

- KESPAIK, J., AND A. DAVYDOV. 1966. Factors determining the cold-hardiness of the *Larus ridibundus* L. on the first day after hatching. Toimetised Eesti NSV Teaduste Akademia XV, Biol. Seeria 4:485-491. In Russian with English summary.
- KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution of ten species of European ducks. Auk 81:281-307.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13-23.
- LASIEWSKI, R. C., W. W. WEATHERS, AND M. H. BERNSTEIN. 1967. Physiological responses of the Giant

- Hummingbird, *Patagona gigas*. Comp. Biochem. Physiol. 23:797-813.
- NEUMANN, R. L., J. W. HUDSON, AND R. J. HOCK. 1968. Body temperatures. Part II. Birds, p. 334-343, Table 59. In P. L. Altman and D. S. Dittmer [eds.], Metabolism. Federation of American Societies of Experimental Biology, Bethesda, Maryland.

Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109. Address of second author: School of Biological Sciences, University of California, Irvine, California 92717. Accepted for publication 12 September 1979.

Condor, 82:105-106
© The Cooper Ornithological Society 1980

CONDUCTANCE, PORE GEOMETRY, AND WATER LOSS OF EGGS OF CASSIN'S AUKLET

T. ROUDYBUSH
L. HOFFMAN
AND
H. RAHN

The ratios of egg mass to body mass in the Alcidae are relatively large (Sealy 1975) when compared with those of most other groups of birds (Rahn et al. 1975). Cassin's Auklet (*Ptychoramphus aleuticus*) weighs about 165 g (Manuwal 1974b, Sealy 1975), and its single egg of about 29 g is twice that predicted from the egg mass-body mass relationship of birds in general (Rahn et al. 1975). The auklets nest in burrows and rock crevices, and during incubation the single egg is held between the lateral incubation patch and the wing (Manuwal 1974a, b). The incubation time of 38 days is considerably longer than the 25 days predicted for eggs of this size. It is of particular interest as it has been suggested that the functional egg characteristics such as conductance, water loss (Rahn and Ar 1974), and metabolism (Rahn et al. 1974) increase not only in proportion to their mass but are inversely related to incubation time. To see whether these generalizations apply also to Cassin's Auklet eggs, we measured the conductance and incubation water loss of these eggs

TABLE 2. Conductance and pore geometry.

	G	L	A _p	N
	mg day ⁻¹ torr	mm	mm ²	
\bar{x}	4.08	0.23	0.419	3,295
S.E.	0.16	0.01	0.034	152
n	21	8	8	8

G = conductance, L = pore length, A_p = total pore area, N = number of pores per egg, and r = radius of pore, where A_p = .447 G · L (Rahn et al. 1974) and $r = [A_p/N\pi]^{0.5} = 6.4 \mu\text{m}$.

and described the physical dimensions of the egg and the shell as well as the pore geometry responsible for the egg conductance.

Eggs were collected in April 1977 and May 1978 on the Farallon Islands, west of San Francisco, California. The water vapor conductance was measured by the method of Ar et al. (1974). Egg volumes were measured by water displacement, and surface area and shell thickness by the method of Paganelli et al. (1974). Initial egg mass was obtained by weighing eggs after the air cell had been displaced with water, using a hypodermic syringe. In order to learn the number of pores the shells were boiled in 2.5% NaOH to remove protein fibers, then briefly etched in concentrated nitric acid. After drying, an aqueous solution of methylene blue was applied to the inner surface of the shell to render the pores more visible (Tyler 1953). Each egg was examined under a compound microscope and twenty fields (0.25 cm²) were counted and averaged.

TABLE 1. Physical dimensions of Cassin's Auklet eggs and shells.

	Egg						Shell			
	Mass g	Vol. cm ³	Density g · cm ⁻³	Area cm ²	Length cm	Width cm	Mass g	Thick- ness mm	Vol. cm ³	Density g · cm ⁻³
\bar{x}	29.74	27.87	1.067	45.7	4.69	3.39	1.88	0.23	1.05	1.79
S.E.	0.6	0.6	.001	0.6	.03	.03	.08	0.01	—	—
n	14	14	14	14	14	14	8	8	8	8
Schönwetter (1963)	n = 80	28.0			4.67	3.37	1.88	0.22		
Manuwal (1974a)	n = 75	27.4			4.62	3.35				

TABLE 3. Observed values and those predicted as a function of egg mass (Prediction I) and as a function of egg mass and incubation time (Prediction II). See text.

	Conductance mg·day ⁻¹ ·torr ⁻¹	Water loss mg·day ⁻¹	Number of pores
Observed	4.08	101	3,295
Prediction I	6.08	186	6,020
Prediction II	4.01	118	—

The total effective pore area was calculated from the conductance and shell thickness values as previously described (Rahn et al. 1976); by dividing this value by the number of pores in each egg, we calculated the mean radius of the average pore. To establish the rate of incubation water loss three eggs were weighed on two occasions, 12, 11, and 9 days apart.

Table 1 gives the physical characteristics of the eggs and shells and compares some of these with values reported by Schönwetter (1963) and Manuwal (1974a). Table 2 provides the data for conductance and pore geometry. The water loss for the three eggs was 105, 107, and 90 mg·day⁻¹ and averaged 101 mg·day⁻¹.

As shown in Table 3, the values predicted as a function of egg mass (Prediction I) for the conductance (Ar and Rahn 1978), the daily water loss (Drent 1970), and pore number per egg (Tullett and Board 1977) are all significantly higher than the measured values. The values predicted as a function of the mass/incubation time ratio (Prediction II; Ar and Rahn 1978) agree well with those observed, supporting the general concept that incubation time is an important determinant of the functional characteristics of avian eggs.

Since the conductance, according to Fick's law of diffusion, is proportional to total pore area (number of pores times the individual pore area) and inversely proportional to the pore length or shell thickness, it is not surprising that the number of pores in Cassin's Auklet eggs is less than their predicted number since their shell thickness is the same as that predicted for eggs of their size (Ar et al. 1974). The product of daily water loss and incubation time predicts the total water loss during incubation, which for Cassin's Auklet is 13% of the initial egg mass and compares well with the average loss of 16% (Drent 1975) and 15% (Ar and Rahn, unpubl. data) established for more than 65 species.

In summary, structural and functional aspects of eggs of Cassin's Auklet are reduced commensurate with their 50% longer incubation period when compared with eggs of the same mass but more typical incubation times.

We thank the California Department of Fish and Game, the U.S. Fish and Wildlife Service, and the Farallon National Wildlife Refuge for their cooperation during this study, and the Farallon Patrol of the San

Francisco Bay Chapter of the Oceanic Society for logistic support. This is Contribution Number 197 of the Point Reyes Bird Observatory. This study was supported by University of California, Davis, Agricultural Experiment Station Project H-2990 and by National Science Foundation Grant PCM 76-20947.

LITERATURE CITED

- AR, A., C. V. PAGANELLI, R. B. REEVES, D. C. GREENE, AND H. RAHN. 1974. The avian egg: water vapor conductance, shell thickness and functional pore area. *Condor* 76:153-158.
- AR, A., AND H. RAHN. 1978. Interdependence of gas conductance, incubation length and weight of the avian egg, p. 227-236. *In* J. Piiper [Ed.], *Respiratory function in birds, adult, and embryonic*. Springer, Berlin-New York.
- DRENT, R. H. 1970. Functional aspects of incubation in the herring gull. *Behaviour*, Suppl. 17:1-132.
- DRENT, R. H. 1975. Incubation, p. 334-420. *In* D. S. Farner and J. R. King [Eds.], *Avian biology*. Vol. 5. Academic Press, New York.
- MANUWAL, D. A. 1974a. The natural history of Cassin's Auklet (*Ptychoramphus aleuticus*). *Condor* 76:421-431.
- MANUWAL, D. A. 1974b. The incubation patches of Cassin's Auklet. *Condor* 76:481-484.
- PAGANELLI, C. V., A. OLSZOWKA, AND A. AR. 1974. The avian egg: surface area, volume and density. *Condor* 76:319-325.
- RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. *Condor* 76:147-152.
- RAHN, H., C. V. PAGANELLI, AND A. AR. 1974. The avian egg: air-cell gas tension, metabolism and incubation time. *Respir. Physiol.* 22:297-309.
- RAHN, H., C. V. PAGANELLI, AND A. AR. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.
- RAHN, H., C. V. PAGANELLI, I. C. T. NISBET, AND G. C. WHITTOW. 1976. Regulation of incubation water loss in seven species of terns. *Physiol. Zool.* 49:245-259.
- SCHÖNWETTER, M. 1963. *Handbuch der Oologie*, Lief. 8, p. 471. W. Meise [Ed.]. Akademie, Berlin.
- SEALY, S. G. 1975. Egg size of murrelets. *Condor* 77:500-501.
- TULLETT, S. G., AND R. G. BOARD. 1977. Determinants of avian eggshell porosity. *J. Zool. (Lond.)* 183:203-211.
- TYLER, C. 1953. Studies on egg shells. II. A method for marking and counting pores. *J. Sci. Food Agric.* 4:266-272.

Departments of Avian Sciences and Animal Physiology, University of California, Davis, California 95616. Address of third author: Department of Physiology, State University of New York at Buffalo, Buffalo, New York 14214. Accepted for publication 9 August 1979.