

Metabolic Rate of Laysan Albatross and Bonin Petrel Chicks on Midway Atoll¹

GILBERT S. GRANT^{2,3} AND G. CAUSEY WHITTOW²

ABSTRACT: The resting metabolic rates of Laysan albatross and Bonin petrel chicks of known age were measured on Midway Atoll in the North Pacific Ocean. The mass-specific metabolism peaked at hatching and then declined to adult levels in Laysan albatross nestlings. The mass specific metabolism of hatching Bonin petrels was similar to that of adults, but it tripled shortly after hatching. Fasting and feeding episodes affected day-to-day changes in petrel chick metabolism.

THE RESTING METABOLIC RATES of chicks represent the major part of their energy expenditure, as they do not fly and their level of activity is generally low (Blem 1978). The metabolic rate increases as the chick grows but the relationship between metabolic rate and body mass varies during growth, the particular pattern of variation depending on a number of factors (Ricklefs 1974). In the Procellariiformes, which have relatively long nestling periods, the metabolic rate of growing chicks is known only for Leach's storm-petrel, *Oceanodroma leucorhoa* (Ricklefs, White, and Cullen 1980a). The present note stems from the opportunity to study the relationship between metabolism and growth in two other procellariiform species that differed greatly in body size, and for which the metabolic rates of the developing embryos are known (Pettit et al. 1982a, 1982b). The two species studied (Laysan albatross, *Diomedea immutabilis*; Bonin petrel, *Pterodroma hypoleuca*) share the same nesting sites in the Northwestern Hawaiian Islands.

METHODS

The metabolic rates of Laysan albatross chicks of known age on Sand Island, Midway Atoll (28°13' N, 177°23' W) were measured in a building immediately adjacent to the nesting sites. The chicks were placed in a small plexiglas chamber or in an air-tight wooden box (0.7 m on all sides), depending on the size of the chick. In the latter instance, a plexiglas cover allowed observation during a series of measurements. Ambient air was drawn through the metabolic chamber by means of a vacuum pump. The flow rate (1–5 liters · min⁻¹) was adjusted to obtain a decrease of approximately 1 percent in the O₂ concentration from the air inlet to the outlet. The birds were weighed, to the nearest gram, on a Terrillon balance, immediately after the final metabolic measurements. All albatross metabolic measurements were made between 1000–1800 hr, 21 January–14 May 1981. Chamber temperatures ranged from 19.3 to 26.0°C during these measurements. Measurements could be made only until the 107th day of nestling life, when we had to leave Midway; the birds fledged at 165 days.

Metabolic measurements on Bonin petrel chicks of known age were made in a small plexiglas chamber (kept in the building adjacent to the nesting site) at chamber temperatures of 21.3 to 29.0°C. All measurements were between 1000–1900 hr, 2 March to 19 May 1981. The flow rate (ca. 200–500 cm³ · min⁻¹) was also adjusted to achieve

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²University of Hawaii, John A. Burns School of Medicine, Department of Physiology, and the PBRC Kewalo Marine Laboratory, Honolulu, Hawaii 96822.

³Present Address: North Carolina State Museum of Natural History, P.O. Box 27647, Raleigh, N.C. 27611.

a decrease of approximately 1 percent in the O_2 concentration between the inlet and outflow from the chamber. Petrels were weighed on a torsion balance (DWL 5) to the nearest 0.01 g, immediately after the metabolic measurements. Measurements were made until a few days prior to fledging (mean age of fledging = 82 days; Pettit, Grant, and Whittow 1982).

Chicks of both species settled down within a few minutes and remained calm in the metabolic chambers during a series of measurements that typically lasted 3–5 hours. Metabolic values obtained for each individual on a particular day were similar and were averaged.

Gas samples were collected in glass syringes, the barrels of which were coated with mineral oil, and analyzed with a Scholander micro-gas analyzer. All gas values are converted to standard temperature and pressure for the dry gas (STPD). Two methods were used in the field to ascertain the accuracy of the gas analyzer: (1) the composition of fresh air, measured by the gas analyzer, averaged 20.90 percent O_2 and 0.04 percent CO_2 (the expected values), and (2) analysis of exhaust gases from the combustion of ethanol in the chamber. The respiratory quotient (RQ) of combusted ethanol should be 0.67. We measured an ethanol RQ of 0.66 with the Scholander micro-gas analyzer, providing confirmation of its accuracy. The resting metabolism was calculated from the measured oxygen consumption (\dot{V}_{O_2}) and RQ. Chamber temperatures were measured with a calibrated Kane-May Limited Dependatherm instrument.

RESULTS

The resting metabolism and mass of albatross chicks from hatching to 107 days of age are presented in Figure 1. Hatchling (age < 1 day) albatross metabolism was measured by the open flow system and compared to values obtained with the closed manometric system used by Pettit et al. (1982a). The \dot{V}_{O_2} for a hatchling measured via the open system average $190 \text{ cm}^3 O_2 \cdot \text{hr}^{-1}$, compared with a mean value of $159 \text{ cm}^3 O_2 \cdot \text{hr}^{-1}$

measured by Pettit et al. (1982a). The RQ of albatross chicks averaged 0.78 (Figure 1). The mass-specific metabolism ($\dot{V}_{O_2} \div \text{mass}$) peaked near hatching ($0.77 \text{ cm}^3 O_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) and declined steadily, reaching adult levels at approximately 75 days (Figure 1).

The resting metabolism and mass of petrel chicks from hatching to 76 days of age (within a week of fledging) are shown in Figure 2. The RQ of petrel chicks averaged 0.76. Mass-specific metabolism tripled between hatching and 2 days of age and declined to adult levels at 20 days of age (Figure 2).

DISCUSSION

The mass-specific oxygen uptake of the Laysan albatross hatchling was $0.77 \text{ cm}^3 O_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ —45 percent higher than the adult rate of oxygen consumption of the Laysan albatross ($0.53 \text{ cm}^3 O_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$; Grant and Whittow 1983) and also greater than that of the adult wandering albatross (*Diomedea exulans*; $0.5 \text{ cm}^3 O_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$; Brown and Adams 1984). The hatchling \dot{V}_{O_2} of Bonin petrels ($1.1 \text{ cm}^3 O_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$; Pettit et al. 1982b) was similar to that of adults ($1.1 \text{ cm}^3 O_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$; Grant and Whittow 1983). Mass-specific metabolism peaked to levels nearly three times hatchling and adult values during the first few days of nestling life in petrels but not in albatrosses. This fundamental difference between the albatross and petrel may be related to differences in the relative incubation periods and embryonic growth in the two Procellariiformes (Pettit et al. 1982a, 1982b). According to Ricklefs (1974), the maximal mass-specific metabolic rate occurs earlier in the precocial than in the altricial chick. By this criterion, the Laysan albatross is more precocial than is the Bonin petrel. However, by other criteria (e.g., yolk content of the egg) petrels are considered to be semiprecocial (Nice 1962, Carey, Rahn, and Parisi 1980, Ricklefs, White, and Cullen 1980b) while albatross are semialtricial (Nice 1962). Clearly, additional information is needed on the metabolism during growth of other species.

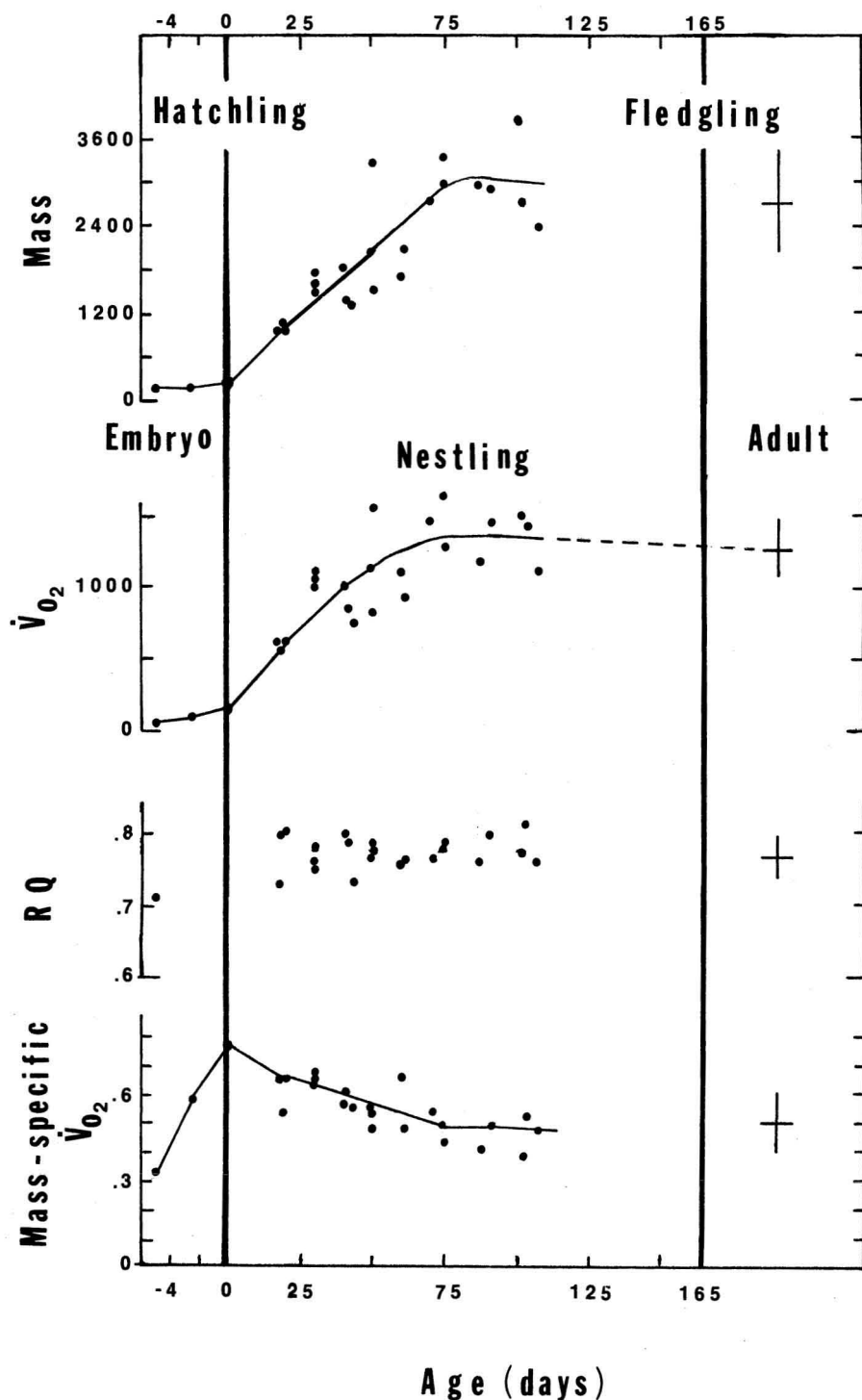


FIGURE 1. Mass (g), metabolism (\dot{V}_{O_2} ; $\text{cm}^3 \text{O}_2 \cdot \text{hr}^{-1}$), RQ, and mass-specific metabolism (\dot{V}_{O_2} ; $\text{cm}^3 \text{O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$) of Laysan albatross embryos, nestlings, and adults in relation to age. Adult values (from Grant and Whittow 1983) are presented as mean (horizontal bar) \pm two standard deviations (vertical bar). Embryo and hatchling values are from Pettit et al. (1982a). Curves are fitted by eye. The broken line indicates extrapolated values (see text).

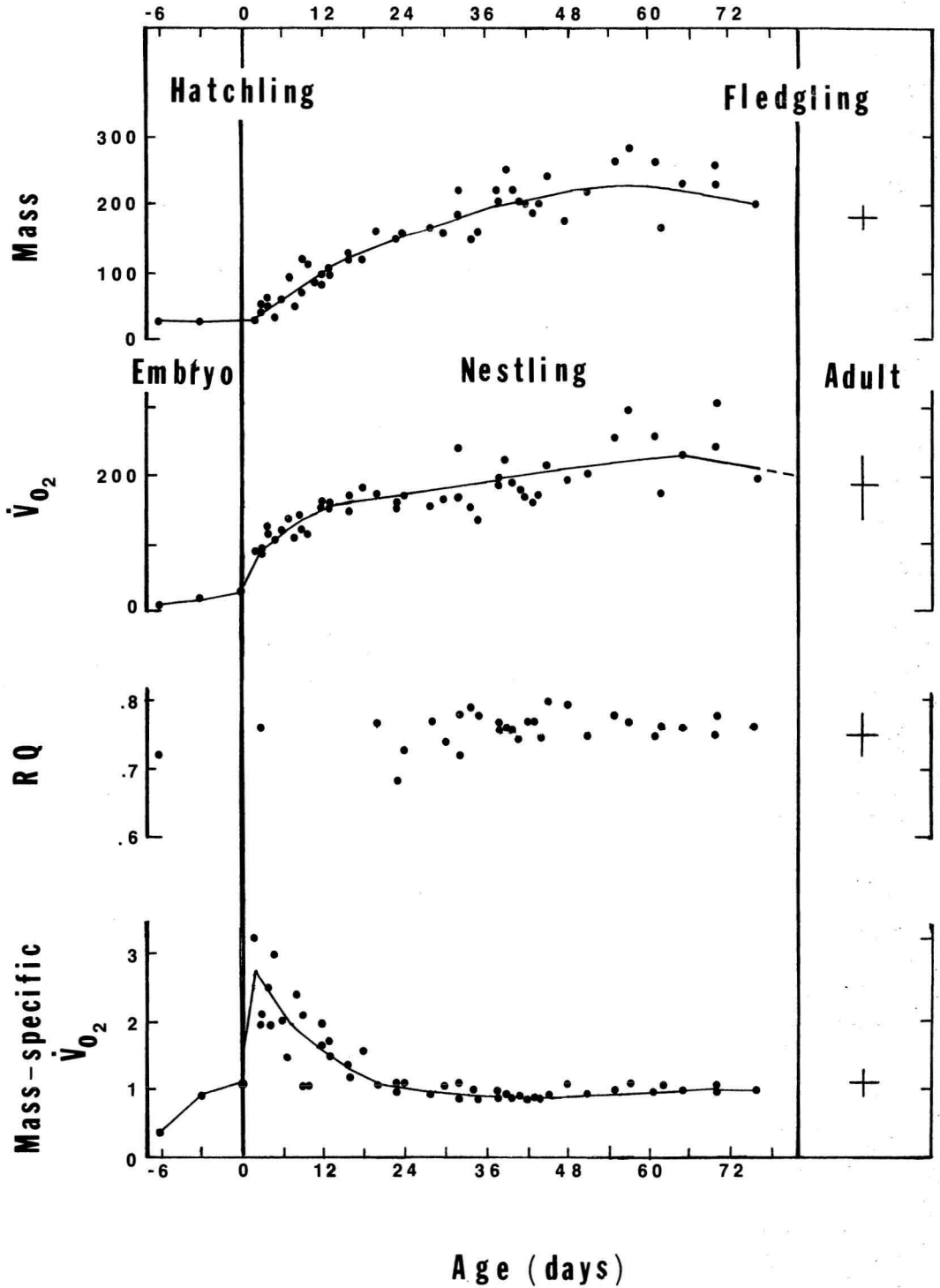


FIGURE 2. Mass (g), metabolism ($\dot{V}O_2$; cm³·O₂·hr⁻¹), RQ, and mass-specific metabolism ($\dot{V}O_2$; cm³·O₂·g⁻¹·hr⁻¹) of Bonin petrel embryos, nestlings, and adults. Adult values (from Grant and Whittow 1983) are presented as mean (horizontal bar) ± two standard deviations (vertical bar). Embryo and hatching values are from Pettit et al. (1982b). Curves are fitted by eye. The broken line indicates extrapolated values (see text).

TABLE 1
OXYGEN COST OF DEVELOPMENT IN THREE PROCELLARIIFORM CHICKS

SPECIES	TOTAL O ₂ COST OF CHICK DEVELOPMENT (liters)	FLEDGLING MASS-HATCHLING MASS (g)	OXYGEN COST PER GRAM OF CHICK* (liters·g ⁻¹)
<i>Oceanodroma leucorhoa</i>	209.3 [†]	40.5 [‡]	5.17
<i>Pterodroma hypoleuca</i>	393.4	177 ^{§,}	2.22
<i>Diomedea immutabilis</i>	4,439	1,792 ^{#,**}	2.48

* Total O₂ cost/fledgling mass-hatchling mass.

[†]From Ricklefs, White, and Cullen 1980a.

[‡]From Palmer, 1962.

[§]From Pettit et al. 1982b.

^{||}From Pettit, Grant, and Whittow 1982.

[#]From Pettit et al. 1982a.

^{**}From Fisher 1967.

TABLE 2
OXYGEN COST OF EMBRYONIC AND CHICK DEVELOPMENT

	O ₂ COST OF EMBRYONIC DEVELOPMENT		O ₂ COST PER GRAM OF YOLK-FREE HATCHLING		O ₂ COST OF CHICK DEVELOPMENT		TOTAL O ₂ COST OF DEVELOPMENT (chick + embryo) (liters)
	(liters)	% OF TOTAL	(liters·g ⁻¹)	(liters)	% OF TOTAL		
<i>Pterodroma hypoleuca</i>	5.6*	1.4	0.218	393	98.6	398.6	
<i>Diomedea immutabilis</i>	29.7 [†]	0.7	0.178	4439	99.3	4468.7	

* Pettit et al. 1982b.

[†]Pettit et al. 1982a.

The total amount of oxygen consumed throughout the nestling period can be estimated by measuring the area under the \dot{V}_{O_2} curve (Figures 1 and 2). Bonin Petrel chicks consumed approximately 373 liters of oxygen during the first 78 days of nestling life. The average fledging time for this species was 82 days (Pettit, Grant, and Whittow 1982); extrapolation of the \dot{V}_{O_2} curves in Figure 2 to 82 days yielded an estimate of 393.4 liters for the total oxygen cost of chick development (Table 1). The estimate for the Laysan albatross required a greater degree of extrapolation and the resulting figure of 4439 liters is correspondingly less exact. Table 1 also includes an estimate for Leach's storm-petrel, which is smaller than the Bonin petrel. When the total amount of oxygen consumed is divided by the mass of body tissue synthesized (fledgling mass minus hatchling mass), it is clear that the oxygen cost per gram of tissue is higher in

Leach's petrel than in the Bonin petrel or Laysan albatross. It is possible that the metabolic rate of Leach's petrel was elevated at the air temperature at which the measurements were made so that its higher oxygen cost of development might be construed to imply a higher energy allocation to thermoregulation. The figure for the oxygen cost per gram of tissue is even higher (6.11 liter·g⁻¹) in the dark-rumped petrel (*Pterodroma phaeopygia*), a species that breeds at high altitude in the Hawaiian Islands (Simons and Whittow, pers. comm.).

Using data published previously (Pettit et al. 1982a, 1982b) it is possible to compare the cost of embryonic development with that of development of the chick, and also to compute the total oxygen cost of embryonic and chick growth (Table 2). As expected, the cost of growth of the chick greatly exceeds the cost of embryonic growth. The cost of embryonic

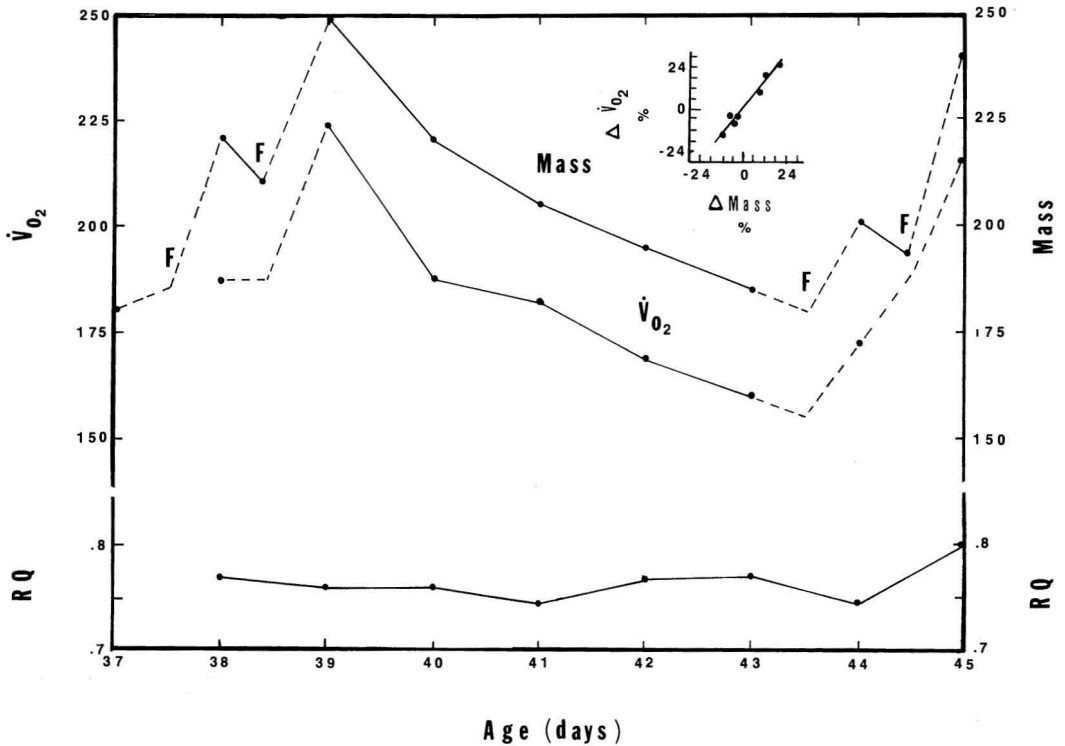


FIGURE 3. Simultaneous mass (g), \dot{V}_{O_2} ($\text{cm}^3 \text{O}_2 \cdot \text{hr}^{-1}$), and RQ values for a Bonin petrel chick during 8 days, involving four feeding (F) episodes and several fasting episodes (up to 4 days long in one instance). The inset shows the relationship between the increases in \dot{V}_{O_2} and mass associated with feeding and decreases during fasting intervals. The regression line for this relationship is as follows: $\Delta \dot{V}_{O_2} = 1.21 \Delta \text{mass} + 0.543$; ($r^2 = 0.980$, $n = 7$).

growth in the Bonin petrel, which has the relatively longer incubation period, is a slightly greater percentage of total costs than in the Laysan albatross. Comparison of Tables 1 and 2 reveals also that the oxygen cost of a unit mass of chick is considerably greater than that of an embryo.

Much of the day-to-day variation in \dot{V}_{O_2} (Figure 2) in the petrel chick can be attributed to feeding history. In Figure 3 we have plotted \dot{V}_{O_2} , mass, and RQ of a petrel chick over 8 days involving four feeding episodes and several days of fasting. The insert shows the concurrent changes in \dot{V}_{O_2} with changes in mass. \dot{V}_{O_2} and mass increased with feeding and decreased during prolonged fasts.

The relatively low RQ values for both the Laysan albatross and Bonin petrel suggest that they were largely metabolizing fats during the fasting periods and also after being fed. This would be in accord with the high

proportion of stomach oils in the diets of Procellariiform chicks (Fisher 1972, Imber 1976).

The resting metabolism of a growing chick represents the energy expended in the synthesis of new tissue, thermoregulation, and physiological activity (maintenance). The present data do not permit an analysis of the resting metabolism into these components. However, the similar values for mass-specific metabolic rates of hatchlings and adults in the Bonin petrel, and the post-hatching increase in mass-specific metabolism, were phenomena not observed in the Laysan albatross. They seem to be worthy of further study in terms of the allocation of energy to various functions in the chicks of small and large species.

In summary, the mass-specific metabolism peaked at hatching, and declined to adult levels during the first third or half of nestling life in the Laysan albatross. In the Bonin

petrel, the mass-specific metabolism was similar in the hatchling and adult but increased considerably shortly after hatching. The RQ remained essentially constant throughout the nestling period in both species and most of the day-to-day changes in metabolism in the Bonin petrel were due to episodes of fasting and feeding.

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