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Egg Dimensions and Shell Characteristics of Bulwer's Petrels, *Bulweria bulwerii,* on Laysan Island, Northwestern Hawaiian Islands[1]

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ABSTRACT: Measured values for Bulwer's Petrel eggs and eggshells from Laysan Island, Northwestern Hawaiian Islands, were within 10% of predicted values available in the literature. In the absence of published predictive equations for egg volume, fresh-egg contents, and total functional pore area of the shell, in Procellariiformes, new logarithmic relationships were developed for tropical Procellariiformes. Data are now needed for species breeding at higher latitudes to determine if these relationships are representative of all Procellariiformes.

BULWER'S PETREL IS a small, procellariiform seabird of the tropical Atlantic, Pacific, and Indian Oceans (Warham 1990, Megyesi and O'Daniel 1997). In the Hawaiian Archipelago, it breeds on islands from Pearl and Hermes Reef in the Northwestern Hawaiian Islands, to offshore islands of Hawai'i in the main Hawaiian Islands (Harrison 1990). Previously, data were presented for, inter alia, the incubation period and the incubation weight loss of eggs on Mānana, a small offshore island of O'ahu, in the main Hawaiian Islands (Whittow 1994). The purpose of this report is to provide information on the dimensions of Bulwer's Petrel eggs and on some of the characteristics of the eggshells, collected on Laysan Island (25° 46′ N, 171° 44′ W) in the Northwestern Hawaiian Islands, and to compare the measured data with predicted values for Procellariiformes compiled by Rahn and Whittow (1988).

MATERIALS AND METHODS

Egg dimensions were measured with dial calipers, and the weight of the freshly laid egg was determined by weighing the egg after replacing the air in the aircell with distilled water (Grant et al. 1982*a*). Egg volumes were measured by weighing the eggs in air and in water (Rahn et al. 1976). Shell weight and shell thickness were determined on shells that had been dried in a desiccator for at least 3 days. Shell weight was measured by weighing the dried shells on a Mettler balance (Model H6) to the nearest 0.1 mg. Shell thickness was determined with micrometer calipers (Starrett No. 230) fitted with a ball attachment on the spindle to accommodate the curvature of the eggshell. The water-vapor conductance of the shell and shell membranes was measured by weighing the eggs daily, for 5 days; the eggs were kept in a desiccator at a constant temperature of 25°C. Under these conditions, the water-vapor conductance can be calculated from the weight loss and the known water-vapor pressure difference between the contents of the eggs and the air in the desiccator. The water-vapor pressure of the egg contents is equal to the vapor pressure of water at 25°C, and that of the air in the desiccator is zero (Ar et al. 1974). The measure of variation used in this report is the standard deviation (SD); n = number of observations; r = correlation coefficient.

RESULTS AND DISCUSSION

The dimensions of the eggs and the characteristics of the eggshells of the Bulwer's

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TABLE 1

MEASURED AND PREDICTED VALUES FOR EGGS AND EGGSHELLS OF BULWER'S PETRELS

PARAMETER	MEASURED	PREDICTED
Egg		
Length (cm)	4.22 ± 0.18 (29)	4.22
Width (cm)	3.04 ± 0.08 (29)	3.12
Volume (cm^3)	19.89 ± 1.57 (29)	
Fresh-egg weight (g)	21.077 ± 1.782 (19)	19.145
Eggshell		
Weight (g)	1.2476 ± 0.1948 (20)	1.3366
Thickness (mm)		
Shell	0.138 ± 0.011 (8)[a]	
Shell + membranes	0.187 ± 0.013 (11)[b]	0.186
Inner shell membrane	0.008 ± 0.004 (3)[c]	
Water-vapor conductance	2.53 ± 0.36 (11)	2.79
(mg day^{-1} $torr^{-1}$)		2.56

NOTE: Mean measured values (±1 SD) are shown; numbers of eggs are in parentheses. Predicted values are from Rahn and Whittow (1988).
[a] 25 measurements on 8 eggs.
[b] 49 measurements on 11 eggs.
[c] 6 measurements on 3 eggs.

Petrel are given in Table 1, together with the predicted values for a procellariiform egg with the incubation period (45.2 days [Whittow 1994]) and fresh-egg weight (Table 1) of a Bulwer's Petrel weighing 92.8 g (Whittow 1994).

Measured egg dimensions were either identical to (egg length) or 97.4% of (egg width) the predicted value; measured fresh-egg weight was 10.1% higher than the value predicted for Procellariiformes (Table 1). Few direct measurements of egg volume have been made on procellariiform eggs (Warham 1990), probably because it is not easy to measure accurately under field conditions. Consequently, there is no published, predictive equation for the egg volumes of Procellariiformes. This is unfortunate, because the egg volume provides more comprehensive information about the size and dimensions of an egg than does any other *single* measurement. This report provides data for the volume of the eggs of the smallest tropical procellariiform species on which information is available, the Bulwer's Petrel. Taken together with previously published information obtained in this laboratory, on the largest tropical species (Black-footed Albatross, *Phoebastria nigripes*) and five other tropical species, it is possible to investigate a relationship between egg volume (V_{egg}) and the weight (W_{egg}) of the freshly laid egg for tropical Procellariiformes (Figure 1). The species included in Figure 1 range in egg weight from 21.1 g (Bulwer's Petrel) to 304.9 g (Black-footed Albatross). The relationship between egg weight and volume is linear on logarithmic coordinates.

The mean shell weight (Table 1) was 6.7% lower than the value predicted by Rahn and Whittow's (1988) equation for Procellariiformes. The mean shell (including the shell membranes) thickness was almost identical to the predicted value according to Rahn and Whittow's (1988) criteria (Table 1). Rahn and Whittow (1988) assembled two predictive equations for the water-vapor conductance of the shells and shell membranes that take into account both the fresh-egg weight and the incubation period. The measured value was either 9.3% or 1.2% lower than the predicted value, depending upon which equation was used (Table 1). In summary, the measured egg length, width, fresh-egg weight, shell thickness, and water-vapor conductance of the shell were within 10% of predicted values.

The water-vapor conductance (G_{H_2O})

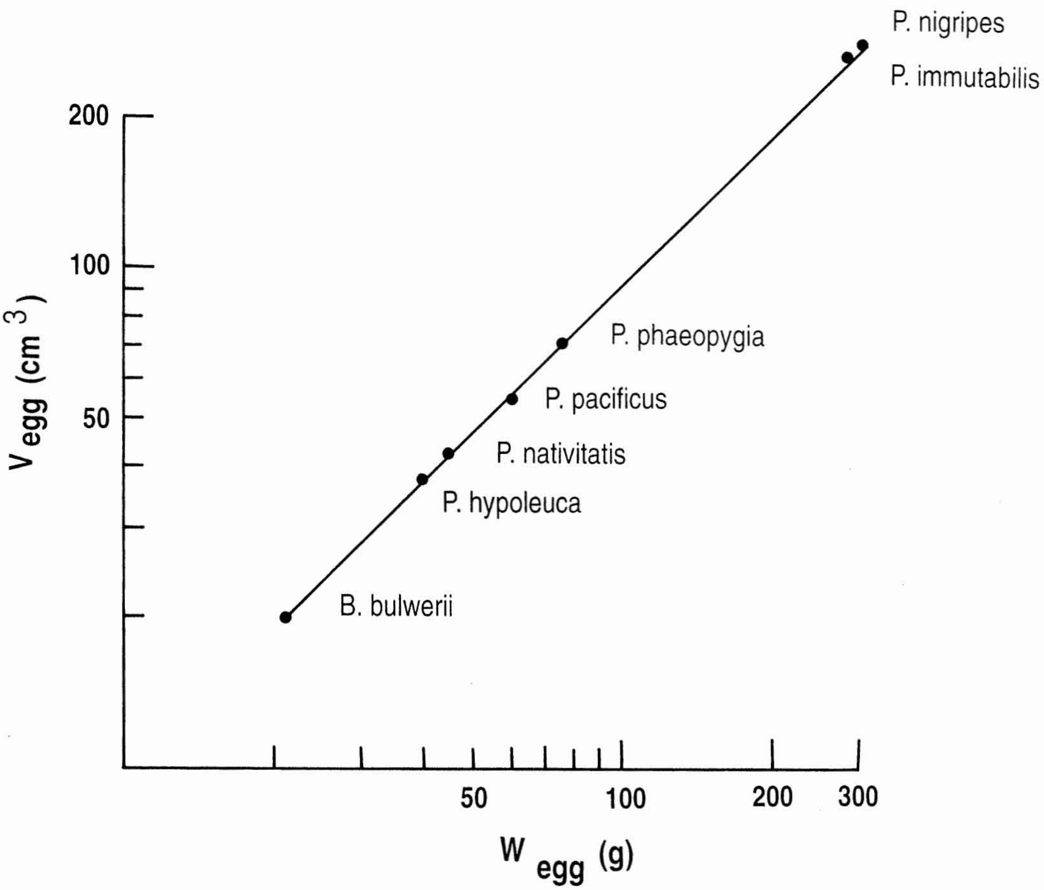

FIGURE 1. Relationship between egg volume (V_{egg}) and fresh-egg weight (W_{egg}) in seven tropical Procellariiformes. The line represents the equation: $V_{egg} = 0.939 \cdot W_{egg}{}^{0.998}$ ($r = 0.999$). Data sources: *Phoebastria nigripes* and *P. immutabilis* (Grant et al. 1982*b*), *Pterodroma phaeopygia* (Whittow et al. 1984), *Puffinus pacificus* (Ackerman et al. 1980), *P. nativitatis* (Whittow and Naughton 1999), *Pterodroma hypoleuca* (Grant et al. 1982*c*), *Bulweria bulwerii* (this report).

and shell (including membranes) thickness (L) data (Table 1) may be used to calculate the total functional pore area (A_p) of the shell from Rahn et al.'s (1976) equation: $Ap\ (mm^2) = 0.447 \cdot G_{H_2O}\ (mg \cdot 24\ hr^{-1} \cdot torr^{-1}) \cdot L\ (mm)$, yielding a value of 0.2115 mm^2. The total functional pore area provides an indication of the pore area involved in diffusion of oxygen into the egg and diffusion of water vapor and carbon dioxide out of the egg. It is, therefore, an important measure of the facility with which gas exchange can occur between the egg and its environment. The rate of gas exchange, in turn, determines the growth and metabolic rates of the embryo (Whittow 1984). This report provides data for the functional pore area of the eggs of the smallest tropical procellariiform species on which information is available, the Bulwer's Petrel. It is possible to investigate a relationship between functional pore area (A_p) and the weight (W_{egg}) of the freshly laid egg for the seven tropical Procellariiformes that provided the data for Figure 1. It is clear (Figure 2) that log A_p is linearly related to log W_{egg}.

Subtraction of the shell weight from the weight of the freshly laid egg (Table 1) yields the weight of the *contents* of the freshly laid

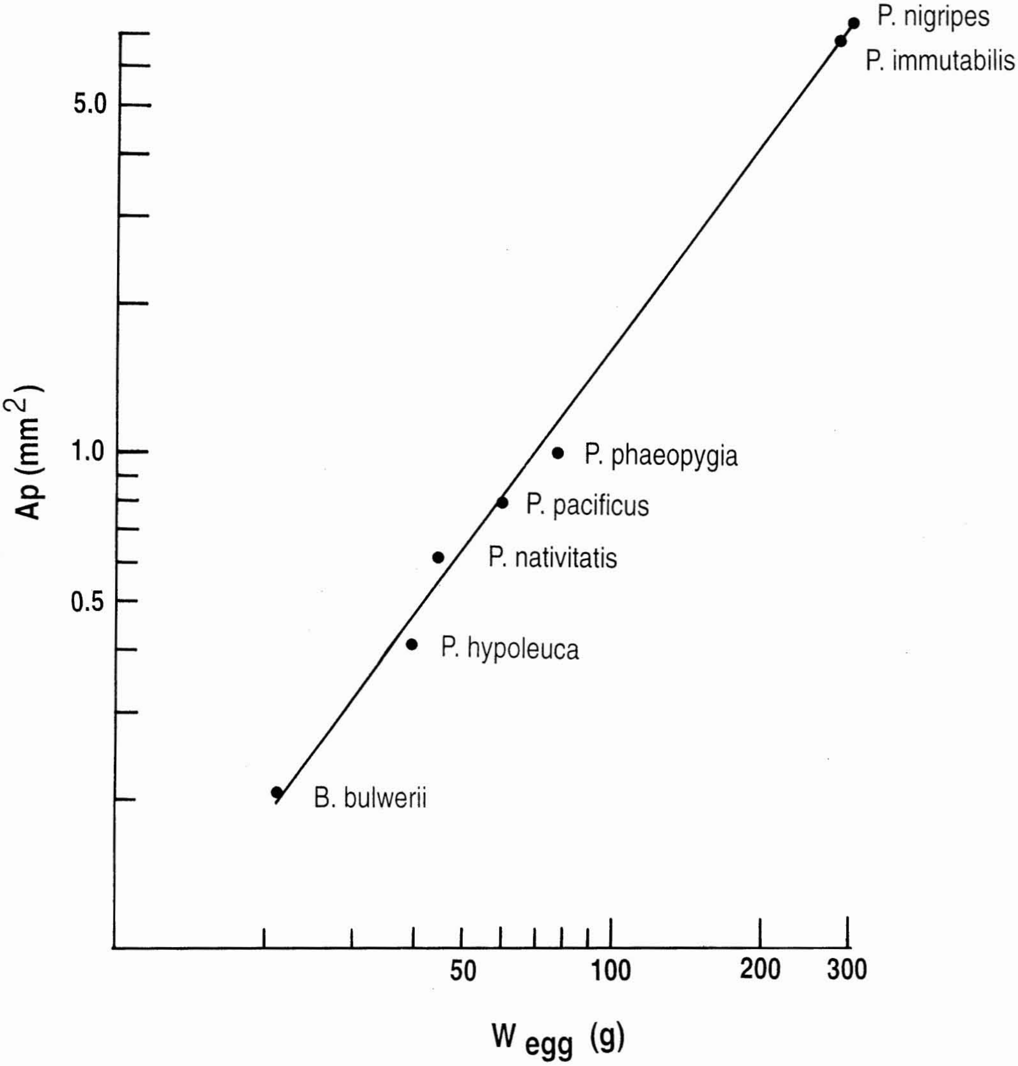

FIGURE 2. Relationship between total functional pore area (A_p) and fresh-egg weight (W_{egg}) in seven tropical Procellariiformes. The line represents the equation: $A_p = 3.15 \cdot 10^{-3} \cdot W_{egg}{}^{1.36}$ ($r = 0.998$). Data sources: *Phoebastria nigripes* and *P. immutabilis* (Grant et al. 1982*b*), *Pterodroma phaeopygia* (Whittow et al. 1984), *Puffinus pacificus* (Whittow et al. 1982), *P. nativitatis* (Whittow and Naughton 1999; G. S. Grant, T.N.P., and G.C.W., unpubl. data), *Pterodroma hypoleuca* (Grant et al. 1982*c*), *Bulweria bulwerii* (this report).

egg. The fresh-egg contents represent the total amount of organic substrates, salts, and water available for the embryo's growth, metabolism, and water balance (Pettit et al. 1984). Again, there are no predictive equations for egg contents in the literature, and, again, it is possible to establish a relationship between egg contents and egg weight in the seven tropical species (Figure 3).

When sufficient data become available for Procellariiformes breeding outside the Tropics, it will be possible to determine if the relationships for tropical Procellariiformes shown in Figures 1–3 represent all Procel-

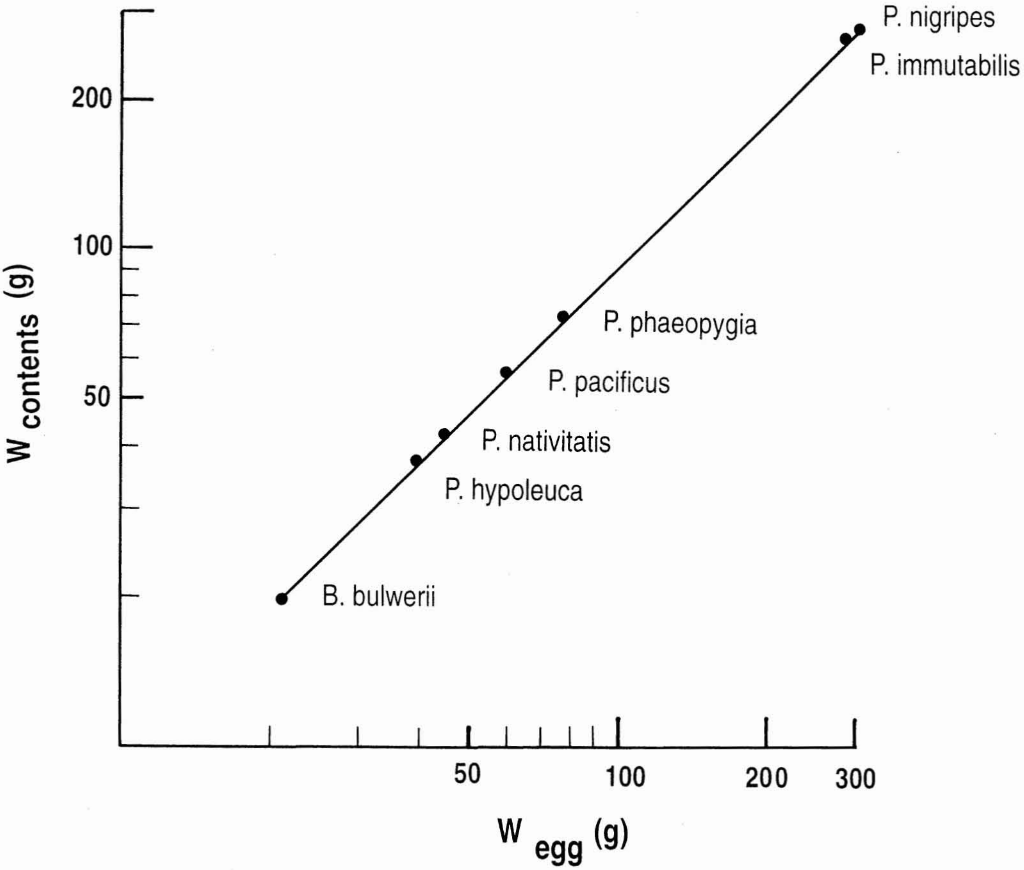

FIGURE 3. Relationship between weight of the contents of the freshly laid egg ($W_{contents}$) and the fresh-egg weight (W_{egg}) in seven tropical Procellariiformes. The line represents the equation: $W_{contents} = 0.964 \cdot W_{egg}^{0.993}$ ($r = 0.999$). Data sources: *Phoebastria nigripes* and *P. immutabilis* (Grant et al. 1982*b*), *Pterodroma phaeopygia* (Whittow et al. 1984), *Puffinus pacificus* (Ackerman et al. 1980, Whittow et al. 1982), *P. nativitatis* (Whittow and Naughton 1999), *Pterodroma hypoleuca* (Grant et al. 1982*c*), *Bulweria bulwerii* (this report).

lariiformes. The expectation is that they will do so, because latitudinal variations in the allometric relationships of eggs are rare in procellariiform birds (Whittow and Naughton 1999).

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