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Incubation Energetics of the Laysan Albatross

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Abstract
The energy expenditure of incubating and foraging Laysan Albatross (Diomedea immutabilis, mean body weight 3.07 kg) was estimated by means of the doubly-la- belled water technique. During incubation, the energy expenditure was similar to that of resting birds that were not incubating an egg. The energy expenditure of foraging albatross (2072 kJ/day) was 2.6 times that of resting birds. It was concluded that the energy expenditure of the tropical Laysan Albatross was not less than that of species foraging over cold, high-latitude oceans. An energy budget compiled for an incubating pair of albatross revealed that the energy expenditure of the female was greater than that of the male bird, during the incubation period

Keywords
Energetics, Albatross, Incubation, Foraging, Seabirds

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Incubation energetics of the Laysan Albatross

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Summary. The energy expenditure of incubating and foraging Laysan Albatross (*Diomedea immutabilis*, mean body weight 3.07 kg) was estimated by means of the doubly-labelled water technique. During incubation, the energy expenditure was similar to that of resting birds that were not incubating an egg. The energy expenditure of foraging albatross (2072 kJ/day) was 2.6 times that of resting birds. It was concluded that the energy expenditure of the tropical Laysan Albatross was not less than that of species foraging over cold, high-latitude oceans. An energy budget compiled for an incubating pair of albatross revealed that the energy expenditure of the female was greater than that of the male bird, during the incubation period.

Key words: Energetics – Albatross – Incubation – Foraging – Seabirds

Grant and Whittow (1983) reported that the oxygen consumption of incubating Laysan Albatross (*Diomedea immutabilis*) was significantly *lower* than that of birds that were also at rest but not incubating an egg. These were the first direct measurements of the metabolic cost of incubation in an albatross. Subsequently, Brown and Adams (1984) reported that the metabolic rate of the Wandering Albatross (*Diomedea exulans*) during incubation, measured directly, was 1.4 times *greater* than the basal metabolic rate of the birds. An earlier estimate (Croxall and Ricketts 1983), based on the rate of loss of body mass, had also led to the conclusion that the energy expenditure of incubating Wandering Albatross was greater than the predicted basal metabolic rate. The energy expenditure of incubating Grey-headed (*Diomedea chrysostoma*) and Black-browed (*Diomedea melanophyris*) Albatross, derived from rates of loss of body mass, was also estimated to be higher than the calculated standard metabolic rate (Prince et al. 1981). This discrepancy between the energy cost of incubation in the tropical Laysan Albatross on the one hand, and the subantarctic species (Wandering, Grey-headed and Black-browed Albatross) on the other, might be explained by the greater energy expenditure for thermoregulatory purposes in birds that incubate their eggs in cold, southern latitudes. However, doubts have been expressed concerning the validity of both the technique of measuring the oxygen consumption in the Wandering Albatross and also the estimation of energy expenditure from the rate of mass loss (Brown and Adams 1984; Obst et al. 1987). Grant and Whittow's (1983) measurements of oxygen consumption in the Laysan Albatross were made over relatively short periods of time (4–6 hours) and it was conceivable that a method that measured energy expenditure over a more extended period might yield different results. Consequently, the main purpose of the present investigation was to measure the energy expenditure of incubating Laysan Albatross using the doubly-labelled water technique that permitted the measurements of the energy expenditure of incubating birds over a period of several days. An ancillary purpose was to determine the energy expenditure of Laysan Albatross when they were foraging, also using the doubly-labelled water technique. It seemed likely that the energy costs of foraging might also be relatively low in the Laysan Albatross which feeds in tropical and sub-tropical ocean waters around the Hawaiian Islands. Air and sea temperatures are considerably higher in the Hawaiian Archipelago than in southern oceans, so that heat loss both when flying and alighting on the water is likely to be lower. Consequently the energy expenditure for thermoregulation during foraging would be expected to be minimal. With the information on incubating and foraging energetics obtained in this study, the energy budget of a pair of Laysan Albatross during the entire incubation period could be compiled.

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Methods

The study was conducted during January and February, 1982, on Tern Island, French Frigate Shoals (23°52′N; 165°18′W) in the Northwestern Hawaiian Islands. The breeding population of Laysan Albatross at French Frigate Shoals numbers approximately 1000 pairs (Pettit et al. 1984). The birds nest in flat grassy areas adjacent to the shore. For identification purposes, the birds selected for study were captured by hand and marked with spray paint on the breast-feathers or the back of the head. The birds were captured soon after the onset of an incubation shift, when the parent bird returned from a foraging trip at sea to relieve the other parent attending the nest. In three study nests, both members of the pair were captured; at other nest sites only one of the parent birds was caught. Some of the study birds had been banded by the U.S. Fish and Wildlife Service in previous years and the age of these birds could be estimated from the banding records. Marked birds were observed twice daily in order to record the duration

Table 1. Energy expenditure of incubating and foraging Laysan Albatross. Mean vlaues ± S.D.; number of birds in parentheses

	Body mass (g)	Change in body mass (%/day)	Measurement interval (days)	CO_2 production (l/day)	Energy expenditure (kJ/day)
Incubating birds	3073 ± 230 (8)	−1.88 ± 0.40 (8)	3.03 ± 0.52 (8)	27.9 ± 5.1 (8)	689.1
Foraging birds	3064 ± 413 (4)	+1.09 ± 2.77 (4)	3.09 ± 1.35 (4)	83.9 ± 23.6 (4)	2072.3

Table 2. Body water and water turnover rates in Laysan Albatross. Mean values ± S.D.; number of birds in parentheses

	Total body water (% of body mass)	Water influx		Water efflux	
		(ml/day)	(ml/kg·day)	(ml/day)	(ml/kg·day)
Incubating birds	47.3 ± 2.8 (6)	59 ± 23 (8)	19 ± 7 (8)	85 ± 24 (8)	28 ± 7 (8)
Foraging birds	47.6 ± 2.3 (4)	537 ± 89 (4)	180 ± 47 (4)	525 ± 77 (4)	174 ± 37 (4)

of their incubation spans, or their guard spans after the chicks had hatched.

On the day of the injection of doubly-labelled water, the bird was weighed on a Manostat Terraillon balance to the nearest gram, and an injection of 0.34 ml of water containing 0.10 millicuries of tritium and 95 atoms % of oxygen-18 was then made into the pectoral muscles. The bird was held for 2.5–3.2 hours to allow equilibration of the isotopically labelled water with the body fluids. A blood sample of 6–8 ml was then collected by venipuncture of the tibial or tarsometatarsal vein and the bird was released at the nest site. While birds were being held, their eggs were also collected, incubated at 35° C, and returned to the nest with the birds. An artificial albatross egg (Grant et al. 1982) was substituted for the bird's egg, in the nest, in case the other parent bird returned during this period. Incubating birds were recaptured approximately 72 h later and foraging birds were caught as soon as possible after their return to Tern Island (48–140 h after being released). The birds were weighed and second blood samples were taken.

The successful application of the doubly-labelled water technique to the measurement of the metabolic rate of free-ranging animals hinges largely on the recapture of the injected animals after a relatively short period of time. This does not present any difficulty in the case of incubating birds; consequently, the energy expenditure of incubating birds may be measured at any time during the incubating period. However, the long absences of foraging Laysan Albatross in the early part of the incubation period (Rice and Kenyon 1962; Fisher 1971) add to the uncertainties of the technique for the measurement of the metabolic cost of flying and feeding in the early part of incubation. This difficulty was avoided in the present investigation by selecting the part of the breeding cycle immediately before and after the chicks had hatched, when both incubation and foraging spans are relatively short (Rice and Kenyon 1962; Fisher 1971). An added advantage of this period is that the foraging member of the pair is known to be at sea foraging for 95% of the time (Fisher and Fisher 1969), so that there can be reasonable certainty that the metabolic cost of foraging is measured at this stage.

The blood samples were vacuum distilled to obtain pure water for analysis of tritium by liquid scintillation spectrometry and for ^{18}O by proton activation analysis (Wood et al. 1975). Total body water at the time of injection was determined from the oxygen-18 dilution space (Nagy 1980). Water flux rates were calculated from equation 4 in Nagy and Costa (1980) and carbon dioxide production was calculated according to equation 2 in Nagy (1980).

Energy expenditure was calculated from CO_2 production in the birds using the conversion factor: 1 ml CO_2 = 24.7 Joules. This conversion factor is based upon the known composition of the diet of Laysan Albatross in the Northwestern Hawaiian Islands (Harrison et al. 1983), the proportions of fat, protein and carbohydrate in the dietary items and the CO_2 yields of protein, fat and carbohydrate (Schmidt-Nielsen 1975).

Maximal and minimal air temperatures, wind speed, barometric pressure, rainfall and cloud cover were measured daily.

The results of this investigation are reported as means ± standard deviations and the numbers of birds are shown in parentheses.

Results

Body mass

Incubating Laysan Albatross lost body mass at the rate of 57.5 g ± 11.2/day (10). Two albatross recaptured after foraging had gained body mass but two other birds had lost 0.8–1.6% of their body mass.

Energy expenditure

The carbon dioxide production was measured in eight incubating and four foraging birds (Table 1). The carbon dioxide production and calculated energy expenditure were three times greater in the foraging than in the incubating birds and the variability in the carbon dioxide production was also greater in the foraging birds.

Total body water and water flux

The total body water was similar in the incubating and foraging birds (Table 2). The water turnover rates, on the other hand, were considerably higher in the foraging birds. There was a net loss of body water in the incubating birds amounting to 9 ml H_2O per kg body mass each day but the foraging birds experienced a net gain of 6 ml H_2O/kg·day, in body water.

Incubation shifts and guard spans

Daily inspection of 21 Laysan Albatross nests during the two weeks prior to hatching of the egg revealed that incubating birds remained on the nest until relieved by their partners for a mean period of 3.48 days ± 1.12. The values ranged from 2 to 5 days.

Seventy-six percent of the eggs in the study nests hatched successfully. Fisher (1971) records a hatching success of "about 70%" for the Laysan Albatross. After the chick had hatched, it was guarded by one of the parents and the mean duration of the guard spans for each parent was 2.04 days ± 1.04 (26).

Weather data

The climate on Tern Island during the study period was relatively warm, wet and cloudy with moderate winds. The mean maximum temperatures for January and February were 23.6° C ± 1.2 (range = 20.6–25.6° C) and 23.3° C ± 0.8 (range = 21.7–24.4° C), respectively. The mean minimum temperatures were 17.8° C ± 1.4 (range = 15.0–21.1° C) for January and 17.9° C ± 1.0 (range = 15.6–18.9° C) for February. The mean wind speeds were 12.3 knots ± 4.5 (range = 5–33 knots) for January and 15.7 knots ± 5.3 (range = 3–45 knots) for February. Monthly rainfall totalled 19.6 cm for January and 10.7 cm in February.

Discussion

Incubation energetics

The carbon dioxide production of incubating Laysan Albatross (0.38 ml/g.h. CO_2 ± 0.07) measured by the doubly-labelled water procedure in the present investigation was higher than that (0.26 ml/g.h. CO_2 ± 0.02) reported by Grant and Whittow (1983) for incubating Laysan Albatross at Midway Islands. Grant and Whittow (1983) used a different technique and they measured the CO_2 production for a relatively short period of time. It is, perhaps, not surprizing that the value obtained by the doubly-labelled water technique over a three-day period would be higher than that recorded over a period of a few hours, as the longer period would be more likely to include any bouts of activity such as rising from the egg, bill-clapping at other birds (Grant et al. 1982) and other episodes of minor activity. The value obtained in the present study for incubating birds was identical to that reported by Grant and Whittow (1983) for albatross that were at rest but not incubating an egg. Thus, it can be concluded from the present results, and those of Grant and Whittow (1983), that the metabolic rate of incubating Laysan Albatross, even under cloudy skies, is not greater than that of resting birds that are not incubating. In this respect, the Laysan Albatross appears to differ from the Wandering Albatross, the Grey-headed Albatross and the Black-browed Albatross (*Diomedea melanophris*), in which the metabolic rate of incubating birds is higher than that of resting birds (Prince et al. 1981; Croxall and Ricketts 1983; Brown and Adams 1984). A possible explanation for this difference might be the higher thermoregulatory cost of incubation in the sub-antarctic species than in the tropical Laysan Albatross. Calculation of the energy expenditure from the body mass loss, using the factors employed by Prince et al. (1981) for the "lower limit" of energy expenditure, yielded values considerably higher than the values directly measured by the doubly-labelled water technique. Similar discrepancies between metabolic rates measured by the doubly-labelled water technique and values calculated from rates of body mass loss were noted by Obst et al. (1987) for Wilson's Storm Petrel (*Oceanites oceanicus*).

Foraging energetics

Are the metabolic rates of Laysan Albatross foraging in tropical waters lower than those of Wandering Albatross foraging in high-latitude cold oceans? Their energy expenditures during foraging cannot be compared directly because of the differences in body mass between the two species. The ratio of foraging energy expenditure to basal or resting metabolic rate was higher (2.6 times) in the Laysan Albatross than in the Wandering Albatross (1.8 times). A more direct comparison may be made with the sub-antarctic Grey-headed Albatross. The energy expenditure of foraging Grey-headed Albatross was 2393 kJ/day (Costa and Prince 1987) ie. 15% higher than that of the Laysan Albatross (2072 kJ/day). However, Grey-headed Albatross are 18% heavier so that the energy expenditure of the two species during foraging is very similar. Thus, comparisons with neither the Wandering Albatross nor the Grey-headed Albatross yield any evidence that the energy expenditure during foraging is substantially lower in the tropical Laysan Albatross than in the sub-antarctic species, in spite of the probable differences in their thermoregulatory costs. A possible explanation for this discrepancy is that the meagre food resources of tropical and sub-tropical oceans (Lack 1968) require Laysan Albatross to spend a relatively large part of their foraging time, in flight, seeking food. In spite of these differences, the energy cost of foraging in the Laysan Albatross is low compared with that of other species of birds (Ellis 1984). In this respect, the Laysan Albatross resembles other albatross and it may be attributed to the low energy cost of the "dynamic soaring" flight (Wilson 1975) of albatross.

Incubation-period energy budget

This study is the first in which the energy expenditure of incubating albatross has been measured simultaneously with that of the foraging member of the breeding pair, using the same method (Grant 1984). It seems justifiable, therefore, to compile an energy budget for a breeding pair of Laysan albatross for the entire incubation period even though measurements were made only during the latter part of the incubation period. Table 3 compiles the time and energy budgets of a single breeding pair of Laysan Albatross based on the energetic data obtained in the present investigation and the behavioral observations of others (Fisher 1967; Fisher and Fisher 1969). Although the male Laysan Albatross is larger than the female, and would therefore be expected to have a greater energy expenditure on these grounds, it spends less time foraging during the incubation period. Consequently the overall energy expenditure of the female parent is higher than that of the male.

It is interesting to relate the data contained in Table 3 to Grant and Whittow's (1984) estimate of the total amount

Table 3. Time[a] and energy budgets of Laysan Albatross during incubation of the egg

		Male (3000 g)[a]	Female (2700 g)[b]
On nest	Time (days)	44	21
	Energy expenditure rate (kJ/day)	760	684
	Total energy expenditure (MJ)	33.4	14.4
At sea	Time (days)	21	44
	Energy expenditure rate (kJ/day)	2029	1825
	Total energy expenditure (MJ)	42.6	80.3
Total	Time (days)	65	65
	Energy expenditure (MJ)	76	94.7

[a] Estimated from Fisher and Fisher (1969)
[b] Estimated from Fisher (1967)

of energy consumed by the embryo of the Laysan Albatross. Thus, the total energy consumption of the embryo was 0.6 MJ, only a small percentage (0.3%) of the energy expenditure of the two parents during the incubation period. It is useful also to compare these data with similar estimates for the Wandering Albatross, obtained by Adams et al. (1986). The main difference between the two species is that the total energy expenditure of the male Wandering Albatross is greater than that of the female bird, during the incubation period, largely reflecting the greater disparity in body mass between the two sexes, in the Wandering Albatross.

Food requirements

It is possible to estimate the amount of food required to satisfy the energy expenditure of a Laysan Albatross during the incubation phase of the breeding season. The average energy expenditure would be 1313 kJ/day (Table 3). The metabolizable energy content of squid, the primary prey species of these birds (Harrison et al. 1983), is 2.68 kJ/g wet mass (Pettit et al. 1984). Thus, each bird would consume, on the average, about 490 g/day of fresh squid, if it fed exclusively on squid. This represents approximately 17% of the body mass of the birds.

Water flux

The body water content (47.3–47.6% of body mass) of Laysan Albatross is very similar to that (47.5%) reported for the Wandering Albatross (Adams et al. 1986). These values are lower than those of a variety of other species of marine birds (Mahoney and Jehl 1984). There are several possible explanations for this difference: the long wings and flight feathers result in a greater proportion of tissue with a low water content in albatross than in many other birds (Adams et al. 1986). In addition, albatross are long-lived birds (Fisher 1980) and it is known that the water content of avian tissues diminishes with age (Sturkie 1986). Data from the leg bands of birds used in the present study indicated that they were at least ten years old. A relatively high body fat content would also predispose towards a low value for body water content. Body fat was not measured in the present study but it is worth noting that the relatively high body water content (57.9%) of the Grey-headed Albatross (Costa and Prince 1987) may be attributed to the fact that the birds were lean (D.P. Costa, unpublished work). Other procellariiform birds with a relatively low body water content are Leach's Storm Petrel (38.9–50.5%; Ricklefs et al. 1986), Wilson's Storm-petrel (45.9%; Obst et al. 1987) and Giant Petrels (51.7%1 B.S. Obst and K.A. Nagy, unpublished work).

The daily water influx of foraging albatross (537 ml ± 89) represented 36.8% of the total body water, similar to the figure of 34.9% reported for foraging Wandering Albatross (Adams et al. 1986). The daily energy expenditure of a foraging albatross (2072 kJ/day) may be used to compute the water intake. Thus, the metabolizable energy content of squid, the primary prey species (Harrison et al. 1983), is 2.68 kJ/day (Pettit et al. 1984). A foraging albatross with an energy expenditure of 2072 kJ/day would, accordingly, require 773 g squid/day. Using this estimate and the water content of squid (0.76 ml/g; Pettit et al. 1984), it is possible to calculate the water intake to be 587 ml/day. This figure is probably too high because it is based on a diet made up exclusively of squid, which have a relatively high water content. It is, however, close enough to the measured value to conclude, albeit tentatively, that the Laysan Albatross does not drink any appreciable amount of sea water, deriving its water mainly from its food. The mean daily water intake of incubating Laysan Albatross was 59 ml ± 23. Of this, approximately 17 ml represented metabolic water production (calculated from CO_2 production, Nagy 1983). Of the remaining 42 ml/day, some was probably due to vapor exchange (Nagy and Costa 1980). The only source of liquid water to incubating albatross is rain water. Incubating Laysan Albatross have been observed to snap at raindrops and also to allow rain water to run down their upturned bills into their mouths (Rice and Kenyon 1962; observations made by the present authors). Grant and Whittow (1983) concluded that the water loss of incubating Laysan Albatross was balanced by the metabolic water production. The turnover of tritiated water measured in the present study suggests that they incur a water deficit of 26 ml/day, a deficit that has to be made good during foraging. The water deficit also accords with the decrease in body mass during incubation.

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