds using flapping flight [predicted from Eq. (6), Birt-Friesen et al. 1989]. Values for northern gannets were 106 and 19% higher, respectively. The particularly high values for northern gannets partly reflect their relatively high energy costs while at the nest. When expressed as a multiple of at-nest costs, overall FMRs of northern and Cape gannets were 1.4 and 1.6 respectively, within the range (1.3 to 3.2) determined for other seabirds (data from Birt-Friesen 1989).

Overall FMR of Cape gannets was $4.7 \times$ BMR. This value and the overall FMR of northern gannets of $6.6 \times$ BMR exceed $4 \times$ BMR, a value suggested to be the maximum sustainable metabolic rate for birds (Drent & Daan 1980). In contrast to many pelagic seabirds, the period of continuous adult attendance at the nest extends throughout most of chick-rearing for gannets. The potential foraging time of each adult is halved and any accompanying energy constraints operating on the adult, potentially compounded by these high metabolic rates, will be maintained throughout chick rearing. The ability to maintain these high metabolic rates may be dependent on these birds exploiting productive areas of ocean with large populations of surface shoaling fish. We concur with Birt-Friesen et al. (1989) that additional measurements of FMR of seabirds coupled with activity

data are required to elucidate the energetic consequences of different flight modes. Studies of the energy budgets of tropical boobies should prove particularly enlightening.

Foraging efficiency

Nagy et al. (1984) defined the foraging efficiency of an animal as the ratio of metabolizable energy gained while foraging to the energy used while foraging. This index does not account for food energy fed to chicks and consequently underestimates foraging efficiency. Assuming a 48 h at-sea/nest attendance cycle for breeding Cape gannets, total energy consumption is 6760 kJ. During an at-sea period of 24 h Cape gannets utilize 4670 kJ. Foraging efficiency is then 1.45. This value is similar to the 1.4 calculated for breeding grey-headed albatrosses *Diomedea chrysostoma* (Costa & Prince 1987), but lower than that of breeding jackass penguins *Spheniscus demersus* (2.1) (Nagy et al. 1984). That the foraging efficiency of non-breeding jackass penguins was 6.8 indicates foraging efficiencies may vary considerably.

Therefore, given the large differences in locomotory and foraging techniques among the 3 species above, this similarity of the values is striking. This lends further support to the suggestion that birds with costly foraging techniques are restricted to breeding at sites adjacent to areas of high food availability (Furness & Monaghan 1987). In the Benguela upwelling region such conditions arise from the presence of large biomass of migratory pelagic fish confined largely to coastal waters (Crawford et al. 1987).

Energy requirements of chicks

The FMR of Cape gannet chicks of estimated age 19 to 45 d ranged from 877 to 1496 kJ d⁻¹ for chicks of 850 g and 2210 g respectively. This measurement includes the energy costs of maintenance, thermoregulation, synthesis costs associated with growth of new tissue and any activity costs. It does not include the chemical potential energy required for growth which may be calculated from the mass increase of the chick and knowledge of the energy content of chick tissue. The mean daily increase in chick mass during this period of rapid growth was 133 g d⁻¹. Energy density of Cape gannet chicks increases linearly with age (R. Navarro pers. comm.) in a similar way to that of northern gannet chicks (Montevecchi et al. 1984) and for chicks of 19 and 45 d was estimated at 5.9 and 7.9 kJ g⁻¹, respectively. Therefore, the rate of chemical potential energy accumulation in body tissue of Cape gannet

chicks ranged between 785 and 1051 kJ d⁻¹. Total energy requirements during the period of growth would be between 1662 and 2547 kJ d⁻¹ of metabolizable energy.

This rate of energy accumulation represents 47 and 41% respectively of the total metabolizable energy utilized by the Cape gannet chicks of 19 and 45 d. Requirements of northern gannet chicks between 21 and 42 d averaged 1718 kJ d⁻¹ of which approximately 43% was allocated to growth. Montevecchi et al. (1984) attributed most of the energy requirements of growth of northern gannet chicks over 3 wk of age to lipid accumulation. It is clear that Cape gannet chicks also accumulate such lipid reserves (R. Navarro pers. comm.).

Feeding rates

During December 1981 and January 1982 the diet of Cape gannets at Lambert's Bay consisted of 100 and 80% anchovy by mass respectively (Sea Fisheries Research Institute, Cape Town unpubl.). For the purposes of calculating feeding rates we assumed the diet was 100% anchovy for both months.

Because at least one adult Cape gannet is in attendance at the nest while breeding, the proportions of time allocated to on- and off-nest periods by an individual bird were in the ratio 1:1. Energy expenditure during incubation and chick rearing averages 3380 kJ d⁻¹ (Table 1) which is equivalent to 691 g anchovy bird⁻¹ d⁻¹. Incubation and chick-rearing periods of Cape gannets are 44 and 97 d respectively. Food consumption over the lay-to-fledge period is then 97.4 kg bird⁻¹ or 194.8 kg pair⁻¹ not including food delivered to chicks.

Food consumption rates may also be calculated from water-flux measurements. Predicted water-flux of breeding Cape gannets assuming 50% of the time is spent away from the nest is 336 ml d⁻¹. If we assume that no water is directly ingested at sea and that all water is obtained from metabolism of food, then the estimated feeding rate of a breeding Cape gannet is 391 g anchovy bird⁻¹ d⁻¹, 43% lower than estimated from energy calculations. This is a large discrepancy and suggests that labelled gannets may have been eating fish with a higher lipid content and less water than analyses suggest. In addition, if gannets were in negative energy balance, calculations of feeding rates from FMR should overestimate actual rates somewhat. Although rates of body mass change of breeding Cape gannets were not significantly different from zero over measurement periods of about 2 d, the significantly lower body mass of brooding gannets in January 1982 compared to incubating adults in December 1981 suggest Cape gannets are in negative energy balance while breeding. The higher water content of brooding

birds indicates adults were using body fat and becoming leaner through the season. Data from several doubly labelled water studies indicate this situation is common among breeding seabirds (see Birt-Friesen et al. 1989). Similar estimates of the metabolizable energy intake of northern gannets calculated from water-flux measurements were also lower than those estimated from FMR by 27 % (Birt-Friesen et al. 1989). Because estimates of feeding rates from water-flux require more assumptions than those based on FMR (Nagy 1980, Nagy & Costa 1980), calculations of total food consumption have been based on FMR.

Assuming the average daily metabolizable energy required by Cape gannet chicks to meet the energy requirements of growth and maintenance are approximated by that of a chick at 45 d (about half way through the chick rearing period), the cost is 2547 kJ d⁻¹. This is equivalent to a feeding rate of 521 g d⁻¹ or 51 kg of anchovy during its 97 d chick rearing period. The average food intake of Cape gannet chicks hand-fed on anchovy to near satiation over 97 d was 426 g d⁻¹, with food intake peaking at 587 g d⁻¹ in chicks of 70 to 71 d (Cooper 1978). This suggests our approach may overestimate average intake. At 45 d chicks are growing rapidly yet are also approaching 67 % of peak mass (Jarvis 1971), consequently both energy requirements for growth and maintenance are large and such a conclusion is not surprising. However, in the absence of a comprehensive data set we have no justification for adjusting our estimate.

Northern gannet chicks were estimated to consume only 24 kg of food over the 91 d nestling period, equivalent to 265 g d⁻¹ (Montevecchi et al. 1984). The difference between this figure and that of Cape gannets is largely attributable to the higher energy value of food fed to northern gannet chicks (Montevecchi et al. 1984).

Total food requirements for a pair of Cape gannets raising a chick to fledging would be 195 kg for the adults and 51 kg for the chick, giving a total of 246 kg of fish over the 141 d breeding season. Based on the

above measurements we can also estimate the total consumption of food by Cape gannets in the region.

There are 2 Cape gannet colonies off the southwestern coast of South Africa that lie within the area utilized by the purse-seine fishery (Berruti 1987). We assumed that birds were present in the fishing area throughout the year and that field metabolic rates measured for breeding gannets were representative of energy costs of adult birds throughout the year. Calculations based on such assumptions are likely to overestimate actual consumption but in the absence of any data we cannot quantify this at present. These data were combined with estimates of population sizes and diet composition (Berruti 1987) to calculate annual energy expenditure and food consumption (Tables 2 & 3). Total consumption was estimated at 23 400 t per annum, considerably higher than the 9500 t estimated for the same population by Duffy et al. (1987). Duffy et al. (1987) based their estimate on an allometric equation which underestimated field metabolic rates, at least during breeding.

Comparison of our consumption estimate with fishery catches (Crawford et al. 1987) indicated that between 1980 and 1985, Cape gannets were consuming, on average, 16 and 3 % of the total pilchard and anchovy catch (both restricted by quota), respectively. Acoustic surveys carried out in November 1984 and 1985 (Hampton 1987) suggested that the Cape anchovy spawner biomass (the most economically important of the pelagic fish species) was in the order of a million tonnes. Average annual gannet catch of anchovy was, therefore, only 0.9 % of adult fish biomass. Consequently, in spite of our revised consumption figure which suggests gannets consume more than double that estimated by Duffy et al. (1987), only a small proportion of the annual production of anchovy is being removed by gannets. Cape gannets are one of the 3 major resident seabird consumers in the region and the conclusion of Duffy et al. (1987) that seabird consumption is relatively unimportant compared with that of other predators in the system appears still valid. It is

Table 2. *Morus capensis*. Estimated annual energy expenditure of Cape gannets in the southern Benguela upwelling system

	Location	No. of birds	No. of days present	Energy expenditure (kJ d ⁻¹)	Total energy expenditure (kJ × 10 ⁹)
Breeding adults ^a	Lambert's Bay	18 456	365	3380	22.8
	Malgas Island	60 018	365	3380	74.0
Fledglings ^b	Lambert's Bay	4 060	97	2547	1.0
	Malgas Island	13 203	97	2547	3.2
				Total	101.0

^a From Berruti (1987); means of counts 1980–1985

^b Assuming 44 % breeding success (N. J. Adams unpubl.)

Table 3. *Morus capensis*. Annual estimated food consumption of Cape gannets in the southern Benguela upwelling system

Prey species	Metabolizable energy content ^a (kJ g ⁻¹)	Malgas Island		Lambert's Bay		Total consumption (t)
		% in diet ^b	Mass consumed (t)	% in diet ^b	Mass consumed (t)	
Cape anchovy	4.89	32.8	5940	63.2	3340	9280
Pilchard	4.78	22.5	4070	7.2	380	4450
Saury	2.91	7.7	1390	9.2	490	1880
Hake	3.61	29.6	5360	4.8	240	5600
Other	4.04	7.4	1340	15.6	820	2160
Total			18100		5270	23370

^a South African Fishing Industry Research Institute (1980), Cooper (1978)
^b Mean of diet composition sampled between 1977 and 1986 (Berruti 1987)

now clear that there may be considerable short- and long-term natural variability in pelagic fish populations and their seabird predators (Duffy & Siegfried 1987) and single estimates of total consumption, such as presented here, must be evaluated in this light.

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LITERATURE CITED

- Adams, N. J., Brown, C. R., Nagy, K. A. (1986). Energy expenditure of free-ranging wandering albatrosses *Diomedea exulans*. *Physiol. Zool.* 59: 583-591
- Berruti, A. (1987). The use of Cape gannets *Morus capensis* in management of the purse-seine fishery of the Western Cape. Ph.D. thesis, University of Natal
- Berruti, A., Colclough, J. (1987). Comparison of the abundance of pilchard in Cape gannet and commercial catches off the Western Cape, South Africa. *S. Afr. J. mar. Sci.* 5: 863-871
- Birt-Friesen, V. L., Montevecchi, W. A., Cairns, D. K., Macko, S. A. (1989). Activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology* 70: 357-367
- Cooper, J. (1978). Energetic requirements for growth and maintenance of the Cape gannet (Aves: Sulidae). *Zool. Africana* 13: 305-317
- Cooper, J., Siegfried, W. R. (1976). Behavioural responses of young Cape gannets *Sula capensis* to high ambient temperatures. *Mar. Behav. Physiol.* 3: 211-220
- Costa, D. P., Prince, P. A. (1987). Foraging energetics of grey-headed albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis* 129: 149-158
- Crawford, R. J. M., Shannon, L. V., Pollock, D. E. (1987). The Benguela ecosystem. Part IV The major fish and invertebrate resources. *Oceanogr. mar. Biol. A. Rev.* 25: 353-505
- Croxall, J. P. (1987). Conclusions. In: Croxall, J. P. (ed.) *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, p. 369-381
- Drent, R. H., Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252
- Duffy, D. C., Siegfried, W. R. (1987). Historical variations in the food consumption by breeding seabirds of the Humboldt and Benguela upwelling regions. In: Croxall, J. P. (ed.) *Seabirds feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge, p. 327-346
- Duffy, D. C., Siegfried, W. R., Jackson, S. (1987). Seabirds as consumers in the southern Benguela region. *S. Afr. J. mar. Sci.* 5: 771-790
- Ellis, H. I. (1984). Energetics of free-ranging seabirds. In: Whittow, G. C., Rahn, H. (eds.) *Seabird energetics*. Plenum Press, New York, p. 203-234
- Furness, R. W., Cooper, J. (1982). Interactions between breeding seabirds and pelagic fish populations in the Southern Benguela region. *Mar. Ecol. Prog. Ser.* 8: 243-250
- Furness, R. W., Monaghan, P. (1987). *Seabird ecology*. Chapman and Hall, New York
- Gabrielsen, G. W., Mehlum, F., Nagy, K. A. (1987). Daily energy expenditure and energy utilization of free ranging black-legged kittiwakes. *Condor* 89: 126-132
- Gessaman, J. A. (1987). Energetics. In: Giron Pendleton, B. A., Millsap, B. A., Cline, K. W., Bird, D. M. (eds.) *Raptor management techniques manual*. National Wildlife Federation, Washington D.C., p. 289-320
- Hampton, I. (1987). Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. *S. Afr. J. mar. Sci.* 5: 901-917
- Hill, R. N. (1972). Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J. appl. Physiol.* 33: 261-263
- Jarvis, M. J. F. (1971). Ethology and ecology of the South African Gannet *Sula capensis*. Ph.D. thesis, University of Cape Town
- Kendeigh, S. C., Dol'nik, V. R., Gavrilov, V. M. (1977). Avian energetics. In: Pinowski, J., Kendeigh, S. C. (eds.) *Granivorous birds in ecosystems*. Cambridge University Press, Cambridge, p. 127-204
- Levy, A. (1964). The accuracy of the bubble meter method for gas flow measurements. *J. Sci. Instrum.* 41: 449-453
- Lifson, N., McClintock, R. (1966). The theory of the use of the turnover rates of body water for measuring energy and material balance. *J. theor. Biol.* 12: 46-74

- Montevicchi, W. A., Ricklefs, R. E., Kirkham, I. A., Gabaldon, D. (1984). Growth energetics of nestling northern gannets (*Sula bassanus*). *Auk* 101: 334–341
- Nagy, K. A. (1980). CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* 238: R466–R473
- Nagy, K. A. (1987). Field metabolic rates and food requirements scaling in mammals and birds. *Ecol. Monogr.* 57: 111–128
- Nagy, K. A., Costa, C. P. (1980). Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* 238: R454–R465
- Nagy, K. A., Siegfried, W. R., Wilson, R. P. (1984). Energy utilization by free ranging Jackass Penguins *Spheniscus demersus*. *Ecology* 65: 1648–1655
- Nelson, J. B. (1978). The sulidae. Oxford University Press, Oxford
- Obst, B. S., Nagy, K. A., Ricklefs, R. E. (1987). Energy utilization by Wilson's Storm-Petrel (*Oceanites oceanicus*). *Physiol. Zool.* 60: 200–210
- Pennycuick, C. J. (1987a). Flight of auks (alcidae) and other northern seabirds compared with southern Procellariiformes: ornithodolite observations. *J. exp. Biol.* 128: 335–347
- Pennycuick, C. J. (1987b). Flight of seabirds. In: Croxall, J. P. (ed.) *Seabirds: feeding ecology and role in marine ecosystems*. Cambridge University Press, Cambridge
- Pennycuick, C. J. (1989). *Bird flight performance. A practical calculation manual*. Oxford University Press, New York
- Pettit, T. N., Nagy, K. A., Ellis, H. I., Whittow, G. C. (1988). Incubation energetics of the Laysan albatross. *Oecologia* 74: 546–550
- Roby, D. D., Ricklefs, R. W. (1986). Energy expenditure in least auklets and diving petrels during the chick rearing period. *Physiol. Zool.* 59: 661–678
- South African Fishing Industry Research Institute (1980). Thirty-fourth annual report of the director, January–December 1980. University of Cape Town
- Schmidt-Nielsen, K. (1979). *Animal physiology. Adaptations and environment*. Cambridge University Press, Cambridge
- Tucker, V. A. (1973). Bird metabolism during flight: evaluation of a theory. *J. exp. Biol.* 58: 689–709
- Wiens, J. A., Scott, J. M. (1975). Model estimation of energy flow in Oregon coastal seabird populations. *Condor* 77: 439–452

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