

- STAPLES, J. 1977. Vegetational succession, soil characteristics, and primary production and energetics on surface mines. Unpublished M.S. thesis. Morgantown, West Virginia, West Virginia Univ.
- STEELE, R. G., & J. H. TORRIE. 1960. Principles and procedures of statistics. New York, McGraw-Hill.
- WEBB, W. L., D. F. BEHREND, & B. SAISON. 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildl. Monogr.* 55: 6-35.
- WHITMORE, R. C., & G. A. HALL. 1978. The response of passerine species to a new resource: reclaimed surface mines in West Virginia. *Amer. Birds* 32: 6-9.
- WIENS, J. A. 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* No. 8.
- WRAY, T., P. B. WACKENHUT, & R. C. WHITMORE. 1978. The reproductive biology of passerine birds breeding on reclaimed surface mines in northern West Virginia. Pp. 333-334 in *Proc. Conf. on Surface Mining and Fish/Wildlife Needs in the Eastern United States*, Morgantown, West Virginia, December 3-6, 1978. U.S.D.I. FWS/OBS-78/81.

Received 13 November 1978, Accepted 2 April 1979.

The Incubation Temperature of Leach's Storm-Petrel

ROBERT E. RICKLEFS¹ AND HERMANN RAHN²

¹Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 USA and

²Department of Physiology, State University of New York, Buffalo, New York 14214 USA

The Procellariiformes are pelagic, surface-feeding seabirds, all of which nest on islands, lay a single egg, and have prolonged development periods compared with other birds. Leach's Storm-Petrel (*Oceanodroma leucorhoa*), one of the smallest species in the order, lays a 10-g egg, has an incubation period (laying to hatching) of 40-42 days (Palmer 1962), which is twice as long as that of other birds having eggs of similar size (Rahn and Ar 1974, Drent 1975), and has a nestling period (hatching to flight) of 63-70 days (Palmer 1962, Wilbur 1969). The single-egg clutch and slow postnatal growth have been related to the food supply, which is distant, patchy, and apparently unpredictable, especially when storms prevent feeding (Lack 1966, 1968). But because the embryo is provided with all its food at the beginning of incubation, food limitation cannot directly cause the prolonged period of embryonic development. To explain the long incubation periods of procellariiform birds, Lack (1968) suggested that rates of embryonic and postembryonic growth have a common genetic basis, and therefore selection of slow postnatal growth to reduce energy requirements would necessarily prolong the incubation period. This hypothesis may be rejected, however, because the growth rates of Procellariiforms do not differ greatly from those of species in other orders (e.g. Galliformes, Charadriiformes) having much shorter incubation periods (Ricklefs 1973).

Warham (1971) contended that the long incubation periods of Procellariiformes derive from low incubation temperatures, but Drent (1975) could find no evidence to support this view. According to Drent, the reported incubation temperatures of 25 species of birds varied between 34 and 38°C, with those of most species being between 35 and 36°C. Incubation temperatures of four Procellariiformes varied between 34.8 and 36.6°C, the lowest value being Drent's unpublished measurement for Leach's Storm-Petrel. Drent dismissed many extremely low values included in Warham's summary as being caused by faulty technique and by the failure to allow sufficient time for full equilibration of egg temperature after disturbance. Here we report two independent measurements of the incubation temperature of Leach's Storm-Petrel of about 32 and 33°C, the lowest yet recorded by direct, reliable measurement for any species (cf. Burger and Williams 1979).

Studies were conducted by RER on Baccalieu Island, Newfoundland, between 21 and 24 July 1978, and by HR on Kent Island, Grand Manan, New Brunswick, during the last week of June and first two weeks of July 1978. On Baccalieu Island, nest burrows were dug into steep, west-facing, grassy slopes. Temperatures were obtained using a Yellow Springs Instruments thermistor thermometer. Body temperatures were measured by extending the thermistor probe into the proventriculus of adults immediately after they were removed from the nest. Brood patch temperatures were obtained from adults removed from their nests. The birds were provided artificial nests, with a petrel egg to which a thermistor had been taped, in a box at an ambient temperature (T_a) of 15°C. The birds readily incubated the eggs. The

TABLE 1. Egg, brood patch, and adult body temperatures of Leach's Storm-Petrel.

	Sample size	Average	Standard deviation	Range	Source
Egg (T_e)	—	34.8	—	—	Drent
	8	32.3	1.35	30.8–34.2	Ricklefs
	2	33.1	—	32.1–33.9 ^a	Rahn
Brood patch (T_p)	—	34.4	—	—	Drent
	5	36.4	1.00	35.0–37.5	Ricklefs
	17	36.7	0.90	34.6–38.1	Rahn
Body (T_b)	—	37.9	—	—	Drent
	5	38.9	0.40	38.4–39.6	Ricklefs
	13	38.1	0.52	37.2–38.8	Rahn

^a Temperature for each egg is the average of 3 or 4 series of 10–18 separate measurements over periods of 30–60 min over 1 or 2 days. For one egg, the extreme temperatures recorded were 31.0 and 33.0°C, and for the other, 32.5 and 34.9°C.

temperature of the brood patch was recorded after it had remained at a steady level for at least 5 min. Temperatures of incubated eggs in burrows were obtained immediately after the eggs were taken from brooding adults. A 2-mm-diameter hole was made in the shell and the thermistor probe was inserted through it to a depth of 5 mm. About 20 s elapsed between reaching into the burrow and inserting the thermistor into the egg, during which time the egg was cradled in the hand in order to prevent cooling. We determined that the temperature of one egg fully exposed to air 10°C cooler than the egg decreased by less than 0.5°C per min. We feel, therefore, that the recorded measurement adequately reflects the true incubation temperature.

On Kent Island, nest burrows were located within a forest of white spruce. Temperatures were measured with a temperature-compensated thermocouple device (Kane-May Instrumentation) using copper-constantan junctions, calibrated against a registered thermometer and read to 0.1°C. Adult temperatures were obtained as above. Brood patch temperatures were obtained by placing the thermocouple on the bare skin of the brood patch where it was held firmly, the overlying feathers being used to insulate the thermocouple from the finger. We do not know the degree to which handling might have affected this measurement. To measure incubation temperature, a thermocouple junction was placed at the center of a fresh egg and its lead secured to the shell by epoxy cement. The egg was put into a nest and its temperature recorded periodically. Air temperatures within burrows and outside the nest were measured over 7-day periods with a *Tempscribe* (Bachrach Instrument Co., Pittsburgh, Pa.).

Temperatures are presented in Table 1. In this study, average body (proventricular) temperature (T_b) of incubating adults (38.3°C) was within the range of temperatures obtained for adults of most species under resting conditions (Warham 1971), although it was somewhat higher than the value (37.2°C) given by Folk (1951). Temperatures of the brood patch averaged 36.6°C. On Bacallieu Island, burrow temperatures (T_a) varied between 13 and 16°C. Air temperature outside the burrows was about 20°C in the afternoon. On Kent Island, the temperature of one burrow varied between 7.8°C and 8.9°C over a 12-day period, over which air temperature outside the burrow varied between 7 and 20°C (average 12.6°C), and agreed with measurements reported from the same colony by D. Ainley (unpubl.).

The average egg temperature (T_e) of Leach's Storm-Petrel (10 eggs, $\bar{x} = 32.5^\circ\text{C}$) is 3°C below the mean of those reported for 25 species by Drent (1975). Temperatures of neonates vary between 32 and 39°C, but the minimum increased rapidly to about 37°C during the first week of development (P. Walls, unpubl.). The gradient between the temperature of the brood patch and the egg (4.1°C) falls within the range reported for other species (1.5–5.5°C, av. 3.2°C, Drent 1975). The gradient between the body core and the brood patch (1.7°C) is toward the higher end of the range reported for other species (0.4–2.4°C, av. 1.0°C, Drent 1975).

The low incubation temperature of Leach's Storm-Petrel raises two questions. First, what is the basis for the observed egg temperature? Second, what consequence does it have for embryonic development? Egg temperature is an equilibrium between heat applied to the egg by the brood patch and heat lost to the nest and surrounding air. Petrels lay their eggs in cool, moist burrows and supply little nest material to insulate the exposed surface of the egg. At about 10 g fresh weight, the egg is 20–25% of adult body weight (Palmer 1962). The conductance of a 10-g egg uniformly exposed to air is about 0.0237 watts (W)· C^{-1} (Kendeigh 1973). Assuming $T_e = 32.5^\circ\text{C}$, $T_a = 10^\circ\text{C}$, and 80% of the egg surface is exposed (Drent 1973), the rate of heat loss from the egg would be 0.43 W. The metabolic rate of resting adult petrels (RMR) is 0.80 W (Ricklefs, unpubl.). Thus our crude estimate of heat loss from the egg is on the

order of 50% RMR. According to this calculation, the additional heat required to raise T_e by 3°C to 35.5°C would be a maximum of 0.07 W, or 9% RMR. It would be less if the nest material were warmed by the brooding adult or if part of the exposed surface of the egg were covered by feathers. In spite of the fact that incubation spells are several days, during which the adult does not feed, energy conservation resulting from reduced incubation temperature would seem to be of minor importance (see King 1973, Walsberg and King 1978). Furthermore, low incubation temperature may not be an adaptation, *per se*, over and above the egg temperature determined by brood patch temperature, egg size, clutch size, and the conformation of the nest. Conceivably, the observed egg temperature is the highest possible equilibrium between heat supplied by the parent and that lost to the environment.

In the domestic fowl, incubation period is inversely related to incubation temperature with a Q_{10} between 36°C (22.7 days) and 39°C (19.4 days) of about 1.7 (Barott 1937, Romanoff 1960). If this relationship applied to all species, the 3°C difference between the incubation temperature of Leach's Storm-Petrel and the average of those of other species might prolong the incubation period 15–20%, far less than the approximate doubling of incubation period observed. Even if the Q_{10} were 2.5, the incubation period would be prolonged only 33%.

This interpretation suggests that incubation temperature is probably a minor factor in the prolongation of incubation by Procellariiformes. This is further emphasized by the observation that the eggs of another storm-petrel, *Hydrobates pelagicus*, required 35 days to hatch at a constant temperature (presumably 37°C) in a chicken incubator (Bent 1922), and by the fact that in three other species of Procellariiformes with prolonged incubation periods, incubation temperatures averaged between 35.8 and 36.3°C (Drent 1975).

We are indebted to C. E. Huntington, Director, Bowdoin Scientific Station, and W. E. Montevecchi, Memorial University of Newfoundland, for advice, cooperation, and logistical assistance. R. Fogler and K. Matthew ably assisted in the field. This study was supported in part by National Science Foundation Grants Nos. PCM76-20947 (HR) and DEB77-27071 (RER). This is Contribution No. 45 from the Bowdoin Scientific Station.

LITERATURE CITED

- BAROTT, H. G. 1937. The effect of temperature, humidity, and other factors on hatch of hens' eggs and on energy metabolism of chick embryos. U.S. Dept. Agr. Bull. 553: 1–45.
- BENT, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U.S. Natl. Mus. Bull. 121.
- BURGER, A. E., & A. J. WILLIAMS. 1979. Egg temperatures of the Rockhopper Penguin and some other penguins. *Auk* 96: 100–105.
- DRENT, R. 1973. The natural history of incubation. Pp. 262–311 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.
- . 1975. Incubation. Pp. 333–420 in *Avian biology*, vol. 5 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- FOLK, G. E. 1951. Observations on the body temperature of Leach's Petrel. *Anat. Rec.* 111: 541–542.
- KENDEIGH, S. C. 1973. Pp. 311–320 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.
- KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78–107 in *Breeding biology of birds* (D. S. Farner, Ed.). Washington, D.C., Natl. Acad. Sci.
- LACK, D. 1966. *Population studies of birds*. London, Oxford Univ. Press.
- . 1968. *Ecological adaptations for breeding in birds*. London, Methuen.
- PALMER, R. S. (Ed.). 1962. *Handbook of North American birds*, vol. 1. New Haven, Yale Univ. Press.
- RAHN, H., & A. AR. 1974. The avian egg: incubation time and water loss. *Condor* 76: 147–152.
- RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115: 177–201.
- ROMANOFF, A. L. 1960. *The avian embryo*. New York, Macmillan.
- WALSBERG, G. E., & J. R. KING. 1978. Energetic consequence of incubation for two passerine species. *Auk* 95: 644–655.
- WARHAM, J. 1971. Body temperatures of petrels. *Condor* 73: 214–219.
- WILBUR, H. M. 1969. The breeding biology of Leach's Petrel, *Oceanodroma leucorhoa*. *Auk* 86: 433–442.

Received 15 January 1979, accepted 23 April 1979.