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EGGSHELL CONDUCTANCE AND OTHER PHYSICAL CHARACTERISTICS OF AVIAN EGGS LAID IN THE PERUVIAN ANDES[1]

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Certain physical characteristics of eggs laid by both wild and domesticated birds at high altitudes differ from comparable values of eggs laid by conspecific or congeneric species at sea level. In a few cases, masses and dimensions of montane eggs are larger than those laid at low altitudes (Carey et al. 1983, 1989a), possibly because body masses of montane adults often exceed those of lowland relatives (Carey and Morton 1976, Carey et al. 1983).

One feature that consistently differs between montane and lowland eggs is the conductance of the eggshell to gases (G) (Wangensteen et al. 1974; Packard et al. 1977; Rahn et al. 1977; Sotherland et al. 1980; Carey et al. 1983, 1987, 1989a, 1989b; Leon-Velarde et al. 1984). The degree and direction of variation depends on the altitude at which the eggs were laid. The conductance (standardized to 760 torr) of eggs laid up to 3,000–3,500 m decreases in approximate proportion to the reduction in barometric pressure at the breeding site (Rahn et al. 1977, Packard et al. 1977, Sotherland et al. 1980, Carey et al. 1983). Standardized conductance of eggs laid above 3,500 m is not reduced in the same proportion as the barometric pressure at the collecting location; in fact, conductance of eggs of some species exceeds the sea level value (Wangensteen et al. 1974; Rahn et al. 1977; Leon-Velarde et al. 1984; Carey et al. 1987, 1989a, 1989b). Since eggshell thickness of most species does not vary altitudinally, most of the variation in conductance in montane eggs results from alterations in the functional pore area, which in turn is attributable to changes in the number of pores rather than in pore dimensions (Carey et al. 1987, 1989a, 1989b).

While we were involved in studies on eggs of other species nesting in the puna, the dry grassland habitat above 3,400 m in the Peruvian Andes (Parker et al. 1982), we had the opportunity to collect a small number of eggs from three species nesting above 4,000 m. The Andean Goose (*Chloephaga melanoptera*) breeds only on the puna, though this species may winter at altitudes as low as 2,000 m (Blake 1977, Parker et al. 1982). The Speckled Teal (*Anas flavirostris oxyptera*) is most common on the puna but occasionally occurs at slightly lower altitudes in the humid and arid temperate montane areas of the Andes (Blake 1977, Parker et al. 1982). The White-tufted Grebe (*Rollandia rolland*, formerly *Podiceps chilensis morrisoni*; Koepcke 1970, Blake 1977) is common both in the puna and at sea level in Peru (Parker et al. 1982). The goals of this paper are to present data on characteristics of eggs of these rarely studied species and to assess the extent to which the characteristics of eggs fitted or conflicted with the patterns of variation observed previously in eggs of other species breeding above 4,000 m.

METHODS

Andean Goose eggs were collected in January from nests located on rocky outcroppings above Laguna Yanacocha (4,400 m) in the Department of Junin, Peru. The eggs were gathered from five different clutches; clutch size averaged 3.6 (range = 2–5). Speckled Teal eggs were gathered from a single nest in December. The nest was located on a floating island of vegetation on Lake Junin (4,150 m), Department of Junin, Peru. Eggs of White-tufted Grebes, also from a single clutch located on a floating mat of wet vegetation, were collected in December from Laguna Tapatapa (4,478 m), 3 km east of Huaychoa, Department of Cerro de Pasco, Peru.

Eggs were wrapped in plastic wrap and taken by car to the Universidad Peruana Cayetano Heredia in Lima (altitude = 50 m). Eggshell conductance to water vapor, G_{H_2O}, of Andean Goose eggs was measured by placing eggs over dry silica gel in a 26- × 21-cm desiccator at 25°C and by weighing them daily for 5 days on a Mettler analytical balance. Since the embryos were dead in these eggs, metabolism did not affect water loss. Then G_{H_2O} was calculated according to the equations given by Ar et al. (1974). Values were discarded from several eggs which proved to be fresh because the G_{H_2O} of such eggs averaged 30% lower than that of eggs containing advanced embryos (developed to an equivalent of stage 15 or more in chicken embryos; Hamburger and Hamilton 1951).

Since previous studies have shown that G_{H_2O} of fresh

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TABLE 1. Physical characteristics of eggs ($\bar{x}$ ± SE) laid by three species in the Peruvian Andes. Sample sizes are given in parentheses.

Species	Mass g	Length cm	Width cm	Volume cm³
Andean Goose	111.94 ± 1.7 (18)	7.47 ± 0.07 (18)	5.01 ± 0.03 (18)	95.49 ± 1.7 (18)
Speckled Teal	46.39 ± 0.32 (2)	5.39 ± 0.01 (2)	3.86 ± 0.05 (2)	40.90 ± 1.0 (2)
White-tufted Grebe	21.81 ± 0.39 (3)	4.65 ± 0.09 (3)	2.92 ± 0.02 (3)	20.21 ± 0.21 (3)

eggs of certain species is substantially below that of eggs which have been incubated (see Carey 1983), we used a different method for measuring G_{H_2O} of Speckled Teal and White-tufted Grebe eggs, which were fresh when collected. This method, developed by Hoyt et al. (1979), is much less accurate than the gravimetric one used above on Andean Goose eggs (see Hoyt et al. 1979). The pore openings on the inside of the shell were photographed with scanning-electron microscopy. The area of each pore was calculated using planimetry in conjunction with a computer program. G_{H_2O} in mg·day⁻¹·torr⁻¹ was then estimated by the equation of Hoyt et al. (1979):

$$G_{H_2O} = (2.24P_A \cdot N)/L \qquad (1)$$

where P_A is the average area of 20 pores per egg in mm², N = pores per egg, and L = eggshell thickness in mm.

The fresh mass of eggs of the three species was determined by injecting water into the air cell until no air bubbles escaped, blotting the egg dry, and weighing it. The thickness of the shell, with membranes removed, was measured using a micrometer caliper. Volume, surface area, and permeability were calculated using equations described previously (Carey et al. 1983). Pore counts were made using the method outlined by Ar and Rahn (1985), with the exception that aniline blue was used for marking the pores. The average area per pore and the radius of individual pores were calculated using equations given by Ar and Rahn (1985).

Mean ± standard error of the mean (SEM) values are presented. The existence and importance of any variation between montane and lowland eggs is most ideally assessed by comparing the characteristics of montane eggs with those of lowland relatives. Unfortunately, two of the species evaluated in this study do not breed at sea level and lowland eggs of the White-tufted Grebe were unavailable. Therefore, we have compared our results with previously published values of similarly sized eggs of lowland congeneric and confamilial relatives. While it would have been desirable to compare our data with eggs of similar mass and incubation period (see Ar and Rahn 1978), we have no information on the incubation period of these three species. The means for each species are not compared statistically with those of related species available in the literature since the sample sizes of Speckled Teal and White-tufted Grebe data are too small to make meaningful statistical comparisons and since no error limits are published for comparable data of congeners of Andean Geese. Our results on total pores per egg (N) and eggshell thickness (L, in mm) of Andean Goose and Speckled Teal eggs were compared with predictions generated by an equation provided by Hoyt et al. (1979):

$$N = 1041 \cdot W^{0.504} \qquad (2)$$

and by an equation calculated from data given by Hoyt et al. (1979):

$$L = 0.25 + 0.00157W \qquad (3)$$

where W = fresh egg mass in g. Because of the variance around estimates provided by such equations is large, such comparisons are less than ideal but they provide some indication of the direction that egg features vary from the predicted value.

RESULTS

ANDEAN GOOSE

If the average G_{H_2O} of Andean Goose eggs were to be reduced in exact proportion to the reduction in barometric pressure at 4,400 m, it would be reduced to approximately 58% of the value of a similarly sized egg laid by a lowland relative. The average conductance of Andean Goose eggs (standardized to 760 torr) was 49.9% and 85.5% of the comparative value for 106-g and 100-g eggs of the Greater Magellan Goose (*Chloephaga picta leucoptera*) and the Ruddy-headed Goose (*C. rubidiceps*), respectively (Hoyt et al. 1979; Tables 1 and 2). The average number of pores and shell thickness of Andean Goose eggs is 70.2% and 104.5% of the value predicted by equations 2 and 3, respectively (Table 3).

SPECKLED TEAL

The average barometric pressure at 4,150 m is approximately 60% of that at sea level. The average G_{H_2O} of eggs of this species is 52.0%, 66.8%, and 88.2% of the comparable values of similarly sized eggs laid at low altitude by captive Mexican Ducks (*Anas platyrhynchos diasi*), Hawaiian Ducks (*A. p. wyvilliana*), and Puna Teal (*A. versicolor puna*) (Hoyt et al. 1979; Tables 1 and 2). The average number of pores and shell thickness of Speckled Teal eggs averaged 65.5% and 78.1%, respectively, of the values predicted by equations 2 and 3 (Table 3).

WHITE-TUFTED GREBE

Eggs of White-tufted Grebes laid at 4,478 m, where the barometric pressure was approximately 57% of sea level,

Table 2. Characteristics ($\bar{x}$ ± SE) of shells of eggs laid by three species in the Peruvian Andes. Sample sizes are in parentheses. Values for G_{H_2O} are "standardized."

Species	G_{H_2O} $\text{mg}\cdot\text{day}^{-1}\cdot\text{torr}^{-1}$	Pore area mm^2	Permeability cm^3 (STP)$\cdot\text{sec}^{-1}\cdot\text{cm}^{-2}\cdot\text{torr}^{-1}\cdot 10^{-6}$	Shell thickness mm	Surface area cm^2
Andean Goose	11.89 ± 0.23 (12)	2.31 ± 0.05 (11)	1.66 ± 0.04 (11)	0.44 ± 0.008 (17)	103.31 ± 1.2 (18)
Speckled Teal	6.35 ± 0.15 (2)	0.69 ± 0.02 (2)	1.55 ± 0.17 (2)	0.24 ± 0.001 (2)	58.71 ± 0.95 (2)
White-tufted Grebe	14.37 ± 0.17 (3)	1.58 ± 0.01 (3)	5.65 ± 0.10 (3)	0.25 ± 0.006 (3)	36.70 ± 0.31 (3)

averaged 118.9% and 146.9% of comparable values of 29-g eggs of Pied-billed Grebes (*Podilymbus podiceps*) and Eared Grebes (*Podiceps nigricollis*), respectively (Davis et al. 1984, Sotherland et al. 1984; Tables 1 and 2). Total pore area, numbers of pores per egg, and shell thickness of White-tufted Grebe eggs averaged slightly larger (107.3%, 111.1%, and 104.2%, respectively) than comparable values for Pied-billed Grebe eggs, while the area per pore and pore radius averaged slightly smaller (95.6% and 97.9%, respectively) (Davis et al. 1984; Tables 2 and 3).

DISCUSSION

An important problem confronted by birds breeding at high altitude is that the diffusion coefficient for gases ($\mathscr{D}$) increases inversely with barometric pressure (Paganelli et al. 1975). An important result of this phenomenon is that eggs laid at altitude could lose more water daily than would conspecific eggs at sea level (Ar et al. 1974). Most water birds breeding in Lake Junin at 4,150 m have relatively long (about 6 months) breeding seasons that span both the rainy and dry seasons (Harris 1981). Therefore, these species do not minimize water loss by breeding solely in the periods of high humidity associated with rainfall. However, previous studies have observed that the increased diffusion of water vapor is offset in some species breeding up to 3,500 m by a reduction in the conductance of the egg to gases that parallels approximately the reduction in barometric pressure (Rahn et al. 1977, Carey et al. 1983, Leon-Velarde et al. 1984). The average G_{H_2O} of eggs laid above 3,500 m is not reduced to the same extent as the reduction in barometric pressure, with the consequences that water loss is higher than at sea level, but air cell oxygen tension is higher than if compensation were complete (Leon-Velarde et al. 1984; Carey et al. 1987, 1989a, 1989b).

Hoyt et al. (1979) found an average difference of 10% between values of G_{H_2O} measured by the method of Ar et al. (1974) and those calculated using equation 1. That difference coupled with our small sample sizes and the variation inherent in allometric predictions makes it difficult to assess accurately whether significant differences exist between the eggs of the three montane species and their lowland counterparts. However, the data generally fit the trends noted previously. In most comparisons, the average G_{H_2O} of Andean Goose and Speckled Teal eggs were reduced below sea-level values, but not to the same extent as the reduction in barometric pressure at the breeding site. The eggs of White-tufted Grebes were collected at the highest altitude at which eggs have been studied so far. They reflect a pattern noted previously that G_{H_2O} of eggs of certain species laid above 4,000 m exceed those of sea-level controls (Carey et al. 1989a; Leon-Velarde et al., unpubl. data). The data for Andean Goose eggs also agree with previously noted trends that most of the variation in pore area results from variation in the total pore area rather than eggshell thickness.

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Table 3. Number of pores per egg, area per pore, and pore radius of shells of eggs ($\bar{x}$ ± SE) of three species laid in the Peruvian Andes. Sample sizes are in parentheses.

Species	Pores/egg	Area/pore μm^2	Pore radius μm
Andean Goose	7,896 ± 247 (12)	297.7 ± 10.9 (11)	9.72 ± 0.18 (11)
Speckled Teal	4,719 ± 70 (2)	145.8 ± 2.8 (2)	6.48 ± 0.05 (2)
White-tufted Grebe	9,724 ± 121 (3)	162.2 ± 9.1 (3)	7.19 ± 0.11 (3)

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