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EMBRYONIC METABOLISM OF THE FORK-TAILED STORM PETREL:  
PHYSIOLOGICAL PATTERNS DURING PROLONGED  
AND INTERRUPTED INCUBATION<sup>1</sup>

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Embryos of the fork-tailed storm petrel survived exposure to 26, 30, and 34 C. However, during artificial incubation at 26 C, metabolic rate did not increase, and presumably development did not progress. When incubated at 30 and 34 C, eggs showed a gradual increase in metabolism commensurate with development, but success of pipping and hatching was much greater at 34 C than at 30 C. The reduction of metabolic  $Q_{10}$  to 1.55 at temperatures above 34 C suggests that the optimum incubation temperature is near 34 C. Embryos tolerated periodic chilling—24-h exposure to 10 C every fourth day, which simulates environmental conditions when parents neglect the egg during foraging trips. During chilling to 10 C, metabolic rate was only 5% of that at 34 C, and development was presumably arrested. The energy expended by embryos during absence of the parents should thus be negligible. However, the total incubation period is increased, and development is slow even when the egg is warm. Low conductance of the eggshell to water vapor,  $2.1 \text{ mg H}_2\text{O (day}\cdot\text{torr)}^{-1}$ , is an adaptation which minimizes water loss during incubation. Natural incubation of the one-egg clutch is prolonged because of periodic chilling, low temperature of incubation in the subterranean burrow, and slow rate of development. Tolerance of a broad range of temperatures during development and a slow rate of development represent a suite of physiological adaptations which facilitate breeding success of a species with patterns of parental behavior that impose unusual physiological demands on the developmental process.

INTRODUCTION

Fork-tailed storm petrels (*Oceanodroma furcata*) are small (ca. 60 g) procellariiform birds of the family Hydrobatidae which lay a single egg incubated by both parents in a burrow or rock crevice (Wheelwright and Boersma 1979). They are strong fliers and commute over great distances between

feeding and breeding grounds, even during the reproductive season. As a result of the temporal and energetic constraints of this commuting pattern, both parents are often absent from the egg for periods of several hours to several days at a time. These periods of neglect impose delays in development, and incubation is prolonged (see Boersma and Wheelwright [1979] for a review).

<sup>1</sup> We thank P. D. Boersma for her encouragement of this study and for arranging for the eggs from Alaska, and T. Simon and U. Wilson for observing and collecting those eggs in the field. P. D. Boersma and R. T. Paine provided the bird and egg from Tatoosh Island, Washington. We thank P. D. Boersma, D. Hoyt, D. Vleck, and N. Wheelwright for comments on the data and the manuscript. Partially supported by NSF grants PCM 77-05397 and DEB 77-06706 to G. J. K.

In an Alaskan population of fork-tailed storm petrels, the mean cumulative duration of neglect was 11 days for 33 nests, and the resulting incubation periods ranged from 37 to 68 days (mean = 50). The temperature to which the eggs were exposed during neglect was about 10 C (Boersma and Wheelwright 1979). No air-cell temperature greater than 27.5 C was recorded during field observations of incubation (Wheelwright and Boersma 1979). Because of the unusual pattern of incubation in this spe-

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cies, we designed experiments to investigate embryonic metabolism in the laboratory. Measurements of metabolism offer a non-invasive means to assess development and allow us to evaluate the embryonic responses to temperature that have evolved in eggs with a pattern of incubation that is prolonged, frequently interrupted by cooling, and characterized by low maximum and average temperatures.

The allometric equations of Rahn and Ar (1974) predict an incubation period of 21 days for an egg the size of that of the fork-tailed storm petrel; this is less than half the actual mean incubation period of 50 days. Rahn, Paganelli, and Ar (1974) and Ar et al. (1974) have suggested that eggs with relatively long incubation periods should have an eggshell conductance to gases and a rate of embryonic metabolism that are relatively low. Recent tests of these predictions with the large and slowly developing eggs of ratites (Calder 1978; Vleck, Vleck, and Hoyt 1980) support these ideas only in part. Our data on the fork-tailed storm petrel provide a test of these predictions in a small egg with an extremely long incubation period.

#### MATERIAL AND METHODS

##### EGG SOURCES AND DATES

Twenty-four eggs of the fork-tailed storm petrel were collected from nests on East Amatuli Island, Alaska (lat. 59° N, long. 152° W, located in the Barren Islands) on June 16, 1978, and brought to Seattle on June 18. Nests had been inspected six times beginning in early May; four of the eggs were laid prior to May 11, and all others were laid between May 11 and June 9. The midpoint of each inspection interval (or May 11 in the case of the first four eggs) was used as laying date to estimate incubation period. We shall use the term "age" to refer to estimated days since eggs were laid, regardless of the thermal history of the eggs, and not to refer to the developmental stage of the embryo. The eggs were weighed on June 18 (day 0) upon arrival in the laboratory, and then left overnight at 26 C. We measured the length ( $L$ ), breadth ( $B$ ),

and—after hatching—the eggshell thickness at the equator of each egg with a micrometer accurate to 0.0025 cm.

On June 19 (day 1) the metabolic rate of each egg at 26 C was used to rank the eggs. Eggs were distributed evenly on the basis of metabolic rate among the three following groups: (1) Eight eggs incubated at 26 C. Three of these were transferred to a 10 C incubator for about 24 h every fourth day, a procedure intended to simulate the thermal regime of an egg during absence of the adult. On day 10 the temperature of the eggs remaining in group 1 was raised to 28 C. (2) Five eggs incubated at 30 C, without periodic chilling. (3) Eight eggs incubated at 34 C; four of these received 24-h exposure to 10 C every fourth day, as in group 1. All eggs in group 3 were held at 30 C on day 2 of the experiment and then transferred to 34 C permanently on day 3. The only exceptions to the above incubation program were four eggs in group 3 in which we measured the effect of temperature on metabolism ( $Q_{10}$ ). In the last third of incubation these four eggs were incubated at 30 or 37 C for no more than 2 h while rate of oxygen consumption was measured, and then returned to the 34 C incubator.

We maintained eggs in two forced-draft egg incubators and two controlled-environment chambers. All eggs were turned at least once a day. Temperature settings were maintained to  $\pm 0.5$  C. Relative humidity varied between 40% and 60%.

##### MEASUREMENT OF OXYGEN CONSUMPTION

We measured oxygen consumption with an Applied Electrochemistry dual-channel oxygen analyzer, model S-3A. Most determinations were made with closed respirometer chambers consisting of 250 cm<sup>3</sup> acrylic syringes, following the method of Vleck, Hoyt, and Vleck (1979). The egg was left in the syringe until oxygen concentration was decreased by about 0.5%, which required as much as several hours or as little as 8 min, depending on metabolic rate of the egg. Runs of less than 30-min duration were timed to the nearest second from closure of the syringe until 15 s after initiation of

expulsion of the sample. At the end of the determination, the air in the syringe was expelled into the oxygen analyzer with an infusion pump at a uniform rate of about  $50 \text{ cm}^3 \cdot \text{min}^{-1}$ . Prior to entering the oxygen sensor, the sample was passed through a tube containing Drierite ( $\text{CaSO}_4$ ) and Ascarite (NaOH-coated asbestos), which removed water vapor and  $\text{CO}_2$ . A second syringe containing ambient air of the same fractional concentration of  $\text{O}_2$  as initially in the egg syringe was simultaneously expelled in identical fashion into the analyzer. A differential readout ( $F_I - F_E$ ) of oxygen concentration readable to 0.001% in the two syringes indicated the depression in oxygen concentration due to metabolism. Rate of oxygen consumption ( $\dot{V}_{\text{O}_2}$ ) was calculated using equation 1 of Vleck et al. (1979).

For several days prior to hatching, embryonic oxygen consumption of some eggs was also measured continuously in an open-flow system, using a 200-cm<sup>3</sup> chamber held within the incubator. Air was pulled through the chamber, through Drierite and Ascarite, and into the oxygen analyzer using an Applied Electrochemistry R-1 pump module calibrated against a Fisher-Porter rotameter. Signals from the oxygen analyzer were recorded continuously on a Leeds and Northrup two-channel millivolt recorder. We calculated  $\dot{V}_{\text{O}_2}$  in the open-flow system using equation 4a of Withers (1977).

#### ADDITIONAL GAS MEASUREMENTS

Because of the accuracy with which we could determine fractional oxygen concentrations and the fact that the presence or absence of other gases affects the fractional concentration of oxygen in air, we were able to calculate the amount of  $\text{CO}_2$  in our gas samples. This technique is discussed further by Withers (1977) and D. Vleck (1978). We determined the initial volume of  $\text{CO}_2$  in the closed chambers before an egg was placed in the chamber and embryonic  $\text{CO}_2$  production ( $\dot{V}_{\text{CO}_2}$ ) by measuring fractional concentrations of oxygen in the gas samples with and without the removal of carbon dioxide by Ascarite. This method is summarized by

equations 11 and 12 of D. Vleck (1978). We used  $\dot{V}_{\text{CO}_2}$  to calculate the respiratory quotient ( $\text{RQ} = \dot{V}_{\text{CO}_2} / \dot{V}_{\text{O}_2}$ ).

We measured the rate of oxygen consumption of each egg at least once a day until the embryo hatched or died. When two or more measurements were made on the same egg at the same incubator temperature, we report the mean of the measurements for that day.

#### METABOLISM AND BODY TEMPERATURE OF AN ADULT

##### *Oceanodroma furcata*

An adult, nonmolting fork-tailed storm petrel was netted at 0200 hours PST on October 3, 1978, at Tatoosh Island, Washington (lat.  $48^\circ 24' \text{ N}$ , long.  $124^\circ 42' \text{ W}$ ) and brought to the laboratory at 2000 hours. We measured  $\dot{V}_{\text{O}_2}$  of this animal in an open-flow respirometry system similar to that used for open-flow measurements on eggs, except that the respirometry chamber consisted of a gallon jar. We measured body temperature with a 36-gauge thermocouple inserted 2 cm into the cloaca, recorded with a Leeds and Northrup Speedomax 250 multipoint recorder, corrected with a mercury thermometer traceable to the National Bureau of Standards. Temperature in the chamber ranged from 25.6 to 28.0 C. For nighttime measurements (2100–0600 hours) the chamber was dark, and for daytime measurements (0600–0730 hours) the lights were on.

#### WATER-VAPOR CONDUCTANCE

We measured the water-vapor conductance of eight eggs which did not hatch by using the method of Ar et al. (1974) in which water loss of eggs in a desiccator at constant temperature and pressure is monitored by measuring change in mass. Reported values are corrected to 760 mm Hg and 25 C (Paganelli, Ackerman, and Rahn 1978).

#### RESULTS

Embryonic oxygen consumption of eggs artificially incubated at 26 C showed no increase; after 9–12 days  $\dot{V}_{\text{O}_2}$  fell to negligible levels, indicating death of the embryos (fig. 1). Estimated ages of these eggs on day 1 ranged from 32 to more than 46 days

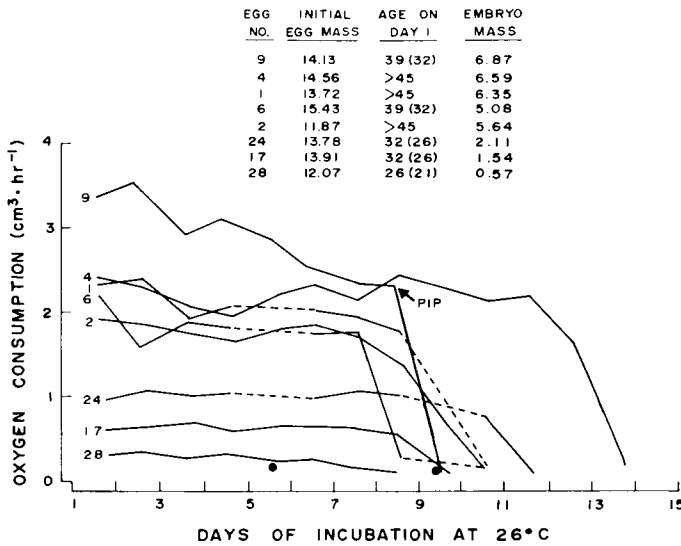


FIG. 1.—Oxygen consumption of fork-tailed storm petrel eggs incubated at 26 C. Day 1 is June 19, 1978.  $\dot{V}_{O_2}$  is plotted against clock time on the day of each measurement. Eggs 1, 6, and 24 were cooled to 10 C on days 5 and 9, and mean  $\dot{V}_{O_2}$  of all these eggs on these days is indicated by a filled circle. Egg 9 pipped, but died without hatching. Inset shows estimated initial mass (g) at laying; estimated maximum (minimum) possible age, in days, on day 1 (see Material and Methods) and measured yolk-free mass (g) of embryo at death.

and the yolk-free masses of the dead embryos ranged from 0.57 to 6.87 g (fig. 1). Only one of these eggs (no. 9) pipped, but the chick never hatched. (It is, of course, possible that chicks which develop in nature may be assisted in hatching by a parent.) Eggs 1, 6, and 24, which were exposed to 10 C every fourth day, showed a decrease in  $\dot{V}_{O_2}$  during chilling to 12.3% the rate at 26 C (SD = 2.6; six measurements on three eggs). Usually  $\dot{V}_{O_2}$  returned to precooling level upon rewarming of the egg the following day.

Oxygen consumption of embryos incubated at 30 C increased, at least initially (fig. 2). Egg 30, with the highest initial metabolic rate, hatched on day 8, 1 day after pipping. The next most advanced egg, no. 12, pipped on day 10, but failed to hatch. The other three embryos died at earlier stages of development after 9–14 days of incubation. The embryo with the lowest initial metabolic rate died first and that with the highest died last.

At 34 C eggs hatched whether incubated continuously or chilled at 4-day intervals.

Two were broken in handling and did not hatch; one of these pipped. Five of the other six eggs hatched within 1 or 2 days of pipping. Metabolic rate of the six eggs that pipped increased throughout incubation (fig. 3). The  $\dot{V}_{O_2}$  prior to pipping was similar in all of these eggs (table 1); but the overall rate of increase in  $\dot{V}_{O_2}$  of a periodically chilled egg (no. 27) was less than that of the eggs which were not chilled. The  $\dot{V}_{O_2}$  at 10 C was only 5.3% (SD = 1.4, 22 measurements on four eggs) the rate at 34 C. Another egg was not plotted in the figure because it was broken in handling and failed to pip; this egg was chilled every fourth day and showed the same pattern as egg 27 during 35 days of measurements. Egg 5 pipped following only one bout of chilling, so that we cannot evaluate the effect of repeated chilling on its rate of development.

The respiratory quotient (RQ) measured in eggs at 34 C was 0.721 (SD = 0.099, 34 measurements on four eggs); at 30 C, RQ was 0.724 (SD = 0.064, five measurements on three eggs); and at 37 C, RQ was 0.751

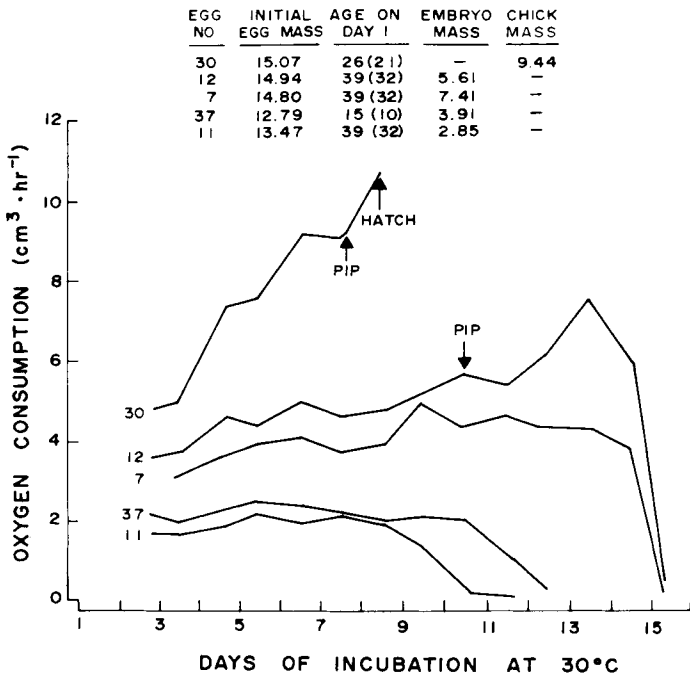


FIG. 2.—Oxygen consumption of fork-tailed storm petrel eggs incubated at 30 C. Plotting and inset as in fig. 1. Mass of chick includes yolk reserve.

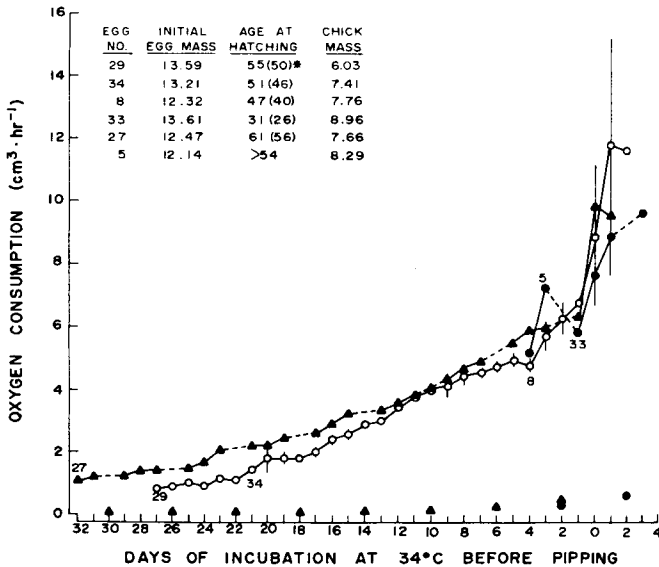


FIG. 3.—Oxygen consumption of fork-tailed storm petrel eggs incubated at 34 C.  $\dot{V}O_2$  is plotted vs. days before and after pipping; this common reference point normalizes the original data, which were obtained from eggs of different ages. Eggs 29, 34, 8, and 33 were incubated continuously at 34 C. Open circles represent mean and bars represent  $\pm 1$  SD for these four eggs; egg number (29, 34, 8, and 33) is shown on the first day on which data were obtained for each egg. Egg 27 (solid triangles) and egg 5 (solid circles) were cooled to 10 C every fourth day;  $\dot{V}O_2$  on these days is seen near the bottom of the graph. Inset shows initial mass (g) of the egg at laying and estimated maximum (minimum) age, in days, at hatching. Chick 29 died after pipping; age shown (\*) is age at pipping, and mass does not include yolk. Mass of all other chicks, which hatched, includes yolk reserve.

(SD = 0.065, nine measurements on four eggs). These values, which are near those reported for a variety of eggs (Rahn et al. 1974), indicate that fats were the principal substrate for metabolism. When  $RQ = 0.727$ , the mass of oxygen incorporated into metabolic water is equal to the mass of carbon excreted as  $CO_2$ . Therefore, at this  $RQ$ , cellular metabolism results in no change in mass. Because the measured  $RQ$  values were close to this value of 0.727, we can say that the loss of mass from the eggs during incubation was due primarily to water loss and not metabolism.

The effect of temperature on rate of  $O_2$  consumption over any range of temperature can be conveniently expressed as a  $Q_{10}$  value. Between 30 and 34 C,  $Q_{10} = 2.41$  (SD = 0.52, 45 measurements on four eggs); between 34 and 37 C,  $Q_{10} = 1.55$  (SD = 0.30, 43 measurements on four eggs). The  $Q_{10}$  between 34 and 37 C is significantly lower than between 30 and 34 C ( $P < .001$ ).

Physical measurements of the eggs are reported in table 2. On experimental day 0 the eggs had lost a mean of 10.8% (range 3.2%-19.7%) of their estimated initial mass.

In addition, we obtained one egg of Leach's storm petrel (*Oceanodroma leucorhoa*) collected from Tatoosh Island, Washington, on July 6, 1978. Because we had already observed low developmental success in the fork-tailed storm petrel eggs at low incubation temperatures, we incubated this single egg of unknown age at 37 C. It pipped on the twentieth day of incubation in the laboratory and hatched on the twenty-third day. The pattern of gradual increase in  $\dot{V}_{O_2}$  throughout the incubation period was similar to that in fork-tailed storm petrel eggs incubated at 34 C. Oxygen consumption of the term embryo was  $5.12 \text{ cm}^3 \cdot \text{h}^{-1}$ , measured on the day prior to pipping (egg mass = 9.28 g). Oxygen consumption of the

TABLE 1  
OXYGEN CONSUMPTION OF TERM EMBRYOS (1 DAY PRIOR TO PIPPING),  
NEWLY HATCHED CHICKS, AND ADULT FORK-TAILED STORM PETRELS

Material Measured	$\dot{V}_{O_2}$ ( $\text{cm}^3 \cdot \text{h}^{-1}$ )	SD	Sample Size	T Air (°C)	T Body (°C)	Egg or Body Mass (g ± SD)
Embryo.....	6.90	2.50	2	30	...	15.01 ± .09
Embryo.....	6.75	.74	6	34	...	12.89 ± .66
Chick.....	9.31	...	1	30	...	9.44
Chick.....	10.99	2.04	2	34	...	7.54 ± .18
Adult:						44.6
Nighttime....	79.36	.59	2	25.6	39.1	...
Nighttime....	79.13	.72	4	28.0	39.1	...
Daytime.....	81.33	3.89	3	28.0	39.1	...

NOTE.—Sample size of eggs and chicks indicates number of individuals measured once each; sample size for adult indicates number of measurements on the single individual.

TABLE 2  
EGG AND INCUBATION PARAMETERS

Parameter	Units	Mean	SD	Sample Size
Egg length (L).....	cm	3.490	.119	24
Egg breadth (B).....	cm	2.677	.083	24
Eggshell thickness.....	cm	.0135	.002	23
Initial egg mass (M) <sup>a</sup> .....	g	13.61	.471	24
Conductance of shell to water vapor ( $G_{H_2O}$ ).....	$\text{mg} (\text{day} \cdot \text{torr})^{-1}$	2.096	.471	8
Age at hatching (approx.) <sup>b</sup> .....	Days	43.9	12.3	6

<sup>a</sup> We estimated initial egg mass at laying from length and breadth according to the equation  $M = 0.54 LB^2$  (Hoyt 1979).

<sup>b</sup> To determine age at hatching we took day of laying as the midpoint of the interval during which the egg was known to have been laid (see Material and Methods).



newly hatched chick was  $12.85 \text{ cm}^3 \cdot \text{h}^{-1}$  (body mass = 6.31 g).

In order to test Warham's (1971) suggestion that adult procellariiformes have a relatively low metabolic rate and body temperature which contribute to low incubation temperature, we measured these parameters in one adult fork-tailed storm petrel (table 1). Daytime  $\dot{V}_{O_2}$  was only slightly higher than nighttime  $\dot{V}_{O_2}$ , and body temperature was 39.1 C (see Discussion).

#### DISCUSSION

##### EFFECTS OF TEMPERATURE ON HATCHING

Embryos of the fork-tailed storm petrel hatched at temperatures below the reported optimum for most other species, and development was normal at temperatures which result in abnormal development in other species (Drent 1975). However, we conclude that there was little or no development during artificial incubation at 26 C, since metabolic rate did not increase with time in these eggs. Hatching success of the eggs we incubated was greatest at 34 C. We suggest that the optimum temperature for development lies near 34 C or slightly higher. This is supported by the reduced  $Q_{10}$  of metabolism above 34 C. ( $Q_{10}$  between 34 and 37 C was 1.55, as compared with  $Q_{10} = 2.41$  between 30 and 34 C.) Other ectothermic vertebrates also have a reduced  $Q_{10}$  in the normal or optimal range of temperatures (Aleksiuk 1976; Bennett and Dawson 1979), implying physiological compensation for temperature.

The apparent optimum temperature for hatching which we measured in artificial incubation lies substantially above the reported air-cell temperature of about 26 C measured during incubation in the field (Wheelwright and Boersma 1979). Data for a variety of species indicate that natural incubation temperature and the artificial incubation temperature of greatest hatching success or of optimal development are nearly identical (Drent 1970, and references therein; White and Kinney 1974; Weinrich and Baker 1978). The optimum temperature for artificial incubation may, of course, be slightly less than 34 C, and the actual tem-

perature of embryos in natural incubation is undoubtedly somewhat greater than that of the measured air-cell temperature, for reasons discussed by Drent (1970). We suggest that the embryonic physiology of this species is characterized by thermal flexibility within a broad range of incubation temperatures. Even at 30 C some eggs developed. However, as demonstrated by our measurements of  $Q_{10}$ , the rate of development below 34 C remains strongly temperature dependent.

Other hydrobatid species may also have a wide range of permissible temperatures for development. Ricklefs and Rahn (1980) report incubation temperatures of 32–33 C in the eggs of Leach's storm petrels. This species nests in a cool burrow similar to that of the fork-tailed storm petrel. Our successful hatching of one Leach's storm petrel chick after 22 days incubation at 37 C indicates that a temperature 5 C higher than that observed in nature is effective for incubation in this species.

When cooled to 10 C at 4-day intervals, eggs otherwise incubated at 34 C showed a reduction in metabolic rate to 5.3% the rate at 34 C. Despite these interruptions, which simulate egg neglect by parents, we found a pattern of development in these eggs which is similar to that of continuously incubated eggs, except that each day of chilling simply added about another day's time to the total incubation period, as also observed in the field (Boersma and Wheelwright 1979). Figure 4 compares the ontogeny of oxygen consumption in continuously incubated eggs with that of a periodically chilled egg, for which the days of chilling have been subtracted from the plot. The data from the egg with days of chilling subtracted coincide with the pattern in eggs continuously incubated at 34 C, indicating that the rate and course of development are similar when the eggs are warm, whether they are intermittently cooled or not.

Eggs of other storm petrels are known to tolerate chilling throughout incubation (Roberts 1940; Matthews 1954; Boersma and Wheelwright 1979). Embryonic tolerance to chilling decreases during incubation

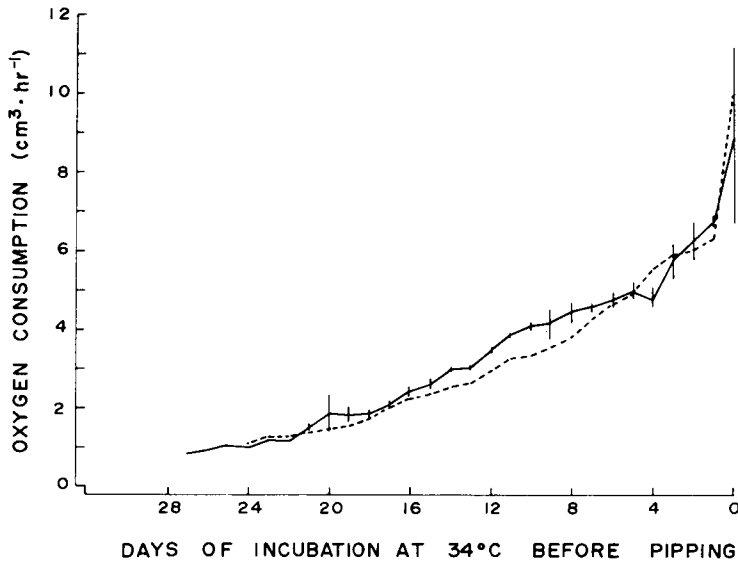


FIG. 4.—Oxygen consumption of fork-tailed storm petrel eggs incubated at 34 C. The solid line connects mean values ( $\pm 1$  SD) for four eggs incubated continuously at 34 C, as shown in fig. 3. Egg 27 was cooled to 10 C every fourth day, as shown in fig. 3, but days of chilling are now removed from the plot, and the broken line thus represents actual days of incubation at 34 C before pipping.

in a variety of species of other orders (Baldwin and Kendeigh 1932; Moreng and Bryant 1956; Norton 1972). Still other birds, such as estrildid finches (Ziswiler 1959) and hummingbirds (Calder and Booser 1973; C. Vleck 1978), are tolerant to chilling late in incubation. It is difficult to assess comparative patterns among these other species because of the paucity of data, but it seems clear that the Hydrobatidae are extreme among birds in the duration of chilling which they survive.

The low incubation temperature of the fork-tailed storm petrel is probably not due to a reduction in adult metabolic rate or body temperature; rather, it is cool conditions of the burrow and the scant nest, together with the behavior of the incubating adults, which interact to result in low incubation temperatures. Adult metabolic rate (table 1) conforms to the prediction of Lasiewski and Dawson (1967) ( $73.3 \text{ cm}^3 \cdot \text{h}^{-1}$ ) and lies between the predictions of Aschoff and Pohl (1970) for daytime and nighttime oxygen consumption ( $83.6$  and  $66.4 \text{ cm}^3 \cdot \text{h}^{-1}$ , respectively). Similar results are reported by Iverson and Krog (1972). Body tem-

perature (table 1) falls slightly above the mean for 31 species of procellariiformes (Warham 1971), and is only 0.9 C below the mean reported for other birds under standard conditions (King and Farner 1961).

#### INCUBATION PERIOD

The period of incubation is lengthened by a slow intrinsic rate of development as well as by recurrent interruptions and low temperature of incubation. Intrinsic rate of development, even at 34 C, in these birds is characterized by an unusually low daily rate of increase in oxygen consumption [mean  $\approx 0.18 \text{ cm}^3 \cdot (\text{h} \cdot \text{day})^{-1}$ ]. This is less than one-third the rate of increase in an egg of similar size, *Coturnix* (Vleck et al. 1979). These *Coturnix* eggs were studied at a typical environmental incubation temperature of about 37 C. We can estimate the rate of development of our eggs at 37 C using the  $Q_{10}$  value of 1.55 for the interval 34–37 C. The rate of development at 37 C would be only 14% greater than at 34 C.

#### GAS EXCHANGE IN THE EGG

A long incubation period increases the possibility of embryonic dehydration. The

minimum incubation period of fork-tailed storm petrels in the field, 37 days, is 75% longer than the incubation period predicted for an egg of this size (table 3). However, mean percent loss in egg mass during incubation in the field was 14.6% (Boersma and Wheelwright 1979), which is similar to water loss in eggs of other birds (Drent 1970).

Rate of water loss is decreased in the fork-tailed storm petrel by an adaptive reduction in conductance of the eggshell to water vapor ( $G_{H_2O}$ ). Measured  $G_{H_2O}$  is near the value predicted when incubation period is taken into account (table 3). The minimum incubation period, 37 days, is used in this analysis because it is a better representation of actual days of parental incubation than either mean or maximum incubation period, which includes days of neglect. The gradient in water-vapor pressure between the egg and environment together with  $G_{H_2O}$  determine water loss. Only when the parent incubates will a substantial gradient develop in water-vapor pressure and elevate water loss to measurable levels.

The structural characteristics of the eggshell which determine  $G_{H_2O}$  also determine the conductance of the eggshell to oxygen ( $G_{O_2}$ ), since these gases follow the same diffusion pathway (Paganelli et al. 1978). Although  $G_{O_2}$  is also low in eggs of the fork-tailed storm petrel,  $\dot{V}_{O_2}$  is not necessarily limited by this low shell porosity. High oxygen flux can also be achieved across a low-porosity shell by maintenance

of a steep gradient of partial pressure in oxygen across the shell which is due to high embryonic demand. We found that  $\dot{V}_{O_2}$  prior to pipping was much higher than predicted on the basis of mass and incubation period (table 3). Embryonic metabolic rate is not reduced as an adaptation to lengthy incubation, but is near the value predicted for an egg of this size (table 3).

#### ENERGETICS AND THERMAL RELATIONS OF THE EMBRYO

What energetic demands are placed upon the egg by its slow intrinsic rate of development? By measuring the area under the curve of mean oxygen consumption during development at 34 C (fig. 3) and extrapolating to nearly zero oxygen consumption at onset of development, we can estimate the total energy utilized during development from onset through hatching. A total of about 2.83 liters  $O_2$  is consumed during this time. Assuming an energy equivalent of 19.64 kJ·liter  $O_2^{-1}$ , corresponding to the oxidation of mixed lipids (RQ = 0.72), this is equivalent to about 55.6 kJ. The formula of Ar and Rahn 1978 (90 cm<sup>3</sup>  $O_2$  per gram initial egg mass) predicts a total oxygen consumption during development of the eggs we studied (table 3, mass = 12.89 g) amounting to 1.16 liters  $O_2$  (=22.78 kJ). The value of total oxygen consumption which we observed under these conditions is therefore greater than twice the predicted value.

TABLE 3

OBSERVED AND PREDICTED VALUES OF INCUBATION PERIOD ( $I$ ), EGGSHELL CONDUCTANCE TO WATER VAPOR ( $G_{H_2O}$ ), AND OXYGEN CONSUMPTION OF TERM EMBRYOS AT 34 C ( $\dot{V}_{O_2}$ )

Parameter	Units	Observed	Predicted	Equation Used for Prediction	Source of Equation
$I$	Days	37 <sup>a</sup>	21	12.03 $M$ . <sup>217</sup>	Rahn and Ar 1974
$G_{H_2O}$	mg(day·torr) <sup>-1</sup>	2.10	3.32 <sup>b</sup>	0.432 $M$ . <sup>78</sup>	Ar et al. 1974
			1.92 <sup>b</sup>	5.2 $M/I$	Rahn and Ar 1974
$\dot{V}_{O_2}$	cm <sup>3</sup> ·h <sup>-1</sup>	6.75	6.79 <sup>c</sup>	25.2 $M$ . <sup>78</sup>	Hoyt, Vleck, and Vleck 1978
			3.88 <sup>c</sup>	267 $M/I$	Rahn et al. 1974

NOTE.— $G_{H_2O}$  and  $\dot{V}_{O_2}$  have been predicted on the basis of mass alone ( $M$ ) and on the basis of mass and incubation period combined ( $M/I$ ).

<sup>a</sup> Minimum incubation period observed in field (mean = 50, maximum = 68) by Boersma and Wheelwright (1979).

<sup>b</sup> Based on mean initial mass of the eggs used to measure  $G_{H_2O}$  (13.64 g).

<sup>c</sup> Based on mean initial mass of the eggs used to measure  $\dot{V}_{O_2}$  at 34 C (12.89 g). These values have been divided by 24 h to convert from units of the equations.

We expect that the energy supply originally deposited in the egg of the fork-tailed storm petrel should be higher than that of most eggs of the same size because of this high total metabolic expenditure for development. The chick produced in this energy-intensive process weighs only slightly less than is typical; the yolk-free mass of chicks we hatched was 50% of initial egg mass, whereas the mean for 19 other species is 57% (Vleck et al. 1980). Furthermore, an additional component of the energy supply is still available at hatching; we found the unassimilated yolk reserve at hatching to be about 24% of yolk-free chick mass, which represents energy supply available for the first week of posthatching growth.

Although the total energy cost of development is high in these eggs, the energy cost during parental absence is small because of the precipitous drop in metabolism when eggs are cooled. We can estimate the energy cost of neglect for an egg neglected for 28 days, as reported by Boersma and Wheelwright (1979). By assuming a decrease in oxygen consumption during cooling to about 5% of the normal rate, and by assuming that the normal rate of oxygen consumption in the field is similar to that which we measured in the laboratory at 34 C, we calculate that 28 days of neglect increase total energy consumption by about 2.3 kJ. This is only about 4% more than if the egg were not neglected.

The relative energy cost of neglect would be greater at higher burrow temperatures or at lower incubation temperatures. For example, if eggs were cooled by about 10 C when neglected, from 34 down to 24 C, energy consumption during neglect would be reduced by only about 50%. In this case, the energy cost of neglect in the nest discussed above would be about 21.6 kJ, i.e., an increase of 40% rather than 4% in

the total cost of development. These hypothetical periods of neglect at 24 C would also increase the total incubation period because the high rate of metabolism would support maintenance, but probably not growth, as we found in eggs incubated at 26 C (fig. 1). Clearly, extended egg neglect is only possible where burrow temperatures are sufficiently cool to ensure energy savings to the embryo through physiological dormancy, yet warm enough not to kill the embryo.

Measurements of metabolism indicate that embryonic development in the fork-tailed storm petrel differs from the typical avian pattern in several ways. (1) Embryos develop over a range of temperatures that extends downward to at least 30 C, even though the optimum temperature for development lies within a few degrees of that of other birds. (2) Oxygen consumption decreases to nearly negligible levels when eggs are chilled to the temperature of natural burrows, and the embryos tolerate repeated bouts of such cooling. (3) Rate of development, as characterized by daily rate of increase in oxygen consumption, is slow compared with that in other avian embryos. The unusual physiological aspects of this pattern of development appear to be adaptations in response to special patterns of behavior in the adults. The habit of foraging at great distances from the breeding grounds and returning to the nest only at night has operated as a selective pressure for the evolution of tolerance to chilling. The habit of laying the egg in a cool burrow or crevice with little or no nest insulation has probably contributed to the evolution of the ability to develop at suboptimal temperatures. The functional significance and evolution of the slow intrinsic rate of development remain to be explained.

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