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Foraging energetics of Grey-headed Albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia

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At-sea metabolism (CO_2 production) and water turnover of six breeding Grey-headed Albatrosses *Diomedea chrysostoma* were measured, using the doubly labelled water method, at Bird Island, South Georgia. Mean food consumption (estimated from a water influx rate of 1·01 l d^{-1} and data on dietary composition) was 1200 g d^{-1} or 50·4 W. At-sea metabolism (derived from a rate of CO_2 production of 3·98 l h^{-1}) was 27·7 W, 2·5 times the estimated basal metabolic rate (BMR). On average the birds ingested nearly twice as much food energy as they expended to obtain it. The metabolic rate during flight (estimated from at-sea metabolism and activity budget data) was 36·3 W (range 34·7–39·0 W) or 3·2 (range 3·0–3·4) times the predicted BMR. This is the lowest cost of flight yet measured, but consistent with the highly developed adaptations for economic flight shown by albatrosses. These results are briefly compared with data for other polar vertebrates (penguins, fur seals) exploiting similar prey.

A significant part of the costs to parents of rearing offspring is the energy consumed in foraging activities. These costs are likely to be particularly important in species which need to travel long distances (e.g., because they feed on widely dispersed resources) and in species using energetically expensive modes of locomotion (e.g., flapping flight). Although field studies of energy expenditure have been carried out on a variety of birds and mammals (e.g., Mullen 1970, Utter & Lefebvre 1972, Shoemaker *et al.* 1976, Bryant & Westerterp 1983), little attention has been given to species adapted for long-distance travel. Of birds, pelagic seabirds of the Order Procellariiformes contain many such species and pre-eminent amongst these, in terms of specializations for economy of long-distance flight, are the albatrosses Diomedeidae, which are essentially dependent on soaring and gliding (Pennycuick 1975, 1982, 1986). The metabolic rate during free-ranging gliding flight has not yet been estimated for any bird; the energy costs of foraging trips have not been measured for any procellariform and there is only one previous study of a seabird, the Sooty Tern *Sterna fuscata* (Flint & Nagy 1984).

We used the doubly labelled water method, coupled with behavioural and dietary data, to measure the rate of water and energy flux in breeding Grey-headed Albatrosses *Diomedea chrysostoma* making foraging trips to sea from Bird Island, South Georgia (54°00′S, 38°02′W) during the austral summer of 1983–84. This species has been extensively studied at this site and much information is available on its reproductive biology and ecology (reviewed in Prince 1985), including unique data on activity budgets at sea (Prince & Francis 1984).

Methods

Energy and water flux

At-sea metabolism (CO_2 production) and water turnover were measured using the doubly labelled water method (Lifson & McClintock 1966, Nagy 1980, Nagy & Costa 1980). This method is based on the equilibration of oxygen in respired CO_2 with oxygen in the body water, via the action of carbonic anhydrase in blood (Lifson *et al.* 1949). When known amounts of tritium and oxygen-18 labelled water are injected into an animal, the oxygen-18 water freely equilibrates with the animals CO_2 and water pools, and dilutes as a function of water influx and CO_2 production. In contrast, tritiated water equilibrates only with the water pool and dilutes as a function of water influx. Therefore, the difference between oxygen-18 turnover and tritiated water turnover is a measure of the animal's CO_2 production. The initial dilution of these isotopes (determined by measuring their specific activity in a blood sample) after an equilibration period allows the determination of the total body water (TBW) volume (the CO_2 pool is insignificant compared to the total body water). The dilution of these isotopes is a function of their turnover rate and is monitored by taking serial blood samples through time.

For reasons of economy, it was important to use relatively low concentrations of isotope, which in turn required recapturing experimental birds within five or six days after initial injection. We selected six breeding adults at the very end of the incubation period (late December) because foraging trips are short at this time. We attempted to obtain data for adults later in the chick-rearing phase (March), but the unusually long foraging trips (3–10 days compared with 1-2 days normally) in the 1983–84 season meant that for only one (of six) birds initially injected were isotope levels on recapture high enough for analysis.

Utilizing the low-level enrichment methodology (Schoeller & van Santen 1982), breeding birds that had just been relieved of nest duties were injected intramuscularly with 1 ml of 95% oxygen-18 water and 0·1 mCi tritiated water in 1 ml of sterile saline. After injection, the birds were held in a large holding pen. Two hours later, an initial 1 to 5 ml blood sample was taken from the intertarsal vein (Hector 1984). Body-weights were measured to a precision of 50 g using a mesh bag and a 5 kg Pesola scale. Birds were then returned to the area near their nests where they interacted briefly with their mates before departing to sea within 30 minutes. Upon returning from a foraging trip, birds were recaptured after they relieved their mates and/or fed their chicks. Subsequently, a blood sample and body mass were taken, followed by a final TBW determination made by re-injection of 1 ml of 0·1 mCi/ml tritiated water (HTO) with a blood sample two hours later. In all cases, TBW was determined by the initial dilution of HTO (Nagy & Costa 1980). Ten additional blood samples (five each from departing and arriving birds) were collected from non-experimental birds for determination of natural oxygen-18 background variation. A third group of six experimental birds was used to determine the time required for isotopic equilibration in the total body water pool. These birds were given a 1 ml injection of sterile saline containing 0·1 mCi/ml HTO. Blood samples were taken from pairs of birds at 30, 60, and 90 minutes and all were sampled at 120 minutes after injection.

Tritium specific activity was determined by scintillation spectrometry of triplicate aliquots of 50 μl of pure water in 10 ml of Betaphase cocktail (Westchem, San Diego, CA) vacuum distilled from the serum samples. The specific activity of oxygen-18 water was determined by mass ratio spectrometry (Global Geochemistry, Canoga Park, CA) of pure water distilled from plasma samples. CO_2 production and water influx was calculated using the equations presented in Nagy (1980) and Nagy &

Costa (1980) assuming an exponentially changing body water pool. A constant of 25·2 J ml^{-1} was used to convert CO_2 production to energy consumption, calculated from the diet composition values given below.

Food intake

Estimates of food consumption were derived from the water influx measurements coupled with data on dietary composition and energy content assuming that food and metabolic water comprise the only avenues of water influx. Theoretically, in a non-drinking animal water influx is only derived from preformed water in the food and water produced by metabolism (Nagy 1975). Since metabolic water production (MWP) can be estimated from the rate of CO_2 production, the difference between total water influx and MWP should be equivalent to the rate of preformed water in the ingested food. Therefore, if we know the water content of the diet, we can estimate the rate of food consumption for a given water influx and metabolism by dividing the rate of preformed water entry by the water content of the diet. Preformed water influx was determined by subtracting metabolic water production from the total water influx as determined by tritium dilution. Metabolic water production was calculated from metabolism using a conversion of 0·026 ml H_2O kJ^{-1} (Schmidt-Nielsen 1982). The diet by mass was assumed to be 16% crustaceans, 49% squid and 35% fish (Prince 1980). Data on prey energy protein, lipid and water contents were taken from Croxall & Prince (1982) for squid, Clarke (1980) for krill and Crawford (1979) for fish. This diet was estimated to have a mean composition of 1·42% fat, 16·1% protein, 0·2% carbohydrate, 79·1% water and 3·873 kJ g^{-1} wet mass. This procedure assumes that food is the only source of exogenous water and that sea-water ingestion and/or unlabelled exchange of HTO across the respiratory surface is minimal (Nagy & Costa 1980). The implications of sea-water ingestion are treated in the discussion. Similar estimates of prey intake in penguins via water influx measurements gave realistic rates of food ingestion and it is unlikely that significant sea-water ingestion occurred (Kooyman *et al.* 1982, Davis *et al.* 1983, Nagy *et al.* 1984). Furthermore, validation studies on pinnipeds indicate excellent agreement between actual food intake and food intake estimated from water influx measurements (differences of −2·3% in Northern Fur Seals *Callorhinus ursinus* (Costa & Gentry 1986) and 1 and 10% in California Sea Lions *Zalophus californianus* (Costa 1984). It is not unreasonable, therefore, to make similar assumptions for Procellariiformes, but it should be noted that they have highly developed salt glands (presumably for removing salt from ingested water) and feed their chicks meals in which water is a major constituent of the liquid fraction (Clarke & Prince 1980).

Results

All incubating birds were recovered after a single foraging trip lasting 1·9 to 4·9 days (Table 1) (although one set of samples was lost during distillation), but only one bird was recovered from the chick-rearing study group. The control studies showed that variation in natural 0–18 abundance was low (mean of 0·199762 ± 0·0001185 s.d. atoms %, $n = 10$) and that there were no significant differences between birds returning and departing from the rookery (returning mean: 0·199763 ± 0·000111 s.d. atoms %; departing mean: 0·199761 ± 0·000139 atoms %, $n = 5$). Equilibration of isotope in some cases occurred within 30 minutes, but was always complete within 120 minutes. An injection enrichment of 0·0487 atoms % excess proved entirely appropriate for recapturing birds up to five days after initial sampling (Bird *48* final

Table 1. *Rates of water influx CO_2 production, power consumption and the ratio of at sea metabolism to predicted basal metabolic rate (BMR) for foraging Grey-headed Albatrosses at South Georgia*

Animal (*n*)	Time interval* d	Water influx 1 d^{-1}	Metabolism CO_2 1 h^{-1}	Metabolism Power W	Ratio of at sea/BMR†
8	3·083	1·33	4·53	31·7	2·88
48	4·916	1·08	3·96	27·7	2·49
59	3·101	0·86	5·48	38·4	2·86
61	1·876	0·80	3·10	21·7	2·20
70	4·126	1·11	2·99	20·9	1·90
29	3·015	0·89	3·79	26·6	2·54
Mean	3·353	1·01	3·98	27·8	2·47
s.e.	0·427	0·08	0·38	2·7	0·16

Notes: * Between intial and final samples.
† Estimated from $BMR = 381{\cdot}8\ M^{0{\cdot}721}$ (Ellis 1984), using mean body mass values (see Table 2).

Table 2. *Rates of food consumption, assimilated power and metabolic power expended by foraging Grey-headed Albatrosses at South Georgia*

Animal (*n*)	Mass* Initial g	Mass* Final g	Mass g	Mass change g d^{-1}	Food consumption† g d^{-1}	Food consumption† W	Assimilated power‡ W	Metabolic power W
8	3250	3850	600	195	1600	71·6	57·3	31·7
48	(3600)		?	?	1290	57·7	46·1	27·7
59	4600	4750	150	48	980	44·1	35·3	38·4
61	2950	3150	200	107	950	42·5	34·0	21·7
70	3300	3800	500	121	1340	60·1	48·1	20·9
29	(3300)		?	?	1050	47·1	37·7	26·6
Mean	3525	3888	363	118	1200	53·9	43·1	27·8
s.e.	367	329	111	30	100	4·6	3·7	2·7

Notes: * Estimated values in parenthesis.
† Using dietary composition and energy values as referenced on p. 6.
‡ Assuming all food is ingested and assimilation efficiency of 0·80 (Wiens 1984).

level of 0·00319 atoms % excess) but inadequate for birds resampled after seven days or more.

Mass-specific water influx rates (Table 1) showed a two-fold variation between individuals, but mean TBW was relatively consistent between birds at 57·9% ± 2·5 ($n = 5$). In three birds, TBW decreased by a mean of 3·3%, increasing only in the bird (59) with the lowest mass gain over the at-sea interval. There was no relationship between mass-specific metabolism and body mass. The variation in at-sea metabolism was lower than for water flux, with a standard error of only 2·7% of the mean value of 27·8 W. This at-sea metabolism is equivalent to 2·5 times the predicted basal metabolic rate (BMR) for seabirds (Ellis 1984). The water influx and metabolic rate of Bird 29, rearing a large chick, is within the range for the incubating birds.

In the four birds for which there were data, mass increased by a mean of 118 g d^{-1} while foraging at sea (Table 2). On average, Grey-headed Albatrosses ingested nearly twice as much food energy than they expended to obtain it, with extreme values of 1·15 times (Bird *29*) and 2·9 times (Bird *70*). If all of the food energy was assimilated, all birds except *59* had an energy surplus available. There was no relationship between metabolic effort and food consumption and mass gain, but the sample size is very small. For example, Bird *8* expended the greatest metabolic effort and consumed most prey, whereas Bird *70* expended the least amount of effort, but consumed the second greatest amount of food.

Discussion

Before making relevant comparisons with data from other species, we need to consider potential errors due to technical limitations. First, if sea-water is ingested, we would overestimate food intake and foraging efficiency. The following analysis suggests that, if anything, we may have underestimated actual food intake. Consequently, it is unlikely that significant sea-water ingestion occurred. Secondly, and probably more important, calculation of food intake depends on accurate assessment of the dietary content and composition. Here we assume that each bird consumed the average diet for the species. If individuals took disproportionate amounts of high or low energy content prey, significant changes in energy balance might result. For instance, if Bird *59*, estimated to be in energy deficit (Table 2), had eaten only krill, it would have shown an energy surplus of 4·4 W, more consistent with its observed increase in mass. Thirdly, we do not know whether the injected isotope had equilibrated to any extent with the contents of the birds stomach and proventriculus. If no equilibration took place, then no allowance has been made for the undigested food brought ashore by incoming birds, which can be used to supplement their reserves during the next incubation/brooding fast and/or to sustain their newly hatched chicks. Thus our adult mass change data may partly reflect the presence of undigested food and we would underestimate food consumption and hence foraging efficiency (see later).

If complete equilibration occurred, we can examine our food intake calculations in the light of the potential uses of surplus energy. In simple terms, it can be used to increase adult body energy reserves or to feed to the chick, or both. If assimilated energy not expended for metabolism (assimilated energy minus metabolic energy in Table 2) is entirely converted to fat and stored as adipose tissue (fat: 39·4 kJ g^{-1}; adispose tissue: 90% fat) then on average the study albatrosses could store 37 ± 11 g (range 27–66 g, excluding Bird *59* with a deficit of 8 g) of adipose tissue. This would sustain a fasting adult for 1·2 days (range 1–2 days) at a time when fasts last an average 3·3 days (range 1–6 days) (Prince *et al.* 1981). Some of these albatrosses, therefore, might be able nearly to maintain energy balance throughout a complete at-sea/onshore cycle at this time of the season, which is consistent with more detailed data on mass loss in the species (Prince *et al.* 1981).

Alternatively, the food mass remaining after meeting metabolic requirements (total food energy–metabolic energy/assimilation efficiency/food energy content) and assuming no adipose storage, averages 425 ± 127 g (range 310–758 g, excluding Bird *59* with a deficit of 86 g). Newly hatched chicks increase in mass by *c.* 50 g d^{-1} in their first week (Ricketts & Prince 1981, Prince unpubl. data) and if they received all the food, then it would last them about 2–3 days, compared with the approximate 2-day changeover frequency of the parents at the nest. It is likely that some combination of fat deposition and chick feeding actually occurs (the decrease in

TBW in three adults indicates an increase in lipid store and we know that young chicks are fed very soon after hatching), but without data on the composition of the mass gained by adults, we cannot estimate the relative importance of each.

Metabolic rate

The at-sea metabolism of Grey-headed Albatrosses measured in this study (2·5 times BMR with a range of 1·9 to 2·9) can be compared with similar measurements for other marine mammals and birds. The at-sea metabolism for foraging female Northern Fur Seals was 2·5 times BMR (Costa & Gentry 1986), whereas the at-sea cost of foraging was 6·6 times BMR in Jackass Penguins *Spheniscus demersus* (Nagy *et al.* 1984) and only 2·6 times BMR in Little Penguins, *Eudyptula minor* (Costa, Dann & Disher 1986). Further comparisons can be made if we calculate a mean field metabolism for Grey-headed Albatrosses that includes both the at-sea and onshore components. Just prior to hatching, the average duration of incubation shifts is 3·3 days (Prince unpubl. data) and our birds spent 3·4 days at sea (Table 2). Therefore, the birds spent 49·3% of their time incubating and 50·7% at sea. The cost of incubation for a 3708 g albatross is 11·9 W (Croxall 1982). Therefore, the total energetic cost for both onshore and at-sea components is (11·9 W × 0·493) + (27·8 W × 0·507) = 20·0 W, which is 1·76 times the predicted BMR (Ellis 1984). This value is significantly lower than comparable values of 2·8 for King Penguins *Aptenodytes patagonicus* (Kooyman *et al.* 1982), 2·6 and 2·9 for Gentoo *Pygoscelis papua* and Macaroni *Eudyptes chrysolophus* Penguins (Davis *et al.* 1983); 2·2 for Little Penguins (Costa *et al.* 1986) and 2·6 for Jackass Penguins (Nagy *et al.* 1984). Extensive studies of hirundines, for which flight costs are a significant portion of field metabolism, have yielded values between 2·2 and 5·3 (Hails & Bryant 1979).

Flight costs

An estimate of the metabolic rate during flight can be derived from the overall at-sea metabolic rate if we know the time spent in flight and can estimate the cost of non-flight activity, which, in the case of these albatrosses, is exclusively sitting on the sea surface. Activity recorders (see Prince & Francis 1984 for details of equipment, techniques and calculations) attached to the legs of breeding Grey-headed Albatrosses on foraging trips during February and March 1984 showed that birds spent on average 35% (range 30–41) of their time away from the nests on the sea surface (Prince & Morgan 1986). These data are directly applicable to Bird *29*, which was sampled during March, and we assume that the incubating birds had similar at-sea activity budgets, which seems reasonable given the similar duration of foraging trips (Table 1). If we assume further that sitting on the water and sitting on a nest have roughly similar power requirements, i.e., 11·9 W, then the average Grey-headed Albatross expends 27·8 W while at sea (from Table 2), and of this 4·2 W (11·9 × 0·35) would be spent sitting on the sea. The remaining 23·6 W (27·8 W–4·2 W) would be expended during the 15·6 hr of flying time (65% of the time at sea). This is equivalent to an expenditure during flight of 36·3 W (23·6 W/0·65) or 3·2 times the predicted BMR for a seabird of equal size (Ellis 1984). This estimate relies on data derived from other situations or birds at different times. Using the above calculations we can substitute alternate data to determine the precision of our estimate of flight energetics. For example, a 10% error in the metabolic rate while on the sea surface would introduce only a 2% error in the estimate of flight power. Time spent sitting on the sea surface varied from 30 to 41% and would result in a range of flight costs between 34·7 to 39·0 W or 3·0–3·4 times the predicted BMR. Our mean value of 3·2

times BMR is higher than the 2 times BMR measured for gliding flight in Herring Gulls *Larus argentatus* (Baudinette & Schmidt-Nielsen 1974). The fact that our overal power consumption during flight is higher than predicted might indicate that these birds are doing more than just gliding or soaring. This is not unreasonable, since our estimate of flight power includes the power consumed while taking off and landing on the sea surface to feed. Regardless, our measure of power expenditure while flying is lower than the 4·8 times BMR measured for Sooty Terns (Flint & Nagy 1984) and considerably lower than costs of flapping flight measured in Ring-billed *Larus delawarensis* and Laughing *L. atricilla* Gulls (respectively 7·5 times BMR (Berger *et al.* 1970) and 9·5–11·1 times BMR (Tucker 1972). However, the lower flight (and hence also at-sea metabolism) costs of Grey-headed Albatrosses is not unexpected considering the species' flight adaptations. Albatrosses are renowned for their ability to glide for long periods without a wing beat, utilizing specialized techniques (Pennycuick 1982, 1986). In addition to the basic structural adaptations for this characteristic gliding flight, albatross energy costs are further reduced by a morphological adaptation (specifically a tendinous 'wing-lock') holding the wing in a gliding position without involving the use of musculature (Pennycuick 1982). Analysis of their flight dynamics suggests that they are among the most economical of flying birds; the values for flight energy costs reported here are entirely consistent with this view.

Our estimates of the energy costs of flight by albatrosses, probably amongst the most economical of flying birds, can also be compared with the cost of locomotion in penguins, the most highly adapted of swimming birds. Surface swimming in Humboldt Penguins *Speniscus humboldti* (Hui 1983) costs only 3·1 times BMR and is 2·5 times BMR in the Little Penguin (Stahel & Nicol 1982, Baudinette & Gill 1985), rather similar to the albatross values. However, both these studies were performed with captive birds operating in restricted areas and Nagy *et al.*'s (1984) estimate of six times BMR for free-swimming Jackass Penguins on foraging trips, and nine times BMR for active swimming, may be more realistic.

Foraging efficiency

If we define foraging efficiency as the energy cost per unit of food energy obtained, how do Grey-headed Albatrosses, with their substantial rates of energy gain (1·1–2·9 times costs), compare with the limited data for other marine seabirds and seals consuming similar resources? In studies of Jackass Penguins (Nagy *et al.* 1984) foraging efficiency was defined as the metabolic energy expended at sea to acquire the total assimilated energy necessary for the trip at sea and time onshore. The resulting value of 2·1 takes into account only the energy consumed by the adult for its own maintenance. It does not include the additional food energy acquired for its chick and, therefore, underestimates the true foraging efficiency. However, a similar measure of foraging efficiency can be derived for Grey-headed Albatrosses using the data involved in estimating flight energy costs. We know that an average bird spends 27·8 W while foraging at sea and 11·6 W while onshore and that they spend 3·4 days at sea and 3·3 days onshore. The total energy consumption of one complete cycle is 11·5 MJ (3·4 d × 27·8 W + 3·3 d × 11·6 W) and the bird expends 8·2 MJ (3·4 d × 27·8 W) acquiring this energy. Therefore, the foraging efficiency is 1·4 (11·5/8·2), a slightly lower value than for the penguins.

Similarly derived values for Northern Fur Seals (Costa & Gentry 1986) and Antarctic Fur Seals *Arctocephal gazella* (Costa *et al.* 1986) give averages of 1·2 and 1·1, respectively. With the present limited data, it is difficult to interpret these indices relating energy costs of foraging to the amount of food acquired, especially

for such different animals as albatrosses, penguins and fur seals. There are considerable differences in the maximum food loads that can be transported by albatrosses and penguins (*c.* 15% and 30% of body mass, respectively; Pennycuick *et al.* 1984), Croxall & Lishman (1986) and offspring growth rates and/or energy contents of meals also differ widely between the three groups. Furthermore, albatrosses on typical 58-hr foraging trips while rearing offspring have a range of 500–800 km (Prince & Francis 1984) compared with *c.* 100 km for Macaroni Penguins (*c.* 30-hr trips) and Antarctic Fur Seals (*c.* 100-hr trips) (Croxall *et al.* 1984). Nevertheless, further data on foraging efficiencies may be of value in understanding the foraging strategies employed by marine vertebrates.

The main purpose of this paper was to obtain estimates of the energy costs of foraging trips to sea by albatrosses. While these data have an intrinsic interest, as the first results from free-ranging birds employing gliding as their principal mode of flight, they have additional relevance as pilot studies for the estimation of procellariiform energy budgets and for investigations of seabird foraging performance. Further studies using these techniques in conjunction with activity recorders (Prince & Francis 1984) and systems recording the mass of meals delivered to chicks (Prince & Walton 1984) should permit accurate estimates of the performance of adults at various stages of the chick-rearing period and, ultimately, realistic comparisons between different species.

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References

BAUDINETTE, R.V. & GILL, P. 1985. The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. J. Comp. Physiol. B. 155: 373–380.

BAUDINETTE, R.V. & SCHMIDT-NIELSEN, K. 1974. Energy costs of gliding flight in herring gulls. Nature 248: 83–84.

BERGER, M., HART, J. S. & ROY, O.Z. 1970. Respiration, oxygen consumption and heart rate in some birds during rest and flight. Z. vergl. Physiol. 66: 201–214.

BRYANT, D. M. & WESTERTERP, K. R. 1983. Time and energy limits to brood size in House Martins *Delichon urbica*. J. Anim. Ecol. 42: 905–925.

CLARKE, A. 1980. The biochemical composition of krill *Euphausia superba* from South Georgia. J. Exp. Mar. Biol. Ecol. 43: 221–236.

CLARKE, A. & PRINCE, P. A. 1980. Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 122: 488–494.

COSTA, D.P. 1984. Assessment of the impact of the California Sea Lion and Elephant Seal on commercial fisheries. R/F-92. *In* California Sea Grant College Program Biennial Report, 1982–84 Institute of Marine Resources, University of California, San Diego, CA.

COSTA, D.P. & GENTRY, R.L. 1986. Free-ranging and reproductive energetics of the Northern Fur Seal. *In* Gentry, R.L. & Kooyman, G.L. (eds), Fur Seals: Maternal Strategies on Land and at Sea: 79–101. Princeton: Princeton University Press.

COSTA, D.P., THORSON, P.H., HERPOLSHEIMER, J.G. & CROXALL, J.P. 1985. Reproductive bioenergetics of the Antarctic Fur Seal *Arctocephalus gazella*. Antarct. J. U.S. (In Press).

COSTA D.P., DANN, P., DISHER, W. 1986. Energy requirements of free ranging Little Penguin, *Eudyptula minor*. Comp. Biochem. Physiol. (In press).

CRAWFORD, R.E. 1979. Effect of starvation and experimental feeding on the proximate composition and caloric content of Antarctic teleost, *Notothenia coriiceps neglecta*. Comp. Biochem. Physiol. 62A: 321–326.

CROXALL, J. P. 1982. Energy costs of incubation and moult in petrels and penguins. J. Anim. Ecol. 51: 177–194.

CROXALL, J.P. & LISHMAN, G.S.F. 1986. The food and feeding ecology of penguins. *In* Croxall, J.P. (ed.), Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge: Cambridge University Press (In press).

CROXALL, J.P. & PRINCE, P.A. 1982. Calorific content of squid (Mollusca: Cephalopoda). Bull. Br. Antarct. Surv. 55: 27–31.

CROXALL, J.P., RICKETTS, C. & PRINCE, P.A. 1984. The impact of seabirds on marine resources, especially krill, at South Georgia. Pp. 285–318. *In* Whittow, G.C. & Rahn, H. (eds), Seabird Energetics. New York: Plenum Press.

DAVIS, R.W., KOOYMAN, G.L. & CROXALL, J.P. 1983. Water flux and estimated metabolism of free-ranging gentoo and macaroni penguins at South Georgia. Polar Biol. 2: 41–46.

ELLIS, H.I. 1984. Energetics of free-ranging seabirds: 203–234. *In* Whittow, G.C. & Rahn, H. (eds), Seabird Energetics. New York: Plenum Press.

FLINT, E.N. & NAGY, K.A. 1984. Flight energetics of free-living Sooty Terns. Auk 101: 288–294.

HAILS, C.J. & BRYANT, D.M. 1979. Reproductive energetics of a free-living bird. J. Anim. Ecol. 48: 411–482.

HECTOR, J.A.L. 1984. Techniques for the serial collection of blood samples and inspection of gonads in free-living albatrosses. Bull. Br. Antarct. Surv. 71: 127–133.

HUI, C.A. 1983. Swimming in penguins. Unpublished Ph.D. thesis. University of California, Los Angeles.

KOOYMAN, G.L., DAVIS, R.W., CROXALL, J.P. & COSTA, D.P. 1982. Diving depths and energy requirements of King Penguins. Science 217: 726–727.

LIFSON, N. & MC CLINTOCK, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Theor. Biol. 12: 46–74.

LIFSON, N.A., GORDON, G. B., VISSCHER, M. B. & NIER, A. O. C. 1949. The fate of utilized molecular oxygen and the sources of the oxygen of respiratory carbon dioxide, studied with the aid of heavy oxygen. J. Biol. Chem. 108: 803–811.

MULLEN, R.K. 1970. Respiratory metabolism and body water turnover rates of *Perognathus formosus* in its natural environment. Comp. Biochem. Physiol. 32: 259–265.

NAGY, K. 1975. Water and energy budgets of free-living animals: measurement using isotopically labelled water: 207–226. *In* Hadley, N. (ed.), Environmental Physiology of Desert Organisms. Stroudsburg, Pa.: Dowden, Hutchinson & Ross.

NAGY, K.A. 1980. CO_2 production in animals: analysis of potential errors of the doubly labelled water method. Am. J. Physiol. 238: R466–473.

NAGY, K.A. & COSTA, D.P. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. Am. J. Physiol. 238: R454–465.

NAGY, K.A., SIEGFRIED, W.R. & WILSON, R.P. 1984. Energy utilization by free-ranging Jackass Penguins *Spheniscus demersus*. Ecology 65: 1648–1655.

PENNYCUICK, C.J. 1975. Mechanics of flight: 1–75. *In* Farner D.S. & King, J.R. (eds), Avian Biology, Vol. 5. New York: Academic Press.

PENNYCUICK, C.J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Phil. Trans. R. Soc. Lond. B300: 75–106.

PENNYCUICK, C. J. Flight of seabirds. *In* Croxall, J.P. (ed.), Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge: Cambridge Univ. Press. (In press).

PENNYCUICK, C. J., CROXALL, J.P. & PRINCE, P.A. 1984. Scaling of foraging radius and growth rate in petrels and albatrosses. Ornis Scand. 15: 145–154.

PRINCE, P.A. 1980. The food and feeding ecology of Grey-headed Albatross *Diomedea chrysostoma* and Black-browed Albatross, *D. melanophris*. Ibis. 122: 476–488.

PRINCE, P.A. 1985. Population and energetic aspects of the relationships between Black-browed and Grey-headed Albatrosses and the Southern Ocean marine environment: 473–477. *In* Siegfried, W.R., Condy, P.R. & Laws, R.M. (eds), Antarctic Nutrient Cycles and Food Webs. Berlin: Springer-Verlag.

PRINCE, P.A. & FRANCIS, M. 1984. Activity budgets of foraging Grey-headed Albatrosses. Condor 86: 297–300.

PRINCE, P.A. & MORGAN, R.A. 1986. Diet and feeding ecology of Procellariiformes. *In* Croxall, J.P. (ed.), Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge: Cambridge University Press.

PRINCE, P.A. & WALTON, D.W.H. 1984. Automated measurement of feed size and feeding frequency in albatrosses. J. Appl. Ecol. 21: 789–794.

PRINCE, P.A., RICKETTS, C. & THOMAS, G. 1981. Weight loss in incubating albatrosses and its implications for their energy and food requirements. Condor 83: 238–242.

RICKETTS, C. & PRINCE, P.A. 1981. Comparison of growth of albatrosses. Ornis Scand. 12: 120–124.

SCHMIDT-NIELSEN, K. 1982. Animal Physiology. Cambridge: Cambridge University Press.

SCHOELLER, D.A. & VAN SANTEN, E. 1982. Measurement of energy expenditure in humans by double-labelled water method. J. Appl. Physiol. 53: 955–959.

SHOEMAKER, V.H., NAGY, K.A. & COSTA, W.R. 1976. Energy utilization and temperature regulation of jack rabbits (*Lepus californicus*) in the Mojave Desert. Physiol. Zool. 49: 364–375.

STAHEL, C.D. & NICOL, S.L. 1982. Temperature regulation in the Little Penguin *Eudyptula minor* in air and water. J. Comp. Physiol. 148: 93–100.

TUCKER, V.A. 1972. Metabolism during flight in the Laughing Gull *Larus atricilla*. Am. J. Physiol. 222: 237–245.

UTTER, J.M. & LEFEBVRE, E.A. 1973. Daily energy expenditure of Purple Martins *Progne subis* during the breeding season: estimates using $D_2{}^{18}0$ and time budget methods. Ecology 54: 597–603.

WIENS, J.A. 1984. Modelling the requirements of seabird populations: 255–284. *In* Whittow, G.C. & Rahn, H. (eds.), Seabird Energetics. New York: Plenum Press.