PARENTAL ACTIVITY BUDGETS AND ENERGY EXPENDITURES OF NORTHERN GANNETS (SULA BASSANUS)

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PARENTAL ACTIVITY BUDGETS AND ENERGY EXPENDITURES OF NORTHERN GANNETS (*SULA BASSANUS*)

by

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ABSTRACT

Activity budgets and energy expenditures were measured simultaneously using doubly labeled water and activity timers on 19 free-living Northern Gannets (*Sula bassanus*) rearing chicks at Funk Island, Newfoundland, in 1984–1985. Gannets expended a mean of 5140±777 $kJ \cdot d^{-1}$ (n=30 sample intervals), or 6.9 x basal metabolic rate (BMR), about twice the level predicted from allometric equations. Daily energy expenditures (DEE) increased with the proportion of time spent away from the nest ('foraging'). Multiple regression analysis indicated a nest-site metabolic rate (EMR) of 112±36.5 $kJ \cdot h^{-1}$, a flying metabolic rate of 382±115 $kJ \cdot h^{-1}$ and a surface swimming metabolic rate (including resting on water) of 159±96.5 $kJ \cdot h^{-1}$. Time budgets were approximately evenly divided among nest attendance, swimming and flying; 19±8% of DEE was expended in nest attendance, 25±10% swimming and 56±12% flying (n=11). Study birds spent 19% less time in nest attendance than control animals, and time spent resting on water was probably inflated due to handling. Gannets obtained a mean of 2.5±0.7 kJ of food per kJ expended foraging. Thermoregulatory requirements and high costs for plunge-diving could help to explain the high energy expenditures. It is hypothesized that the 4 x BMR maximum sustainable level of energy expenditure for free-living animals may actually be closer to 4 x standard metabolic rate. DEE did not differ between sexes and decreased with chick age, probably due to decreased foraging demands on the parents. Chick-feeding in gannets may be constrained by energy expenditures and/or digestion as opposed to time budgets or food shortages.

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INTRODUCTION

Many calculations in ecological energetics indicate that seabirds consume substantial tonnages of marine prey, and that competition may exist between seabirds and commercial fisheries (Furness 1982, Wiens 1984). The accuracy of such estimates depends largely on measurements of time and energy expenditures and population sizes of the species modeled (Furness 1978, Wiens 1984). Nest-site time budgets have been studied in many species of marine birds (reviewed by Dunn 1979), but there are few data on time budgets of seabirds away from colonies, where, until very recently, detailed meaurements were impossible (Prince and Francis 1984, Kooyman *et al.* 1983, Cairns *et al.* in press a). Estimates of energy expenditures have also tended to be inaccurate, relying on extrapolations of laboratory measurements to field situations (e.g. Arnason and Grant 1978, Furness 1982, Wiens 1984, Gaston 1985, Birt and Cairns in press). These laboratory data involve small sample sizes and limited numbers of species, and are therefore insensitive to inter- and intra-specific differences in morphology, behaviour, breeding requirements and environmental conditions. For example, high latitude (cold water) birds tend to expend much energy on thermoregulation (Weathers 1979, Ellis 1984), and pursuit divers, such as murres, tend to expend more energy than aerial foragers, such as terns (Roby and Ricklefs 1986). Very few studies have simultaneously measured time and energy expenditures of free-ranging seabirds (e.g. Nagy *et al.* 1984, Costa and Prince in press).

Researchers have recently been enabled to study the at-sea activities of free-ranging animals through the development of self-contained, lightweight activity timers that continuously and cumulatively measure time spent flying and swimming (Kooyman *et al.* 1983, Wilson and Bain 1984, Cairns *et al.* in press b). The doubly labeled water (DLW) technique has also become widely applied to measure energy expenditures of free-living animals (seabird studies reviewed by

Ellis 1984, Roby and Ricklefs 1986). In the present study, these two technological advances are integrated to investigate time and energy expenditures in a large, cold water, upper trophic level seabird, the Northern Gannet (*Sula bassanus*).

DLW is used to measure turnover rates of carbon dioxide and water, the end-products of oxidation of body fuels. Lifson *et al.* (1949) demonstrated that the oxygen of CO_2 is in equilibrium with the oxygen of body water through atomic exchange with carbonic acid:

$$CO_2 + H_2O^* \Longleftrightarrow H_2CO_3^* \Longleftrightarrow CO_2^* + H_2O. \qquad (1)$$

If water labeled with oxygen-18 (^{18}O) and either tritium or deuterium (*H) is introduced into an animal's body, ^{18}O will equilibrate with metabolic CO_2 and leave the body as both $C^{18}OO$ and $H_2{}^{18}O$, whereas *H will leave the body only as *HHO. The difference in turnover rates of these 2 isotopes is therefore equal to the rate of CO_2 production. If the proportion of lipid, protein and carbohydrate in the diet is known, the rate of CO_2 production can be directly equated to energy expenditure. The DLW technique has been tested on a variety of vertebrates and found to yield energy estimates within 8% of values determined by respirometry (Lifson *et al.* 1955, McClintock and Lifson 1958a, b, Lee and Lifson 1960, LeFebvre 1964, Lifson and McClintock 1966, Little and Lifson 1975, Nagy 1980).

Northern Gannets are aerially foraging seabirds that feed on large, surface-schooling fish, such as mackerel (*Scomber scombrus*), and squid (*Illex* spp., Nelson 1978, Montevecchi *et al.* 1984), and nest in large colonies. One egg is produced per pair, and chicks are brooded/guarded and fed by both parents until fledging at 13 weeks (Kirkham 1980, Montevecchi and Porter 1980). Parental investment hypotheses concerning monogamous birds predict that males and females should expend equal amounts of energy on offspring (Trivers 1972), but previous activity studies on gannets indicate that relative expenditures vary at different stages of the breeding cycle, and that, overall, males may invest more than females (Montevecchi and Porter 1980, Montevecchi and Kirkham 1981, Montevecchi *et al.* 1984). Twinning experiments also indicate that Northern Gannets can successfully fledge 2 chicks (Nelson 1964).

In the present study, data from DLW, electronic activity timers (Cairns *et al.* in press b), closed-chamber respirometers (Ricklefs *et al.* 1984) and nest watches are integrated to investigate time and energy expenditures of a large number of breeding Northern Gannets. The major objectives of the study are 1) to determine activity-specific energy expenditures during flying, surface swimming and nest attendance; 2) to compare energy expenditures of males and females during chick-rearing; and 3) to compare time/energy budgets of gannets with other seabirds and with allometric equations from the literature to gain insight into factors limiting parental care.

METHODS

Energy Expenditures

Doubly Labeled Water

Energy expenditures were measured using DLW at Funk Island, Newfoundland (49°46' N, 53°11' W, 6075 site-holding pairs, D.N. Nettleship and G. Chapdelaine unpubl. data) on 10 breeding gannets from 10–17 August 1984 and on 30 gannets (10/wk) from 23 August–9 September 1985. Birds were caught either by hand at night using bright lights, or with a leg-hook and movable blind during the day. Birds were given pectoral injections of 1.02 mL of $^{3}HH^{18}O$ containing about 95 atom % ^{18}O and 2.9 $mCi \cdot mL^{-1}$ ^{3}H (1984), or .93 mL $^{3}HH^{18}O$ containing about 95 atom % ^{18}O and 1.7 $mCi \cdot mL^{-1}$ ^{3}H (1985). Gannets were held in canvas bags for 4 h to allow the DLW to spread throughout the body, and then were bled from a brachial vein (3–10 mL), weighed, banded, given individual head markings with colored airplane dope and released. Birds were recaught up to 3 times between 1 and 7 days after injection and were bled and weighed again. Blood samples were kept cold in the field by storage in seawater (~5°C, 1984) or dry ice (–70°C, 1985).

Blood samples were vacuum distilled (Wood *et al.* 1975) and 2 or 3 100 μL aliquots of water (10 μL in 1984) transfered to 10 mL scintillation fluid for tritium analysis in a Beckman LS7500 scintillation counter. One to 4 mL CO_2 were added to the remaining water (generally 1–2 mL) and the oxygen isotopes allowed to equilibrate between the water and CO_2 in a shaking water bath at 25°C for 42–46 h (Eq. 1). The CO_2 was then isolated and the ^{18}O fraction measured in a Micromass 203E mass spectrometer, with output in δ values (ppt, $\delta\ ^{18}O = 1000 \cdot [(R_{sample}/R_{standard})-1]$, where $R = {}^{18}O/{}^{16}O$). δ values were corrected for fractionation during equilibration in the water bath (–40.5 ppt at 25°C) and converted to atom % using the equation

$$\text{atom } \% = \frac{100\ (.0019974\ [(\delta\ /\ 1000) + 1]}{1 + .0019974\ [(\delta\ /\ 1000) + 1]} \tag{2}$$

(derived from Hayes 1982). Background isotope levels were measured on 1 bird in 1984 and 5 in 1985. Standards were prepared by diluting 10.0 μL $^3HH^{18}O$ in 20.0 mL distilled water, and were analyzed in triplicate.

Average daily metabolic rate (ADMR, mL $CO_2 \cdot g^{-1} d^{-1}$) was calculated for each bird for the interval between successive captures assuming that changes in body water between captures were small (Nagy 1980):

$$\text{ADMR} = \frac{25.93\ W\ \ln(O_1H_2/O_2H_1)}{M\ .\ t} \tag{3}$$

where 25.93 converts days to hours and mL H_2O to mL CO_2 at standard temperature and pressure (STP, $0^{\circ}C$ and 1 atm), W is total body water (mL), O_1 and O_2 are initial and final ^{18}O fractions corrected for background (atom % excess), H_1 and H_2 are initial and final ^3H activities corrected for background (dpm), M is minimum body mass (g), and t is time between blood samples (d). Differences in body mass on successive weighings were assumed to be due to the presence of unassimilated fish in the gut (see Discussion), so minimum body mass was taken as the best estimate of true mass. Total body water was estimated from $H_2{}^{18}O$ dilution space; i.e. from the fractional dilution of the injection solution in the initial sample of body water:

$$W = \frac{(O_S - O_D)(V_D/V_S)(V_I)}{(O_0 - O_B)} \tag{4}$$

where O_S, O_D, O_0 and O_B are ^{18}O fractions in the standard, distilled water, body water following injection and background water samples, V_D is the volume of distilled water in the standard, V_S is the volume of $H_2{}^{18}O$ in the standard, and V_I is the volume of $^3HH^{18}O$ injected into the bird (Nagy 1983).

Conversion of ADMR to daily energy expenditure (DEE, $kJ \cdot d^{-1}$) depends on the lipid, protein and carbohydrate composition of the diet (Table 1). Gannet diets vary both seasonally and annually depending on relative abundances of mackerel, capelin (*Mallotus villosus*), herring (*Clupea harengus*), Atlantic saury (*Scomberesox saurus*), sandlance (*Ammodytes hexapterus*) and short-finned squid (*Ilex illecebrosus*, Kirkham *et al.* 1985). Samples of regurgitated food were collected from gannets at Funk Island at the time of heavy water studies in both years and the percentage by mass of different fish species estimated (Table 2). The nutrient compostion of each fish species was obtained from Montevecchi *et al.* (1984). It was assumed that assimilation efficiencies were the same for all nutrients. A conversion factor of 0.02609 kJ·mL CO_2^{-1} was used for birds in 1984 and 0.02615 kJ·mL CO_2^{-1} in 1985.

Measurements of energy expenditures using low ^{18}O enrichments, such as in this study, are highly sensitive to errors in background ^{18}O readings and may become artificially elevated as body water turns over and final ^{18}O fractions approach background (Nagy 1983, Roby and Ricklefs 1986). To correct for this source of error, the number of half-lives of body water between injection and final capture (H) was calculated for each bird and regressed against ADMR. Sample intervals involving large H's were successively eliminated until ADMR became independent of H ($p>.25$, see also Roby and Ricklefs 1986). These data points were excluded from further analyses.

Respirometry

Oxygen consumption was measured volumetrically in 1986 on 4 non-labeled breeding gannets at Funk Island and 6 at Cape St. Mary's, Newfoundland (46°50'N, 54°10'W, 5085 site-holding pairs, D.N. Nettleship and G. Chapdelaine unpubl. data). Gannets were caught at night and placed in large (62 L) air-tight barrels which contained a layer of Drierite and soda lime to absorb H_2O and CO_2, respectively. Birds were left in the dark for 30 min or until quiet before barrels were connected to a Yellow Springs Instrument thermister and a water-filled

Table 1: Conversion factors[A] used in calculating daily energy expenditures and energy intake for Northern Gannets at Funk Island, including J·mL CO_2^{-1}, kJ·g dry matter^{-1} and mL metabolic H_2O·g dry matter^{-1} for protein, lipid and carbohydrate.

CONVERSION	FACTOR		
	PROTEIN	LIPID	CARBOHYDRATE
J·mL CO_2^{-1}	24.8	27.7	20.8
kJ·g dry matter^{-1}	17.8	39.3	17.5
mL H_2O·g dry matter^{-1}	.392	1.07	.556

A) From Nagy 1983.

Table 2: Percent by mass of prey species in regurgitated food collected from Funk Island gannets in August 1984 and September 1985, and organic compositions of prey.

FISH SPECIES	% BY MASS[A]		% WET MASS[B]			
	1984	1985	H_2O	PROTEIN	LIPID	CARBOHYDRATE[C]
Mackerel	23	27	62.3	16.2	18.6	0.9
Capelin	2	0	78.4	14.9	3.3	1.4
Sandlance	0	2	63.5	19.5	8.9	0.8
Atlantic Saury	72	67	70.1	19.6	7.6	1.2
Herring	3	4	62.9	20.0	13.6	0.9[D]
TOTAL						
1984			68.3	18.7	10.2	1.1
1985			67.6	18.7	10.8	1.1

A) Montevecchi unpubl. data.
B) Montevecchi *et al.* 1984.
C) 100 - %H_2O - %protein - %lipid - %ash.
D) not available - value for mackerel.

manometer (Ricklefs *et al.* 1984). Temperature and pressure readings were taken for 8 to 15 min. Assuming that all water vapor and CO_2 were absorbed by the Drierite and soda lime, the change in air pressure in the barrels was converted to O_2 uptake at STP using the equation

$$\frac{\text{mL O}_2}{\text{d}} = \frac{273\ \text{P}\ (61670 - \text{V})}{1033\ \text{t}\ \text{T}} \qquad (5)$$

where 273 is 0°C on the Kelvin scale, 1033 is mean sea level air pressure (cm water), P is the change in air pressure in the barrel (cm water in the manometer), 61670 is the volume of the chamber (mL air), V is body volume (mL), t is trial duration (d) and T is mean chamber temperature (°K, Ricklefs *et al.* 1984). Body volume was estimated from body mass assuming a body density of 1 $g \cdot mL^{-1}$, and O_2 uptake was converted to kJ using a factor of 0.0201 $kJ \cdot mL\ O_2^{-1}$ (Dawson 1974). Because birds were in the rest (nocturnal) phase of their daily cycle, inactive, thermoneutral (16–21°C) and approaching a post-absorptive state (3–8 h since dusk and last possible feeding), this measurement was used as an estimate of basal metabolic rate (BMR).

Activity Budgets

Continuous dawn-to-dusk nest-watches were carried out on all birds injected with DLW to record arrival and departure times. The times of day when gannets first began flying at the colony in the morning and stopped flying in the evening were recorded, and, because gannets do not fly at night (Nelson 1978, pers. obs.), the interval between was used as an estimate of available foraging time. This period varied by up to 2 h according to date, cloud cover, moonlight and wind.

The activities of gannets away from the nest include flying, diving, surface swimming (including sitting on water) and sitting on land. Diving comprises a small fraction of a gannet's foraging time (Nelson 1978) and, due to their strong nest tenacity, breeding gannets are not thought to spend significant amounts of time on land away from their nests (Nelson, 1978). The amount of time that gannets are neither at the nest nor swimming may therefore be assumed to be spent flying. Specially devised timers which cumulatively record time spent on water (Cairns *et al.* in press b) were attached to the legs of study gannets in 1985. 'Complete' activity budgets, including nest attendance, surface swimming and flying, were obtained by combining data from timers and nest watches.

Foraging Efficiencies

Data on time and energy expenditures of individual gannets can be used to calculate foraging efficiencies. Gross foraging efficiency (FE_G) is the amount of energy acquired per unit energy expended foraging (daylight time away from the nest). Assuming that 1) gannets balance their daily budgets and 2) males and females each provide half the daily energy requirements of the chick (Montevecchi and Porter 1980), then

$$FE_G = \frac{EA}{EE} = \frac{(DEE_A/.80) + 0.5\,(DEE_C/.76)}{E_D \cdot D_a} \qquad (6)$$

where EA and EE are energy acquired and energy expended during foraging ($kJ \cdot d^{-1}$), DEE_A is adult DEE ($kJ \cdot d^{-1}$), .80 is adult assimilation efficiency (Ricklefs 1974), DEE_C is chick DEE ($kJ \cdot d^{-1}$, derived from Montevecchi *et al.* 1984), .76 is chick assimilation efficiency (Montevecchi *et al.* 1984), E_D is foraging metabolic rate ($kJ \cdot h^{-1}$), and D_a is daylight time away from the nest ($h \cdot d^{-1}$).

Daylight time away, and therefore FE_G, includes both surface swimming and flying; net foraging efficiency (FE_N) involves energy expended in flight only:

$$FE_N = \frac{EA}{E_F \cdot T_F} \qquad (7)$$

where E_F is flying metabolic rate ($kJ \cdot h^{-1}$) and T_F is time spent in flight ($h \cdot d^{-1}$).

Energy Expenditures and Reproduction

Gannets were sexed according to head coloration and behavioural characteristics (Nelson 1978). Wing lengths (wrist joint to tip of longest primary) and body masses were measured on chicks of study birds after final capture. Chick age (d) was calculated from winglength (cm) using Kirkham and Montevecchi's (1982) equation:

$$\text{Age} = 3.969 + 1.805\ \text{Winglength} \tag{8}$$

Twinning experiment

An additional egg or chick was added to each of 6 nests at Funk Island on 22 August 1985 to produce 1 nest with 2 eggs, 1 with 2 hatchlings, 1 with 2 1-week old chicks, 2 with 2 2-week old chicks, and 1 with 2 3-week old chicks. On 28 August, 2 additional nests were created with 2 2-week old chicks and 2 3-week old chicks. Adults were given 1 to 2 weeks to adjust to these changes before energy expenditures were measured.

Evaluation of the DLW Procedure

The accuracy of the DLW technique has been verified by several researchers (Lifson *et al.* 1955, McClintock and Lifson 1958a, b, Lee and Lifson 1960, LeFebvre 1964, Lifson and McClintock 1966, Little and Lifson 1975, Nagy 1980). To determine the precision of the laboratory assays, ^{3}H activities and ^{18}O fractions were measured in duplicate or triplicate on 13 blood and water samples ranging from 0.20614 to 0.25471 atom %. ^{18}O fractions were also measured on 6 fractional dilutions of 0.5202 atom % $H_2{}^{18}O$ in distilled water (0:5, 1:4, 2:3, 3:2, 4:1 and 5:0) to check the calibration of the mass spectrometer at high enrichments. As a further check on ^{18}O readings, percent body water (as estimated from ^{18}O dilution space) was calculated and compared with values obtained by other researchers:

$$\% \mathrm{W} = \frac{100 \mathrm{W}}{\mathrm{M}} \quad (9)$$

Water turnover rates

Water turnover rates (WTO, $\mathrm{mL \cdot kg^{-1} \cdot d^{-1}}$), measured by the rate of depletion of hydrogen isotopes only, can be used to calculate total energy intake of an animal if the energy:water ratio of the diet is known. WTO of gannets on Funk Island were calculated using Nagy and Costa's (1980) equation for animals with constant body water:

$$\mathrm{WTO} = \frac{1000 \mathrm{W} \ln (\mathrm{H_1/H_2})}{\mathrm{M \cdot t}} \quad (10)$$

where 1000 converts g to kg. The amount of energy ingested per mL H_2O turned over depends on the nutrient and water compositions of the diet. The nutrient composition of the gannets' diet was determined from the proportion by mass of fish in the diet and nutritional data for each species. Total water content was calculated as the sum of preformed water and metabolic water formed on catabolism of the dry matter (Davis *et al.* 1983). A conversion factor of 9.00 $\mathrm{kJ \cdot mL\ H_2O^{-1}}$ was used for the 1984 diet and 9.30 $\mathrm{kJ \cdot mL\ H_2O^{-1}}$ for the 1985 diet (Tables 1, 2).

Statistics

Statistical tests were run using $\mathrm{SPSS^X}$ and Minitab statistical packages and are described as they are used. Means are reported ±1 standard deviation.

RESULTS

Energy Expenditures

Eight of 10 study gannets were recaptured a total of 9 times in 1984, and 22 of 30 birds were recaught 37 times in 1985. ADMR for all sample intervals was correlated with both final ^{18}O fraction ($r=-.49$, $n=46$, $p<.001$) and number of half-lives of body water between injection and final capture (Appendix A, Fig. 1, $r=.68$, $n=46$, $p<.001$, see also Roby and Ricklefs 1986). After samples for which more than 4.0 biological half-lives of H_2O had elapsed were discarded (5 in 1984 and 11 in 1985), ADMR was independent of final ^{18}O fraction ($r=.11$, $n=30$, $p=.29$). Energy expenditures of the remaining 19 gannets ($n=30$ sample intervals) averaged $2.63 \pm .42$ mL $CO_2 \cdot g^{-1} \cdot d^{-1}$ or 5140 ± 777 $kJ \cdot d^{-1}$ and were highly variable, ranging from 1.70 mL $CO_2 \cdot g^{-1} d^{-1}$ or 3542 $kJ \cdot d^{-1}$ to 3.77 mL $CO_2 \cdot g^{-1} d^{-1}$ or 6960 $kJ \cdot d^{-1}$ (Appendix B). Minimum body masses averaged $3.11 \pm .23$ kg ($n=19$).

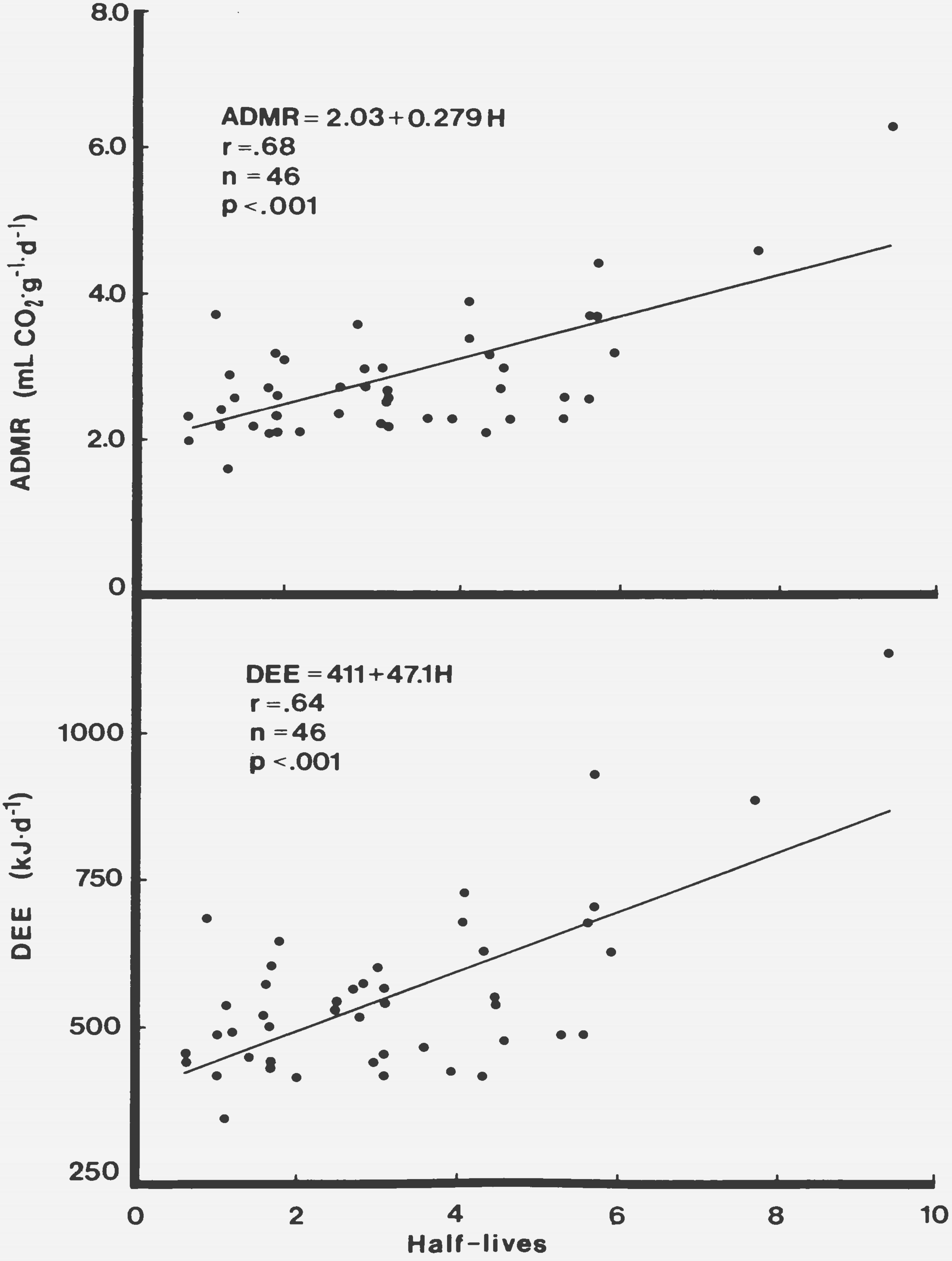
Basal metabolic rate

BMR's of gannets at Cape St. Mary's and Funk Island were not statistically different ($t=1.95$, $n=10$, $p=.09$) and averaged 696 ± 127 $kJ \cdot d^{-1}$ (range=525−984 $kJ \cdot d^{-1}$). Masses of study birds averaged $3.03 \pm .14$ kg.

Simultaneous Time and Energy Budgets

Overall, gannets spent a mean of 9.3 ± 3.0 h in nest attendance ($39 \pm 13\%$ total time, $N=25$), 14.7 ± 3.0 total $h \cdot d^{-1}$ away from the nest ($61 \pm 13\%$ total time) and 9.6 ± 2.2 daylight $h \cdot d^{-1}$ away ('foraging', $40 \pm 9\%$ total time). DEE tended to increase with total time away from the nest ($r=.26$, $n=25$, $p=.11$), and increased significantly with daylight time away (D_a, $h \cdot d^{-1}$, Fig. 2, $DEE = 4060 + 109\ D_a$, $r=.35$, $n=25$, $p=.042$). The y intercept of this equation (4060 ± 596 $kJ \cdot d^{-1}$ or 169 ± 24.8 $kJ \cdot h^{-1}$) is the predicted metabolic rate of a 'non-foraging' bird, and the slope (109 ± 60.4 $kJ \cdot h^{-1}$) represents the cost of foraging. If the cost of foraging is

Fig. 1 Average daily metabolic rates (ADMR, mL $CO_2 \cdot g^{-1} d^{-1}$) and daily energy expenditures (DEE, $kJ \cdot d^{-1}$) of gannets as a function of number of half-lives of body water between injection and final capture (H).


ADMR = 2.03 + 0.279 H
r = .68
n = 46
p < .001
ADMR (mL CO2·g-1·d-1)
8.0
6.0
4.0
2.0
0
DEE = 411 + 47.1H
r = .64
n = 46
p < .001
DEE (kJ·d-1)
1000
750
500
250
0
2
4
6
8
10
Half-lives

assumed to be additive to non-foraging metabolism (Flint and Nagy 1984, Nagy *et al.* 1984, Tatner and Bryant 1986), then foraging metabolism is 278 ± 85.2 $kJ \cdot h^{-1}$. These 25 gannets therefore expended a mean of 2672 ± 618 $kJ \cdot d^{-1}$ or $53 \pm 12\%$ of their daily energy budget in foraging (Table 3).

'Complete' time and energy budgets were obtained for 11 gannets in 1985. These birds spent a mean of 8.6 ± 2.9 $h \cdot d^{-1}$ in nest attendance ($36 \pm 12\%$ of total time), 7.9 ± 2.7 $h \cdot d^{-1}$ surface swimming (including sitting on water, $33 \pm 11\%$ of total time) and 7.5 ± 2.1 $h \cdot d^{-1}$ flying ($31 \pm 9\%$ of total time). Time spent flying accounted for 57% of variability in DEE (Fig. 3, $r=.75$, $n=11$, $p<.008$); flying and swimming together accounted for 60% of variability in DEE ($r=.77$, $n=11$, $p=.027$, $DEE = 2694 + 270\ T_F + 47.1\ T_S$, where T_F is time flying and T_S is time swimming in $h \cdot d^{-1}$). The y intercept (2694 ± 877 $kJ \cdot d^{-1}$ or 112 ± 36.5 $kJ \cdot h^{-1}$, Table 3) is the predicted metabolic rate of a bird at the nest site (0 time flying, 0 time swimming) and may be considered to be an approximation of existence metabolic rate (EMR, the metabolic rate of a caged bird, including costs of digestion, thermoregulation and limited activity, Kendeigh 1970), although the nest site metabolic rate also includes costs of nest defense and other activities. If the costs of flying (270 ± 78.6 $kJ \cdot h^{-1}$) and swimming (47.1 ± 60.0 $kJ \cdot h^{-1}$) are each assumed to be additive to EMR (Flint and Nagy 1984, Nagy *et al.* 1984, Tatner and Bryant 1986), then flight metabolism is estimated to be 382 ± 115 $kJ \cdot h^{-1}$ and swimming metabolism, 159 ± 96.5 $kJ \cdot h^{-1}$ (Table 3). These 11 gannets therefore expended a mean of $19 \pm 8\%$ of their daily energy budget in nest attendance, $25 \pm 10\%$ swimming and $56 \pm 12\%$ flying.

Foraging Efficiencies

Gross foraging efficiency of study gannets averaged $3.04 \pm .84$ ($n=22$) and was highly variable both between and within individuals (Appendix B), ranging from 1.9 to 5.5. Efficiency did not differ between sexes or years (t-test, $p>.10$) but increased with adult mass ($r=.38$, $n=22$, $p=.039$), chick age ($r=.50$, $n=22$, $p=.009$) and chick mass ($r=.46$, $n=21$, $p=.02$).

Fig. 2 Daily energy expenditures (DEE, $kJ \cdot d^{-1}$) of gannets as a function of daylight time spent away from the nest (D_a, $h \cdot d^{-1}$).

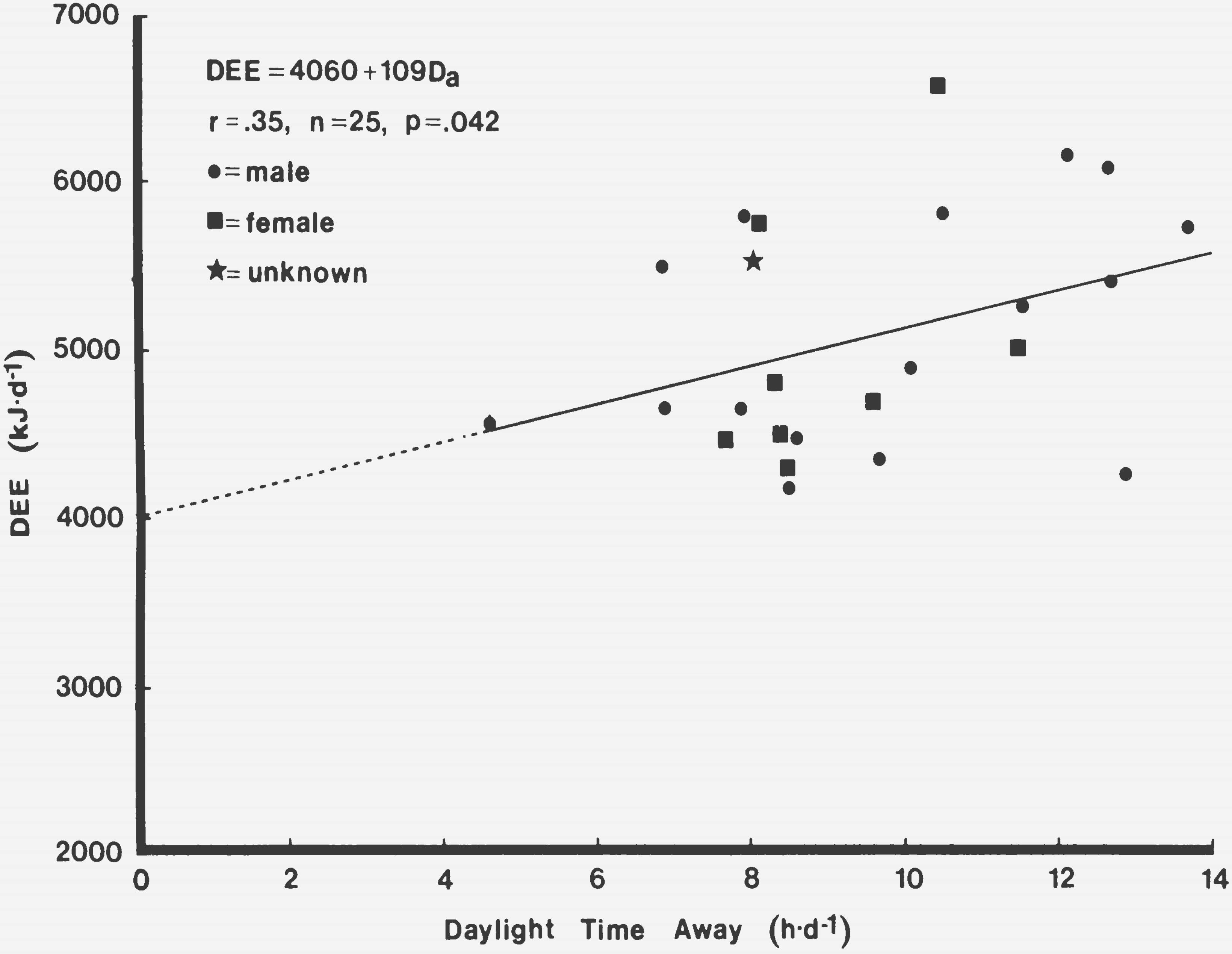

DEE = 4060 + 109Da
r = .35, n = 25, p = .042
● = male
■ = female
★ = unknown
DEE (kJ·d-1)
7000
6000
5000
4000
3000
2000
0
2
4
6
8
10
12
14
Daylight Time Away (h·d-1)

Table 3 Estimates of activity-specific metabolic rates, including nest attendance, flying, surface swimming[A] and foraging[B], for gannets breeding on Funk Island in 1985.

ACTIVITY	N	METABOLIC RATE			
		$kJ \cdot h^{-1}$	xBMR[C]	xSMR[D]	xEMR[E]
NEST ATTENDANCE	11	112	3.6	1.9	1.0
FLYING	11	382	12.3	6.5	3.4
SURFACE SWIMMING[A]	11	159	5.1	2.7	1.4
'FORAGING'[B]	25	278	9.0	4.7	2.5
TOTAL	11	212	6.8	3.6	1.9

A) including sitting on water.

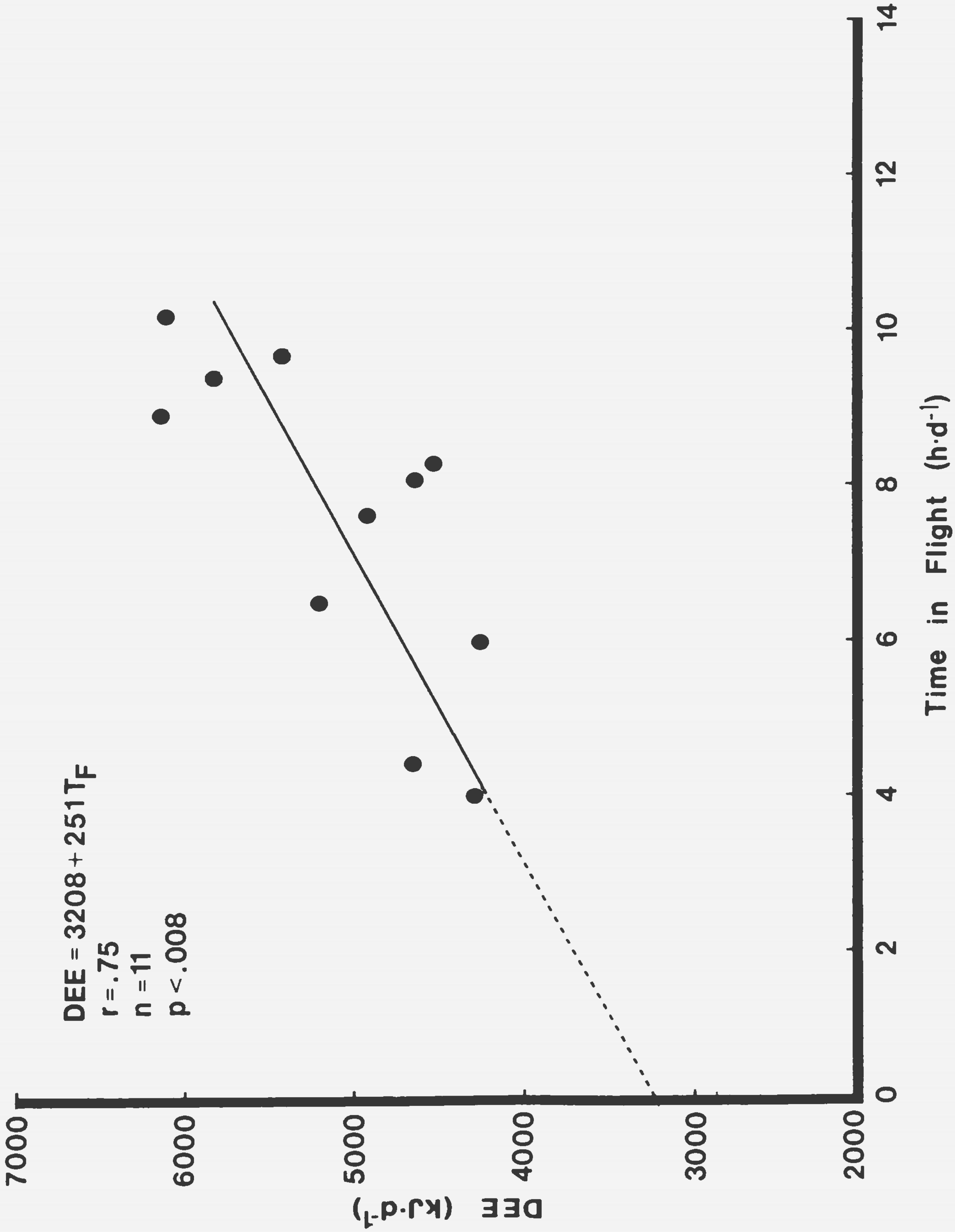
B) daylight time away from the nest.

C) 31.0 $kJ \cdot h^{-1}$ (Lasiewski and Dawson 1967).

D) 58.9 $kJ \cdot h^{-1}$ (1.9 x BMR, Johnson and West 1975, Ricklefs and Mathews 1983, Roby and Ricklefs 1986).

E) 112 $kJ \cdot d^{-1}$ (nest-site metabolic rate).

Fig. 3 Daily energy expenditures (DEE, $kJ \cdot d^{-1}$) of gannets as a function of time spent in flight (T_F, $h \cdot d^{-1}$).


DEE = 3208 + 251 T_F
r = .75
n = 11
p < .008
DEE (kJ·d⁻¹)
7000
6000
5000
4000
3000
2000
0
2
4
6
8
10
12
14
Time in Flight (h·d⁻¹)

Net foraging efficiency of the 11 gannets for which simultaneous time and energy budgets were known averaged 2.6±.47 (range=1.9–3.6) and was not significantly different from FE_G (t-test for paired observations, n=11, p=.45).

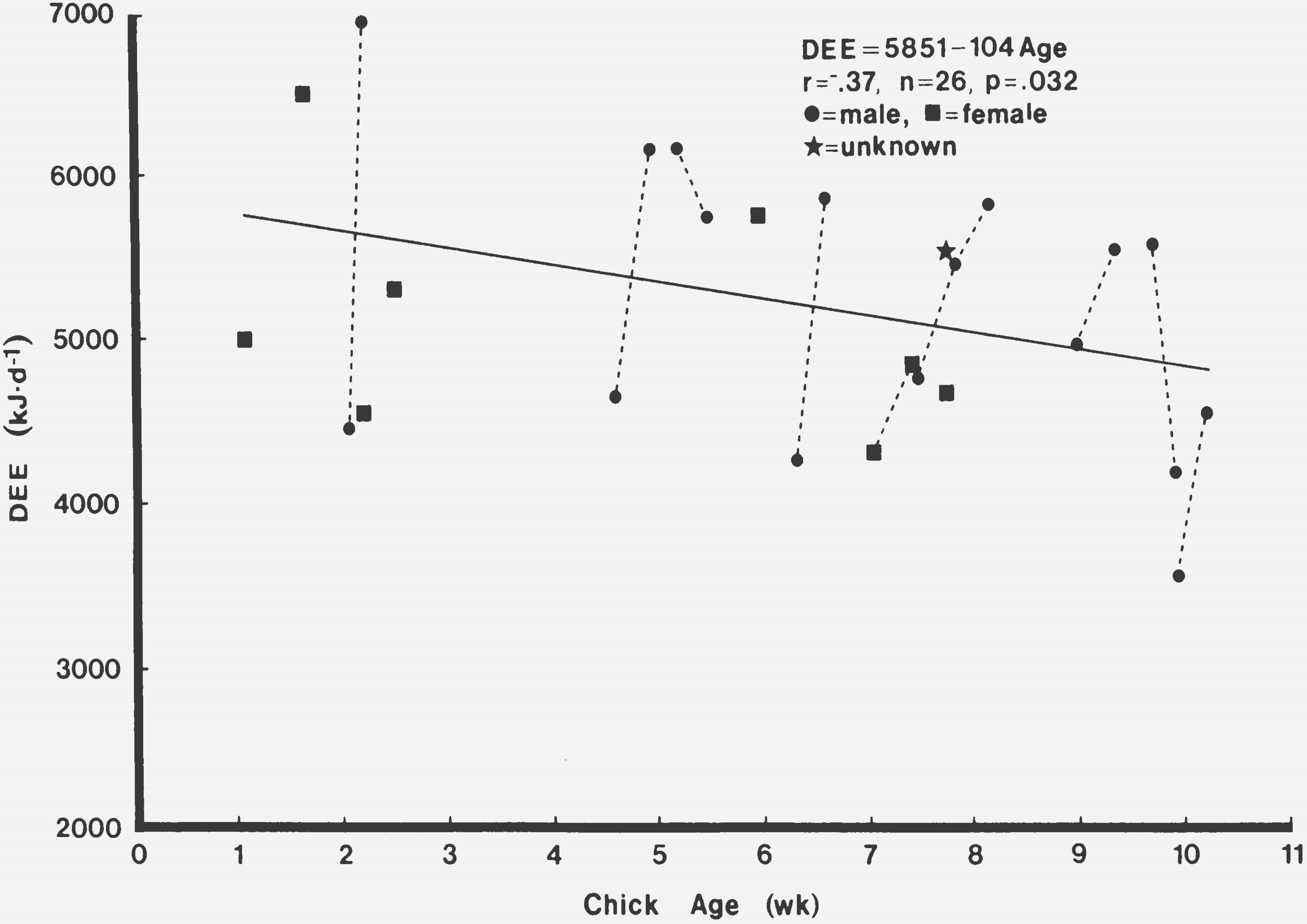
Energy Expenditures and Reproduction

Male and female gannets did not differ in ADMR, DEE, total time away from the nest or daylight time away ('foraging time', t-tests, $p>.10$). DEE for both sexes decreased significantly with chick age (Fig. 4, r=–.37, n=26, p=.032) and chick mass (r=–.46, n=24, p=.012). These relationships appeared to be linear, and the regression slopes of the sexes did not differ. Daylight time away for both sexes tended to decrease with chick age, although this trend was not significant (r=–.33, n=22, p=.067).

Twinning experiment

Three adults from 2 experimentally twinned nests were injected with DLW but only 1 gannet was recaptured. This bird had 2 2–3 week old chicks and was found to expend 2.81 mL $CO_2 \cdot g^{-1} \cdot d^{-1}$ or 5523 $kJ \cdot d^{-1}$. It spent 14.5 total $h \cdot d^{-1}$ and 8.0 daylight $h \cdot d^{-1}$ away from the nest and had an FE_G of 3.10. These values are within the ranges for other gannets with small chicks.

Fig. 4 Daily energy expenditures (DEE, $kJ \cdot d^{-1}$) of gannets as a function of chick age (wk). Broken lines connect data points for the same adult.


DEE = 5851 − 104 Age
r = ⁻.37, n = 26, p = .032
● = male, ■ = female
★ = unknown
DEE (kJ·d⁻¹)
7000
6000
5000
4000
3000
2000
0
1
2
3
4
5
6
7
8
9
10
11
Chick Age (wk)

DISCUSSION

Activity-Specific Energy Expenditures

ADMR and DEE of gannets at Funk Island were high compared to other seabirds studied with tritiated or doubly labeled water (Table 4, Fig. 5). Many equations are available in the literature for estimating activity-specific energy expenditures of free-living birds, and estimates for basal, standard, existence, surface swimming, flying and daily metabolic rates of gannets are compared with observed values in Table 5. Table 6 summarizes measurements of activity-specific energy expenditures on various seabirds.

Basal metabolic rate (BMR)

There was generally close agreement between measured BMR and values predicted by allometric equations, although BMR was low compared to some estimates and to some other seabirds (Tables 5, 6).

Existence metabolic rate (EMR)

EMR of gannets at Funk Island was 2 x higher than Kendeigh *et al.*'s (1977) prediction of 1262–1318 $kJ \cdot d^{-1}$ for a 3.11 kg bird at 5–10°C during summer (Table 5). This discrepancy may be due in part to thermoregulatory costs additional to those for low temperatures alone. The weather at Funk Island in late August and September is wet, cloudy and windy, and these three factors all incur energy costs (Ricklefs 1974). The frequent, energetically-expensive aggressive activities of nesting gannets could also raise estimates of EMR (Nelson 1978). Davis *et al.* (1983) found that metabolic rates of Macaroni Penguins (*Eudyptes chrysolophus*) brooding chicks at South Georgia were 1.2 x higher than predicted, and they suggested that this was due to climate and/or aggressive activity.

Table 4 Masses, water turnover rates (WTO), average daily metabolic rates (ADMR) and daily energy expenditures (DEE) of seabirds studied with tritiated and doubly labeled water. See Appendix C for scientific names.

SPECIES	N	MASS	WTO	ADMR	DEE			
		g	mL·kg^{-1}d^{-1}	mL·g^{-1}h^{-1}	kJ·d^{-1}	xBMR^{A}	xBMR^{B}	SOURCE
Gentoo Penguin	5	6200	155	-	3800	-	3.1	Davis *et al.* 1983
King Penguin	3	13000	169	-	6320	-	3.0	Kooyman *et al.* 1982
Macaroni Penguin	3	3600	184	-	2830	-	3.4	Davis *et al.* 1983
Little Penguin^{C}	4	1089	82	1.19	798	1.7	2.1	Costa *et al.* 1986
Jackass Penguin	10	3170	91	0.99	1940	-	2.6	Nagy *et al.* 1984
Grey-Headed Albatross^{C}	6	3707	-	-	1725	-	2.0	Costa & Prince in press
Wandering Albatross	9	8417	161	0.66	3354	1.8	2.2	Adams *et al.* 1986
Wedge-Tailed Shearwater	10	384	-	2.48	614	4.8	3.7	Ellis 1984
Wilson's Storm-Petrel	13	42	-	6.12	159^{D}	-	4.8	B. Obst unpubl.^{E}
Leach's Storm-Petrel	5	45	515	4.46	123	2.8	3.5	Ricklefs *et al.* 1986
South Georgia Diving Petrel	10	109	918	6.53	464	4.2	7.0	Roby & Ricklefs 1986
Common Diving Petrel	13	137	888	6.34	557	4.3	7.1	Roby & Ricklefs 1986
Northern Gannet	30	3110	156	2.63	5140	7.4	6.9	present study
Sooty Tern^{C}	5	187	-	2.12	241	2.8	2.5	Flint & Nagy 1984
Brown Noddy	9	195	-	2.81	352	5.2	3.5	Ellis 1984
Common Murre	4	940	442	3.18	1789	3.0	5.7	D.K. Cairns unpubl.
Thick-Billed Murre	5	834	-	2.75	1420^{D}	2.3	4.9	A.J. Gaston unpubl.^{E}
Black Guillemot	6	420	-	2.37	616^{D}	-	3.5	A.J. Gaston unpubl.^{E}
Least Auklet	24	84	874	6.69	358	3.1	6.5	Roby & Ricklefs 1986

A) Measured values

B) Lasiewski and Dawson (1967) prediction.

C) Mean of at-sea and nest-site rates.

D) DEE = $\mathrm{mL\ CO_2 \cdot g^{-1} \cdot h^{-1} \times 24\ h \cdot d^{-1} \times 0.0258\ kJ \cdot mL\ CO_2^{-1} \times M}$.

E) Cited in Roby and Ricklefs (1986).

Fig. 5 Daily energy expenditures (DEE, $kJ \cdot d^{-1}$) of seabirds studied with tritiated and doubly labeled water as a function of body mass (M, kg). See Table 4 for references. Symbols denote foraging mode: circles = pursuit-diving, triangles = gliding flight, squares = flapping flight.

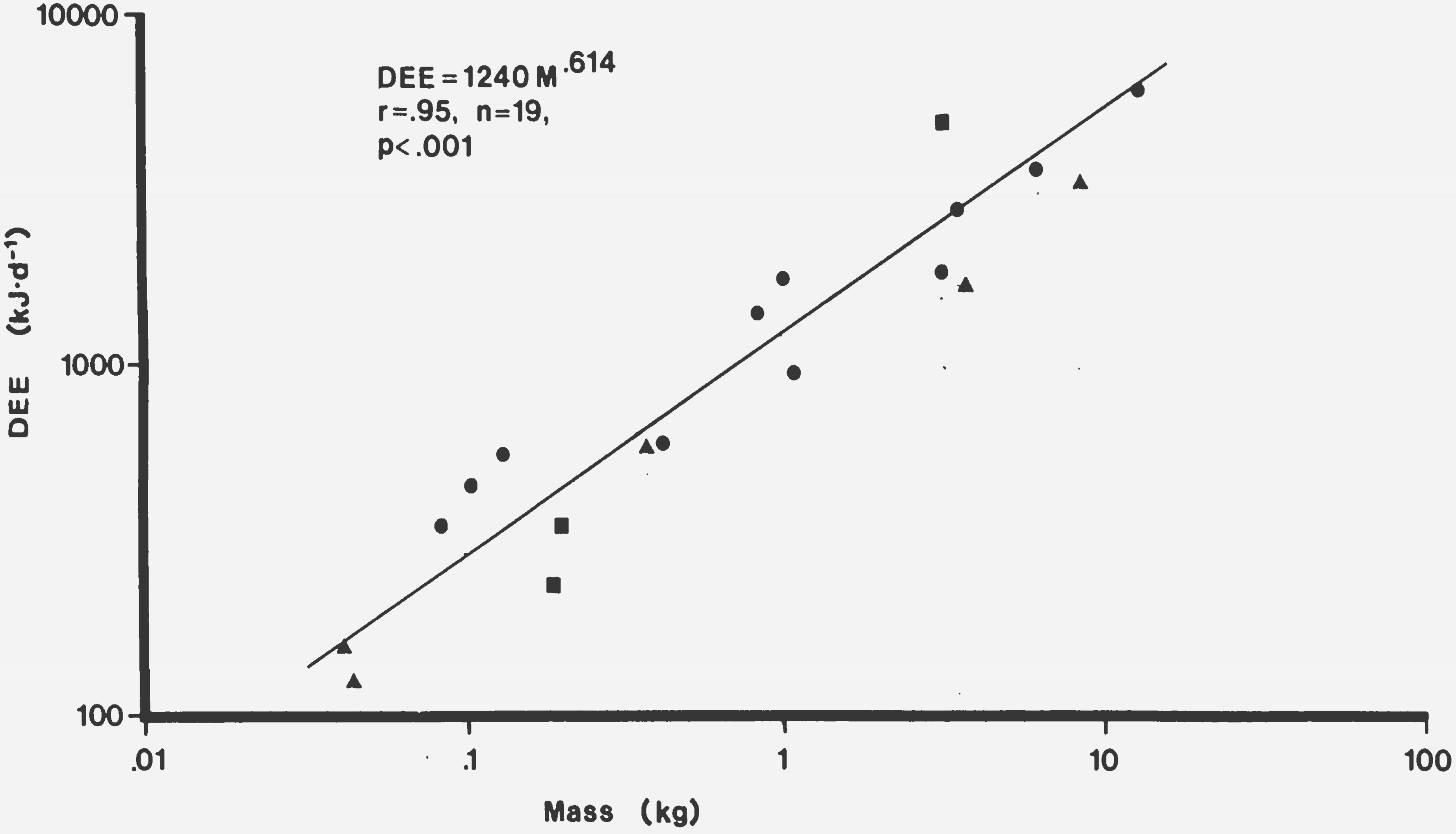

DEE = 1240 M^.614
r=.95, n=19,
p<.001
DEE (kJ·d⁻¹)
10000
1000
100
.01
.1
1
10
100
Mass (kg)

Table 5 Equations for predicting activity-specific energy expenditures of birds according to body mass, estimates for a 3.11 kg gannet (3.03 kg for BMR and SMR estimates), and ratios of observed to predicted values (O/P).

EQUATION	UNIT OF MASS	ENERGY $kJ \cdot d^{-1}$	O/P	SPECIFICATIONS	SOURCE
BASAL METABOLIC RATE (696 $kJ \cdot d^{-1}$)					
BMR = 328 $M^{.723}$	kg	731	1.0		Lasiewski & Dawson 1967
BMR = 2.15 $M^{.717}$	g	674	1.0		Kendeigh 1969
BMR = 308 $M^{.734}$	kg	695	1.0	night	Aschoff & Pohl 1970
BMR = 381 $M^{.729}$	kg	854	0.8	day	Aschoff & Pohl 1970
BMR = 2.37 $M^{.728}$	g	811	0.9	summer night	Kendeigh *et al.* 1977
BMR = 382 $M^{.721}$	kg	849	0.8	seabirds	Ellis 1984
BMR = 417 $M^{.804}$	kg	1016	0.7	pelecaniform birds	Rahn & Whittow 1984
BMR = 397 $M^{.744}$	kg	905	0.8	seabirds	Rahn & Whittow 1984
STANDARD METABOLIC RATE^{A}					
SMR = 14.0 $M^{.526}$	g	949	1.4^{B}	0°C	Kendeigh 1969
$b^{C,D} = 9.2\ t^{E}$		903	1.3^{B}	5°C (949 - 5 b)	
		857	1.2^{B}	10°C (949 - 10 b)	
SMR = 11.0 $M^{.571}$	g	1069	1.5^{B}	0°C	Kendeigh *et al.* 1977
$b^{C} = .270\ M^{.573}$	g	(26.7)			Kendeigh *et al.* 1977
		936	1.3^{B}	5°C (1069 - 5 b)	
		802	1.2^{B}	10°C (1069 - 10 b)	
EXISTENCE METABOLIC RATE (2694 $kJ \cdot d^{-1}$)					
EMR = 2.26 $M^{.755}$	g	980	2.7	30°C	Kendeigh 1969
EMR = 18.1 $M^{.530}$	g	1285	2.1	0°C	Kendeigh 1969
$b^{C.D} = 10.1\ t^{E}$		1234	2.2	5°C (1285 - 5 b)	
		1184	2.3	10°C (1285 - 10 b)	
EMR = 4.47 $M^{.664}$	g	932	2.9	30°C, summer	Kendeigh *et al.* 1977
EMR = 17.3 $M^{.544}$	g	1374	2.0	0°C, summer	Kendeigh *et al.* 1977
$b^{B} = -1.16\ M^{.282}$	g	(11.2)			Kendeigh *et al.* 1977
		1318	2.0	5°C (1374 - 5 b)	
		1262	2.1	10°C (1374 - 10 b)	
FLYING METABOLIC RATE (9168 $kJ \cdot d^{-1}$)					
$E_F = 29.5\ M^{.73}$	g	10460	0.9	all birds	Hart & Berger 1972
$E_F = 7.31\ M^{1.0}$	g	22726	0.4	at speed of lowest cost of transport	Tucker 1973
$E_F = 15.2 \times \mathrm{BMR}$	-	10579	0.9	all birds	King 1974
$E_F = 31.7\ M^{.698}$	g	8690	1.1	for birds < 1 kg	Kendeigh *et al.* 1977
DEE (5140 $kJ \cdot d^{-1}$)					
DEE = 1329 $M^{.705}$	kg	2957	1.7		King 1974
DEE = 13.1 $M^{.605}$	g	1700	3.0		Walsberg 1983b
DEE = 14.2 $M^{.607}$	g	1872	2.7	aerial foragers only	Walsberg 1983b
DEE = 4 x BMR	-	2784	1.8		Drent & Daan 1980

A) Lower critical temperature = 47.2 $M^{-.181}$ = 11°C (Kendeigh *et al.* 1977, M in g).
B) SMR / BMR (measured).
C) Temperature coefficient = $kJ \cdot {}^{\circ}C^{-1}$.
D) Derived from Kendeigh's (1969) estimates for SMR at 0°C and 30°C assuming a linear increase in metabolism with decrease in temperature.
E) Temperature (°C).

Table 6 Masses, BMR's and activity-specific energy expenditures of various seabird species. See Appendix C for scientific names.

SPECIES	MASS g	ENERGY $kJ \cdot d^{-1}$	xBMR[A]	SPECIFICATIONS	SOURCE
BMR					
Adelie Penguin	3500	1582	2.0		Ricklefs & Mathew 1983
Laysan Albatross	3103	620	.8		Grant & Whittow 1983
Southern Giant Fulmar	3280	1418	1.8	female	Ricklefs & Mathew 1983
Brown Pelican	3510	1105	1.4		Benedict & Fox 1927
Brown Pelican	3038	896	1.2		Ellis 1984
Northern Gannet	3028	696	1.0		present study
EMR					
Macaroni Penguin	3600	1739	2.1	-2-9°C	Davis *et al.* 1983
Little Penguin	1106	619	1.8		Costa *et al.* 1986
Jackass Penguin	3170	1250	1.7		Nagy *et al.* 1984
Grey-Headed Albatross	3708	1027	1.2		Croxall 1982
Wandering Albatross	7930	2415	1.6	females	Brown and Adams 1984
Northern Gannet	3110	2694	3.6	5-15°C	present study
Sooty Tern	188	141	1.4		Flint & Nagy 1984
FLYING METABOLIC RATE					
Little Penguin	1200	878	2.3	diving	Baudinette & Gill 1985
Jackass Penguin	3170	7430	9.8	diving	Nagy *et al.* 1984
Grey-Headed Albatross	3707	3132	3.7	gliding	Costa and Prince in press
Wandering Albatross	8417	4590	3.0	gliding	Adams *et al.* 1986
Northern Gannet	3110	9168	12.3		present study
Herring Gull	-	-	3.1	gliding	Baudinette & Schmidt-Nielsen 1974
Laughing Gull	322	2114	14.6	$13\ m \cdot s^{-1}$	Tucker 1973
Ring-billed Gull	440	1899	10.5	short flights	Berger *et al.* 1970
Sooty Tern	184	407	4.2	flapping	Flint & Nagy 1984
SWIMMING METABOLIC RATE (surface)					
Little Penguin	1200	663	1.8	resting	Baudinette & Gill 1985
Little Penguin	1200	1035	2.8	$<.5\ m \cdot s^{-1}$	Baudinette & Gill 1985
Jackass Penguin	3170	2921	3.9		Nagy *et al.* 1984
Peruvian Penguin	-	-	3.2		Hui 1983 *in* Ellis 1984
Northern Gannet	3110	3816	5.1		present study
FORAGING METABOLIC RATE					
Gentoo Penguin	6200	3798	3.1		Davis *et al.* 1983
King Penguin	13000	5608	2.7		Kooyman *et al.* 1982
Macaroni Penguin	3600	2826	3.4		Davis *et al.* 1983
Little Penguin	1072	982	2.8		Costa *et al.* 1986
Jackass Penguin	3170	4960	6.6		Nagy *et al.* 1984
Grey-Headed Albatross	3707	2390	2.8		Costa and Prince in press
Wandering Albatross	8417	3354	2.2		Adams *et al.* 1986
Leach's Storm-Petrel	45	123	3.5		Ricklefs *et al.* 1986
Northern Gannet	3110	6676	9.0		present study
Sooty Tern	184	340	3.5		Flint & Nagy 1984

A) Lasiewski and Dawson (1967) prediction.

Study gannets spent 39% of their time in nest attendance (Fig. 6, n=25), 20–31% less than gannets rearing chicks at other North American colonies in previous years (Montevecchi and Porter 1980, unpubl. data). This difference probably resuls from disturbance. Jackass Penguins at South Africa, and Grey-headed Albatrosses (*Diomedea chrysostoma*) at South Georgia also spent more time in nest attendance than study gannets (Fig. 6, Nagy *et al.* 1985, Costa and Prince in press). Gannets were estimated to spend 20% of their energy in nest attendance (Fig. 6, n=25), less than estimates of 32% for Jackass Penguins and 29% for Grey-headed Albatrosses (Nagy *et al.* 1984, Costa and Prince in press).

Flying metabolic rate

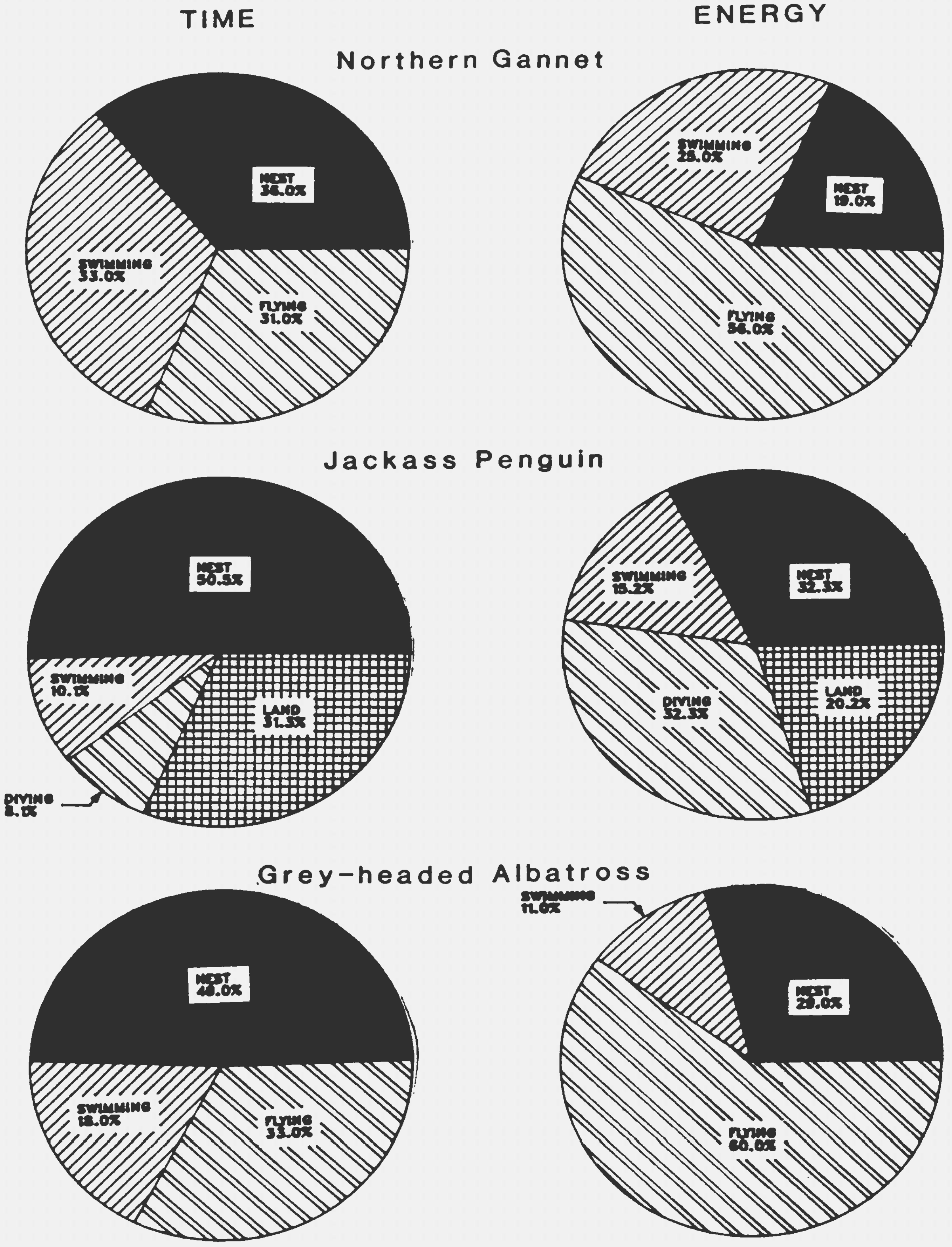
Gannets are capable of prolonged gliding, and consequently were expected to expend relatively little energy in flight (Kirkham 1980). Flying metabolism was lower than predicted by several allometric equations (Table 5), but higher than estimates for most other seabirds (Table 6). Plunge diving may however incur high energy costs (Ellis 1984), and gannets use flapping flight extensively while travelling to and from feeding sites (Nelson 1978, pers. obs.).

Study gannets spent 31% of their time and 56% of their energy in flight (Fig. 6, n=11). Time spent in flight was similar to the amount predicted by Walsberg's (1983a) equation:

$$\%\ T_F = 44.3\ M^{-.603} = 35\% \qquad (11)$$

(M in g), and the proportion of time and energy spent in flight were also similar to values of 33% and 60%, respectively, for Grey-headed Albatrosses (Fig. 6, Costa and Prince in press). In contrast, Least Auklets were speculated to spend only about 5% of their time and 11% of their energy in flight, and 2 species of diving petrels, about 9% of their time and 19–23% of their energy in flight (Roby and Ricklefs 1986).

Fig. 6 Proportions of daily time and energy budgets expended in flying or pursuit diving, surface swimming, nest attendance and resting on land by Northern Gannets, Jackass Penguins (Nagy *et al.* 1984) and Grey-headed Albatrosses (Costa and Prince in press).


TIME
ENERGY
Northern Gannet
NEST 36.0%
SWIMMING 33.0%
FLYING 31.0%
SWIMMING 25.0%
NEST 19.0%
FLYING 56.0%
Jackass Penguin
NEST 50.5%
SWIMMING 10.1%
LAND 31.3%
DIVING 8.1%
SWIMMING 15.2%
NEST 32.3%
DIVING 32.3%
LAND 20.2%
Grey-headed Albatross
NEST 48.0%
SWIMMING 18.0%
FLYING 33.0%
SWIMMING 11.0%
NEST 29.0%
FLYING 60.0%

Surface swimming metabolic rate

Swimming metabolism of gannets was 1.4 x EMR and was higher than that of any other seabird studied (Table 6). Funk Island is located in the Labrador Current, which has surface water temperatures between 0 and 5°C in summer (Pickard and Emery 1982); swimming on this water would probably increase thermoregulatory costs above nest-site requirements.

Gannets spent 33% of their time swimming, requiring 25% of their energy (Fig. 6). In contrast, Jackass Penguins spent only 10% of their time and 15% of their energy resting on water (Nagy *et al.* 1984), and Grey-headed Albatrosses spent 18% of their time and 11% of their energy on water (Fig. 6, Costa and Prince in press). Much of the time gannets spent swimming probably resulted from handling (see below).

Foraging metabolic rate

Estimated foraging metabolic rate of gannets was also higher than that of any other seabird (Table 6), probably owing to high costs for plunge diving, flapping flight and surface swimming. Roby and Ricklefs (1986) proposed that aerial foragers would have lower DEE's than pursuit divers, a prediction that is at variance with the present results. Gannets spent 40% of their time and 52% of their energy away from the nest during the day (n=25).

Daily energy expenditure

The high daily energy expenditures of Funk Island gannets probably result from high costs for plunge diving, flapping flight and thermoregulation (see below). The strong correlation between time in flight and DEE (Fig. 3, r=.75, p=.004) indicates the importance of flight in the daily energy budget, and Roby and Ricklefs (1986) also suggested that the high DEE's of Least Auklets and diving petrels resulted partly from their foraging mode (pursuit diving). Several researchers have found DEE's of seabirds at high latitudes to be 1.2 to 2 x higher than predicted by Walsberg's (1983a) equation (Table 4): e.g. Common and South Georgia Diving Petrels and Gentoo and King Penguins (*Aptenodytes patagonica*) at South Georgia (54°S, Kooyman *et al.* 1982, Davis *et al.* 1983, Roby and Ricklefs 1986), Least Auklets at St. George Island, Alaska (56°N, Roby and Ricklefs 1986), and Thick-billed Murres (*Uria lomvia*) and Black Guillemots (*Cepphus grylle*) at Digges Sound, Canada (62°N, A.J. Gaston unpubl. data *in* Roby and Ricklefs 1986). Birds in more temperate areas often have lower DEE's than predicted by Walsberg's (1983a) equation (Table 4): e.g. 0.9 x for Sooty Terns (*Sterna paradisaea*, Flint and Nagy 1984) and 0.8 x for Leach's Storm-Petrels (*Oceanodroma leucorhoa*, Ricklefs *et al.* 1986). Kendeigh (1969) suggested that nonpasserines are affected by cold more than passerines, and the white plumage of gannets may be an additional disadvantage in cold climates (Ellis 1984).

Foraging Efficiency

The foraging efficiency of gannets at Funk Island can be roughly compared with estimates for other seabirds. FE_G was higher than that of Jackass Penguins ($\bar{x}$=3.0 *vs.* 2.1), although the estimate for the penguins does not include either energy acquired for the chick or digestive efficiency (Nagy *et al.* 1984). FE's of these 2 species were considerably higher than those of Little Penguins (1.3, Costa *et al.* 1986), Leach's Storm-Petrels (1.4, Ricklefs *et al.* 1986), Grey-headed Albatrosses (1.4, Costa and Prince in press), Least Auklets (1.2, Roby and Ricklefs 1986) and 2 species of diving petrels (1.3 and 1.2, Roby and Ricklefs 1986). Estimates for all species except gannets involve energy expended during total time away from the nest rather than daylight time, which may account for some of the differences. Except for the albatrosses, which were incubating, all these birds were caring for young chicks.

An animal's foraging efficiency depends on feeding mode, individual ability and environmental influences. Auklets, petrels and albatrosses are lower trophic level consumers than gannets and penguins, which may explain their lower FE, and auklets and petrels are smaller, so must balance higher energy turnovers. Gannets also experience little competition either from other seabirds or from commercial fisheries (Nelson 1978, Montevecchi unpubl. data). FE also reflects food needs: when needs are low birds may loaf or 'play', and their efficiency would therefore decline (R.E. Ricklefs, pers. comm.). This suggests that food needs of study gannets were high. Gannet FE was highly variable (range=1.9−5.5), and this variability may reflect a large degree of plasticity in foraging behaviour, enabling the exploitation of ephemeral prey patches. Many more estimates of FE's different seabird species under varying environmental conditions are needed before these points can be assessed in more detail.

Energy Expenditures and Reproduction

There were no overall differences in parental energy expenditures between male and female gannets in the present study, a finding similar to Montevecchi *et al.* (1984). Several researchers have found that chick energy requirements and parental energy expenditures peak simultaneously (Hails and Bryant 1979, Ricklefs and Williams 1984, Ricklefs *et al.* 1985, Masman 1986): Montevecchi *et al.* (1984) showed that food requirements of gannet chicks are greatest around 8 weeks post-hatch, but gannets with chicks older than 8 weeks were found both to expend less energy and to have higher foraging efficiencies than those with younger chicks (Fig. 4). Parental energy expenditures in gannets may be related less to the amount fed to young chicks than to the frequency of feeds. Young chicks are fed frequent, small meals, and, because adult gannets probably cannot slow their digestion, they are probably forced to make frequent foraging trips (Nelson 1978, Montevecchi and Porter 1980). Older chicks can consume a 600 g (or larger) mackerel in 1 meal and can survive off fat stores for many days, and parental feeds are much less frequent than for younger chicks (Montevecchi and Porter 1980, Montevecchi *et al.* 1984). In the present study, a decrease in adult foraging demands is suggested both by the decrease in DEE with chick age and by a decrease in daylight time away with chick age, although this correlation did not attain statistical significance ($p=.067$).

Ricklefs (1983) proposed that the brooding stage is the most energetically demanding for seabirds because potential foraging time is halved. In gannets, parents must attend the chick continuously until fledging, and this may impose strong energetic constraints throughout chick-rearing. The chick-rearing period is also shorter in gannets than in low latitude sulids (e.g. Blue-footed Boobies, *Sula nebouxii*, Nelson 1978), possibly further increasing parental foraging demands.

At least 3 other studies have compared energy expenditures of male and female birds during chick-rearing. Expenditures of female House Martins (*Delichon urbica*) were relatively constant throughout the nestling stage whereas expenditures of males increased (Hails and Bryant 1979). Female European Kestrels (*Falco tinnunculus*) and European Starlings (*Sturnus vulgaris*) increased expenditures between incubation and fledging, whereas the energy investments of male European Kestrels remained fairly constant throughout the nestling stage (Masman 1986, Ricklefs and Williams 1984).

Limitations on Parental Care

Parental care, and therefore reproductive success, may be limited by 1) constraints on foraging time, 2) food shortages and/or 3) metabolic limits on energy expenditures (Ashmole 1963, Trivers 1972, Walsberg 1983b). 1) Northern Gannets spend 11–15%, of their daylight time paired at the nest rather than foraging (Nelson 1978, Montevecchi and Porter 1980, Montevecchi unpubl. data), suggesting that their daily activity budgets are not tightly constrained. 2) Even if gannets expend twice the energy predicted by allometric equations it is unlikely that they would deplete local fish stocks given the seasonally high productivity of North Atlantic waters and the mobility of forage fish, enabling rapid renewal of local stocks (Ashmole 1963, Nelson 1983). 3) Because gannets are expending much more than the suggested maximum sustainable level of 4 x BMR, it is possible that they are approaching a metabolic ceiling in DEE and are forced to spend much time 'resting' and/or digesting rather than foraging (Diamond *et al.* 1986, Krebs and Harvey 1986). The importance of this time for resting and/or digesting is further suggested by the relatively constant proportion of time mates spend paired between years, colonies and breeding stages (Nelson 1978, Kirkham 1980, Montevecchi and Porter 1980, Montevecchi unpubl. data).

Despite the high energy requirements indicated in the present study, Northern Gannets have been shown to be able to raise 2 chicks to fledging (Nelson 1964, *c.f.* Jarvis 1974). The high foraging efficiencies of gannets and of Jackass Penguins, which generally raise 2 chicks, also supports these findings. A physiological limit on energy expenditures may however prevent parents from obtaining sufficient food for chicks to lay down the fat deposits necessary for post-fledging survival (W.A. Montevecchi unpubl. data). Heightened energy expenditures imposed by raising twins may also decrease adult survival, and in long-lived species such as gannets, adult survivorship over a breeding season is more important to lifetime reproductive fitness than breeding success (Ashmole 1963, Nelson 1983). Low fledgling and adult survivorship would effectively select against a brood size of 2.

Evaluation of the DLW Data

The high metabolic rates and DEE's reported in the present study indicate possible problems with the DLW data. To evaluate the reliability of the results, several checks were run on both the laboratory procedure and the effects of handling on energy expenditures.

Evaluation of the laboratory procedure

The mass spectrometer used in the present study was standardized against Vienna Standard Mean Ocean Water (SMOW), Standard Light Antarctic Precipitation (SLAP) and National Bureau of Standards (NBS) CO_2 standards. Seawater from Logy Bay, Newfoundland, was measured to contain .1983 atom % $H_2{}^{18}O$, which is within the range expected from geographical studies (Craig and Gordon 1965, J. Whelan unpubl. data). Fresh water at high latitudes is generally depleted in $H_2{}^{18}O$ compared to SMOW (.1997 atom %), and accordingly, water distilled from the St. John's municipal water supply was measured at .1982 atom % $H_2{}^{18}O$. ^{18}O readings for fractional dilutions of .5202 atom % $H_2{}^{18}O$ were in close agreement with expected values. These results indicate that the mass spectrometer was correctly calibrated for measurement of ^{18}O at the enrichments used in this study. Gannet blood averaged .1991 atom % $H_2{}^{18}O$, which is within the range of values for other seabirds (.199–.203 atom % $H_2{}^{18}O$, Nagy 1980, Costa *et al.* 1986, Costa and Prince in press, Ricklefs *et al.* 1986). Percent body water estimated from $H_2{}^{18}O$ dilution space averaged 66±4.8% (n=19), and was similar both to estimates of 69% determined by drying (Ricklefs *et al.* 1984), and to values of 60–69% for other birds (Kooyman *et al.* 1982, Davis *et al.* 1983, Ricklefs and Williams 1984, Costa *et al.* 1986, Masman 1986, Roby and Ricklefs 1986). Percent body water estimated from ^3HHO dilution space (67±4.6%, n=19) was similar to that estimated from $H_2{}^{18}O$ dilution space, and tritium activities in standards and initial blood samples were in agreement with values expected from quantitative dilution of the injection solutions.

The maximum difference between $H_2{}^{18}O$ fractions for replicate measurements on individual blood samples was 3.0%, and differences were generally less than 1%. Tritium activities showed a maximum difference of 3.5% between replicate measurements, but when the amount of water used for analysis was increased from 10 μL (1984) to 100 μL (1985), differences were generally less than 2%. These errors probably result from fractionation during distillation, and could alter energy estimates by up to 20%.

ADMR and DEE for all samples were strongly correlated with the number of half-lives of body water between injection and final capture (Appendix A, Fig. 1, $r=.68$, $n=46$, $p<.001$ and $r=.64$, $n=46$, $p<.001$ respectively), but samples involving more than 4.0 half-lives were not used in analyses. Exclusion of samples for which more than 3.5 half-lives had elapsed (n=3) did not lower the mean estimate for energy expenditure (2.63±.44 mL $CO_2 \cdot g^{-1} d^{-1}$ or 5159±794 $kJ \cdot d^{-1}$), and exclusion of samples involving more than 3.0 half-lives (n=5) lowered it only slightly (2.62±.47 mL $CO_2 \cdot g^{-1} d^{-1}$ or 5134±809 $kJ \cdot d^{-1}$).

The amount of energy released per mL CO_2 depends on the diet. The conversion factors used in the present study were derived from the organic composition of food samples collected at the time of DLW studies. Variations in diet produce only slight changes in conversion factors. For example, Nagy (1983) suggested a factor of 0.0258 $kJ \cdot mL\ CO_2^{-1}$ for piscivorous birds; use of this number decreased mean DEE for gannets by only 1.3%. If study gannets had not fed between captures and burned body fat only (0.0277 $kJ \cdot mL\ CO_2^{-1}$), mean DEE would be 5587±929 $kJ \cdot d^{-1}$, and if they burned only protein (0.0248 $kJ \cdot mL\ CO_2^{-1}$), mean DEE would be 5002±831 $kJ \cdot d^{-1}$.

Water turnover rates

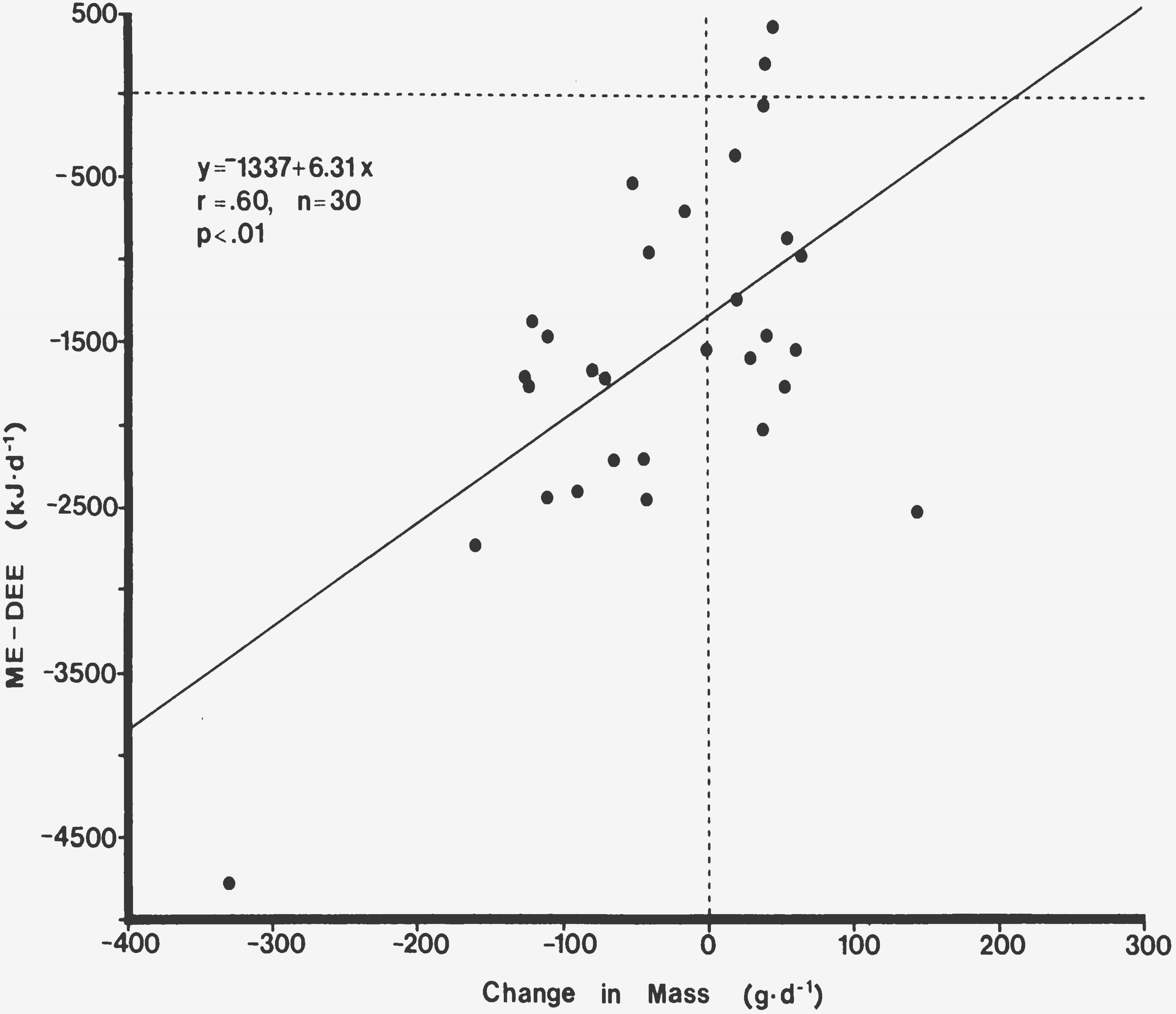
WTO averaged 156±38.3 $mL \cdot kg^{-1} \cdot d^{-1}$ and was within the range of rates for other seabirds of similar mass (Table 4). Energy intake calculated from WTO averaged 4489±1082 $kJ \cdot d^{-1}$. Assuming an assimilation efficiency of .80 (Ricklefs 1974), metabolizable energy (ME) calculated from WTO averaged 3590 $kJ \cdot d^{-1}$, 29% lower than the mean estimate of DEE. This suggests that values of either DEE or ME are in error. It is possible that the estimates of DEE from DLW are inflated (Nagy 1980, K.A. Nagy and R.E. Ricklefs pers. comm.), however it is more likely that estimates of WTO are low because the WTO procedure involves more assumptions than the DLW technique (Nagy 1980, Nagy and Costa 1980). For example, estimates of WTO and ME would be low if there was incomplete isotopic equilibration of body water with gut contents, as may occur in animals which regurgitate food to their young. WTO and ME estimates would also be low if there was fractional concentration of tritium in the body, e.g. during excretion or respiration (Nagy and Costa 1980).

The equations used to calculate energy expenditure and WTO in this study assume that total body water remains constant between captures. Nagy (1980) and Nagy and Costa (1986) reported that use of an inappropriate equation may result in large errors in estimates of WTO, but only small errors in estimates of energy expenditures. The decrease in body masses of many study gannets (up to 470g) may have involved a decrease in total body water. For example, Davis *et al.* (1983) found that total body water of 1 Gentoo Penguin (*Pygoscelis papua*) decreased by 6% over a 15% drop in body mass. Such a change may result from the presence of unassimilated food in the gut. Nagy (1980) and Nagy and Costa (1980) provide equations for calculating energy expenditures and WTO assuming that body water changes linearly between captures as a constant proportion of body mass. Use of these equations resulted in a small decrease in estimates of DEE ($\bar{x}=-0.8\pm3.5\%$, n=30, max.=−8.6%) and an increase in estimates of WTO ($\bar{x}=5.3\pm3.5\%$, n=30, max.=73%).

The difference between ME and DEE in this study may also indicate that study gannets were in a negative energy balance (ME−DEE, Davis *et al.* 1983). Nagy *et al.* (1984) also found that water turnover rates of Jackass Penguins were 13% below the expected rates and explained this on the basis of utilization of body fat. Energy balance of study gannets was positively correlated with change in mass between captures (Fig. 7, r=.60, n=30, p=.0005). Fat contains about 39.3 $kJ \cdot g^{-1}$ of energy (Nagy 1983), so catabolism of body fat could account for much of the discrepancy between DLW and WTO data. Some birds that gained mass however were also calculated to be in a negative energy balance (see Fig. 7). These discrepancies may be accounted for by (i) the presence of unassimilated food in the gut, (ii) use of inappropriate conversion equations, and/or (iii) erroneous isotope readings.

DEE and WTO of Common Murres (*Uria aalge*) have also been measured using the same analytical procedure as in the present investigation (D.K. Cairns unpubl. data). Mean DEE of these birds was similar both to predicted values and to estimates for other seabirds of similar mass (Table 4). Energy intake of murres calculated from WTO was 10% higher than DEE ($\bar{x}=1960\pm168$ *vs.* 1789 ± 265 $kJ \cdot d^{-1}$, n=4), indicating that these birds were approximately in energy balance.

Fig. 7 Energy balance (ME – DEE, $kJ \cdot d^{-1}$) of gannets as a function of change in body mass between captures ($g \cdot d^{-1}$).


y=⁻1337+6.31x
r =.60, n=30
p<.01
ME-DEE (kJ·d⁻¹)
500
-500
-1500
-2500
-3500
-4500
-400
-300
-200
-100
0
100
200
300
Change in Mass (g·d⁻¹)

Effects of handling on behaviour and energy expenditures

Recapture rates for gannets were as high as those for other seabird species studied with tritiated or doubly labeled water (Davis *et al.* 1983, Costa *et al.* 1986).

Ricklefs *et al.* (1986) and Flint and Nagy (1984) reported that few of their study birds lost chicks. In the present study, 6 chicks from 40 study nests died during initial handling of the parent, and 2 died shortly after. (Survival of chicks after completion of DLW studies was not monitored.) All of these chicks were less than 3 weeks of age and probably died from exposure. Under normal conditions, chick masses increase roughly linearly from hatching to 60 d and then asymptote (Montevecchi *et al.* 1984). Nelson (1964) provides an equation relating chick mass to age (d) for this period:

$$M = -257.45 + 75.55 \text{ Age} \tag{12}$$

When age-specific masses of study chicks were compared with masses predicted by this equation (assuming an asymptote of 4275 g, mass at day 60), there was no significant difference ($t=.32$, $n=15$, $p=.75$).

Study gannets did not differ statistically from undisturbed gannets rearing chicks at Cape St. Mary's in 1985 in the frequency of changeovers in nest duties (t-test, $p>.10$, unpubl. data). Most study birds returned to nests within 24 h of initial handling, although 1 bird did not return for 46 h ($\bar{x}=14.1\pm12.1$ h, $n=28$). On average, these gannets took longer foraging trips ($\bar{x}=7.8\pm6.6$ h, $n=90$) than undisturbed gannets rearing chicks at other nests at Funk Island and Great Bird Rock, Quebec, in 1979 ($\bar{x}=6.3\pm0.9$ h, $n=451$, Montevecchi and Porter 1980). Study gannets spent only 39±13% of daylight time ($n=25$) in nest attendance, 20–31% less time than undisturbed gannets rearing chicks at other North American gannetries in previous years (Montevecchi and Porter 1980, unpubl. data). These discrepancies probably result from study gannets spending large amounts of time resting on water after handling.

To determine if handling elevated gannet energy turnovers, expenditures of birds which lost their chick, spent more than 65% of their time away from the nest, or did not return to the nest within 24 h of handling were compared with expenditures of less disturbed birds. Neither ADMR nor DEE ($t=.61$, $n=30$, $p=.54$ and $t=.28$, $n=30$, $p=.78$ respectively) differed between these 2 groups. Both ADMR and DEE were independent of number of recaptures ($t=1.12$, $n=30$, $p=.28$ and $t=1.35$, $n=30$, $p=.20$ respectively), recapture interval ($r=-.14$, $n=30$, $p=.23$ and $r=-.19$, $n=30$, $p=.16$ respectively) and use of activity timers ($t=.435$, $n=30$, $P=.67$ and $t=.234$, $n=30$, $P=.82$ respectively). Energy expenditures may have been elevated by the large proportion of time spent resting on cold water. If study gannets had spent the same amount of time in nest attendance as undisturbed gannets elsewhere, and only 10% or less of total time on water, and if the estimates of activity-specific metabolic rates given in Table 3 are correct, then estimated DEE would be up to 8% lower (4724–4810 $kJ \cdot d^{-1}$ or 6.3–6.5 x BMR). This estimate is still higher than for other seabirds.

Conclusions

DEE and activity-specific metabolic rates in different animals are often directly correlated with BMR (Ricklefs 1974, Kendeigh *et al.* 1977, Drent and Daan 1980, Ellis 1984), and several researchers have suggested the existence of a maximum sustainable level of energy expenditure, generally around 4 x BMR (King 1974, Drent and Daan 1980, Ellis 1984, Table 4). This energy maximum may be a result either of metabolic constraints in the ability of tissues (such as flight muscle) to mobilize energy reserves, or of limitations in rates of digestion and assimilation (Ricklefs 1974, Walsberg 1983b, Diamond *et al.* 1986, Krebs and Harvey 1986). Animals engaging extensively in energetically expensive modes of transport or living in cold climates tend to have elevated DEE's (Table 4), and most also have have high BMR's (Weathers 1979, Hails 1983, Ellis 1984). For example, BMR's of Common and Thick-billed Murres in Alaska (Johnson and West 1975) and Least Auklets in South Georgia (Roby and Ricklefs 1986) were 1.9 x higher than predicted by Lasiewski and Dawson's (1967) equation. Gannet BMR was similar to values predicted by most allometric equations, but DEE and activity-specific metabolic rates expressed as multiples of BMR were all about 2 x higher than expected (Tables 4, 5, 6). The 4 x BMR hypothesis was derived largely from observations on birds living in thermoneutral environments. Unlike most other cold water seabirds, gannets winter at low latitudes and probably evolved in tropical to temperate areas (Nelson 1978), so may have retained the low BMR of ancestral stocks. Thermoregulatory costs would therefore be additive to BMR, resulting in a more flexible thermoregulatory system than in other high latitude seabirds. Thermoregulatory requirements at Funk Island would probably raise standard metabolic rate (SMR, the metabolic rate of a resting, postabsorptive animal which is not necessarily in a thermoneutral environment) to 1.5–2 x BMR (Tables 5, 6). I suggest, therefore, that DEE and activity-specific metabolic rates may be a function not of BMR, but of SMR under the prevailing weather conditions. Thermoregulation of free-ranging gannets has not been studied, but EMR includes thermoregulatory costs, and DEE and activity-specific metabolic rates expressed as multiples of EMR were similar to values found in other studies (Table 7). If SMR of gannets at Funk Island in late August and early September was 1.5 to 2 x BMR, then DEE would fall closer to the expected range (3.5–4.6 x).

Future work

Several lines of experimentation could help to explain the apparently high energy expenditures of Northern Gannets and the discrepancies between DLW and WTO results. Heart-rate telemetry could give an indication of the effect of disturbance on DEE, and SMR measurements at controlled temperatures could help to resolve the importance of climatic factors in raising DEE. Simultaneous gravimetric and isotopic measurements of energy expenditures of seabirds would determine the accuracy of the DLW technique. A cross-validation between our results and those generated by K.A. Nagy's laboratory is currently in progress.

Table 7 Total, flying/pursuit-diving, swimming and foraging metabolic rates expressed as multiples of EMR for seabirds studied with tritiated and doubly labeled water. See Appendix C for scientific names.

SPECIES	DEE	FLYING/ DIVING	SWIMMING	FORAGING	SOURCE
Macaroni Penguin	1.6	-	-	1.6	Davis *et al.* 1983
Little Penguin	1.3	1.4	1.1	1.6	Costa *et al.* 1986
Jackass Penguin	1.6	5.9	2.3	4.0	Nagy *et al.* 1984
Grey-Headed Albatross	1.7	3.0	-	2.3	Croxall 1982 and Costa and Prince in press
Wandering Albatross	1.4	1.9	-	1.4	Adams *et al.* 1986 and Brown and Adams 1984
Northern Gannet	1.9	3.4	1.4	2.5	present study
Sooty Tern	1.7	2.9	-	2.5	Flint and Nagy 1984

LITERATURE CITED

Adams, N.J., C.R. Brown and K.A. Nagy. 1986. Energy expenditure of free-ranging Wandering Albatrosses *Diomedea exulans*. *Physiol. Zool.* 59:583-591.

Arnason, E. and P.R. Grant. 1978. The significance of kleptoparasitism during the breeding season in a colony of Arctic Skuas *Stercorarius parasiticus* in Iceland. *Ibis* 120:38–54.

Aschoff, J. and H. Pohl. 1970. Rhythmic variations in energy metabolism. *Fed. Proc.* 29:1541–1552.

Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b:458–473.

Baudinette, R.V. and P. Gill. 1985. The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. *J. Comp. Physiol.* 155B:373-380.

Baudinette, R.V. and K. Schmidt-Nielsen. 1974. Energy cost of gliding flight in Herring Gulls. *Nature* 248:83–84.

Benedict F.G. and E.L. Fox. 1927. The gaseous metabolism of large wild birds under aviary conditions. *Proc. Amer. Philos. Soc.* 66:522–534

Berger, M., J.S. Hart and O.Z. Roy. 1970. Respiration, oxygen consumption and heart rate in some birds during rest and flight. *Z. Vergl. Physiol.* 66:201–214.

Birt, V.L. and D.K. Cairns. In press. Kleptoparasitic interactions of Arctic Skuas *Stercorarius parasiticus* and Black Guillemots *Cepphus grylle* in northeastern Hudson Bay, Canada. *Ibis* 129.

Brown, C.R. and N.J. Adams. 1984. Basal metabolic rate and energy expenditure during incubation in the Wandering Albatross (*Diomedea exulans*). *Condor* 86:182-186.

Cairns, D.K., K.A. Bredin and W.A. Montevecchi. In press a. Activity budgets and foraging ranges of breeding Common Murres. *Auk*.

Cairns D.K., K.A. Bredin, V.L. Birt and W.A. Montevecchi. In press b. Electronic activity recorders for aquatic wildlife. *J. Wildl. Manage.* 51:393-397.

Costa, D.P., P. Daan and W. Disher. 1986. Energy requirements of free ranging Little Penguin, *Eudyptula minor*. *Comp. Biochem. Physiol.* 85A:135-138.

Costa, D.P. and P.A. Prince. In press. Foraging energetics of Grey-headed Albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis*.

Craig, H. and L.I. Gordon. 1965. Deuterium and oxygen 18 variations in the ocean and marine atmosphere. *In* Proc. Conf. Stable Isotopes in Oceanographic Studies and Paleotemperatures, Spoleto. pp.9-130.

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

Davis, R.W., G.L. Kooyman and J.P. Croxall. 1983. Water flux and estimated metabolism of free-ranging Gentoo and Macaroni Penguins in South Georgia. *Polar Biol.* 2:41–46.

Dawson, R.W. 1974. Appendix: conversion factors for units used in symposium. *In* R.A. Paynter, Jr. (ed.), Avian energetics. Publ. Nuttall Ornithol. Club No. 15, Cambridge, Mass. p. 334.

Diamond, J.M., W.H. Karasov, D. Phan and F.L. Carpenter. 1986. Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature* 320:62–63.

Drent R.H. and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.

Drent, R.H. and B. Stonehouse. 1971. Thermoregulatory responses of the Peruvian Penguin, *Spheniscus humboldti*. *Comp. Biochem. Physiol.* 40A:689–710.

Dunn, E.H. 1979. Time-energy use and life history strategies of northern seabirds. *In* J.C. Bartonek and D.N. Nettleship (eds.), Conservation of marine birds of northern North America. Wildl. Res. Rep. #11, U.S. Dept. Interior, Washington. pp.141-166.

Ellis, H.I. 1984. Energetics of free-ranging seabirds. *In* G.C. Whittow and H. Rahn (eds.), Seabird energetics. Plenum Pub. Corp., New York. pp. 203–234.

Flint, E.N. and K.A. Nagy. 1984. Flight energetics of free-living Sooty Terns. *Auk* 101:288–294.

Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. *J. Anim. Ecol.* 47:39–53

Furness, R.W. 1982. Competition between fisheries and seabird communities. *Adv. Mar. Biol.* 20:225-307.

Gaston, A.J. 1985. Energy invested in reproduction by Thick-billed Murres (*Uria lomvia*). *Auk* 102:447–458.

Grant, G.S. and G.C. Whittow. 1983. Metabolic cost of incubation in the Laysan Albatross and Bonin Petrel. *Comp. Biochem. Physiol.* 74A:77–82.

Hails, C.J. 1983. The metabolic rate of tropical birds. *Condor* 85:61–65.

Hails, C.J. and D.M. Bryant. 1979. Reproductive energetics of a free-living bird. *J. Anim. Ecol.* 48:471–482.

Hart, J.S. and M. Berger. 1972. Energetics, water economy and temperature regulation during flight. *Proc. XV Intern. Ornithol. Congr.*:189–199.

Hayes, J.M. 1982. Fractionation, *et al.*: an introduction to isotopic measurements and terminology. *Spectra* 8:3-8.

Jarvis, M.J.F. 1974. The ecological significance of clutch size in the South African gannet (*Sula capensis* Lichtenstein). *J. Anim. Ecol.* 43:1–17.

Johnson, S.R. and G.C. West. 1975. Growth and development of heat regulation in nestlings, and metabolism of adult Common and Thick-billed Murres. *Ornis Scand.* 6:109–115.

Kendeigh, S.C. 1969. Tolerance of cold and Bergmann's rule. *Auk* 86:13–25.

Kendeigh, S.C. 1970. Energy requirements for existence in relation to size of bird. *Condor* 72:60–65.

Kendeigh, S.C., V.R. Dol'nik and V.M. Gavrilov. 1977. Avian energetics. *In* J. Pinowski and S.C. Kendeigh (eds.), Granivorous birds in ecosystems. Cambridge Univ. Press, Cambridge.

King, J.R. 1974. Seasonal allocation of time and energy resources in birds. *In* R.A. Paynter, Jr. (ed.), Avian energetics. Publ. Nuttall Ornithol. Club No. 15, Cambridge, Mass. pp. 4–85.

Kirkham, I.R. 1980. Chick development and parental care in the Northern Gannet. M.Sc. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland.

Kirkham, I.R., P.L. McLaren and W.A. Montevecchi. 1985. The food habits and distribution of Northern Gannets, *Sula bassanus*, off eastern Newfoundland and Labrador. *Can. J. Zool.* 63:181–188.

Kirkham I.R. and W.A. Montevecchi. 1982. Growth and thermal development of Northern Gannets (*Sula bassanus*) in Atlantic Canada. *Col. Waterbirds* 5:66–72.

Kooyman, G.L., J.O. Billups and W.D. Farwell. 1983. Two recently developed recorders for monitoring diving activity of marine birds and mammals. *In* A.J. MacDonald and I.G. Priede (eds), Experimental biology at sea. Academic Press, London. pp. 197-214.

Kooyman, G.L., R.W. Davis, J.P. Croxall and D.P. Costa. 1982. Diving depths and energy requirements of King Penguins. *Science* 217:726–727.

Krebs, J.R. and P.H. Harvey. 1986. Busy doing nothing – efficiently. *Nature* 320:18-19.

Lasiewski, R.C. and W.R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.

Lee, J.S. and N. Lifson. 1960. Measurement of total energy and material balance in rats by means of doubly labeled water. *Am. J. Physiol.* 199:238–242.

LeFebvre, E.A. 1964. The use of D_2O^{18} for measuring energy metabolism in *Columba livia* at rest and in flight. *Auk* 87:405–416.

Lifson, N., G.B. Gordon and R. McClintock. 1955. Measurement of total carbon dioxide production by means of D_2O^{18}. *J. Appl. Physiol.* 7:704–710.

Lifson, N., G.B. Gordon, M.B. Visscher and O. Nier. 1949. The fate of utilized molecular oxygen and the source of the oxygen of respiratory carbon dioxide, studied with the aid of heavy oxygen. *J. Biol. Chem.* 180:803–811.

Lifson, N. and R. McClintock. 1966. Theory of the use of the turnover rates of body water for measuring energy and material balance. *J. Theoret. Biol.* 12:46–74.

Little, W.W. and N. Lifson. 1975. Validation study of $D_2{}^{18}O$ method for determination of CO_2 output of the eastern chipmunk (*Tamias striatus*). *Comp. Biochem. Physiol. A* 50:55–56.

Masman, D. 1986. The annual cycle of the Kestrel *Falco tinnunculus.* Ph.D. Thesis. University of Groningen, Haren, The Netherlands. 227pp.

McClintock, R. and N. Lifson. 1958a. Determination of the total carbon dioxide outputs of rats by the $D_2{}^{18}O$ method. *Amer. J. Physiol.* 192:76–78.

McClintock, R. and N. Lifson. 1958b. CO_2 output of mice measured by $D_2{}^{18}O$ under conditions of isotope re-entry into the body. *Amer. J. Physiol.* 195:721–725.

Montevecchi, W.A. and I.R. Kirkham. 1981. The relative investments of male and female Northern Gannets (*Morus bassanus*). *Col. Waterbirds* 4:199.

Montevecchi, W.A. and J.M. Porter. 1980. Parental investments by seabirds at the breeding area with emphasis on Northern Gannets, *Morus bassanus.* *In* J. Burger, B.L. Olla and H.E. Winn (eds.), Behavior of marine animals, Vol. 4. Plenum, New York. pp. 323–365.

Montevecchi, W.A., R.E. Ricklefs, I.R. Kirkham and D. Galbaldon. 1984. Growth energetics of nestling Northern Gannets (*Sula bassanus*). *Auk* 101:334–341.

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

Nagy, K.A. 1983. The doubly labeled water ($^3HH^{18}O$) method: a guide to its use. UCLA Publ. No. 12-1417, Los Angeles.

Nagy, K.A. and D.P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* 238:R454–465.

Nagy, K.A., W.R. Siegfried and R.P. Wilson. 1984. Energy utilization by free-ranging Jackass Penguins, *Spheniscus demersus. Ecol.* 65:1648-1655.

Nelson, J.B. 1964. Factors influencing clutch-size and chick growth in the North Atlantic gannet *Sula bassana. Ibis* 106:63–77.

Nelson, J.B. 1978. The gannet. Buteo Books, Vermillion, South Dakota.

Nelson, J.B. 1983. Contrasts in breeding strategies between some tropical and temperate marine Pelecaniformes. *Stud. Avian Biol.* 8:95–114.

Pickard, G.L. and W.J. Emery. 1982. Descriptive physical oceanography, an introduction. Pergamon, Oxford.

Prince, P.A. and M.D. Francis. 1984. Activity budgets of foraging Grey-headed Albatrosses. *Condor* 86:297–300.

Rahn, H. and G.C. Whittow. 1984. Introduction. *In* G.C. Whittow and H. Rahn (eds.), Seabird energetics. Plenum, New York.

Ricklefs, R.E. 1974. Energetics of reproduction in birds. *In* R.A. Paynter, Jr. (ed.), Avian energetics. Publ. Nuttall Ornithol. Club No. 15, Cambridge, Mass. pp. 152–297.

Ricklefs, R.E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* 8:84–94.

Ricklefs, R.E., C.H. Day, C.E. Huntington and J.B. Williams. 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. *J. Anim. Ecol.* 54:883–898.

Ricklefs, R.E., D. Galbaldon and W.A. Montevecchi. 1984. Postnatal development of the Northern Gannet *Sula bassanus*, and the general relationship between growth rate and adult size in birds. *Ornis Scand.* 15:204–210.

Ricklefs, R.E. and K.K. Mathew. 1983. Rates of oxygen consumption in four species of seabird at Palmer Station, Antarctic Peninsula. *Comp. Biochem. Physiol.* 74A:885–888.

Ricklefs, R.E., D.D. Roby and J.B. Williams. 1986. Daily energy expenditure of adult Leach's Storm-Petrels during the nesting cycle. *Physiol. Zool.* 59:649-660.

Ricklefs, R.E. and J.B. Williams. 1984. Daily energy expenditure and water-turnover rate of adult European Starlings (*Sturnus vulgaris*) during the nesting cycle. *Auk* 101:707–716.

Roby, D.D and R.E. Ricklefs. 1986. Energy expenditure in adult Least Auklets and diving petrels during the chick-rearing period. *Physiol. Zool.* 59:661-678.

Tatner, P. and D.M. Bryant. 1986. Flight cost of a small passerine measured using doubly labeled water: implications for energetics studies. *Auk* 103:169–180.

Trivers, R.L. 1972. Parental investment and sexual selection. *In* B. Campbell (ed.), Sexual selection and the descent of man 1871–1971. Aldine, Chicago. pp. 136–179.

Tucker, V.A. 1973. Bird metabolism during flight. *J. Exp. Biol.* 58:689–709.

Walsberg, G.E. 1983a. Avian ecological energetics. *In* D.S. Farner, J.R. King and K.C. Parkes (eds.), Avian biology, Vol. VII. Academic Press, New York. pp. 161–220.

Walsberg, G.E. 1983b. Ecological energetics: what are the questions. *In* A.H. Brush and G.A. Clark, Jr. (eds.), Perspectives in ornithology. Cambridge Univ. Press, Cambridge. pp. 135–158.

Weathers, W.W 1979. Climatic adaptation in avian standard metabolic rate. *Oecol.* 42:81–89.

Wiens, J.A. 1984. Modelling the energy requirements of seabird populations. *In* G.C. Whittow and H. Rahn (eds.), Seabird energetics. Plenum, New York. pp. 255–284.

Wilson, R.P. and C.A.R. Bain. 1984. An inexpensive speed meter for penguins at sea. *J. Wildl. Manage.* 48:1360–1364.

Wood, R.A., K.A. Nagy, N.S. MacDonald, S.T. Wakakuwa, R.J. Beckman and H. Kaaz. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Anal. Chem.* 47:646–650.

APPENDIX A Calculation of the half-life of body water.

The $H_2{}^{18}O$ and ^3HHO fractions in body water decrease logarithmically as body water turns over. In this study, ^3HHO enrichments were high enough that activities were well above background levels for all water samples, with the result that measurements of water turnover rates were reliable for all sample intervals. A log-log regression of $H_2{}^{18}O$ fraction (atom % excess) *vs.* total water turnover (TWTO, $mL \cdot kg^{-1}$) for all samples gave the equation

$$H_2{}^{18}O = .0646\ TWTO^{-.0525}$$

($r = -.98$, $n = 75$, $p < .0001$). The half-life (L) of body water for individual birds was calculated as

$$L = \frac{(O_1/2)^{-1/.0525}}{.0646}$$

where L is in $mL\ H_2O \cdot kg^{-1}$ and O_1 is initial ^{18}O enrichment corrected for background (atom % excess). The number of half-lives of body water (H) between injection and final capture was calculated as

$$H = \frac{TWTO}{L}$$

APPENDIX B Energy expenditures and breeding parameters of Northern Gannets studied with doubly labeled water at Funk Island in 1984 and 1985. ΔT = time between captures; Mass = minimum body mass; ΔMass = change in mass between captures, %BW = % body water estimated from ^{3}HHO and $H_2{}^{18}O$ dilution spaces; WTO = water turnover rate; ADMR = average daily metabolic rate; DEE = daily energy expenditure ; FE_G = gross foraging efficiency.

BIRD	ΔT d	MASS kg	Δ MASS $g \cdot d^{-1}$	%BW ^3H	%BW ^{18}O	WTO $g \cdot kg^{-1} d^{-1}$	ADMR $mL \cdot g^{-1} h^{-1}$	DEE $kJ \cdot d^{-1}$	SEX	CHICK AGE wk	FE_G
1984											
9a	1.76	2.95	- 85	71.3	76.4	157	2.71	5014	f	-	-
21	1.98	3.32	152	58.0	70.3	165	3.16	6571	f	1.7	2.34
24a	1.36	2.95	73	70.6	75.9	161	2.43	4480	m	2.1	1.98
24b	1.07		-352			102	3.77	6960		2.3	-
1985											
2a	3.89	2.91	-121	68.4	65.4	174	2.85	5213	f	1.1	1.65
3	3.87	3.02	-119	71.6	69.0	121	2.73	5173	m	-	-
5a	1.86	2.98	59	67.6	67.0	196	3.27	6124	m	5.2	2.42
5b	2.99		-137			145	3.07	5735		5.5	1.98
10a	1.52	2.90	- 72	74.3	64.7	179	3.06	5570	m	9.7	-
10b	2.41		46			216	2.31	4207		9.9	2.35
13a	1.84	3.51	44	66.6	66.6	102	2.12	4679	m	7.5	2.21
13b	2.70		41			206	2.47	5436		7.7	1.93
13c	1.54		-169			117	2.63	5804		8.1	3.30
14a	1.84	2.99	-131	69.0	67.4	130	2.28	4284	m	6.4	1.58
14b	1.70		- 53			239	3.11	5831		6.7	2.46
16a	3.53	2.79	- 45	67.6	68.7	179	2.68	4687	f	7.8	2.28
17a	2.51	3.11	20	62.8	64.5	170	2.20	4294	f	7.1	2.42
17b	3.53		- 45			101	2.45	4788		7.5	2.67
19a	2.49	3.15	- 92	68.9	66.8	105	2.48	4899	m	9.0	2.23
19b	2.97		20			183	2.78	5503		9.4	3.58
20a	2.50	3.32	56	64.6	63.4	114	1.70	3542	m	9.9	-
20b	1.53		- 46			100	2.20	4586		10.3	4.61
22	3.47	3.06	- 3	60.5	61.4	166	2.37	4543	f	2.2	2.14
23	2.45	3.76	- 16	55.5	56.1	164	2.25	5306	f	2.5	-
24a	2.45	2.91	41	63.3	63.8	136	2.45	4475	m	-	-
24b	1.99		40			211	2.39	4362		-	-
25a	2.47	3.16	65	63.9	65.4	134	2.35	4660	m	4.6	3.05
25b	1.95		-139			187	3.10	6149		5.0	2.21
27a	2.38	3.25	34	65.8	64.3	172	2.84	5788	f	6.0	3.38
28	4.38	3.13	- 68	68.2	68.4	146	2.81	5523	-	7.8	3.10
MEAN	2.43	3.11	- 34	66.3	66.6	156	2.63	5140			3.04
S.D.	0.84	0.23	100	4.6	4.6	38	0.42	777			1.88
MAX.	4.38	3.76	-352	74.3	76.4	239	3.77	6960			5.49
MIN.	1.07	2.79	152	55.5	56.1	100	1.70	3542			0.84

APPENDIX C Scientific names of seabirds listed in tables.

COMMON NAME	SCIENTIFIC NAME
Adelie Penguin	*Pygoscelis adeliae*
Gentoo Penguin	*Pygoscelis papua*
King Penguin	*Aptenodytes patagonicus*
Macaroni Penguin	*Eudyptes chrysolophus*
Fjordland Penguin	*Eudyptes pachyrynchus*
Little Penguin	*Eudyptula minor*
Jackass Penguin	*Spheniscus demersus*
Peruvian Penguin	*Spheniscus humboldti*
Grey-Headed Albatross	*Diomedea chrysostoma*
Wandering Albatross	*Diomedea exulans*
Laysan Albatross	*Diomedea immutabilis*
Southern Giant Fulmar	*Macronectes giganteus*
Wedge-Tailed Shearwater	*Puffinus pacificus*
Wilson's Storm-Petrel	*Oceanites oceanicus*
Leach's Storm-Petrel	*Oceanodroma leucorhoa*
South Georgia Diving Petrel	*Pelecanoides georgicus*
Common Diving Petrel	*Pelecanoides urinatrix*
Brown Pelican	*Pelecanus occidentalis*
Blue-Eyed Shag	*Phalacrocorax atriceps*
Herring Gull	*Larus argentatus*
Laughing Gull	*Larus atricilla*
Ring-Billed Gull	*Larus delawarensis*
Sooty Tern	*Sterna fuscata*
Brown Noddy	*Anous stolidus*
Common Murre	*Uria aalge*
Thick-Billed Murre	*Uria lomvia*
Black Guillemot	*Cepphus grylle*
Least Auklet	*Aethia pusilla*