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EGG SIZE, EGGSHELL POROSITY, AND INCUBATION PERIOD IN THE MARINE BIRD FAMILY ALCIDAE

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ABSTRACT.—Although the ultimate factors that influence the duration of avian incubation periods are well known, we know much less about the proximate mechanisms by which birds adjust incubation period in response to selection. We tested the hypothesis that an adjustment in eggshell porosity is one such proximate mechanism (i.e., that avian species with higher ratios of incubation period to egg size lay eggs with less porous shells). Eggshell porosity affects the rate of gaseous exchange between the developing embryo and the external environment; thus, to the extent that embryonic metabolism is diffusion-limited, eggshell porosity could directly determine incubation period. To test that hypothesis, we collected eggs from seven species of Alcidae, a family of marine birds that exhibits an unusual degree of interspecific variation in incubation period, and measured egg mass and eggshell porosity (determined by the number and size of pores and the thickness of the shell). Incubation periods were obtained from the literature. Egg mass and eggshell porosity combined explained 87% of the variation in incubation period among the seven species, which included at least one member of each of the six main alcid lineages. As predicted, eggshell porosity and incubation period were negatively related, after controlling for egg mass. Our results are consistent with the hypothesis that evolutionary changes in avian incubation period may be attributed, at least in part, to adjustments in eggshell porosity. *Received 21 December 2004, accepted 14 March 2006.*

Key words: Alcidae, egg mass, eggshell porosity, evolution, incubation period.

Taille de l'Œuf, Porosité de la Coquille et Période d'Incubation chez les Oiseaux Marins de la Famille des Alcides

RÉSUMÉ.—Les facteurs fondamentaux qui influencent la durée de la période d'incubation chez les oiseaux sont bien connus. En revanche, nous connaissons peu les mécanismes immédiats par lesquels les oiseaux ajustent leur période d'incubation en réponse à la sélection naturelle. Nous avons testé l'hypothèse qu'un ajustement de la porosité de la coquille soit l'un de ces mécanismes immédiats (i.e. les espèces aviaires dont les rapports de la période d'incubation sur la taille de l'œuf sont élevés pondent des œufs avec des coquilles moins poreuses). La porosité de la coquille affecte le taux d'échanges gazeux entre l'embryon en développement et l'environnement extérieur; ainsi, dans la mesure où le métabolisme embryonnaire est limité par la diffusion, la porosité de la coquille peut directement déterminer la période d'incubation. Pour tester cette hypothèse, nous avons récolté des œufs de sept espèces d'alcidés, une famille d'oiseaux marins qui présente un degré inhabituel de variation interspécifique de la période d'incubation, de la masse des œufs mesurée et de la porosité de la coquille (déterminée par le nombre et la taille des pores et l'épaisseur de la coquille).

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Les périodes d'incubation ont été obtenues à partir de la littérature. La combinaison de la masse des œufs et de la porosité de la coquille expliquait 87% de la variation de la période d'incubation parmi les sept espèces, incluant au moins un membre de chacune des six principales lignées d'alcidés. Comme prévu, après avoir tenu compte de la masse des œufs, la porosité de la coquille et la période d'incubation étaient négativement reliées. Nos résultats soutiennent l'hypothèse que les changements évolutifs de la période d'incubation chez les oiseaux peuvent être attribués, du moins en partie, aux ajustements de la porosité de la coquille.

INCUBATION PERIODS VARY widely among avian species (Rahn and Ar 1974). This is true even for species that lay eggs of similar size, though egg size and incubation period are strongly, positively correlated in comparisons among species (Carey et al. 1980). That relationship appears to be largely evolutionary, in that egg size has little, if any, effect on incubation period within species (Martin and Arnold 1991). About 80% of the Class-wide variation in incubation period resides at the taxonomic levels of Order and family-within-order (Ricklefs and Starck 1998, Bennett and Owens 2002). Thus, this key life-history trait is evolutionarily conservative in birds. That is not surprising, given that embryonic development is a tightly constrained process (Starck 1998) and that egg size is equally conservative (Ricklefs and Starck 1998, Bennett and Owens 2002). Nonetheless, the existence of so much interspecific variation in incubation period, even among eggs of similar size, indicates that this trait can and does respond strongly to natural selection. The role of ecological factors, particularly food supply, predation risk, and disease, in driving evolutionary divergence in incubation periods has been well studied, though their relative importance remains poorly resolved (Conway and Martin 2000, Martin 2002, Lloyd and Martin 2003, Møller 2005). However, few studies have considered what proximate mechanisms birds might use to adjust incubation period in response to selection (Tieleman et al. 2004).

Here, we test a simple hypothesis: that an adjustment in eggshell porosity is one such proximate mechanism (i.e., that species with higher ratios of incubation period to egg size lay eggs with less porous shells). The rate at which metabolic gases—water vapor, oxygen, and carbon dioxide—are exchanged between the external environment and the developing embryo is determined by the porosity of the shell and the partial pressure gradients of each

of the gases across the shell (Paganelli 1980, Vleck and Bucher 1998). Thus, to the extent that embryonic metabolism is a diffusion-limited process (Burton and Tullett 1983), eggshell porosity could directly determine the incubation period (Massaro and Davis 2005).

To test this hypothesis, we collected eggs from seven species of Alcidae, a family of marine birds that exhibits an unusual degree of interspecific variation in incubation period, and measured egg mass and eggshell porosity. Porosity is determined by the number and size of pores in the shell and its thickness (Ar et al. 1974). Among avian families, the alcids are noteworthy for the extent of interspecific variation in their incubation periods and for the apparent lack of relationship between egg size and incubation period (Barrett et al. 1995). Those features of alcid biology not only indicate the strength of selection on incubation period in the family, they also raise the possibility that coevolved proximate factors may be especially apparent.

METHODS

Egg collections.—We obtained eggs from seven species of Alcidae that breed in British Columbia: Common Murre (*Uria aalge*; $n = 6$ eggs); Pigeon Guillemot (*Cepphus columba*; $n = 7$), Ancient Murrelet (*Synthliboramphus antiquus*; $n = 1$), Marbled Murrelet (*Brachyramphus marmoratus*; $n = 2$), Cassin's Auklet (*Ptycoramphus aleuticus*; $n = 12$), Rhinoceros Auklet (*Cerorhinca monocerata*; $n = 11$), and Tufted Puffin (*Fratercula cirrhata*; $n = 9$). Those seven species include at least one member of each of the six "distinct lineages" of the alcids (Friesen et al. 1996); only one lineage is replicated (Rhinoceros Auklet and Tufted Puffin, of the Fraterculini). Most eggs were collected on Triangle Island, British Columbia, within 48 h of laying and immediately frozen. Exceptions were the Ancient Murrelet egg, which was abandoned without

having been incubated, at East Limestone Island, British Columbia; and the Marbled Murrelet eggs, one of which was laid in the hand of a researcher by a bird captured at sea in Desolation Sound, British Columbia.

Laboratory methods.—To obtain whole eggshells, we lightly etched around the midline of the shells of the frozen whole eggs with a saw blade, placed the eggs in lukewarm water, removed the shells, and air-dried them.

Methods used to measure eggshell porosity followed Tyler (1965). The shells were boiled in a 2.5% solution of sodium hydroxide to remove the inner membrane, then placed into distilled water for 4–5 min and allowed to air dry. Using micrometer calipers, we took four measurements (± 0.01 mm) of shell thickness, excluding the inner membrane, at each of the following locations: the egg's equator, its pointed end, and its blunt end. Each shell was then lightly scratched in concentrated nitric acid for a few seconds to remove any remaining organic compounds and placed into distilled water for 1–2 min, then air dried. An aqueous solution of aniline blue was applied to the inner surface of the shell to make the pores more visible.

The stained shell fragments were placed under a microscope. We then used a paper mat that left an area of 0.25 cm² of shell surface uncovered and counted the number of pores in 30 fields. Ten fields were located near the equator, 10 toward the pointed end, and 10 toward the blunt end. Each count was multiplied by 4 to estimate the number of pores per square centimeter of shell surface, and these 30 values were averaged for each egg. Then, using an objective scale of known value, we measured the diameter of 30 individual pores on the inside surface of the shell (at 160 \times magnification) and 10 on the outside (100 \times). Again, these values were averaged for each egg. The pores were smaller on the inner surface than on the outer surface; thus, inner pore size should offer the greater resistance to diffusion. Therefore, we used inner pore measurements in subsequent calculations (Tullett and Board 1977). Neither the number nor the size of pores differed in any systematic manner between the equator and poles of the eggs.

Calculating eggshell porosity.—Eggshell porosity is defined as Ap/L , where Ap is the total functional pore area (calculated as total number of pores per egg \times mean area of individual pores on the egg; in square centimeters) and L is the pore

length or shell thickness (in centimeters; Ar et al. 1974, Tullett and Board 1977). This assumes that the pores are linear. As in most other avian species (Tullett and Board 1977), the pores in alcid eggs appeared to be straight and funnel-shaped; there were no obvious differences among the seven species. To estimate the number of pores for each egg we used the formula

$$\text{pores egg}^{-1} = \text{mean pores cm}^{-2} \times \text{mean surface area (cm}^2\text{)}$$

For each species, the mean surface area of an average-sized egg was estimated using the mean length and mean breadth of a larger sample of eggs. The values used in these calculations derived from eggs measured at Triangle Island (for most species) and East Limestone Island or nearby Reef Island (for Ancient Murrelet; Birkhead and Gaston 1988, J. M. Hipfner unpubl. data). However, for Marbled Murrelet, we used values from Nelson (1997) because we had so few eggs of that species. We used the formula

$$\text{mean shell surface area (cm}^2\text{)} = (4.393 + 0.394l/b)(0.51lb^2)$$

where l = egg length (cm) and b = maximum egg breadth (cm). We used this formula, as recommended by Smart (1991), because it takes some account of interspecific differences in egg shape (particularly elongation). Those differences are marked in the Alcidae.

To determine the area of the average pore on each egg, we converted our measurements of mean pore diameter (in micrometers) to mean pore radius (in micrometers) by dividing by 2. We assumed that pores were perfectly round, and determined mean pore area (in square centimeters) using the formula

$$\text{mean pore area (cm}^2\text{)} = \pi \times \text{mean pore radius } (\mu\text{m})^2 / 10,000^2$$

Because shell thickness (L) was both maximal and least variable at the equator, we used these measurements to calculate porosity (Ap/L).

Finally, to assess, in a general way, how porous alcid eggs are in relation to their mass, we calculated predicted values using the formula for birds in general (Ar et al. 1974):

$$\text{predicted porosity } Ap/L = 0.18 \times \text{egg mass}^{0.78}$$

RESULTS

All three eggshell features that we measured—pore density, pore radius, and shell thickness—showed marked interspecific variation (Table 1). Given our values for egg mass (Table 2), there was a marginally significant negative relationship between pore density and egg mass ($r^2 = 0.40$, $P > 0.05$), whereas both pore size ($r^2 = 0.75$) and shell thickness ($r^2 = 0.77$) increased significantly with egg mass (both $P < 0.01$). Total number of pores was positively but nonsignificantly related to egg mass ($r^2 = 0.21$, $P > 0.2$).

Our seven study species produced eggs that were between 7% and 70% less porous than predicted for their mass (Ar et al. 1974; Table 3). Eggshell porosity increased with egg mass ($r^2 = 0.63$, $P < 0.05$), whereas incubation period showed little relationship with mass ($r^2 = 0.11$, $P > 0.4$), which is consistent with previous reports for the Alcidae (Barrett et al. 1995). However, when we examined the combined effects of eggshell porosity and egg mass on incubation period in a multiple linear regression,

these variables explained 87% of the variation in incubation period ($F = 13.58$, $df = 2$ and 4 , $P = 0.016$); both eggshell porosity ($t = -4.95$, slope = -52.7 ± 10.66 ; mean \pm SE) and egg mass ($t = 5.06$, slope = 0.32 ± 0.06) contributed significantly (both $P < 0.01$), despite being strongly intercorrelated. Therefore, as predicted, among our seven study species at least, alcids that have longer incubation periods lay eggs with less porous shells, after controlling for egg size effects (Fig. 1).

DISCUSSION

Egg mass and eggshell porosity combined explained most (87%) of the variation in incubation period among the seven species of Alcidae in our study. As in other birds, incubation period tends to increase with egg size in the alcids, but that relationship is otherwise masked (Barrett et al. 1995) by interspecific differences in eggshell porosity. In addition, incubation period is longer in alcid species that lay eggs with less porous shells, after controlling for egg size. That result is consistent with the hypothesis that evolutionary responses to

TABLE 1. Eggshell characteristics in seven species of Alcidae (means \pm SD).

Species	<i>n</i>	Pores (cm ⁻²)	Inner pore radius (μ m)	Shell thickness (<i>L</i> , in cm)
Common Murre	6	36.2 \pm 3.8	15.8 \pm 3.7	0.054 \pm 0.0005
Pigeon Guillemot	7	66.4 \pm 13.3	8.9 \pm 1.6	0.029 \pm 0.0004
Marbled Murrelet	2	78.0 \pm 5.9	6.2 \pm 2.0	0.021 ^a
Ancient Murrelet	1	49.0	5.8	0.027 ^b
Cassin's Auklet	12	49.0 \pm 10.1	4.6 \pm 0.9	0.020 \pm 0.0001
Rhinoceros Auklet	11	43.4 \pm 12.4	7.0 \pm 1.1	0.028 \pm 0.0002
Tufted Puffin	8	44.7 \pm 6.3	9.0 \pm 3.0	0.032 \pm 0.0003

^aNelson 1997.^bGaston 1994.TABLE 2. Egg size measurements in seven species of Alcidae (means \pm SD).

Species	<i>n</i>	Length (cm)	Breadth (cm)	Fresh mass (g)
Common Murre	15	8.55 \pm 0.35	5.05 \pm 0.12	111.8 \pm 8.0
Pigeon Guillemot	7	6.11 \pm 0.14	4.07 \pm 0.11	57.0 \pm 2.3
Marbled Murrelet ^a	11	5.98 \pm 0.22	3.76 \pm 0.14	38.5
Ancient Murrelet	25	5.93 \pm 0.19	3.75 \pm 0.10	44.8 \pm 3.2
Cassin's Auklet ^b	30	4.69 \pm 0.20	3.39 \pm 0.10	29.2 \pm 2.6
Rhinoceros Auklet ^b	30	6.91 \pm 0.22	4.60 \pm 0.10	79.2 \pm 4.2
Tufted Puffin	20	7.10 \pm 0.23	4.90 \pm 0.10	90.0 \pm 4.4

^aNelson 1997.^bHipfner et al. 2004.

TABLE 3. Measurements used to calculate porosity,^a and published values for incubation period.

Species	Surface area of egg (cm ²)	Pores per egg	Mean pore area (μm ²)	Functional pore area (<i>Ap</i>) (×10 ⁵ μm ²)	Porosity (<i>Ap/L</i>)	Predicted porosity	Incubation period (days)
Common Murre	116.9	4,235	783.9	33.198	0.615	0.713	33
Pigeon Guillemot	69.1	4,588	248.7	11.410	0.393	0.422	28
Marbled Murrelet	61.7	4,766	120.7	5.753	0.274	0.310	29
Ancient Murrelet	61.1	2,994	105.6	3.162	0.117	0.349	34
Cassin's Auklet	44.9	2,200	66.4	1.461	0.073	0.250	38
Rhinoceros Auklet	88.3	3,832	153.9	5.897	0.211	0.545	45
Tufted Puffin	97.5	4,358	254.3	11.082	0.346	0.602	44

^aSee text for all formulae.

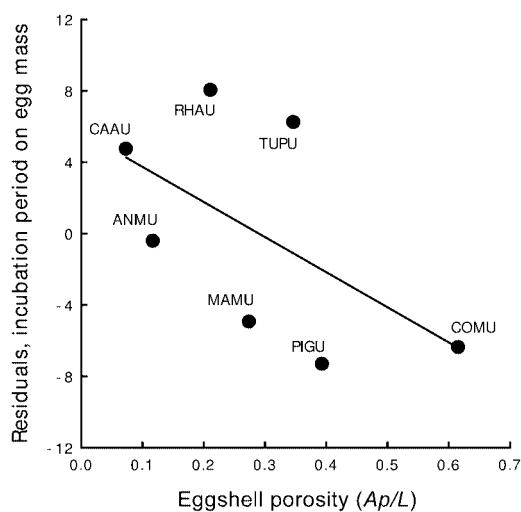


FIG. 1. Relationship between eggshell porosity (*Ap/L*) and the residuals from the regression of incubation period on egg mass in seven species of Alcidae. Species codes: CAAU = Cassin's Auklet, RHAU = Rhinoceros Auklet, TUPU = Tufted Puffin, ANMU = Ancient Murrelet, COMU = Common Murre, MAMU = Marbled Murrelet, and PIGU = Pigeon Guillemot.

selection on avian incubation periods may be achieved, at least in part, through concurrent evolutionary adjustments in eggshell porosity. We expect that any evolved change in eggshell porosity would require concurrent changes in embryonic physiology (presumably the main target of selection).

Evolutionary changes in eggshell porosity could potentially involve pore number, pore size or geometry, and shell thickness. However,

because the shell serves other functions, including conferring structural strength to the egg (Rahn and Paganelli 1989), its porosity would have to evolve in conjunction with interrelated factors (egg size, shell strength). That necessity could influence the nature and type of mechanisms involved. Across birds in general, pore size and the total number of pores increase with egg mass, whereas pore density decreases (Tullett and Board 1977). Shell thickness also increases with egg mass (Rahn and Paganelli 1989). Our seven study species of Alcidae exhibited all four of these trends, though not all were statistically significant. Carey et al. (1989b) found that differences in conductance among various *Anas* spp. were mainly related to differences in pore number. By contrast, differences in porosity in our study could be attributed most strongly to pore density (as in Pigeon Guillemots and Marbled Murrelets), pore size (as in Common Murres, and perhaps Pigeon Guillemots), and shell thickness (as in Common Murres).

Interestingly, several intraspecific studies in which eggshell porosity was experimentally manipulated found that incubation period was unaffected (Tazawa et al. 1971, Carey 1986). Those negative results may be attributable to shell porosity varying widely among individual eggs (Bucher and Barnhart 1984) and the fact that individual embryos can tolerate a wide range of conditions (Carey 1986). By contrast, observational studies of populations breeding under different environmental regimes indicate that eggshell conductance (Sotherland et al. 1980, Carey et al. 1989b) and embryonic metabolism (Carey et al. 1982, 1989a) vary predictably across environmental gradients. Moreover, Massaro and Davis (2005) measured eggshell

porosity and incubation period directly in the A- and B-eggs of Snares Penguins (*Eudyptes robustus*) and found that the more porous B-eggs had shorter incubation periods, despite being larger. Our study complements those intraspecific studies by indicating that eggshell porosity may also be an important mechanism facilitating evolutionary divergence in incubation period.

Our hypothesis rests on the assumption that embryonic development is a diffusion-limited process. But it may not be, and changes in incubation period could instead be achieved through changes in the time at which tissues mature (i.e., hatchling precocity), with little influence of eggshell porosity. However, that is hard to reconcile with studies on single species showing that porosity and incubation period are related (Massaro and Davis 2005). Moreover, Duncan and Gaston (1988) found that hatchling water content was equally low in two alcid species in which offspring leave the nest site long before they are capable of an independent existence (Thick-billed Murre [*U. lomvia*] and Ancient Murrelet). Water content was higher in three species in which offspring remain in the nest until they are capable of living independently (Pigeon Guillemot, Cassin's Auklet, Rhinoceros Auklet). The two species with lower hatchling water content differ quite markedly in relative incubation period, which suggests that precocity is not the primary determinant of incubation period (Ricklefs and Starck 1998). At the same time, assuming that eggshell porosity is similar in Thick-billed and Common murres, the difference in incubation period between Thick-billed Murres and Ancient Murrelets is well described by porosity (Fig. 1).

Proximate traits other than eggshell porosity very likely also play a role in producing responses to selection on avian incubation period. One that merits particular attention is variation in yolk hormone concentrations. Within some avian species, yolk testosterone increases the rate of prenatal development (Groothuis et al. 2005), and Gorman and Williams (2005) detected a negative relationship between yolk testosterone concentration and duration of incubation period in a comparative study of passerine birds. At present, we know very little about the role of yolk hormones in alcid eggs.

Another possibility is that interspecific variation in incubation constancy produces variation

in incubation period (Conway and Martin 2000, Martin 2002; but see Tieleman et al. 2004). Among the alcids, murres almost never neglect their eggs, because of the high risk of losing them to accidents or predators, but all other species involved in our study leave their eggs unattended for short periods (Gaston and Jones 1998). However, normal amounts of egg neglect result in extensions in incubation period on a scale of days (Sealy 1984, Gaston and Powell 1989, Astheimer 1991), whereas incubation periods across the entire family vary on a scale of weeks. Moreover, even in species in which egg neglect occurs frequently, most individuals neglect only rarely, or not at all (Astheimer 1991). Therefore, we suggest that egg neglect is probably not an important mechanism involved in the evolution of incubation period in the Alcidae.

Physical characteristics of nest sites could directly influence incubation periods (Birchard et al. 1984). However, there is no obvious pattern to be found in Figure 1 among species that nest in enclosed sites (Cassin's and Rhinoceros auklets, Tufted Puffin, Ancient Murrelet, Pigeon Guillemot) and open sites (Common Murre and Marbled Murrelet). As for temperature, incubation period varies little with latitude in the widely distributed Common Murre (Ainley et al. 2002), and that species' incubation period (33 days) is identical to that of its Arctic congener, the Thick-billed Murre (Hipfner et al. 2001). By contrast, behavioral, morphological, and physiological traits that influence internal egg temperature—such as the extent of brood patch vascularization or incubation posture—could be important (Webb 1987). Atlantic Puffins (*F. arctica*) have long incubation periods, and adult puffins incubate at lower body temperatures than Common Murres and Pigeon Guillemots, both of which have brief incubation periods (Barrett et al. 1995). Like yolk hormones, regulation of incubation temperature deserves attention as a proximate mechanism that may facilitate responses to selection on incubation period.

In recent years, interest in avian incubation periods among evolutionary ecologists has sharply increased (Bennett and Owens 2002, Martin 2002, Lloyd and Martin 2003, Tieleman et al. 2004, Møller 2005); this may lead to renewed interest in the associated proximate mechanisms (Conway and Martin 2000, Massaro and Davis

2005). The results of the present study on seven species of Alcidae point to eggshell porosity as one potentially important mechanism involved in evolutionary responses to selection on incubation period. It remains to be determined whether the relationship is more widespread in birds.

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LITERATURE CITED

- AINLEY, D. G., D. N. NETTLESHIP, H. R. CARTER, AND A. E. STOREY. 2002. Common Murre (*Uria aalge*). In *The Birds of North America*, no. 666 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- 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.
- ASTHEIMER, L. B. 1991. Embryo metabolism and egg neglect in Cassin's Auklet. *Condor* 93: 486–495.
- BARRETT, R. T., G. W. GABRIELSEN, AND P. FAUCHALD. 1995. Prolonged incubation in the Atlantic Puffin *Fratercula arctica* and evidence of mild hypothermia as an energy-saving mechanism. Pages 479–488 in *Ecology of Fjords and Coastal Waters* (H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas, Eds.). Elsevier Science, Amsterdam.
- BENNETT, P. M., AND I. P. F. OWENS. 2002. *Evolutionary Ecology of Birds: Life History, Mating System and Extinction*. Oxford University Press, London.
- BIRCHARD, G. F., D. L. KILGORE, JR., AND D. F. BOGGS. 1984. Respiratory gas concentrations and temperatures within the burrows of three species of burrow-nesting birds. *Wilson Bulletin* 96:451–456.
- BIRKHEAD, T. R., AND A. J. GASTON. 1988. The composition of Ancient Murrelet eggs. *Condor* 90:965–966.
- BUCHER, T. L., AND M. C. BARNHART. 1984. Varied egg gas conductance, air cell gas tensions and development in *Agapornis roseicollis*. *Respirational Physiology* 55:277–289.
- BURTON, F. G., AND S. G. TULLETT. 1983. A comparison of the effects of eggshell porosity on the respiration and growth of domestic fowl, duck and turkey embryos. *Comparative Biochemistry and Physiology A* 75:167–174.
- CAREY, C. 1986. Tolerance of variation in eggshell conductance, water loss, and water content by Red-winged Blackbird embryos. *Physiological Zoology* 59:109–122.
- CAREY, C., F. LEON-VELARDE, O. DUNIN-BORKOWSKIT, T. L. BUCHER, G. DE LA TORRE, D. ESPINOZA, AND C. MONGE. 1989a. Variation in eggshell characteristics and gas exchange of montane and lowland coot eggs. *Journal of Comparative Physiology B* 59:389–400.
- CAREY, C., F. LEON-VELARDE, O. DUNIN-BORKOWSKIT, AND C. MONGE. 1989b. Shell conductance, daily water loss, and water content of Puna Teal eggs. *Physiological Zoology* 62:83–95.
- CAREY, C., H. RAHN, AND P. PARISI. 1980. Calories, water, lipid and yolk in avian eggs. *Condor* 82:335–343.
- CAREY, C., E. L. THOMPSON, C. M. VLECK, AND F. C. JAMES. 1982. Avian reproduction over an altitudinal gradient: Incubation period, hatchling mass, and embryonic oxygen consumption. *Auk* 99:710–718.
- CONWAY, C. J., AND T. E. MARTIN. 2000. Evolution of passerine incubation behavior: Influence of food, temperature, and nest predation. *Evolution* 54:670–685.
- DUNCAN, D. C., AND A. J. GASTON. 1988. The relationship between precocity and body composition in some neonate alcids. *Condor* 90:718–721.
- FRIESEN, V. L., A. J. BAKER, AND J. F. PIATT. 1996. Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Molecular Biology and Evolution* 13:359–367.
- GASTON, A. J. 1994. Ancient Murrelet (*Synthliboramphus antiquus*). In *The Birds of North America*, no. 132 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences,

- Philadelphia, and American Ornithologists' Union, Washington, D.C.
- GASTON, A. J., AND I. L. JONES. 1998. *The Auks*. Oxford University Press, London.
- GASTON, A. J., AND D. W. POWELL. 1989. Natural incubation, egg neglect, and hatchability in the Ancient Murrelet. *Auk* 106:433–438.
- GORMAN, K. B., AND T. D. WILLIAMS. 2005. Correlated evolution of maternally derived yolk testosterone and early developmental traits in passerine birds. *Biology Letters* 1: 461–464.
- GROOTHUIS, T. G. G., W. MULLER, N. VON ENGELHARDT, C. CARERE, AND C. EISING. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience and Biobehavioural Reviews* 29:329–352.
- HIPFNER, J. M., K. CHARLETON, AND W. E. DAVIES. 2004. Rates and consequences of relaying in Cassin's Auklets *Ptychoramphus aleuticus* and Rhinoceros Auklets *Cerorhinca monocerata* breeding in a seasonal environment. *Journal of Avian Biology* 35:224–236.
- HIPFNER, J. M., A. J. GASTON, D. L. MARTIN, AND I. L. JONES. 2001. Seasonal declines in incubation periods of Brünnich's Guillemots *Uria lomvia*: Testing proximate causes. *Ibis* 143:92–98.
- LLOYD, J. D., AND T. E. MARTIN. 2003. Sibling competition and the evolution of prenatal development rates. *Proceedings of the Royal Society of London, Series B* 270:735–740.
- MARTIN, P. A., AND T. W. ARNOLD. 1991. Relationships among fresh mass, incubation time, and water loss in Japanese quail eggs. *Condor* 93:28–37.
- MARTIN, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London, Series B* 269:309–316.
- MASSARO, M., AND L. S. DAVIS. 2005. Differences in egg size, shell thickness, pore density, pore diameter and water vapour conductance between first and second eggs of Snares Penguins *Eudyptes robustus* and their influence on hatching asynchrony. *Ibis* 147: 251–259.
- MØLLER, A. P. 2005. Parasites, predators and the duration of developmental periods. *Oikos* 111: 291–301.
- NELSON, K. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). In *The Birds of North America*, no. 276 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- PAGANELLI, C. V. 1980. The physics of gas exchange across the avian eggshell. *American Zoologist* 20:329–338.
- RAHN, H., AND A. AR. 1974. The avian egg: Incubation time and water loss. *Condor* 76: 147–152.
- RAHN, H., AND C. V. PAGANELLI. 1989. Shell mass, thickness and density of avian eggs derived from the tables of Schonwetter. *Journal für Ornithologie* 130:59–68.
- RICKLEFS, R. E., AND J. M. STARCK. 1998. Embryonic growth and development. Pages 31–58 in *Avian Growth and Development: Evolution within the Altricial–Precocial Spectrum* (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.
- SEALY, S. G. 1984. Interruptions extend incubation by Ancient Murrelets, Crested Auklets, and Least Auklets. *Murrelet* 65:53–56.
- SMART, I. H. M. 1991. Egg-shape in birds. Pages 101–116 in *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles* (D. C. Deeming and M. W. J. Ferguson, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- SOTHERLAND, P. R., G. C. PACKARD, T. L. TAIGEN, AND T. J. BOARDMAN. 1980. An altitudinal cline in conductance of Cliff Swallow (*Petrochelidon pyrrhonota*) eggs to water vapor. *Auk* 97: 177–185.
- STARCK, J. M. 1998. Structural variants and invariants in avian embryonic and postnatal development. Pages 59–88 in *Avian Growth and Development: Evolution within the Altricial–Precocial Spectrum* (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.
- TAZAWA, H., T. MIKAMI, AND C. YOSHIMOTO. 1971. Effect of reducing the shell area on the respiratory properties of chicken embryonic blood. *Respirational Physiology* 13:352–360.
- TIELEMAN, B. I., J. B. WILLIAMS, AND R. E. RICKLEFS. 2004. Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds. *Functional Ecology* 18:571–577.
- TULLETT, S. G., AND R. G. BOARD. 1977. Determinants of avian eggshell porosity. *Journal of Zoology (London)* 183:203–211.

- TYLER, C. 1965. A study of the egg shells of the Sphenisciformes. *Journal of Zoology* (London) 147:1–19.
- VLECK, C. M., AND T. L. BUCHER. 1998. Energy metabolism, gas exchange, and ventilation. Pages 89–116 *in* *Avian Growth and Development: Evolution within the Altricial–Precocial Spectrum* (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.
- WEBB, D. R. 1987. Thermal tolerance of avian embryos: A review. *Condor* 89:874–898.

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