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DAILY ENERGY EXPENDITURE BY ADULT LEACH'S STORM-PETRELS DURING THE NESTING CYCLE[1]

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We measured metabolic rates of adult Leach's storm-petrels on Kent Island, New Brunswick, in order to determine the energetic costs of reproductive activities in a small, pelagic seabird. Oxygen consumption of captive birds was determined volumetrically, and daily energy expenditure of free-living individuals was estimated by the doubly labeled water technique (DLW). Errors inherent in DLW gave rise to expected standard deviations in estimates of CO_2 production on the order of 20%–30% of the mean, which were similar in magnitude to the variation observed among individual measurements. Furthermore, when final concentrations of ^{18}O in body water were low, an apparent bias in the measurement of background ^{18}O consistently inflated estimates of CO_2 production. Minimum rate of oxygen consumption occurred at 36 C and averaged 90 $cm^3\ h^{-1}$ or 1.92 $cm^3\ g^{-1}\ h^{-1}$. Rate of oxygen consumption increased gradually with decreasing temperature and more rapidly below 16 C, at which point thermal conductance plus evaporative heat loss was 2.6–2.9 $J\ g^{-1}\ C^{-1}\ h^{-1}$. CO_2 production of incubating adults averaged 80 $cm^3\ h^{-1}$. Analysis of individuals collected at the beginning and end of the incubation spell indicated that about two-thirds of the energy for incubation was supplied by fat deposits and the rest by stomach oils and that the ratio of fat to water loss during incubation was about 1.55 by mass. Carbon dioxide production of adults away from the nest during the first half of the nestling period averaged 191 $cm^3\ h^{-1}$. Water turnover rates were 0.136 day^{-1} in incubating adults and 1.01 day^{-1} in adults away from the nest. Estimates of daily energy expenditure (DEE) are consistent with Leach's storm-petrels' spending considerable time resting on the water surface while at sea. Ratios of energy expenditure to water turnover suggest that adults assimilate a less energy-dense diet than that which they feed their chicks.

INTRODUCTION

All procellariiform birds (petrels and their relatives) rear a single, slowly growing chick that accumulates large deposits of fat during the nestling period. These adaptations led Lack (1968), among others, to suggest that such pelagically feeding seabirds are severely limited, compared with nearshore and terrestrial species, in the amount of food that they can deliver to their chicks and that their food supplies are variable and unpredictable. Most attempts to test this idea have involved adding a second chick to the brood. These twinning experiments test whether adults are able to increase their feeding rates sufficiently (i.e., approximately twofold) to rear two offspring to fledging. Procellariiforms have not been able to rear two well-nourished chicks (Rice and Kenyon 1962; Harris 1966, 1969; C. E. Huntington, personal communication).

Even if we accept twinning as a valid test of the ability of adults to deliver more food to their chicks, such experiments address only the problem of the single-chick brood. The amount of food required to sustain a single, rapidly growing chick is less than the amount required by two slowly growing chicks (Ricklefs, White, and Cullen 1980a; Ricklefs and White 1981; Ricklefs 1984). Hence, the inability of petrels to rear twins is not germane to the significance of slow postnatal growth. Shea and Ricklefs (1985) recently demonstrated that adult gray-backed terns (*Sterna lunata*), which also

rear a single, slowly growing chick, can in-
crease food delivery by at least 30%, enough
to successfully rear fostered chicks of the
larger, but closely related, sooty tern (*S.
fuscata*). Furthermore, Ricklefs et al. (1985)
present evidence that the amount of food
consumed by Leach's storm-petrel (*Ocean-
odroma leucorhoa*) chicks is narrowly reg-
ulated, suggesting that rate of food delivery
is determined by the requirements of the
chick rather than by the ability of the par-
ents to gather food. These observations cast
doubt on the idea that reproduction in all
pelagic seabirds is severely limited by food
supply.

With respect to the ability of adult petrels
to provide food for their young, we may
imagine three possibilities: (*a*) adults deliver
as much food as they possibly can gather
over and above their foraging and transport
requirements; (*b*) food delivery to the nest
is limited by ceilings imposed on the fre-
quency of trips from the foraging area to
the nest and the amount the parent can
carry per trip, not by how much it can
gather (Ricklefs 1983); and (*c*) adults deliver
fewer or smaller meals than they potentially
could, the growth rates of the chicks being
limited by factors other than food avail-
ability (Ricklefs, White, and Cullen 1980*b*).
Furthermore, the food requirements of
chicks may be adjusted with respect to food
availability during occasional poor years,
rather than to average or prevailing con-
ditions.

In a discussion of the energetics of
breeding in pelagic seabirds, Ricklefs (1983)
pointed out that adults may be more con-
strained energetically during the incubation
or brooding periods than during the nestling
period. When the egg or chick must be
tended continuously, the potential foraging
time of each adult is halved; during the for-
aging period, each adult must gather
enough energy to support itself and the cost
of either incubating an egg or feeding and
brooding a small chick. Conceivably,
therefore, energy limitation could occur at
a time when energy requirement is inde-
pendent of the postbrooding growth rate of
the chick. If transport of food were limiting,
this problem would be alleviated to the ex-
tent that adults transport energy for their
own metabolic needs in the form of fat de-
posits or stomach oils, having a high energy

density, rather than the fresh or partially
digested meals fed to their chicks (Ricklefs
1983).

In order to evaluate food delivery to the
nest as a factor in the evolution of patterns
of reproduction in seabirds, we must even-
tually measure the energy requirements of
adults and chicks, the forms in which en-
ergy is transported, and the costs to the
adult of foraging and transport. Few of these
data have been obtained for any species.
The present paper attempts to fill in some
of these gaps by presenting for Leach's
storm-petrels (*a*) measurements of oxygen
consumption of adults as a function of
chamber temperature, (*b*) estimates of daily
energy expenditure (DEE) by incubating
adults calculated from changes in body
components during incubation spells, (*c*)
partitioning of the source of energy metab-
olized during the incubation spell between
stomach contents and fat deposits, (*d*) es-
timates of DEE of incubating adults ob-
tained by the doubly labeled water (DLW)
method, and (*e*) estimates of DEE of adults
away from the nest site, presumably while
foraging, by the DLW method. The results
are discussed in the context of limitations
to breeding in pelagic seabirds.

MATERIAL AND METHODS

The study was conducted at the Bowdoin
Scientific Station on Kent Island, New
Brunswick, at the mouth of the Bay of
Fundy, during the summers of 1981–1983.
Here, most female storm-petrels lay their
egg during early June; chicks begin hatching
around mid-July and fledge in September
(Wilbur 1969).

Oxygen consumption was measured in
a closed system having a volume of about
4 liters, similar to that described by Ricklefs
and Roby (1983). We lined chambers with
5-mm thick, dark green scouring pads to
keep subjects from contacting the metal
walls of the chambers and to minimize re-
flectance of long-wave radiation. Ascarite
was placed in the bottom of the chamber
to absorb carbon dioxide; Drierite was
placed there to absorb water vapor. We did
not measure the partial pressures of either
carbon dioxide or water vapor, but, because
we waited after sealing the chambers until
oxygen consumption stabilized before re-
cording data (usually 30 min), we assume

that carbon dioxide and water vapor concentrations reached equilibria. Oxygen was added from a calibrated syringe to keep the pressure in the chamber constant during the equilibrium and trial periods. We used manometers filled with light-gauge oil to detect pressure changes. The volume of oxygen added per unit time, corrected to 0 C and 760 torr, is the rate of oxygen consumption. Ambient temperature was regulated to ±0.5 C by circulating a temperature-controlled mixture of methanol and water through copper coils surrounding the chambers; all calculations were adjusted with respect to chamber temperatures at the beginning and end of each trial. Results obtained with our closed manometric system have been compared with those from an open-flow system using an Applied Electrochemistry Oxygen Analyzer, and we found no significant difference (Williams and Prints 1986). Logistical considerations precluded our using an open system at Kent Island.

Adult subjects for metabolism measurements were removed from their burrows at 0800–0900 hours and returned before nightfall. Eight adults were exposed to a variety of chamber temperatures from 36 to −3 C for 30-min trials. Body temperatures were measured after each trial by inserting a thermistor about 5 cm into the proventriculus.

For calculating energy expenditures, we assumed the energy equivalent of oxygen consumption to be 20.1 kJ/liter O_2.

Temperatures within our chambers were measured by 36-gauge copper-constantan thermocouples connected to a Bailey BAT-12 thermometer. Adults were weighed with an electronic balance (readable to 0.01 g) in the laboratory and calibrated Pesola spring balances (±0.5 g) in the field.

In order to determine the water content of adults and to determine the composition of adults at the beginning and end of the incubation spell, we collected two sets of adults at the end of July 1983. The first had been incubating eggs for 3 consecutive days and was obtained between 2200 and 2400 hours on the third day. The mates of these six birds were collected between 0000 and 0400 hours, after they had returned to the nest to commence their incubation spells. The specimens were frozen for later analysis.

Thawed birds were dissected, and their components were air-dried to constant mass at 60 C and extracted for 24 h in each of at least two fresh baths of a 5:1 mixture of petroleum ether and chloroform. We have found that this technique compares favorably with soxhlet extraction of ground material. In a comparison using 20-g aliquots of coarsely ground, homogenized samples of duck carcasses, ranging in lipid content between 12% and 43% of dry weight, the technique used in this study extracted 90.3% (3.6% SE, $n = 10$) of the mass removed by extraction in boiling ethyl ether using the method of Randall (1974).

Six specimens, three from each of the samples of adult storm-petrels, were dissected into 15 components to determine anatomical proportions. The other six were skinned and opened to allow their muscle masses and viscera to dry rapidly. The stomach contents were removed from all the specimens and analyzed separately. In this study, water = wet mass − dry mass; fat = dry mass − extracted mass (lipid-free dry matter [LFDM]). Total body water was related to mass by a quadratic equation used to estimate the body water content of live birds (see Results). In several calculations, we used metabolizable energy equivalents of 18 kJ g^{-1} LFDM and 38 kJ g^{-1} fat.

Estimates of carbon dioxide production of free-living birds were obtained using a technique somewhat modified from protocols developed by Nagy (1975, 1980), as applied, for example, by Williams and Nagy (1984a, 1984b) and Ricklefs and Williams (1984). Adults were captured in their nest burrows at night and injected intraperitoneally with 0.30 cm^3 of a mixture of tritiated (^{3}H) water (0.3 mCi cm^{-3}) and ^{18}O-enriched water (98 atom %). Injected adults were immediately placed back in the nest. Incubating birds were recaptured after 24 or 48 h, at which time a blood sample of approximately 0.20 cm^3 was obtained by puncturing the brachial vein and drawing blood into heparinized capillary tubes. The tubes were flame sealed and stored at 4 C until further analysis. Adults foraging at sea were trapped in their nest burrows after 48 or 72 h, and blood samples were taken in the same manner. Ricklefs et al. (1985) found that 2 and 3 days were the most fre-

quent foraging periods. One month after the blood samples were taken, the chicks of all the adult subjects in this study appeared healthy and well nourished, indicating that the procedure had no long-term effect on parental care.

The initial level of ^{3}H and the initial ratio of ^{18}O to ^{3}H in the body water of injected birds were estimated from the average values for blood samples obtained from eight adults after 1 h, which allows equilibration of isotopes in birds ranging in size from 20 to 600 g (Degen et al. 1981; Williams 1985). We did not obtain initial blood samples from subjects released for the measurement of field metabolism because a pilot study indicated that the trauma of bleeding following an hour of confinement led either to prolonged periods before subjects returned to the nest or to avoidance of our nest traps.

We microdistilled (Wood et al. 1975) the blood samples under vacuum and measured tritium activity according to procedures described by Ricklefs and Williams (1984). Oxygen-18 was measured according to the technique of Wood et al. (1975) by K. Nagy at the Laboratory of Biomedical and Environmental Sciences, UCLA. Carbon dioxide production was calculated by the equations of Lifson and McClintock (1966) and Nagy (1980), as modified by Ricklefs and Williams (1984):

$$CO_2 (cm^3/h)$$
$$= \frac{622.23\,W}{t}\left[\ln\left(\frac{O_i}{H_i}\right) - \ln\left(\frac{O_f}{H_f}\right)\right], \quad (1)$$

where W is total body water (g), t is time (h) between injection and bleeding minus 1 h for equilibration, and O/H are the ratios of ^{18}O to ^{3}H in initial (i) and final (f) samples of water distilled from blood. Values of O and H were first adjusted by subtracting background levels, estimated from distilled blood samples of six uninjected birds. Total body water is the arithmetic mean of the estimated body water at the times of injection and bleeding (see Results).

In this study, we assumed the energy equivalent of CO_2 to be 26.8 J cm^{-3}, which assumes a respiratory quotient (RQ) of 0.75. Iversen and Krog (1972) determined RQ of adult Leach's storm-petrels to be 0.83, but we have arbitrarily used the lower value, which is more generally typical of birds that metabolize lipid and protein (Schmidt-Nielson 1975).

Potential sources of error and bias in the measurements are discussed in detail in Results. Statistical procedures follow Sokal and Rohlf (1981).

RESULTS

OXYGEN CONSUMPTION

Rate of oxygen consumption was least (90.2 cm^3 h^{-1}, 1.92 cm^3 g^{-1} h^{-1}, 1.81 kJ h^{-1}) at 36 C, the highest temperature tested (table 1). Rate of oxygen consumption increased gradually with decreasing chamber temperature down to 15 C and more steeply below that point. Mass-specific thermal conductance of the body surface plus evaporative cooling was 7.6 J g^{-1} C^{-1} h^{-1} at 36 C and decreased to between about 2.6 and 2.9 J g^{-1} C^{-1} h^{-1} at 16 C and below. According to Lasiewski and Dawson's (1967) equation relating basal metabolic rate (BMR) of nonpasserine birds to body mass, the predicted BMR for a mass of 45 g is 1.45 kJ h^{-1}. Measured BMR was 25% greater than predicted. According to equation (14) of Calder and King (1974), expected conductance for a bird with a mass of 45 g is 2.17 J C^{-1} g^{-1} h^{-1}. Thus, the measured value of about 2.75 J C^{-1} g^{-1} h^{-1} was 27% higher. The expected critical gradient (body temperature minus lower critical temperature = BMR/conductance) was 14.0 C. Thus the expected T_{lc} was about 26 C.

INCUBATION SPELL AND DAILY MASS LOSS

Ten nests were checked every day between July 29 and August 6, 1982, toward the end of the incubation period of most pairs. Incubation spells were recorded only when both the beginning and end of the spell could be ascertained, that is, when one adult replaced the other and was in turn replaced by the first bird. Disappearance of an adult, resulting in an unattended egg, disqualified the observation. Chicks hatched in several of the nests during this period, and some of the nests were left unattended for long periods, apparently because the adults were sensitive to daily disturbance.

TABLE 1

MEAN RATES OF OXYGEN CONSUMPTION AS A FUNCTION OF CHAMBER
TEMPERATURE IN ADULT LEACH'S STORM-PETRELS

SAMPLE SIZE	TEMPERATURE (°C)		OXYGEN CONSUMPTION		CONDUCTANCE ($J g^{-1} °C^{-1} h^{-1}$)
	Chamber	Body	($cm^3 h^{-1}$)	($cm^3 g^{-1} h^{-1}$)	
4	35.9	41.0	90.2	1.92	7.56
	(.4)	(.7)	(17.1)	(.37)	
4	30.4	39.9	120.1	2.51	5.31
	(.5)	(.1)	(9.0)	(.18)	
4	25.1	39.9	127.6	2.66	3.61
	(.3)	(.1)	(18.2)	(.35)	
8	19.9	39.8	150.5	3.26	3.29
	(.5)	(.3)	(21.6)	(.42)	
4	15.7	40.8	152.8	3.35	2.76
	(.2)	(.1)	(12.3)	(.17)	
4	9.6	38.9	189.9	4.28	2.94
	(.3)	(.4)	(17.4)	(.59)	
3	5.3	40.7	227.7	4.63	2.62
	(.4)	(.3)	(18.2)	(.25)	
8	−.9	38.7	254.5	5.24	2.65
	(1.5)	(.5)	(13.5)	(.33)	

NOTE.—Numbers in parentheses are ±SDs.

A total of seven incubation spells were two of 2 days, three of 3 days, and one each of 4 and 5 days. The average for the seven observations was 3.1 days (1.6 SD). For these same birds, and others for which we did not determine incubation spells, 27 records of daily mass loss averaged 2.37 g (0.72 SD, 0.14 SE). We calculated daily mass losses of 11 subjects in our study of DEE of incubating birds (late July 1983). Nine of the trial periods were 24 h, three were 48 h. The average daily mass loss was 3.15 g (0.63 SD, 0.19 SE).

ENERGY EXPENDITURE DURING INCUBATION BASED
ON BODY COMPONENTS

The six adults that we collected at the beginning of their incubation spells averaged 53.47 g (4.41 SD), and the six adults collected after 3 days of incubation averaged 41.47 g (2.03 SD). The initial and final masses differed by 12.00 g. The estimated variance of the difference between two samples of independent observations is the sum of the variances of each of the samples; with this assumption, we estimated the standard deviation of the difference between the initial and final masses to be 4.85 g (1.98 SE). The difference was therefore equivalent to a daily loss of 4 g (0.66 SE),

which exceeds significantly that obtained from repeated measurements of individuals during both 1982 and 1983.

Our analyses indicate that adults contained an average of 766 kJ of metabolizable energy at the beginning of the incubation spell and 480 kJ after 3 days (table 2). The difference between these values was 286 kJ, for which the estimated standard deviation was 109 kJ (31 SE). These values are equivalent to 95 kJ per day and 24 kJ (9 SD) per gram of weight lost.

Of the difference in energy content between the initial and final samples, 88% was due to differences in lipid content, and 66% was associated with differences in body components rather than stomach contents. Of the difference in mass between the two samples, 55.6% was fat, 35.9% was water, and 15.4% was LFDW. The total of these percentages exceeds 100% because the difference between the sums of the components (52.48 − 39.66 = 12.82 g) was greater than the difference between the fresh masses of the specimens. The discrepancies (0.99 and 2.13 g) were due to loss of mass during processing. The LFDM did not differ significantly between the initial and final samples. In this study, the difference between samples included about 1.55 times as much

lipid as water. Therefore, if LFDM were ignored, mass loss would have consisted of 61% fat (46% of which was stomach oils) and 39% water, with an associated energy equivalent of 23 kJ g^{-1}.

WATER CONTENT OF ADULTS

Water content was calculated for the 12 specimens collected at the beginning or end of incubation spells. Fresh masses varied between 38.13 and 57.37 g, and, excluding stomach contents, the specimens contained between 17.14 and 22.96 g of water (38.88%–50.45%). We do not know the extent to which processing loss was body water, but this loss could have resulted in body water being underestimated by as much as 1–2 g (i.e., 5%–10%).

We related water content (W) to body mass (M) using a least-squares fit of a quadratic equation to the data. The resulting equation was $W = -40.947$ (21.52 SE) $+ 2.447$ (0.904 SE) $M - 0.023555$ (0.00933 SE) M^2 ($R^2 = .715$). The standard deviation of points about the regression line was 0.95 g.

OXYGEN-18 BACKGROUND LEVELS AND INITIAL ISOTOPE RATIO

Water distilled from the blood of six noninjected adults was analyzed in triplicate to determine the background level of ^{18}O. The resulting values averaged 0.2032 atom % (0.0002 SE, $n = 18$). There was no significant between-adult variation. Initial ratios of ^{18}O to ^{3}H (backgrounds subtracted) were determined for eight adults 1 h after injection. The average of the natural log-transformed values was -11.0920 (0.0056 SE, $n = 8$).

POTENTIAL ERRORS IN THE ESTIMATION OF CARBON DIOXIDE PRODUCTION

Errors can enter the calculation of CO_2 production by equation (1) through errors

TABLE 2

MEANS OF COMPONENTS AND THEIR ENERGY EQUIVALENTS
OF ADULT LEACH'S STORM-PETRELS AT THE BEGINNING
AND END OF THE INCUBATION SPELL

	Water	Lipid	Lipid-free Dry Weight
Initial (weight = 53.47 g, 4.41 SD, $n = 6$)			
Body components ...	22.15 (.69)	9.83 (1.96)	14.10 (1.83)
Stomach contents ...	2.56 (2.35)	3.50 (.46)	.33 (.46)
Final (weight = 41.47 g, 2.03 SD, $n = 6$)			
Body components ...	19.94 (1.57)	5.49 (1.06)	12.65 (.75)
Stomach contents ...	.48 (.32)	1.17 (.39)	−.06 (.09)
Difference			
Body components ...	2.21 (1.71)	4.34 (2.23)	1.45 (1.98)
Stomach contents ...	2.08 (2.37)	2.33 (.60)	.39 (.47)
Energy equivalent of total (kJ)			
Initial		506	260
Final		253	227
Difference			
Body components ...		165	26
Stomach contents		89	7
Total		254	33

NOTE.—Numbers in parentheses are ±SDs.

in estimating several components: backgrounds, ratios of ^{18}O to ^{3}H in body water, and total body water. In addition, biases can be introduced through biases in estimates of body water and, as we shall discuss below, ^{18}O background.

Oxygen-18 background was measured with a standard error of 0.0002%. The two lowest values of ^{18}O concentration measured in this study were 0.2047 and 0.2098%, that is, 0.0015% and 0.0066% above background. Initial concentrations of ^{18}O were at least 1% above background, and most of the final concentrations obtained within 48 h were greater than 0.0600% above background. Thus, the error in estimating O_f owing to error in estimating the background was less than 0.02% of the estimate in most cases and less than 3% in all but one case.

Errors introduced by measurement of isotopes in water distilled from blood water were investigated more directly by repeating measurements of ^{18}O and ^{3}H on the same sample of water and calculating two values of CO_2 production based on the first and second sets of measurements. Variation between replicates represents errors in pipetting water samples and determining isotope levels. First values varied between 62 and 332 cm^3 h^{-1}. In 15 replicates, the ratio of the second value for CO_2 production to the first averaged 0.959 (0.112 SD, 0.029 SE, not significantly different from 1). Thus, the standard deviation of the replicate was about 12% above and below the first value. We analyzed variation between adults and between replicates within adults by one-way analysis of variance. Variation between adults accounted for most of the variance [$F(1,14) = 52$, $P < .0001$, $R^2 = .98$]. The square root of the mean square error (the error standard deviation), was 15.9 cm^3 h^{-1}, or 9.7% of the mean value of CO_2 production. The same ANOVA based on log-transformed values of CO_2 production had an error standard deviation of 0.106. Most of this variation arose from measurement of ^{3}H.

The water content of the adult was estimated with a standard deviation of about 5% and with a potential bias of −5% to −10%. Considering all these sources of error, we feel that individual estimates of daily energy expenditure probably should be assigned confidence limits (approximately

twice the standard deviations of the estimates about the mean) of perhaps 60% above the mean and 40% below the mean, with a potential bias in the mean as high as −10%.

CARBON DIOXIDE PRODUCTION DURING INCUBATION

Twelve measurements varied between 62 and 99.5 cm^3 CO_2 h^{-1} with an average of 80.0 cm^3 CO_2 h^{-1} (13.5 SD, 3.9 SE, 17% CV). Nine of the 12 measurements were obtained over 24-h periods and ranged between 62 and 93 cm^3 CO_2 h^{-1}. The three measurements obtained over 48 h were 78, 99, and 99 cm^3 CO_2 h^{-1}. Mass-specific CO_2 production averaged 1.71 cm^3 g^{-1} h^{-1} (0.33 SD, 0.095 SE, 19% CV). Neither the total nor mass-specific CO_2 production was statistically correlated with the mass of the adult. Because the coefficient of variation in CO_2 production was on the same order as that expected from a consideration of errors in each component of the equation, most of the variation among measurements could be attributable to measurement error rather than inherent variation in the population.

CARBON DIOXIDE PRODUCTION AWAY
FROM THE NEST

We obtained measurements from eight individuals with chicks, four after 48 h, and four after 72 h. It was apparent that the estimate of CO_2 production was biased in relation to the final concentration of ^{18}O such that, as the concentration approached the background level, estimates of CO_2 production increased (fig. 1). Although it is possible that individuals with low final ^{18}O concentrations (related to high WTO rates) might have had higher metabolic rates, we would have expected a similar relationship among individuals measured over 48 h, and there was none. Furthermore, the relationship between CO_2 production and final ^{18}O concentration can be removed by adjusting the background ^{18}O level downward. Carbon dioxide production values calculated with a hypothetical background of 0.2000%, also plotted in figure 1, show this effect.

The bias in the estimate of CO_2 production was relatively small for values of final ^{18}O concentration above 0.24%. These five values (excluding replicates) were 171, 180, 188, 196, and 218 cm^3 CO_2/h ($\bar{X} = 191$, 18 SD, 8 SE, 9.4% CV). On a mass-specific

basis, the average was 4.46 cm^3 CO$_2$ g^{-1} h^{-1} (0.38 SD, 0.17 SE, 8.5% CV).

WATER TURNOVER RATE

Water turnover rate was estimated from concentrations of ^{3}H in the initial and final samples by the equation WTO (day^{-1}) = [ln $(H_i) - \ln (H_f)]/t$, where t is the measurement period in days. The natural logarithm of H_i was estimated from initial (1-h) blood samples obtained from eight birds to be 11.1443 (0.0889 SD, 0.0314 SE). For 12 individuals incubating eggs, WTO averaged 0.136 day^{-1} (0.062 SD, 0.018 SE, 45.4% CV). For nine individuals away from the nest site, WTO averaged 1.009 day^{-1} (0.228 SD, 0.076 SE, 22.6% CV). A large part of the variation in estimates of WTO probably arises from the error in estimating H_i, which we did not measure directly in the experimental subjects.

DISCUSSION

Estimates of energy expenditure of adult Leach's storm-petrels are compared in table 3. Oxygen consumption of adults under standard conditions reported by Iversen and Krog (1972), Ricklefs et al. (1980a), and this study are comparable and suggest a metabolic rate of 55–60 kJ day^{-1} at an ambient temperature of 20 C. The CO$_2$ production of incubating birds, equivalent to 51.5 kJ day^{-1} (0.60 W), was 19% above the lowest level of metabolism that could be estimated from oxygen consumption, even though burrow temperatures were consistently in the range of 10–15 C (Ricklefs and Rahn 1979; this study).

According to equations of Kendeigh (1973), and assuming that 80% of the surface of the 10-g egg is not covered by the brood patch (Drent 1973), the estimated rate of heat loss of an egg incubated at 36 C (Williams and Ricklefs 1984) is 0.62 W. Therefore, taken at face value, our estimate of CO$_2$ production suggests either that the immediate nest microenvironment of the incubating parent is warmed considerably, the egg is well covered by feathers and hence is enclosed within the insulative shell of the adult, some avenues of heat loss or components of metabolism are reduced considerably during incubation, or some combination of these factors. Experience handling particularly docile incubating adults in
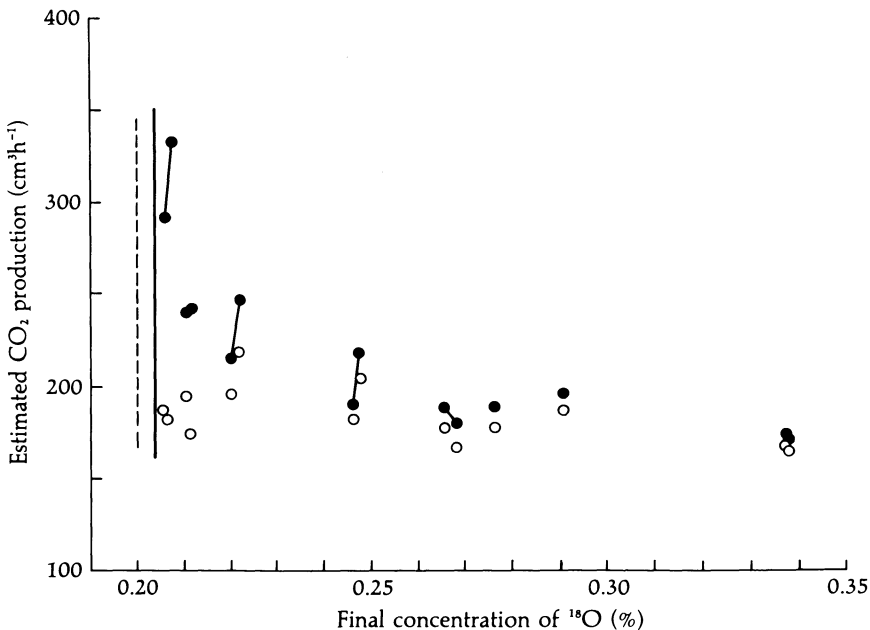

FIG. 1.—Calculated rate of CO$_2$ production (cm^3 h^{-1}) of free-flying adult Leach's storm-petrels as a function of the final concentration of ^{18}O in body water. Solid symbols are based on the measured background level of ^{18}O of 0.2032% (solid vertical line); open symbols are based on a hypothetical background level of 0.2000% (dashed vertical line). Lines between symbols connect replicated values for the same subjects.

TABLE 3

ESTIMATES OF ENERGY EXPENDITURE OF ADULT LEACH'S STORM-PETRELS

	kJ/day	W
Oxygen consumption:		
This study, lowest value (36 C, 90 cm³ h⁻¹)	43.4	.50
This study, at 16 C (153 cm³ h⁻¹)	73.8	.85
Ricklefs et al. (1980a), at 15–25 C (126 cm³ h⁻¹)	60.8	.70
Iversen and Krog (1972), at 20 C (110 cm³ h⁻¹)	53.1	.61
Incubating adults:		
Equation of Croxall (1982), mass = 0.045 kg, mass loss 55% lipid	52.1	.60
This study, mass loss:		
Component difference	96.0	1.11
Injected birds (1983), 3.15 g day⁻¹, 24 kJ g⁻¹	75.6	.88
1982 sample, 2.37 g day⁻¹, 24 kJ g⁻¹	56.9	.66
This study, DLW (80 cm³ CO₂ h⁻¹)	51.5	.60
Free-flying adults:		
This study, DLW (190.6 cm³ CO₂ h⁻¹)	122.6	1.42

burrows suggests that the egg is fully surrounded by body feathers when positioned in contact with the brood patch.

Croxall (1982) presented an equation for estimating incubation energy expenditure from adult mass, based on measurements of rate of mass loss of incubating petrels and assuming that the loss is 55% lipid (ca. 21 kJ g⁻¹). According to his equation, we estimate DEE for Leach's storm-petrel (M = 45 g) to be 52.1 kJ day⁻¹ (0.60 W), which is nearly identical with the DLW estimate from this study. Our estimate of % of mass loss due to lipid was 61%, which did not differ significantly from 55%.

Water turnover rate may be used to check the consistency of the estimate of carbon dioxide production. In this study, we estimated WTO, based on fractional change in ³H, to be 0.14 day⁻¹ during incubation. If water in the stomach and body were in equilibrium with each other, and thus ³H is fully dispersed, the only source of new water during incubation would be oxidative metabolism. At 38 kJ g⁻¹ of lipid, a DEE of 51.5 kJ day⁻¹ is equivalent to burning 1.4 g of fat with the production of about the same amount of water (Schmidt-Nielsen 1975). Divided by an average of 21.7 g of water per individual, this would result in a WTO rate of 0.065 day⁻¹. But if water in the stomach contents were not equilibrated with that of the body, as much as 2 g of water would be produced by assimilation from the gut, bringing the WTO to (2.0 + 1.4)/21.7 = 0.16 day⁻¹, which is

in reasonable agreement. This agreement justifies our not including water present in stomach contents in the calculation of CO₂ production.

Metabolism while away from the nest was estimated to be 123 kJ day⁻¹ (1.42 W) or about 2.4 times the DEE of adults incubating eggs and 2.8 times BMR. We do not know what Leach's storm-petrels do while they are away from the nest. Observations of feeding are primarily of birds sitting on the ocean and grabbing prey at, or within a few centimeters of, the surface (R. Butler, personal communication), in contrast to southern hemisphere species like Wilson's storm-petrel (*Oceanites oceanicus*) that feed while flying slowly close to the surface (Ashmole 1971; Withers 1979; B. Obst, personal communication).

Pennycuick (1975) has provided equations for estimating power requirements of birds in flapping flight at minimum-power speed and maximum-range speed knowing only the body mass, wingspan, and basal metabolism. Using values of 0.045 kg, 0.474 m, and 0.55 W, respectively, we calculated the minimum-power speed (V_{mp}) to be 5.34 m s⁻¹, at which point the minimum-power requirement (P_{min}) is 0.466 W. Assuming a conversion efficiency of 23% (Pennycuick 1975), this translates into a metabolic rate of 2.02 W, somewhat higher than the DEE measured in this study (1.42 W). From Pennycuick's equations we estimated the maximum range speed (V_{mr}) to be 9.66 m s⁻¹, at which point the power

output (P_{mr}) is equivalent to a metabolic rate of 2.60 W. These calculations are consistent with the observation that Leach's storm-petrels spend much of their time resting on the water.

While adults were away from the nest, their WTO rates averaged 1.01 day^{-1} and their body water content averaged an estimated 21.0 g (0.77 SD, $n = 9$). Therefore, the sum of assimilated and metabolically produced water amounts to approximately 21 g per day. An energy expenditure rate of 122.6 kJ day^{-1} would indicate an energy/water ratio in the assimilated portion of their food (plus ingested seawater) of 5.8 kJ g^{-1} of water. Summing the coefficients of variation of each of these estimates suggests a coefficient of variation on the energy/water ratio of about 36%, or 2.1 kJ g^{-1}.

Samples of food collected from the proventriculi of chicks immediately after feeding during the first half of August 1982 contained mostly small crustaceans and consisted of 60% water, 27% lipid, and 13% LFDM, and a total metabolizable energy content (assuming 100% assimilation efficiency) of 12.6 kJ g^{-1}. Using conversion factors from Schmidt-Nielsen (1975), we estimated the total water from this food, including free water plus metabolically produced water, to be 0.95 g g^{-1}, and the energy/water ratio, therefore, to be 13.3 kJ g^{-1}. Leach's storm-petrels are known to feed on fish as well as euphausiids (Linton 1978). From data in Montevecchi et al. (1984) on the composition of several species of fish in the diets of gannets (*Sula bassanus*) in Newfoundland, we calculated energy/water ratios ranging between four for the capelin (*Mallotus villosus*) and 11 for the mackerel (*Scomber scombrus*). Data for several species of fish summarized in Ricklefs (1974) indicate an average value of about 6 kJ g^{-1}. Work on krill has yielded values of about 5 kJ g^{-1} of water (Clarke and Prince 1980, Simons and Whittow 1984). These calculations suggest that the diet of adults has a significantly lower energy density than that which they feed their chicks, or that adults drink seawater. Also, stomach oils from previous chick meals may have been included in the food samples collected from chicks. If the adult diet has a lower energy density than the chick diet, then adults may partition their time away from the nest be-

tween foraging for themselves and foraging on different resources for their chicks, as suggested by observations of Richdale (1963) and Serventy (1967) on sooty and short-tailed shearwaters (*Puffinus griseus* and *P. tenuirostris*). Or they may concentrate lipid in their proventriculi by selective assimilation of water and protein and feed chicks a meal that has a higher energy/water ratio than the food ingested, as suggested by Ashmole (1971). When adult expenditures and chick meals are combined, the estimated energy/water ratio of all food gathered by adult Leach's storm-petrels is 7.0 kJ g^{-1}.

Our measurements indicate that at least 51.5 kJ in food or stored fat must be transported to the nest site for each day of the incubation spell, and half of the requirement of the chick for each parent during the nestling period, or a maximum of 50 kJ day^{-1} (Ricklefs et al. 1980a). Assuming that 123 kJ day^{-1} is expended in foraging, including the cost of flight to and from the feeding grounds, the foraging efficiency during both the incubation and chick-rearing periods is about 0.4 kJ returned per kJ expended.

Ricklefs (1983) suggested that the period during which adults brood small chicks may be the most demanding energetically because parents can feed only half the time yet must support both themselves and their chick at the nest. Ricklefs et al. (1980a) estimated that the average energy requirement of chicks during the first 5 days was 47 kJ day^{-1}. Adding the requirement of a brooding adult on top of this (assuming it is the same as that of the incubating adult) brings the total to 98.5 kJ day^{-1}, or nearly double either the requirement of an incubating parent or one parent's share of the requirement of a large, unattended chick. Each adult probably broods the chick for no more than one spell after it hatches, and it is possible that the parent could support a negative energy balance with its fat reserves at this time. Even after incubation spells of 3 days, adults had an average of 5.5 g of extractable body lipid with an energy content of over 200 kJ. The high cost of brooding may explain the extremely short brooding periods of storm-petrels and many of their relatives.

Incubating adults utilize fat deposits and

food carried in the stomach about equally. Furthermore, our data are consistent with the idea that food is delivered to the chicks at a higher energy density than that utilized by adults while at sea. Adults may store fat during the first part of their foraging bout at sea to be used while they subsequently capture different food with higher energy density to be delivered to the young. Alternatively, they may concentrate energy in the chick meals by selective absorption of water and protein.

The average meal brought to the chick weighs about 10 g (Ricklefs et al. 1985) and contains 12.6 kJ g^{-1}. The addition of 10 g to the mass of the adult increases both the maximum range speed and the power consumption. According to Pennycuick's equations, and with a mass of 0.055 kg, the chemical equivalent of the power at maximum range speed is 3.2 W, or approximately 0.6 W greater than the expenditure at 0.045 kg mass. Maximum-range speed increases to 14 m s^{-1}. If adults transport food 100 km, then it would take 2.0 h at a cost of 4.3 kJ (0.6 W for 2 h). This is only 3%–4% of the energy transported in the meal, suggesting that transport cost does not determine the size of the meal delivered. If the adult accumulated the meal steadily during the foraging period, the cost of carrying it could become much more important. At the extreme, a 10-g meal carried for, say, 16 h of flight during the foraging spell would result in an excess expenditure of 69 kJ, nearly half of the energy content of the meal.

There is undoubtedly a limit to the amount of mass that an adult can take off with, but this does not appear to be approached by adults returning to the nest with chick meals. We have observed chicks to fledge weighing an average of 57 g (SD = 4, n = 10) and a maximum of 63 g, after a week or so of prefledging weight loss. At the end of incubation spells, adults with 5 g of fat weigh about 42 g, not including stomach contents. They weigh 53 g when they begin to incubate, which is consistent with carrying a 10-g meal.

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