METABOLISM, GROWTH, AND ACTIVITY IN ADÉLIE AND EMPEROR PENGUIN EMBRYOS

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ABSTRACT.— The eggs of Adélie (*Pygoscelis adeliae*) and Emperor (*Aptenodytes forsteri*) penguins are smaller than those of large species in other orders. The incubation period in Adélie Penguins was as predicted based on egg mass, but in Emperor Penguins it was 50% longer than predicted. Although penguins have been described as semialtricial using the behavioral and morphological traits in Nice's (1962) classification, total oxygen consumption during incubation was similar to that of eggs of the same masses laid by precocial species. In both penguin species prepipping oxygen consumption was at a level predicted for precocial species.

Adélie embryos grew continuously during the last two weeks of incubation, but the relative growth rate (%/day) of both wet and dry mass decreased steadily until day 32 of incubation. From day 21 to day 31 of incubation, there was no significant change in the wet mass, dry mass, or caloric content of yolk. The mass-specific caloric content of the embryos remained constant at 5.49 kcal/g dry mass. Activity of the embryo between pipping and hatching contributed importantly to measured oxygen consumption (~10% of the total measured during incubation, ~20% in pipped eggs from 3 days to 1 day before hatching, and ~25% on the day of hatching).

We suggest that the limited behavioral repertoire of hatchling penguins evolved as a response to the severity of the environment into which they hatch and because of the skilled predatory behavior that they must learn before they can feed themselves. *Received 21 June 1985, accepted 6 January 1986.*

MANY investigators have measured the energy metabolism of avian embryos and discussed the empirical relationships between this and other functions, including embryonic growth, egg mass at laying, length of incubation, developmental type at hatching, adult mass, adult basal metabolic rate, and conductance of the eggshell (for recent reviews and discussions see C. Vleck et al. 1980, Rahn 1982, Bucher and Bartholomew 1984). A stated or an implicit assumption in most of these studies is that the contribution of activity to the total energy metabolism of avian embryos is minimal. Embryonic oxygen consumption usually has been measured in closed respirometry systems, except for very large eggs (D. Vleck et al. 1980) and in a few recent studies (e.g. Bartholomew and Goldstein 1984). Closed-system respirometry is integrative and gives only average values and rates of energy metabolism over relatively extended time periods. Recently, it has become possible to follow short-term fluctuations in energy metabolism by using flow-through respirometry and calculating instantaneous rates of oxygen consumption (Bartholomew et al. 1981). Continuous monitoring of rates of oxygen consumption of avian embryos over extended periods of time allows one to determine short-term variability in oxygen consumption of an individual due to activity as well as variation due to longer-term ontogenetic change.

All members of the order Sphenisciformes are considered to be semialtricial (Nice 1962). Most lay their eggs in relatively to extremely cold environments characterized by low absolute humidity. Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) penguins breed on the Antarctic continent and its fringe islands and have a circumpolar distribution. There were no published data on embryonic growth and metabolism in penguins, so it was necessary to establish as broad a data base as possible from the combination of materials available to us (see Methods).

We collected Adélie Penguin eggs of known age from colonies near Arctowski Station and Palmer Station in the Antarctic. We made physiological measurements on the eggs of Emperor Penguins and on the eggs and chicks of Adélie

Penguins at Sea World in San Diego, California. Measurements of embryonic mass and accompanying yolk mass were obtained when possible to allow analysis of growth patterns and of energy allocation at specific times during incubation.

METHODS

Egg parameters.—The length (L) and breadth (B) of all eggs were measured with dial calipers and used to calculate initial egg mass (M) and volume (V) according to the equations and constants of Hoyt (1979), except that a species-specific value of $K_m = 0.569$ was determined from three Adélie Penguin eggs and used in all calculations of initial egg mass for that species. Adélie Penguin clutches customarily consist of two eggs. Only second eggs were used to minimize uncertainty about the day of laying and the length of the incubation period (I).

Incubation temperatures.—Incubation temperatures (T_{egg}) maintained by Emperor Penguins were measured with Minimitter Model X telemeters installed in artificial eggs cast of epoxy resin from a mold made from an Emperor Penguin egg borrowed from the Western Foundation of Vertebrate Zoology. Two calibrated telemeters were fitted in cavities drilled in opposite sides of the white, epoxy eggs at their maximum breadth and sealed with threaded plugs 1 cm long.

The epoxy eggs were held in an incubator until they reached an equilibrium temperature of approximately 37°C and then substituted for fertile eggs being incubated by two pairs of Emperor Penguins at Sea World, San Diego that bred successfully on a substrate of pulverized ice in a refrigerated exhibit ($T_{air} = -2$ to -8°C). On four and seven different occasions, respectively, each pair accepted and continuously incubated the artificial eggs until their own eggs were returned to them 2–3 h later.

The telemeter signals were monitored using an antenna buried in the ice and connected to a radio receiver that produced audible clicks at a rate proportional to the temperature of the telemeter. Clicks were counted and timed with a stop watch, and rates were recorded at frequent intervals starting 1 h after the penguins began to incubate the artificial eggs.

Oxygen consumption.—All measurements of energy metabolism were made on eggs being incubated at Sea World in San Diego in 1982. Data were collected both day and night as eggs became available. Rates of oxygen consumption ($\dot{V}_{O_2}$) of Emperor Penguin eggs and the younger Adélie Penguin eggs were measured in a closed system with 1-gallon (~3,850 ml) paint cans used as respirometer chambers for the former and 500-ml plexiglass syringes for the latter. Air samples were analyzed with a Beckman E-2 Paramagnetic Oxygen Analyzer for the Emperor eggs and with an Applied Electro-chemistry S-3A Oxygen Analyzer for the Adélie eggs. $\dot{V}_{O_2}$ was determined using the method of Vleck et al. (1979) as modified by Bucher (1983). The $\dot{V}_{O_2}$ of Adélie Penguin eggs that had been incubated for at least 25 days and of Adélie hatchlings were measured in an open-flow system with the flow rate of dry, CO_2-free air monitored upstream from the metabolic chamber. Flow rates ranged from 65 to 360 ml/min depending on the age of the embryo or hatchling. The incurrent air was humidified before it entered the metabolic chamber. A sample of dried, CO_2-free air from the chamber was directed to an Applied Electro-chemistry S-3A Oxygen Analyzer to determine changes in fractional oxygen content. Inlet and outlet ports were constructed with multiple openings into the metabolic chamber to facilitate mixing of the air within the chamber. When $\dot{V}_{O_2}$ was constant, rates were determined assuming a steady state and using equation 8 of Depocas and Hart (1957). If there was visible movement of either the egg or embryo or if rates were obviously varying, instantaneous rates of oxygen consumption were calculated using 0.5-min time intervals according to the method of Bartholomew et al. (1981). The data presented are from 2 Emperor Penguin eggs and 11 Adélie Penguin eggs, all of which hatched successfully, and from 6 Adélie hatchlings.

Embryo and yolk mass.—A sample of 26 eggs of known incubation age was collected during the 1982–1983 breeding season from an Adélie Penguin colony near the Arctowski Station, King George Island, South Shetland Islands (62°10'S, 58°30'W). The eggs were opened within 1–2 h of collection, and the embryo and yolk sac were separated, blotted, and weighed on preweighed pieces of aluminum foil. All samples were frozen immediately after weighing, shipped to the University of California, Los Angeles, and later freeze-dried, placed in desiccators, and reweighed until constant masses were obtained. They subsequently were stored in desiccators until the caloric equivalences of subsamples were determined by bomb calorimetry with a Gentry Instruments Microbomb and Phillipson Microbomb Calorimeter calibrated with benzoic acid pellets of known mass.

Statistics.—Unless otherwise specified, values are reported as the mean ± standard error of the mean. Regression lines are fitted by the least-squares method. Results are considered significant if $P \leq 0.05$.

RESULTS

Eggs and hatchlings.—Data on eggs and hatchlings are given in Table 1. Because of the variety of power functions and proportionality constants associated with the allometry of fresh egg mass in the various avian orders, it is dif-

TABLE 1. Penguin egg and hatchling masses and corresponding incubation periods.

	Adélie Penguin		
	Sea World	Antarctic	Emperor Penguin
Initial egg mass[a] (g)	119.29 ±2.48 $n = 10$	114.16[b] ±1.8 $n = 27$	465.47 ±14.25 $n = 6$
Hatchling mass (g)	80.96 ±2.38 $n = 12$	80.65[c] $n = 1$	—
Hatchling mass ÷ initial egg mass (%)	68.03 ±2.43 $n = 9$	70.78[c] $n = 1$	—
Incubation period[d] (I)			
Measured (days)	35.2 ±0.8 $n = 10$	—	68.5 ±4.5 $n = 2$
Predicted (days)	33.5	33.2	45.24

[a] According to the equation, mass = 0.569 LB^2 (see Methods).
[b] From Arctowski Station, King George Island.
[c] From Palmer Station, Torgerson Island.
[d] According to the equation, $I = 11.64\ M^{0.221}$ (Ar and Rahn 1978) and based on the mass given in the same column in the table.

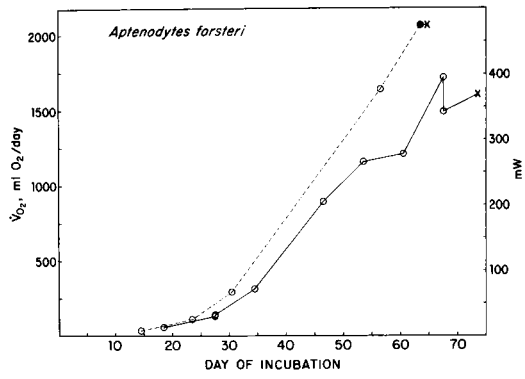

Fig. 1. Oxygen consumption in relation to day of incubation in two Emperor Penguin eggs. The solid and dashed lines connect consecutive measurements on individual eggs; the filled symbol indicates a pipped egg. The curve for each egg was extended at the last measured mean daily level to age at hatching (X) for that egg and was integrated separately. The mean value is reported (see Table 2).

ficult to characterize satisfactorily the relative mass of Emperor and Adélie penguin eggs.

Egg mass as a function of adult body mass in Sphenisciformes (if the log-log relationship is extrapolated to body mass of 100 g) is average for birds as a class (see Rahn et al. 1975: figs. 1, 5). Penguins are large birds, however, and the Emperor and Adélie penguin eggs were smaller than those of birds of similar mass in other orders (see Rahn et al. 1975: fig. 4).

The incubation period of Adélie Penguins had the expected relationship to adult body mass and to fresh egg mass, but in Emperor Penguins it was about 35 and 50% longer, respectively, than predicted. The incubation period of Emperor Penguins was extremely long compared with the periods of other very large eggs. Emperor Penguin eggs had a mean incubation period 29 days longer than that of the Rhea (*Rhea americana*), 17 longer than that of the Emu (*Dromaius novaehollandiae*), and 21–26 days longer than that of the Ostrich (*Struthio camelus*), even though the masses of the eggs of these species are at least 140, 170, and 1,000 g greater, respectively, than the mass of Emperor Penguin eggs.

Adélie hatchling mass, expressed as a percentage of initial egg mass (Table 1), was similar to the 66–74% reported for procellariiform hatchlings (Pettit et al. 1982) and slightly less than the 74% reported for Brown Pelicans (*Pelecanus occidentalis*; Bartholomew and Goldstein 1984). Adélie hatchlings were only 1.6% of adult mass, which is similar to the 2.0% calculated for Brown Pelicans but less than a mean value of 6.5% calculated for Laysan (*Diomedea immutabilis*) and Black-footed (*Diomedea nigripes*) albatrosses (data from Pettit et al. 1982, Dunning 1984).

Incubation temperature.—Temperatures from artificial eggs being incubated by two pairs of Emperor Penguins were obtained on days 14, 23, 30, and 56 of a 73-day incubation period and on days 9, 18, 27, 34, 46, 53, and 60 of a 63-day incubation period. The means of the measurements recorded from both telemeters in each of the eggs were 32.6 ± 0.7°C ($n = 13$) and 32.7 ± 0.4°C ($n = 34$), respectively. Often, there was a temperature difference between the telemeters in the artificial eggs. The mean difference in temperature between the two telemeters in a given egg with the telemeter centers 5.7 cm apart was 3.26 ± 0.47°C ($n = 19$). The largest temperature differential measured across either of the artificial eggs was 7.75°C.

Mean T_{egg} may underestimate the effective incubation temperature, especially for early embryos, which tend to float to the top of the

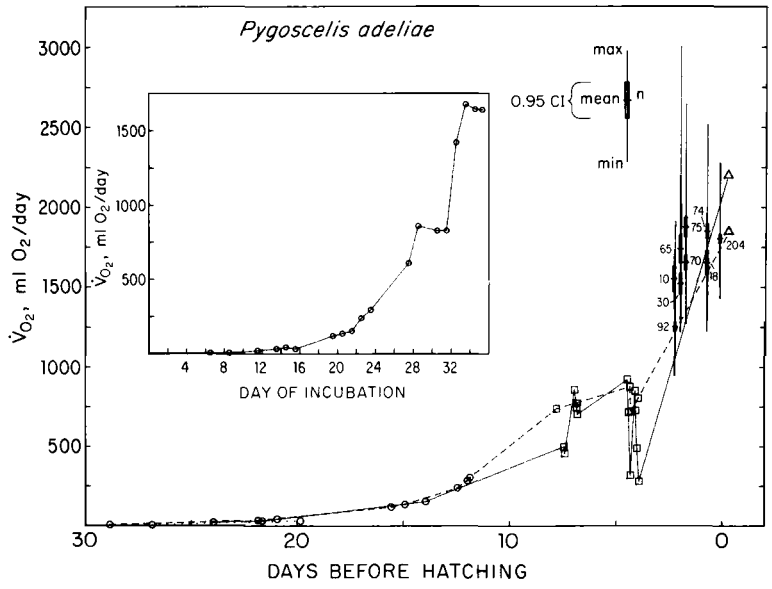

Fig. 2. Oxygen consumption in relation to days before hatching in Adélie Penguin eggs. Circles indicate measurements on unpipped eggs made in a closed system; squares indicate measurements on unpipped eggs made in an open-flow system assuming steady-state oxygen consumption; dicegrams indicate measurements made on pipped eggs in an open-flow system calculating instantaneous rates of oxygen consumption at 0.5-min intervals; numbers indicate sample sizes (see Methods and Fig. 5). Triangles indicate measurements of resting rates of oxygen consumption of hatchlings made in an open-flow system. The solid, dashed, and dotted lines connect consecutive measurements on individual eggs and their hatchlings. Inset: Oxygen consumption in relation to days of incubation. Curve connects daily means based on values collected in the closed system and only during the first hour of measurement in the open-flow system.

egg. Eight of the 47 individual measurements were above 35.0°C; the highest was 36.5°C. Presumably, the highest T_{egg}s were recorded when one of the telemeters was at the part of the egg closest to the ventral body surface of the incubating bird.

Oxygen consumption.—Total oxygen consumption during incubation, determined by integrating the empirical curves for each species (Figs. 1 and 2), was 11.865 l O_2 for Adélie Penguins and 43.997 l O_2 for Emperor Penguins (Table 2). Although penguins have been classified as semialtricial (Nice 1962), these totals are about twice the values expected for eggs of the same masses and incubation periods if laid by altricial species and 9% greater than would be predicted for eggs of the same mass laid by precocial species.

Regardless of which established measure of metabolism one considers, the embryos of both species of penguins function at levels similar to those of semiprecocial and precocial species and not at levels characteristic of semialtricial and altricial species (Table 2). Prepipping $\dot{V}_{O_2}$ is a problematic measure for use in comparing species because the time of pipping can vary widely even within a given species (Bucher and Barnhart 1984). This was certainly true of Adélie Penguin eggs. Pipping preceded hatching by 1–5 days in different eggs used in this study. Even the most conservative measure of prepipping $\dot{V}_{O_2}$ (5 or 6 days before hatching or ~85% of the way through incubation) yielded values that were at levels predicted for precocial species.

Our data suggest that there is a plateau in the ontogeny of $\dot{V}_{O_2}$ of Adélie Penguin embryos, perhaps from as early as day 28 until pipping. This resembles the pattern seen in precocial rather than in altricial species (Vleck et al. 1979). However, because the time of pipping varied, because we did not monitor any single egg continuously throughout this period, and because our data base in terms of numbers of eggs was small, a conclusive statement is premature.

Embryonic growth and yolk mass.—The Adélie Penguin embryos grew continuously through-

TABLE 2. Energy values for penguin development.[a]

	Adélie Penguin	Emperor Penguin
Total metabolism (kJ)		
Measured	235.88	874.66
Predicted	115.11[b]	447.36[b]
	216.19[c]	803.37[c]
Prepipping $\dot{V}_{O_2}$ (mW)		154.67[f]
Measured	≥191.03	≥372.88
Predicted	112.74[d]	195.88[d]
	184.04[e]	386.38[e]
	154.67[f]	
Hatchling $\dot{V}_{O_2}$ (mW)		
Measured	≥377.46	—
Predicted	315.69[g]	—
	311.56[g]	
kJ/g fresh egg mass		
Measured	1.98	1.84
Predicted	2.09 ± 0.15[h]	2.09 ± 0.15[h]
	1.51[i]	1.69[i]
	1.99[j]	2.22[j]

[a] Conversions to SI units for embryos assume RQ = 0.73, kcal/l O_2 = 4.75, ml O_2 = 19.88 J, and cal/h = 1.16 mW = 0.21 ml O_2/h. Masses and incubation periods in Table 1 are used for all predictions.
[b] For altricial species, kJ = 0.456 $M^{0.663}$ $I^{0.663}$ (Bucher 1983: eq. 5).
[c] For precocial species, kJ = 2.303 $M^{0.95}$ (converted to SI units from C. Vleck et al. 1980).
[d] For altricial species, mW = 43.43 $M^{0.767}$ $I^{-0.762}$ (converted to SI units from Bucher 1983: eq. 8).
[e] Hoyt and Rahn 1980: eq. 4; data base of primarily precocial species.
[f] mW = 11.81 G_{H_2O} (Rahn et al. 1974) and G_{H_2O} = 13.1 mg·day^{-1}·torr^{-1} (Rahn and Hammel 1982).
[g] Ackerman et al. 1980: eqs. 5, 6; based on initial egg mass and hatchling mass, respectively.
[h] Predicted as a constant for all species by Rahn (1982).
[i] Bucher and Bartholomew 1984: eq. 1; assumes penguins are semialtricial.
[j] As in footnote i, but assumes penguins are semiprecocial.

out the last two weeks of incubation (Fig. 3). Both wet and dry mass increased at a decreasing relative rate (%/day). Wet yolk mass (24.8 ± 0.8 g, $n = 20$) and dry yolk mass (11.49 ± 0.27 g, $n = 24$), however, did not show a corresponding significant decrease from day 22 and day 14, respectively, to day 31 of incubation (regression analysis: slopes not significantly different from zero; $P > 0.5$ and $P > 0.2$, respectively). The fractional H_2O content of the embryo declined from 94% on day 21 to 83–84% at hatching. The H_2O content of the yolk was variable between day 21 and hatching, with a mean value of 55.4 ± 1.2% ($n = 26$). Two hatchlings with a mean mass of 80.6 ± 5.2 g had a yolk reserve of 10.4 ± 3.0 g, equal to 12.8 ± 2.8% of the hatchling mass and similar to the 15.0% reported by Reid and Bailey (1966) for hatchlings from Cape Hallet.

Caloric content per gram dry mass of embryo (5.49 ± 0.06 kcal/g, $n = 26$) did not vary significantly ($P \gg 0.25$) during the last 13 days of incubation. Caloric content per gram dry mass of yolk changed marginally if at all between day 14 and day 25 ($P \sim 0.05$; Fig. 4) but decreased significantly from day 26 until hatching ($P \ll 0.01$; Fig. 4). Because the yolk presumably supplies the energy for embryonic growth and embryonic caloric content increases throughout incubation, one would expect the total caloric content of the yolk to decrease throughout incubation. However, the total caloric content of the yolk (87.78 ± 2.17 kcal, $n = 24$) did not vary significantly between day 14 and days 21–31 ($P > 0.2$). This may be related to the fact that the yolk reserve has demonstrated survival value under natural conditions (Reid and Bailey 1966).

DISCUSSION

In Adélie Penguin eggs prepipping $\dot{V}_{O_2}$ did not appear to be limited by shell conductance in the manner suggested by Rahn et al. (1974). Although conductance (13.1 mg H_2O·day^{-1}·torr^{-1}, Rahn and Hammel 1982; 12.6 mg H_2O·

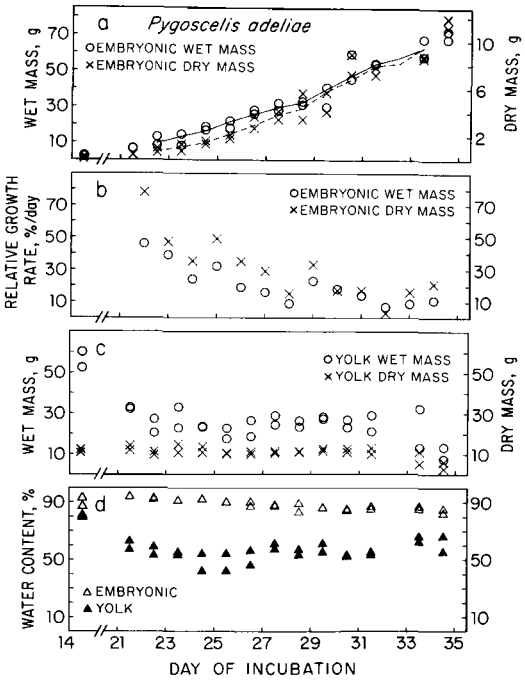

Fig. 3. (a) Adélie Penguin embryonic wet and dry mass in relation to incubation age. Solid and dashed lines connect 3-day running averages of wet and dry masses, respectively. (b) Relative growth rate of embryonic wet and dry mass (based on 3-day running averages) in relation to incubation age. (c) Yolk wet and dry mass in relation to incubation age. (d) Fractional water content of the embryo and the yolk in relation to incubation age.

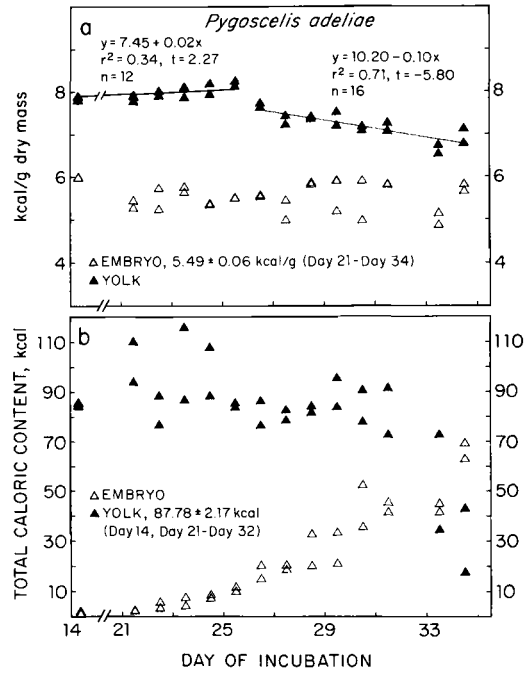

Fig. 4. (a) Caloric content per gram dry mass of Adélie Penguin embryo and yolk in relation to incubation age (see Results). (b) Total caloric content of the embryo and the yolk in relation to incubation age.

day^{-1}·torr^{-1}, R. Ackerman unpubl. data from the Sea World population on which the present study is based) is lower than predicted on the basis of egg mass, $\dot{V}_{O2}$ was not reduced correspondingly. Calculated partial pressures of oxygen in the Adélie air cell (based on G_{H_2O} and $\dot{V}_{O_2}$; see Paganelli et al. 1978) were 84–90 torr with a ΔP_{O_2} of 59 torr. Given the low conductance and high $\dot{V}_{O_2}$, the ΔP_{O_2} necessarily exceeded the value of 42 torr predicted for all eggs (Rahn 1982). The P_{O_2} in the air cell was less than the 104 torr predicted by Hoyt and Rahn (1980) as a constant for all species and less than the 109 torr predicted by D. Vleck et al. (1980) as a function of egg mass.

Most previous estimates of embryonic $\dot{V}_{O_2}$ were made in closed systems and yield only an integrated measure of metabolism for limited time periods. It has been assumed that such estimates are representative of the energy metabolism required for growth and maintenance at a particular age. However, this assumption may not be justified. Our limited long-term measurements show that levels of metabolism are highly variable.

Two important points should be noted regarding the oxygen-consumption data for Adélie Penguins (Figs. 2 and 5). First, on each of three occasions when we monitored the $\dot{V}_{O_2}$ of an unpipped egg continuously for more than 1 h, large changes in $\dot{V}_{O_2}$ occurred. For example, over a 22-h period $\dot{V}_{O_2}$ of one egg (4 days before hatching) fell to 35% of its initial rate, then rose to 92% of the initial rate, and then decreased to only 30% of the initial rate. In two other eggs (7 and 4 days before hatching), over a 3-h and a 1.25-h period $\dot{V}_{O_2}$ fell 20% from the initial rate in each case. The rates measured during the first hour of each of these experiments are probably the rates most equivalent to the published values for other species measured in closed systems (Fig. 2, inset). The fact that the values during the first hour were 1.2–3.3 times the minimal values measured for the same eggs on the same days strongly suggests that a significant proportion of the variability seen by

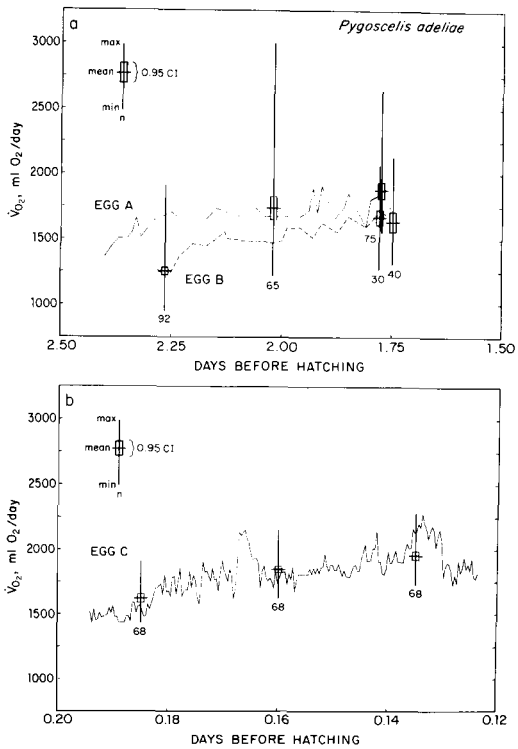

Fig. 5. Oxygen consumption in Adélie Penguin eggs during the last 3 days of incubation. (a) Solid and dashed lines connect data points from 2 eggs when their $\dot{V}_{O_2}$ was relatively constant and calculated assuming steady-state $\dot{V}_{O_2}$. Dicegrams summarize instantaneous $\dot{V}_{O_2}$ calculated during periods when $\dot{V}_{O_2}$ was elevated and the embryos were visibly active (see Fig. 2). (b) A record of instantaneous $\dot{V}_{O_2}$ on the day of hatching. Each dicegram summarizes one-third of the period displayed.

previous investigators and in this study is attributable to embryonic activity and possibly a daily rhythm in activity and metabolism. Second, individual variability in $\dot{V}_{O_2}$ in pipped eggs can be large even within short periods of time. The dicegrams in Figs. 2 and 5 show the mean $\dot{V}_{O_2}$ and the range in $\dot{V}_{O_2}$ in pipped eggs during various time periods (5–102 min). The means are equivalent to the values measured in closed systems. Therefore, the difference between the mean and the minimum, expressed as a percentage of the mean, for each data set of pipped eggs gives an estimate of the percentage of metabolism that may be attributable to embryonic activity during the period of measurement. From three days to one day before hatching this activity component was ~20% in pipped eggs, and on the day of hatching it was ~25%. Based on these estimates, about 9% of the total $\dot{V}_{O_2}$ during incubation is due to embryonic activity between pipping and hatching. This percentage makes no allowance for activity before pipping.

Thus, a substantial portion of embryonic metabolism, both before and after pipping, probably is due to embryonic activity. This has not been quantified previously because measurement techniques have masked the information. The portion of $\dot{V}_{O_2}$ attributable to activity either has been ignored or has been assumed to be negligible in attempts to partition the total energetic costs of embryos among maintenance, growth, and other possible parameters.

Penguins generally are classified as semialtricial species (Nice 1962). Many of the criteria used in Nice's classification are behavioral traits such as the ability to feed independently and to leave the nest and locomote effectively. Such traits need not be associated with a particular level of metabolic activity or of any other physiological capacity. The relations between physiological capacities and the environment are diverse. The limited behavioral repertoire of hatchling penguins may have evolved as a response to the severity of the environment into which they hatch. The very cold environment makes brooding a necessity even though the hatchlings have resting metabolic levels as high as other hatchlings classified as precocial by Nice (Table 2).

A measure of mass-independent metabolism (a MIM value; see Heusner 1985) can be calculated for a species by dividing basal metabolic rate by adult body mass raised to the ⅔ power (MIM = BMR ÷ mass$^{0.67}$). A MIM value also can be calculated for hatchlings by substituting resting metabolic rate at the temperature of incubation for BMR. The ratio of hatchling MIM to adult MIM serves as an index of metabolic precociality (see Bucher 1986 for a list of ratios). Among species for which the necessary data are available, the index for Adélie Penguins (0.56) is equal to or exceeds that of many species that Nice (1962) classified as semiprecocial or precocial.

The young of almost all predatory avian species take considerable time to learn the skills involved in prey capture, and this is presumably true for penguins. Therefore, both because of the harshness of the environment and because of the type of behavior necessary for in-

dependent feeding, there would appear to be no selective advantage for a newly hatched penguin to leave the nest.

Growth and energy allocation.—Penguin embryo mass increases between pipping and hatching in a manner intermediate to those that have been described for altricial and for precocial species (C. Vleck et al. 1980). Absolute growth rate peaks at day 28–29 (80% of incubation) but remains near this level throughout the rest of incubation, neither decreasing as sharply as has been described for precocial species nor continuing to increase as in altricial species (C. Vleck et al. 1980, Bucher 1983). At 60% of incubation the Adélie relative growth rate (~45%/day, Fig. 3) is similar to that of the Zebra Finch (*Poephila guttata*), a very small altricial species, but higher than reported for the altricial *Agapornis roseicollis* and *Pelecanus occidentalis* or the precocial *Coturnix coturnix* (Bucher and Bartholomew 1984). By 80% of incubation, the relative growth rate in Adélie Penguins has dropped to less than 20%/day, as low as or lower than in any of the species just mentioned. Mass-specific oxygen consumption is constant or decreases slightly between 40 and 90% of incubation (Fig. 6). It then increases until hatching, and continues to increase for at least several days after hatching.

The rate of growth or production (P) can be expressed as kcal/day, i.e. (g dry mass/day) × (kcal/g dry mass), as can the rate of energy metabolism. Daily production ratios or "growth efficiency" ratios, $P/(P + \dot{V}_{O_2})$, have been calculated for a number of species during the nestling period (see Williams and Prints 1986). Values range between 0.5 and 0.1, generally declining as the nestling period proceeds and growth rate decreases. At 60% of incubation the daily growth efficiency ratio of Adélie Penguin embryos is 0.62. During the last week of incubation it averages 0.52. The ratio for the total incubation period is 0.54. During the incubation period of *Agapornis roseicollis* daily growth efficiency ratios range between 0.22 and 0.59, but, in contrast to the situation in Adélie Penguins, this ratio increases as relative growth rate decreases and age increases. The ratio for the total incubation period in *Agapornis* is 0.50 (recalculated from data in Bucher and Bartholomew 1984). The same ratio (referred to as an "energetic storage efficiency") has been calculated for incubation through the period prior to internal pipping into the air cell (pre-IP stage) and through hatching for several seabirds (Pettit et al. 1984). Their values for the total period range from 0.52 to 0.72 and are lower for hatchlings than for pre-IP embryos of the same species.

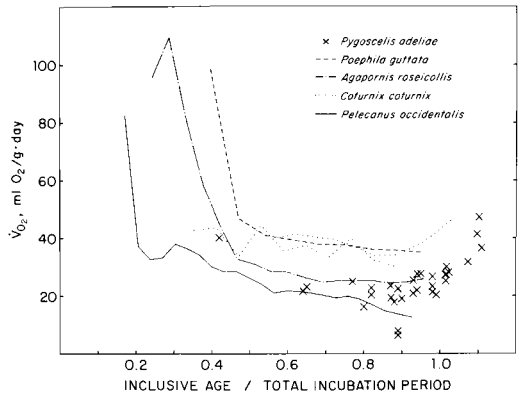

Fig. 6. Mass-specific metabolism in relation to inclusive age/total incubation period (inclusive age is age from the beginning of incubation). Time of hatching equals one. Adélie Penguin data is superimposed on the data from Fig. 2 in Bucher and Bartholomew (1984).

The growth efficiency ratio for *Pygoscelis* is higher than that for *Agapornis* because, for the portion of the incubation period for which we have data, *Pygoscelis* has a relative growth rate nearly as high as or higher than that of *Agapornis*, and at the same time its mass-specific metabolic rate is as low as or lower than that of *Agapornis*. If the maintenance portion of embryonic $\dot{V}_{O_2}$ scales with mass to any power less than one, the measured total metabolizable energy ($TME = P + \dot{V}_{O_2}$) will be proportionately smaller as size increases. Thus, larger (and older) birds will have higher daily efficiencies than smaller birds if their relative growth rates are equal. It may be more appropriate to speak of an allocation ratio rather than an efficiency. The allocation ratio expresses the proportion of metabolizable energy that is being allocated to growth, but it does not indicate the cost of growth independently from the maintenance and activity components of the measured energy metabolism.

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