Pacific Science (1994), vol. 48, no. 2: 136–144

Incubation Biology and Nestling Growth of Bulwer's Petrels on Manana Island, Oahu, Hawaii[1]

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ABSTRACT: Data were gathered on incubation of eggs and growth of nestlings of Bulwer's Petrels nesting on Manana Island in the Hawaiian Islands. Mean incubation period of five eggs was 45.2 days. Duration of pipping period of six eggs, which began with star-fracture of the shell, was 4.5 days. Daily water loss from unpipped eggs was 62.6 mg/day; water loss from pipped eggs was much higher, and 36.3% of total water loss occurred from pipped eggs. Mean nestling period (hatching–fledging) of four nestlings was 62 days; body weight of eight nestlings increased to a maximum 21.2 days before the nestlings fledged and then declined. Body weight of adult Bulwer's Petrels declined over the breeding season.

BULWER'S PETREL (*Bulweria bulwerii* Jardine & Selby) is a tropical procellariiform seabird breeding in the Central Atlantic and Pacific oceans. The species is of particular interest because it is the smallest member of the family Procellariidae and also the smallest of the tropical petrels. Although general information on the Pacific population of Bulwer's Petrels is contained in Berger (1981) and Harrison (1990), they are among the least known of Procellariiformes according to Warham (1990), who summarized the little information available on their breeding biology.

Bulwer's Petrels have been reported to nest on Manana Island, a small island offshore of the main island of Oahu in the Hawaiian Islands, since 1948 (Richardson and Fisher 1950). Although the numbers breeding on Manana are small, visits to the island over the period 1977–1989 presented an opportunity to obtain information that would fill in some of the many gaps in our knowledge of the species.

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MATERIALS AND METHODS

All of the nesting sites studied were on the westerly aspect of Manana Island (lat. 21° 20′ N; long. 157° 40′ W); three of the sites (a, b, c) were on the leeward shore and the remaining site (d) was on the rim of the crater (Figure 1). Eggs were laid in old shell holes in the rock face (c), on ledges within a cave (a), under rock overhangs (b, c), or in rock crevices (d).

Nest sites were examined regularly at the beginning of the breeding season to establish the dates on which the eggs were laid. Toward the estimated end of the incubation period, eggs were examined carefully to detect the first indication of pipping. External pipping (star-fracture of the shell) was recognized both by the appearance of the shell and by touch—the slightly protuberant fractured edge of the shell was often felt before it was seen. Internal pipping (penetration of the aircell of the egg by the embryo's beak) was identified by listening for "cheeping" sounds from the egg (Pettit and Whittow 1983).

Egg dimensions were measured with a dial calipers, the smallest graduation of which was 0.025 mm. The water loss from naturally incubated eggs was measured by weighing the eggs, at the nest site, at intervals of 48 hr to 15 days (Rahn and Ar 1974) using a field

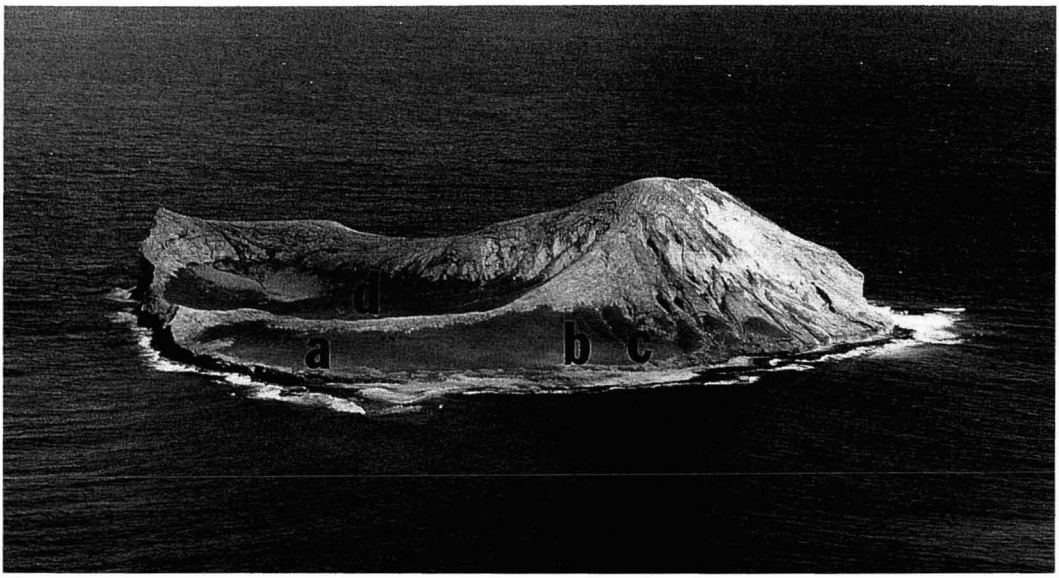

FIGURE 1. A view of Manana Island from Kamehame Ridge on Oahu, looking northeast. The letters identify the nesting areas (immediately below the letters) of the Bulwer's Petrels studied in this report.

balance (Ohaus model 1010-10). Great care was taken to minimize the disturbance to the incubating birds during these measurements, and when eggs were removed for measurements, they were replaced temporarily by an abandoned egg kept for that purpose. Incubated eggs were not collected, but a small number of abandoned eggs, and eggshells remaining at the nest site after the eggs had hatched, were available for additional measurements. Fresh-egg mass was determined by weighing the eggs after the aircell had been filled with distilled water (Grant et al. 1982). Egg volume was measured by weighing the eggs in air and in water (Rahn et al. 1976). The water-vapor conductance of the shell and shell membranes was determined by weighing eggs, which were kept in a desiccator, at daily intervals (Ar et al. 1974). The mass and thickness of the eggshells were measured on shells that had been dried in a desiccator for at least a week. A micrometer calipers (Starrett No. 230), fitted with a ball attachment on the spindle to accommodate the curvature of the eggshell, was used to measure shell thickness. The number of pores in the shells was counted by the method described by Tyler (1953) and Roudybush et al. (1980).

Adults and nestlings were weighed at the nest site with Ohaus Dial Spring Scales that had a range of either 0–100 g or 0–250 g. The scale was checked against a known weight each day. The measurements entailed minimal interference with the birds and nestlings. The measure of variation used in this paper is the standard deviation (SD).

RESULTS

Eggs

INCUBATION PERIOD. The incubation period was measured for five eggs. The mean incubation period was 45.2 days (range, 45–46 days). The earliest date on which an egg was found was 15 May and the latest date was 7 June. Thus, eggs were laid over a period of 24 days. The latest date on which an egg hatched was 23 July; consequently, eggs were present for a period of 70 days. The earliest and latest hatching dates were 29 June and 23

July, respectively. Thus, hatching occurred over a period of 25 days. Part of the egg was often visible under the incubating bird, and an impression was gained that Bulwer's Petrels do not "sit tightly" on their eggs. There was no evidence that the egg was left unattended.

SEQUENCE OF EVENTS DURING PIPPING. The sequence of events during pipping was studied in six eggs. The initial event appeared to be star-fracture of the shell; "cheeping," indicative of internal pipping, was never heard before the shell had been fractured. The mean time between star-fracture of the shell and hatching was 4.5 days, with a range of 2–7 days. A distinct pip hole was seen in only two eggs (Figure 2), 4 days before hatching in both eggs.

EGG DIMENSIONS. The mean length of 11 eggs was 4.167 ± 0.182 cm, and the mean width was 3.048 ± 0.092 cm. The weight of the freshly laid egg was 19.264 and 19.541 g, respectively, in two eggs, and the volume of two eggs was 18.38 and 18.00 ml, respectively.

WATER LOSS. Nineteen measurements of water loss from unpipped eggs were made. The mean water loss was 62.6 ± 13.5 mg/day. Sequential measurements on the same egg revealed a tendency for the water loss from unpipped eggs to increase as incubation proceeded. In four additional instances, the eggs were unpipped on the first occasion that they were weighed and pipped on the second occasion. The mean water loss from these four eggs was 115.5 ± 35.4 mg/day, considerably

FIGURE 2. Bulwer's Petrel egg, showing pip hole.

greater and more variable than that from unpipped eggs. Another egg was pipped on both occasions, and water loss from this egg was 321.9 mg/day.

SHELL CHARACTERISTICS. The mean shell weight for three eggs was 1.189 ± 0.099 g. The mean of 41 measurements of shell thickness (including the shell membranes) of five eggs was 0.193 ± 0.018 mm. The mean shell thickness of six eggs (66 measurements), without the shell membranes, was 0.135 ± 0.014 mm. The measured combined thickness of the inner and outer shell membranes was 0.091 ± 0.031 mm (41 measurements of five eggs). Five direct measurements of the inner-shell membrane thickness yielded a value of 0.010 mm. The mean water-vapor conductance of the shell was 2.1 ± 0.3 mg day^{-1} $torr^{-1}$ for two eggs. The mean pore density of the shell was 67 ± 10 pores per cm for three eggs.

Nestlings

BROODING PERIOD. Precise measurements were not made of the length of time that the hatchlings were brooded by the adult bird. However, for two eggs, it can be said with certainty that the hatchlings were brooded for less than 3 days.

NESTLING PERIOD. The mean nestling period (hatching–fledging) for four nestlings (Figure 3) was 62 ± 3.3 days. The earliest and latest fledging dates were 3 and 19 September, respectively. Consequently, fledging took place over a period of only 16 days.

GROWTH. To reduce the possibility of the hatchling being left unattended during the brooding period, nestlings were not weighed until they were alone. Complete or partially-complete growth data were obtained from eight nestlings, and they are presented in

FIGURE 3. Bulwer's Petrel nestling. The dark area behind the nestling is the entrance to a rock "burrow" in area c (Figure 1).

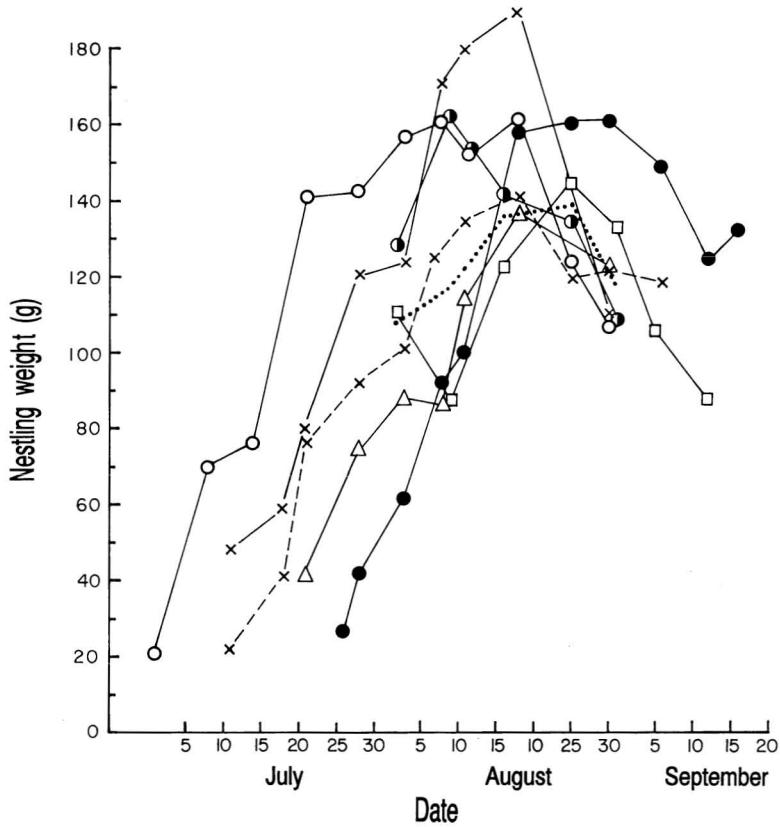

FIGURE 4. Growth of eight Bulwer's Petrel nestlings. Symbols represent different birds.

Figure 4. It is apparent that the weight of each nestling increased to a maximal value and then declined. The mean maximal nestling weight was 142.3 ± 43.0 g. The mean fledging weight (i.e., the final weight before the fledgling left the nest site) was 112.1 ± 13.2 g ($n = 9$). Thus, the fledging weight was 79% of the maximal nestling weight. The maximal nestling weight occurred 21.2 ± 3.8 days ($n = 4$) before the nestlings fledged.

Adults

The earliest sighting of an adult bird at a nest site during the day was on 3 April. During mid-May, before egg laying, adults were rarely seen during the day. The last date on which an adult bird was seen at the nest site during the day was 26 August, 8 days before the earliest fledging date.

Adult birds were weighed as the opportunity to do so presented itself. The identity of the birds was, for the most part, unknown, and nothing was known either about the history of the birds before weighing. The data are shown in Figure 5. There was a general tendency for the birds to weigh less as the season progressed, and an analysis of variance revealed that the differences in body weight between different dates were significant ($F = 4.498$, df = 8, $P < 0.01 > 0.001$). Two birds could be identified because they had been banded. One of these birds was weighed twice during the same season. Its mass decreased from 85 g on 9 April to 83 g on 2 August. The other banded bird was

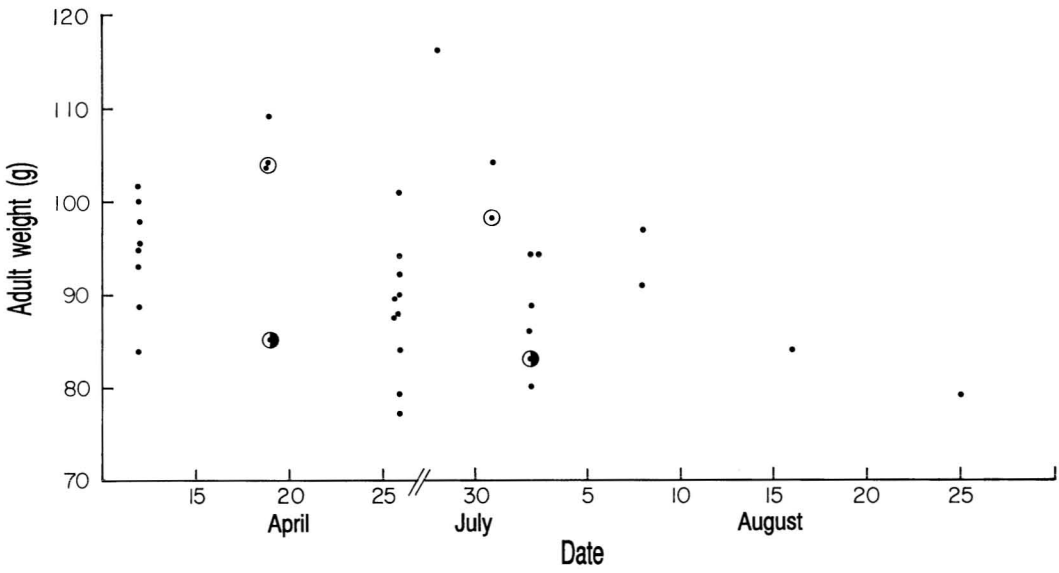

FIGURE 5. Weight of adult Bulwer's Petrels during the breeding season. Each point represents a different bird. ◑, same bird weighed on different dates during the same season; ⊙, same bird weighed during different seasons.

weighed in two consecutive seasons. It weighed 104 g on 19 April during one season and 98 g on 31 July during the following season. This particular bird nested in the same hole in both seasons. The banding information revealed that the two birds were at least 6 yr old.

The mean value of all measurements of adult body weight was 92.8 ± 9.3 g (n = 35).

DISCUSSION

Eggs

Amerson and Shelton (1976) reported that "Two 1968 eggs required at least 44 and 47 days," respectively, of incubation at Johnston Atoll in the North Pacific Ocean. These figures are close to the mean incubation period of 45.2 days recorded in this study. Rahn and Whittow (1988) compiled predictive equations for procellariiform eggs, including an equation for incubation period based on the weight of the freshly laid egg. Using the mean fresh-egg weight of the two eggs measured in the investigation reported here (19.403 g), the predicted incubation period is 45.6 days, very close to the value measured on Manana Island.

The sequence of events during pipping of the eggs of the Bulwer's Petrel had not been described before this report. The sequence seems to be similar to that in other small Procellariiformes (Whittow 1984): the initial event is star-fracture of the shell (external pipping). The duration of the pipping period (external pipping to hatching) was 4.5 days, 10.0% of the total incubation period.

This study has also provided the most definitive data on water loss from eggs of Bulwer's Petrels during natural incubation. Daily water loss from unpipped eggs (62.6 mg/day) was 93% of the expected value (67.1 mg/day) for procellariiform eggs based on the fresh-egg weight (Rahn and Whittow 1988). Robertson and James (1988) reported the mean daily weight loss of 56 eggs at Great Salvage Island (Atlantic Ocean) to be 74 ± 0.02 (SD) mg/day, but it is not clear if pipped eggs were included in the measurements. Using the value of 4.5 days for the duration of the pipping period and 321.9 mg/day for the water loss from a pipped egg (both values

obtained in this study), the total water loss from pipped eggs was estimated to be 4.5 × 321.9 mg = 1448.5 mg. The water loss from unpipped eggs was calculated to be 2546.6 mg [(45.2 − 4.5 days) × 62.6 mg/day]. Thus the total water loss from the eggs during the entire incubation period was 3995.1 mg. This represents 20.6% of the weight of the freshly laid egg, and 36.3% of this water loss occurred from pipped eggs. This latter figure represents the highest percentage of water loss from pipped eggs reported so far in Procellariiformes (Whittow 1984).

The beginning of the laying period on Manana Island (15 May) is similar to that (15 May) reported by Amerson and Shelton (1976) for Bulwer's Petrels on Johnston Atoll (Pacific Ocean) and to the value (19 May) cited by Jouanin et al. (1979) for this bird in Madeira and the Salvages (Atlantic Ocean). The end of the laying season (7 June, Manana; 6 June, Atlantic Ocean) was also similar, but Amerson and Shelton (1976) gave 5 July as the last day on which eggs were laid at Johnston Atoll. However, Amerson and Shelton (1976) stated that eggs laid as late as 5 July did not hatch and were probably produced by young adults laying for the first time. The hatching dates were also similar on Manana Island (29 June–23 July), Johnston Atoll (29 June–15 July), and the Atlantic islands (9–25 July).

Of the other measurements made on eggs, the linear dimensions were made on a sufficiently large sample to justify comparison with the dimensions of Bulwer's Petrel eggs made elsewhere. The mean length and width of the eggs on Manana were 99.2 and 99.6%, respectively, of the mean dimensions of 56 eggs measured on the Atlantic island of Great Salvage (Robertson and James 1988). A comparison of shell thickness, including the shell membranes, with the predicted value for Procellariiformes (Rahn and Whittow 1988) is also valid; the measured value was 93.5% of the expected figure.

Nestlings

The only published data for the growth of Bulwer's Petrel nestlings are those of Jouanin et al. (1979). Their data are fragmentary, and they are for only the first 9 days after hatching. Consequently, they give no intimation of the features of nestling growth noted in this investigation: an increase in nestling body weight to a maximal value that exceeded the weight of the adult bird, followed by a decrease in nestling weight before fledging (Figure 4). This pattern of growth is characteristic of petrels (Warham 1990). The maximal nestling weight was 153.3% of the adult weight, similar to the value for the Bonin Petrel, *Pterodroma hypoleuca* Salvin (Pettit et al. 1982, Warham 1990). Fledging, in petrels, refers to the time when the nestling leaves the nest on its first flight (Warham 1990). The fledging weight for the Bulwer's Petrel was 120.8% of the adult body weight, higher than the value of 113% for the Bonin Petrel. Comparison of the growth rates of Bulwer's Petrel nestlings with those of other petrels is difficult because growth constants are based on growth asymptotes (Ricklefs 1968). In most petrels, nestling weight increases to a maximum and then declines so that, strictly speaking, there is no true asymptote. Another difficulty is that the nature of the growth curve that best represents a particular set of data varies in different species. One index that avoids this latter difficulty is the t_{10-90}, the time interval for growth from 10 to 90% of the asymptote. Using the maximal nestling weight as the value for the asymptotic weight, the mean t_{10-90} for four nestlings of Bulwer's Petrels was 31.8 days. This value is less than that (48.4) for Bonin Petrel nestlings (Pettit et al. 1982), pointing to faster growth in the Bulwer's Petrel. Bulwer's Petrels are smaller than Bonin Petrels, and a higher growth rate would be expected from the inverse relationship between body size and growth rate (Ricklefs 1968). Warham (1990) compiled data for t_{10-90} in petrels. The species closest to the Bulwer's Petrel in body size is the diving petrel (*Pelecanoides georgicus* Murphy & Harper); its t_{10-90} value is 24, indicative of faster growth than in the Bulwer's Petrel.

Amerson and Shelton (1976) reported that nestlings were abandoned several days before fledging. The decline in weight before fledging is consistent with desertion, but, as Warham

(1990) pointed out, smaller meals, fewer parental visits, and the growth of integument rather than heavier tissues may all contribute to weight loss. The last sighting of an adult at the nest site during the day preceded the earliest fledging date, and, again, this is consistent with, but not incontrovertible proof of, desertion.

The mean fledging period of 62 days is identical to that reported by Amerson and Shelton (1976) for Bulwer's Petrels on Johnston Island. The fledging dates for the birds on Manana Island (3–19 September) are also similar to those reported for Johnston Island (26 August–18 September) and a little earlier than in the Atlantic islands (18–25 September). The maximal body weight occurred after 65.8% of the fledging period had elapsed, close to the value of 61% for the Bonin Petrel.

Adults

In general, adults were present on Manana Island for about the same period that they were seen on Johnston Island by Amerson and Shelton (1976) and in the Atlantic (Jouanin et al. 1979). A diminution in body weight during the breeding season has not been reported before for Bulwer's Petrels, but it has been documented in other Procellariiformes (Warham 1990). Because the history of the birds that were weighed was not known, it is not possible to ascribe the weight loss to any known factor except to note that feeding the nestlings coincides with a period of weight loss in several Procellariiformes (Warham 1990). The mean body weight of 92.8 g is rather less than the mean value (94.8 g) for Atlantic birds (Jouanin et al. 1979), but well within the range and standard deviation of the latter. Robertson and James (1988) reported the mean body weight "at first encounter" to be 107.1 g for males and 99.9 g for females at Great Salvage Island, North Atlantic. They also recorded that a female bird weighed only 73 g after an incubation spell of at least 12 days. The total weight loss for 21 birds averaged 20% of initial body weight over an incubation spell of 8–9 days. If the birds do not make up the weight loss incurred during incubation spells, this may also contribute to their decline in weight over the season, as noted in this investigation.

ACKNOWLEDGMENTS

I am grateful to Ted N. Pettit for measuring the fresh-egg weights and shell water-vapor conductance of two eggs. The State of Hawaii Division of Forestry and Wildlife, and the U.S. Fish and Wildlife Service kindly provided permits for this work. Makai Ocean Engineering, Inc. provided assistance with the boat.

LITERATURE CITED

AMERSON, A. B., and P. C. SHELTON. 1976. The natural history of Johnston Atoll, Central Pacific Ocean. Atoll Res. Bull. 192:1–479.

AR, A., C. V. PAGANELLI, R. B. REEVES, D. G. GREENE, and H. RAHN. 1974. The avian egg: Water vapor conductance, shell thickness and functional pore area. Condor 76:153–158.

BERGER, A. J. 1981. Hawaiian birdlife, 2nd ed. University of Hawaii Press, Honolulu.

GRANT, G. S., C. V. PAGANELLI, T. N. PETTIT, and G. C. WHITTOW. 1982. Determination of fresh-egg mass during natural incubation. Condor 84:121–122.

HARRISON, C. S. 1990. Seabirds of Hawaii. Comstock/Cornell, Ithaca, New York.

JOUANIN, C., J.-L. MONGIN, F. ROUX, and A. ZINO. 1979. Le Pétrel de Bulwer *Bulweria bulwerii* dans l'archipel de Madère et aux îles Selvagens. Oiseau Rev. Fr. Ornithol. 49:165–184.

PETTIT, T. N., and G. C. WHITTOW. 1983. Water loss from pipped Wedge-tailed Shearwater eggs. Condor 85:107–109.

PETTIT, T. N., G. S. GRANT, and G. C. WHITTOW. 1982. Body temperature and growth of Bonin Petrel chicks. Wilson Bull. 94:358–361.

RAHN, H., and A. AR. 1974. The avian egg: Incubation time and water loss. Condor 76:147–152.

RAHN, H., and G. C. WHITTOW. 1988. Adapta-

tions to a pelagic life: Eggs of the albatross, shearwater and petrel. Comp. Biochem. Physiol. A Comp. Physiol. 91:415–423.

RAHN, H., C. V. PAGANELLI, I. C. T. NISBET, and G. C. WHITTOW. 1976. Regulation of incubation water loss in eggs of seven species of terns. Physiol. Zool. 49:245–259.

RICHARDSON, F., and H. I. FISHER. 1950. Birds of Moku Manu and Manana Islands off Oahu, Hawaii. Auk 67:285–306.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

ROBERTSON, H. A., and P. C. JAMES. 1988. Morphology and egg measurements of seabirds breeding on Great Salvage Island, North Atlantic. Bull. Br. Ornithol. Club 108:79–87.

ROUDYBUSH, T., L. HOFFMAN, and H. RAHN. 1980. Conductance, pore geometry and water loss of eggs of Cassin's Auklet. Condor 82:105–106.

TYLER, C. 1953. Studies on egg shells. II. A method for marking and counting pores. J. Sci. Food Agric. 4:266–272.

WARHAM, J. 1990. The petrels. Academic Press, New York.

WHITTOW, G. C. 1984. Physiological ecology of incubation in tropical seabirds. Stud. Avian Biol. 8:47–72.