



Published in final edited form as:

Can J Zool. 2015 June ; 93(6): 421–425. doi:10.1139/cjz-2014-0279.

Eggshell porosity covaries with egg size among female House Wrens (*Troglodytes aedon*) but is unrelated to incubation onset and egg-laying order within clutches

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Abstract

In birds, the duration of egg incubation (the time from incubation onset to hatching) can affect multiple components of nest success, but what affects incubation duration? Previous studies suggest that incubation duration is affected by both parental behavior and components of the egg, which have yet to be determined. One egg component that may be related to incubation behavior and the time until hatching is eggshell porosity, which affects the exchange of metabolic gasses and water vapor across the shell and, thus, the speed of embryonic development and incubation duration. We tested whether eggshell porosity was associated with the timing of incubation onset by female House Wrens (*Troglodytes aedon* Vieillot, 1809), and whether porosity varied within clutches in a manner that might be associated with incubation periods and hatching patterns (i.e., synchronous vs. asynchronous hatching). Eggshell porosity was unrelated to the onset of maternal

incubation and did not differ between early and later-laid eggs within clutches, but differed significantly among females and covaried with egg size. We conclude that producing all eggshells of similar porosity within clutches, while adjusting incubation onset once most or all eggs are laid, provide facultative maternal control over variation in hatching patterns.

Keywords

incubation behavior; eggshell porosity; onset of incubation; hatching asynchrony; egg; House Wren; *Troglodytes aedon*

Introduction

In altricial birds, the eggs within a clutch often hatch asynchronously over several days, causing offspring to differ considerably in size shortly after hatching, with last-hatched nestlings usually half the size of their older siblings (e.g., Clotfelter et al. 2000; Maddox and Weatherhead 2008; Johnson et al. 2009). This initial hierarchy is typically maintained throughout the time offspring are in the nest, and often results in the death of the younger, smaller nestlings (Slagsvold 1986; Mock and Parker 1997; Lago et al. 2000; Johnson et al. 2003, 2009; Maddox and Weatherhead 2008). Synchronous hatching of eggs also occurs in a wide variety of avian taxa (Clark and Wilson 1981; Slagsvold and Lifjeld 1989; Hébert and Sealy 1992; Stoleson and Beissinger 1995; Hébert 2002) and occurs when all eggs hatch over a short period of time, typically within a day, which results in nestlings being similar in size throughout their time in the nest (Bowers et al. 2011).

Considerable variation in hatching synchrony has been documented both within and among species (Lack 1954, 1966; Clark and Wilson 1981; Magrath 1990; Stoleson and Beissinger 1995), but the factors that contribute to this variation are not fully understood. Generally, asynchronous hatching occurs when full, diurnal incubation begins before the laying of the penultimate egg of the clutch, staggering embryonic development across the egg-laying sequence, whereas synchronous hatching occurs when incubation commences with the penultimate egg or upon clutch completion, causing development to begin at a similar time for all offspring in the clutch (Clark and Wilson 1981; Wiebe et al. 1998; Badyaev et al. 2003; Ardia et al. 2006; Kontiainen et al. 2010; Arnold 2011; Johnson et al. 2013). However, Wang and Beissinger (2009) found that variation in hatching spans was unrelated to the onset of incubation in five passerine species, despite considerable variation in the onset of incubation relative to clutch completion. Moreover, within clutches, the incubation periods of earlier-laid eggs were actually longer than those of later-laid eggs (Wang and Beissinger 2009; see also Viñuela 1997; Hadfield et al. 2013), suggesting that mechanisms other than differences in the onset of incubation may contribute to variation in incubation periods, including properties of the eggs themselves. However, the properties of the egg that influence incubation periods have yet to be determined (see also Robinson et al. 2008). Ricklefs and Smeraski (1983) cross-fostered eggs among nests of the European Starling (*Sturnus vulgaris*) shortly after laying, and found that the length of the incubation period depended on the incubation behavior of the foster parents, and also on the nest from which the eggs originated. They found that differences in incubation periods were associated with

variation in the composition of eggs laid by both the original and foster mothers, as revealed by both nest-of-origin and nest-of-rearing effects, leading them to suggest that the formation of eggs may be correlated with maternal incubation behavior (see also Stein and Badyaev 2011).

As avian eggshells contain microscopic pores, shell porosity is one component of the egg that may be related to incubation behavior and incubation periods. Eggshell porosity (i.e., the total pore area of the eggshell divided by eggshell thickness) directly affects the exchange of metabolic gasses and water vapor across the shell, which regulates the rate of embryonic development and incubation duration (Ar et al. 1974; Ar and Rahn 1985; Vleck and Bucher 1998; Zimmermann and Hipfner 2007). Indeed, blocking all eggshell pores with light oils has often been used to manage pest species as gas exchange ceases and embryos asphyxiate (Blokpoel and Hamilton 1989; Hindman et al. 2014). Variation in eggshell porosity has also been reported to be associated with egg size and the time elapsed between laying and hatching within clutches; eggs within clutches that exhibited similar porosity hatched more synchronously than eggs within clutches that differed more widely in porosity (Massaro and Davis 2005). Therefore, natural variation in eggshell porosity could contribute to differences in developmental rates and hatching times among siblings within nests, generating variation in hatching synchrony (Massaro and Davis 2005; Boonstra et al. 2010; Clark et al. 2010). In some species, for example, clutches that hatch synchronously exhibit increasing eggshell porosity from earlier- to later-laid eggs within the clutch (Massaro and Davis 2005; Clark et al. 2010). Such a pattern would facilitate enhanced exchange of gas and water vapor across the eggshell in later-laid eggs, thereby allowing them to “catch up,” in terms of embryonic development, to their siblings in earlier-laid eggs.

In this study, we investigated within- and among-clutch variation in eggshell porosity in a population of House Wrens (*Troglodytes aedon* Vieillot, 1809) in which both synchronous and asynchronous hatching of eggs occurs (Harper et al. 1992, 1994; Ellis et al. 2001a,b; Bowers et al. 2011, 2013). Only females incubate eggs, and, as in other species (see above), asynchronous hatching occurs when females begin diurnal incubation prior to laying the penultimate egg of the clutch, whereas synchronous hatching occurs when incubation commences with the penultimate egg or upon clutch completion (Johnson 2014). If variation in eggshell porosity is associated with incubation period (i.e., the time until hatching), then clutches hatching synchronously may exhibit increased eggshell porosity from earlier- to later-laid eggs within the clutch (Massaro and Davis 2005; Clark et al. 2010). Alternatively, clutches that hatch asynchronously may exhibit lower porosity among later-laid eggs, which would constrain embryos in later-laid eggs from catching up developmentally with those in earlier-laid eggs and facilitate hatching across multiple days. Here, we test the hypothesis that eggshell porosity is associated with the female's onset of diurnal incubation by relating when females began fully incubating their eggs with the porosity of the eggshells these females produced. This hypothesis predicts that if eggshell porosity is associated with maternal incubation behavior, then females commencing diurnal incubation at different times relative to clutch completion may exhibit differences in eggshell porosity among their eggs. We also test for an interaction between onset of incubation and egg-laying order, while controlling for variation in egg size, which would be predicted if porosity within clutches

changes across the laying sequence differently for females that initiate incubation at different times relative to clutch completion.

Materials and Methods

Study area and species

We studied a population of House Wrens breeding in secondary deciduous forest in north-central Illinois, USA (40.665°N, 88.89°W) in 2012 and 2013. Nestboxes ($N = 820$) were mounted on 1.5-m poles spaced 30 m apart along north-south transects separated by 60 m, and all nestboxes were protected, to an extent, from ground-dwelling predators (e.g., mammals and snakes) by 48.3-cm diameter aluminum predator baffles mounted on the poles below the nestboxes. Lambrechts et al. (2010) provide further details on nestbox size and construction materials.

House wrens are small (10–12 g), cavity-nesting songbirds with breeding grounds distributed across the mid-latitudes of North America, and birds in the study population winter in the southern United States and northern Mexico (Johnson 2014). In spring, females select a mate that is defending a nest site and eventually lay a clutch of 4–8 eggs (Dobbs et al. 2006), producing one egg per day until their clutch is completed. Clutch size does not differ, on average, between clutches that hatch synchronously or asynchronously (Ellis et al. 2001a; Bowers et al. 2011). Incubation periods generally last 12.5 d. Only females incubate eggs and brood young nestlings, but both parents provision nestlings after hatching. The length of the nestling period is typically 14–17 days (Bowers et al. 2013). The oldest, largest nestlings usually leave the nest first, with the rest of the brood following within a few hours, although some nestlings, typically small, underdeveloped runts, occasionally remain in the nest and die of starvation (Johnson 2014).

Field procedures and measuring porosity

We checked nestboxes at least twice weekly during the 2012 and 2013 breeding seasons for evidence of female settlement and, after nest-building was completed, we visited nests daily between 0600 and 1100 hr Central Daylight Time and collected eggs on the day each was laid. We replaced the fresh eggs with artificial eggs, which females readily accepted. We documented the onset of “full,” diurnal incubation by females (Kendeigh 1952; Johnson 2014) as determined by eggs being noticeably warm to the touch on the morning that we visited nests to collect the eggs. Thus, we have no information on partial heat applied nocturnally to eggs prior to the onset of diurnal incubation (e.g., Kendeigh 1952, 1963; Wang and Beissinger 2009); nonetheless, the onset of incubation as we assessed it here is predictive of whether eggs eventually hatch synchronously or asynchronously (Johnson 2014).

In the laboratory, we weighed each egg on an electronic balance (± 0.001 g; Acculab Pocket Pro 2060D), and measured egg length and breadth using a digital thickness gauge (± 0.01 mm; Mitutoyo 700–121) prior to weighing egg yolks (± 0.0001 g; Mettler Toledo AE163) and storing eggshells for porosity measures. To test for differences in porosity between earlier- and later-laid eggshells within clutches, we compared the porosity of the eggshells

of the first-laid, second-laid, penultimate, and ultimate eggs from each of 28 clutches (14 clutches from 2012 and 14 from 2013). We estimated eggshell porosity following the methods described in Jaeckle et al. (2012), although a novel method has recently been developed using casts that allow for the visualization of three-dimensional pore morphology (Murphy et al. 2015). Estimates of shell porosity and gas conductance across the eggshell have not been compared using these two methods in House Wrens, so we utilized the earlier, more traditional methods used by Jaeckle et al. (2012). Eggshells were first broken into fragments and submerged in boiling 5% NaOH for 12 min to remove any persisting shell membrane and cuticle. After boiling in NaOH, the fragments were rinsed with water and then air-dried prior to viewing with a compound microscope (Nikon E-600). The outer surface of each eggshell fragment ($N = 2,232$ fragments from 112 eggs) was examined and photographed with a digital camera (Nikon MT-5B). Surface area of the fragments was calculated using ImageJ (version 1.46r; average fragment size = 6.65 mm^2). For each egg, we examined at least 80 mm^2 (mean \pm SD = $120.3 \pm 43.5 \text{ mm}^2$) of the eggshell, constituting an average of 19.9% of the eggshell surface. One observer (AW) counted and measured the diameters of each pore within an eggshell fragment ($\times 400$ magnification) using an ocular micrometer ($\pm 2 \mu\text{m}$). Pores were primarily circular in shape, so we calculated pore area as the area of a circle for analysis. We then estimated the total pore area (mm^2) per egg, using estimates of total eggshell surface area and egg volume following Paganelli et al. (1974) and Hoyt (1979), respectively. Eggshell thickness ($\pm 0.01 \text{ mm}$) was estimated as the average of nine randomly selected fragments from each eggshell using a base-mounted thickness gauge (Starrett 2600-1), and we calculated eggshell porosity as the total pore area per egg \times eggshell thickness⁻¹ (Ar et al. 1974). There was no association between eggshell thickness and maternal body mass or tarsus length (linear mixed model with nest identity as a random effect; body mass: $F_{1, 23} = 0.10$, $P = 0.75$; tarsus length: $F_{1, 23} = 0.23$, $P = 0.63$). For 32 eggs (8 clutches), we compared porosity from the basal, equatorial, and apical regions of each eggshell using a total of 345 fragments, and we found no differences in porosity among these regions ($F_{2, 31} = 0.35$, $P = 0.71$). Thus, for the remaining clutches, we sampled eggshell fragments randomly within eggs, and we used a single mean value of porosity for each egg in our statistical analyses.

All research subjects were cared for in accordance with current ethical standards, and all activities complied with current laws of the United States of America, and were in accordance with the Illinois State University Institutional Animal Care and Use Committee, United States Geological Survey, and United States Fish and Wildlife Service (see Acknowledgements).

Data analysis

We obtained porosity measures for early-laid eggs (28 first- and 28 second-laid eggs within the laying sequence) and late-laid eggs (28 penultimate and 28 last-laid eggs within the laying sequence) from 28 clutches. Prior to analysis, we converted data to z-scores to obtain standardized parameter estimates from our analyses following Schielzeth (2010), which provides greater utility for parameter estimates as a measure of effect size. We first characterized among-female variation in eggshell porosity using an analysis of variance (ANOVA) with eggshell porosity as the dependent variable, egg volume and female tarsus

length (as a measure of female skeletal size) as main effects, and maternal identity as a random effect. We then analyzed within-clutch variation in eggshell porosity by testing whether this trait differed between early and late-laid eggs within clutches, and also between clutches for which females differed in the onset of incubation (early vs. late) relative to clutch completion. We did this using a linear mixed model with relative egg-laying order (egg number divided by the clutch size, where egg number is the sequence in which eggs were laid) and maternal onset of incubation as fixed effects and nest identity as a random effect. We also included relative egg size, i.e. the difference between the volume of a given egg and the clutch mean (Krist and Remeš 2004), as a covariate. We used SAS (version 9.3) for all analyses, tests were two-tailed ($\alpha = 0.05$), and the data satisfied assumptions of normality and homogenous variance.

Results

We detected substantial, greater than five-fold, variation in eggshell porosity among clutches (Fig. 1). There was a significant, positive correlation among females in both eggshell porosity and egg size (Table 1a, Fig. 1), and a marginally non-significant trend for large females to produce less porous eggshells than smaller females (Table 1a). Egg size was also positively correlated with the amount of maternally derived yolk deposited in the egg (i.e., wet yolk mass; $r_{98} = 0.536$, $P < 0.001$). Despite the high degree of among-female variation in porosity, variation among eggs within clutches was minimal and there was no association between eggshell porosity and the egg's position within the laying sequence (Table 1b). There was also no difference in the porosity of eggs laid by females initiating incubation at different times relative to clutch completion, nor was eggshell porosity related to differences in egg size within clutches (Table 1b). Removal of the non-significant interaction from the model in Table 1b revealed similarly non-significant main effects for relative laying order, incubation onset, and relative egg size (all $P > 0.5$).

Discussion

If eggshell porosity were associated with the incubation behavior of females, then females commencing full incubation at different times relative to clutch completion should have exhibited differences in the porosity of the eggs they produced. However, we did not observe this, nor did we detect a correlation between eggshell porosity and egg-laying order within clutches. Thus, differences in hatching spans among nests (i.e., synchronous vs. asynchronous hatching) are unlikely to be associated with variation in eggshell porosity, and, therefore, unlikely to contribute substantially to differences in developmental rates and hatching times among siblings within nests.

Intriguingly, not all House Wren populations exhibit synchronous and asynchronous hatching. For example, although asynchronous hatching is slightly less common than synchronous hatching in our study population (Harper et al. 1992, 1993; Ellis et al. 2001a; Bowers et al. 2011), all clutches hatch asynchronously in a Wyoming population and nearly all clutches hatch asynchronously in a Panamanian population (Johnson 2014). On the other hand, other Central-American populations are comprised of entirely synchronously hatching clutches (Johnson 2014). We do not yet have a complete understanding of the ecological

factors contributing to variation in brood hatching patterns, although spatial and temporal variation in food abundance, temperature, and predation risk likely play a role (Lack 1954; Hussell 1972; Slagsvold and Lifjeld 1989; Pennock 1990; Wiebe and Bortolotti 1994; Hébert 2002; Ardia et al. 2006, 2009). Given the highly variable and unpredictable nature of these biotic and abiotic factors, it is likely that selection has favored female control of brood hatching patterns primarily through adjustments to incubation behavior (see also Wiebe 1995; Wiehn et al. 2000), rather than through selection for changes in the female physiology underlying the formation of eggs (Lack 1954; Howe 1976, 1978). Although there may be properties of eggs aside from eggshell porosity that affect variation in hatching patterns, we do know that clutches of eggs hatching synchronously or asynchronously in our study population do not differ in egg mass (E.K. Bowers, personal observation), or in levels of maternally derived androgens within yolks, each of which might be expected to influence variation in incubation periods (Ellis et al. 2001b). Thus, producing all eggshells of similar porosity within clutches, while being able to adjust incubation behavior facultatively once most or all of the eggs have been produced, may facilitate female control over synchrony or asynchrony in hatching under variable conditions. What, then, generates variation in eggshell porosity among clutches? Portugal et al. (2014) recently reported a positive association between estimated rates of gas exchange and egg size across species, consistent with the positive correlation between egg size and shell porosity we detected within our study species. Given the positive association between eggshell porosity and egg size, increases in eggshell porosity with egg size may be necessary to maintain normal rates of gas exchange and embryonic development for larger eggs that have a lower surface area:volume ratio than smaller eggs. Moreover, variation in eggshell porosity may influence the thermal inertia of eggs and, therefore, an incubating parent's ability to regulate the temperature of developing embryos, independently of the effect that eggshell porosity has on gas exchange.

In conclusion, clutches of House Wrens in this population varied widely in eggshell porosity, a variable known to entail consequences for the rate of embryonic development and incubation periods. However, variation in eggshell porosity was not associated with the onset of full incubation by females, nor the order in which eggs were produced within clutches in the study population. Thus, it appears unlikely that variation in porosity is related brood hatching patterns in this population.

Acknowledgments

We thank the 2012 and 2013 Wren Crews for field assistance and the ParkLands Foundation (Merwin Preserve), the Illinois Great Rivers Conference of the United Methodist Church, and the Sears and Butler families for the use of their properties. We also thank two anonymous reviewers for helpful comments on the manuscript. All research activities complied with current laws of the United States of America, and were in accordance with the Illinois State University Institutional Animal Care and Use Committee (Protocol Nos. 05-2010, 04-2013), United States Geological Survey banding permit 09211, and United States Fish and Wildlife Service collecting permit MB692148-0. Financial support was provided by NSF grants IBN-0316580 and IOS-0718140; NIH grant R15HD076308-01; the School of Biological Sciences, Illinois State University; and student-research grants from the Animal Behavior Society, the American Museum of Natural History's Frank M. Chapman Memorial Fund, the Beta Lambda Chapter of the Phi Sigma Biological Honor Society, and the Department of Biology at Illinois Wesleyan University.

References

- Ar A, Rahn H. Pores in avian eggshells: gas conductance, gas exchange and embryonic growth rate. *Respir Physiol.* 1985; 61:1–20.10.1016/0034-5687(85)90024-6 [PubMed: 4035113]
- Ar A, Paganelli CV, Reeves RR, Greene DG, Rahn H. The avian egg: water vapor conductance, shell thickness, and functional pore area. *Condor.* 1974; 76:153–158.10.2307/1366725
- Ardia DR, Cooper CB, Dhondt AA. Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of their range. *J Avian Biol.* 2006; 37:137–142.10.1111/j.0908-8857.2006.03747.x
- Ardia DR, Pérez JH, Chad EK, Voss MA, Clotfelter ED. Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. *J Anim Ecol.* 2009; 78:4–13.10.1111/j.1365-2656.2008.01453.x [PubMed: 18637971]
- Arnold TW. Onset of incubation and patterns of hatching in the American Coot. *Condor.* 2011; 113:107–118.10.1525/cond.2011.100001
- Badyaev AV, Beck ML, Hill GE, Whittingham LA. The evolution of sexual size dimorphism in the house finch. V Maternal effects Evolution. 2003; 57:384–396.10.1111/j.0014-3820.2003.tb00272.x
- Blokpoel H, Hamilton RMG. Effects of applying white mineral oil to chicken and gull eggs. *Wildlife Soc B.* 1989; 17:435–441.
- Boonstra TA, Clark ME, Reed WL. Position in the sequence of laying, embryonic metabolic rate, and consequences for hatching synchrony and offspring survival in Canada Geese. *Condor.* 2010; 112:304–313.10.1525/cond.2010.090043
- Bowers EK, Sakaluk SK, Thompson CF. Adaptive sex allocation in relation to hatching synchrony and offspring quality in house wrens. *Am Nat.* 2011; 177:617–629.10.1086/659630 [PubMed: 21508608]
- Bowers EK, Sakaluk SK, Thompson CF. Sibling cooperation influences the age of nest-leaving in an altricial bird. *Am Nat.* 2013; 181:775–786.10.1086/670244 [PubMed: 23669540]
- Clark AB, Wilson DS. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. *Q Rev Biol.* 1981; 56:253–277.10.1086/412316
- Clark ME, Boonstra TA, Reed WL, Gastecki ML. Intraclutch variation in egg conductance facilitates hatching synchrony of Canada Geese. *Condor.* 2010; 112:447–454.10.1525/cond.2010.100004
- Clotfelter ED, Whittingham LA, Dunn PO. Laying order, hatching asynchrony and nestling body mass in Tree Swallows *Tachycineta bicolor*. *J Avian Biol.* 2000; 31:329–334.10.1034/j.1600-048X.2000.310308.x
- Dobbs RC, Styrsky JD, Thompson CF. Clutch size and the costs of incubation in the house wren. *Behav Ecol.* 2006; 17:849–856.10.1093/beheco/arl019
- Ellis LA, Styrsky JD, Dobbs RC, Thompson CF. Female condition: a predictor of hatching synchrony in the House Wren? *Condor.* 2001a; 103:587–591.10.1650/0010-5422(2001)103[0587:FCAPH]2.0.CO;2
- Ellis LA, Borst DW, Thompson CF. Hatching asynchrony and maternal androgens in egg yolks of House Wrens. *J Avian Biol.* 2001b; 32:26–30.10.1034/j.1600-048X.2001.320104.x
- Hadfield JD, Heap EA, Bayer F, Mittell EA, Crouch NMA. Intraclutch differences in egg characteristics mitigate the consequences of age-related hierarchies in a wild passerine. *Evolution.* 2013; 67:2688–2700.10.1111/evo.12143 [PubMed: 24033176]
- Harper RG, Juliano SA, Thompson CF. Hatching asynchrony in the house wren: a test of the brood reduction hypothesis. *Behav Ecol.* 1992; 3:76–83.10.1093/beheco/3.1.76
- Harper RG, Juliano SA, Thompson CF. Avian hatching asynchrony: brood classification based on discriminant function analysis of nestling masses. *Ecology.* 1993; 74:1191–1196.10.2307/1940489
- Harper RG, Juliano SA, Thompson CF. Intrapopulation variation in hatching synchrony in House Wrens: test of the individual optimization hypothesis. *Auk.* 1994; 111:516–524.
- Hébert, PN. Ecological factors affecting initiation of incubation behaviour. In: Deeming, DC., editor. *Avian incubation: behaviour, environment, and evolution.* Oxford University Press; NY, USA: 2002. p. 270-279.

- Hébert PN, Sealy SG. Onset of incubation in Yellow Warblers: a test of the hormonal hypothesis. *Auk*. 1992; 109:249–255.10.2307/4088193
- Hindman LJ, Harvey WF IV, Conley LE. Spraying corn oil on mute swan *Cygnus olor* eggs to prevent hatching. *Wildfowl*. 2014; 64:186–196.
- Howe HF. Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. *Ecology*. 1976; 57:1195–1207.10.2307/1935044
- Howe HF. Initial investment, clutch size, and brood reduction in the common grackle (*Quiscalus quiscula* L.). *Ecology*. 1978; 59:1109–1122.10.2307/1938226
- Hoyt DF. Practical methods of estimating volume and fresh weight of bird eggs. *Auk*. 1979; 96:73–77.
- Hussell DJT. Factors affecting clutch size of arctic passerines. *Ecol Monogr*. 1972; 42:317–364.10.2307/1942213
- Jaekle WB, Kiefer M, Childs B, Harper RG, Rivers JW, Peer BD. Comparison of eggshell porosity and estimated gas flux between the brown-headed cowbird and two common hosts. *J Avian Biol*. 2012; 43:486–490.10.1111/j.1600-048X.2012.05705.x
- Johnson, LS. House Wren (*Troglodytes aedon*). 2. Poole, A., editor. Cornell Lab of Ornithology and American Ornithologists' Union; Ithaca, NY, USA: 2014. The birds of North America online
- Johnson LS, Wimmers LE, Campbell S, Hamilton L. Growth rate, size, and sex ratio of last-laid, last-hatched offspring in the tree swallow *Tachycineta bicolor*. *J Avian Biol*. 2003; 34:35–43.10.1034/j.1600-048X.2003.02950.x
- Johnson LS, Brubaker JL, Johnson BGP, Masters BS. Evidence for a maternal effect benefiting extra-pair offspring in a songbird, the house wren *Troglodytes aedon*. *J Avian Biol*. 2009; 40:248–253.10.1111/j.1600-048X.2009.04777.x
- Johnson LS, Napolillo FM, Kozlovsky DY, Hebert RM, Allen A. Variation in incubation effort during egg laying in the Mountain Bluebird and its association with hatching asynchrony. *J Field Ornithol*. 2013; 84:242–254.10.1111/jof.12023
- Kendeigh SC. Parental care and its evolution in birds. *Illinois Biol Monogr*. 1952; 18:1–356.10.5962/bhl.title.50337
- Kendeigh SC. New ways of measuring the incubation period of birds. *Auk*. 1963; 80:453–461.10.2307/4082850
- Krist M, Remeš V. Maternal effects and offspring performance: in search of the best method. *Oikos*. 2004; 106:422–426.10.1111/j.0030-1299.2004.13373.x
- Kontiaainen P, Pietiäinen H, Karell P, Pihlaja T, Brommer JE. Hatching asynchrony is an individual property of female Ural owls which improves nestling survival. *Behav Ecol*. 2010; 21:722–729.10.1093/beheco/arq045
- Lack, D. The natural regulation of animal numbers. Clarendon Press; Oxford, UK: 1954.
- Lack, D. Population studies of birds. Clarendon Press; Oxford, UK: 1966.
- Lago K, Johnson LS, Albrecht DJ. Growth of late-hatched, competitively disadvantaged nestling house wrens relative to their older, larger nestmates. *J Field Ornithol*. 2000; 71:676–685.10.1648/0273-8570-71.4.676
- Lambrechts MM, Adriaensen F, Ardia DR, Artemyev AV, Atiénzar F, Ba bura J, Barba E, Bouvier J-C, Camprodon J, Cooper CB, Dawson RD, et al. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. *Acta Ornithol*. 2010; 45:1–26.10.3161/000164510X516047
- Maddox JD, Weatherhead PJ. Egg size variation in birds with asynchronous hatching: is bigger really better? *Am Nat*. 2008; 171:358–365.10.1086/527500 [PubMed: 18217858]
- Magrath RD. Hatching asynchrony in altricial birds. *Biol Rev Camb Philos Soc*. 1990; 65:587–622.10.1111/j.1469-185X.1990.tb01239.x
- Massaro M, Davis LS. 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*. 2005; 147:251–258.10.1111/j.1474-919x.2005.00379.x
- Mock, DW.; Parker, GA. The evolution of sibling rivalry. Oxford University Press; Oxford, UK: 1997.

- Murphy JP, Swanson MT, Jaeckle WB, Harper RG. Corrosion casts: a novel application of a polyurethane resin (PU4ii) for visualizing eggshell pore morphology. *Auk: Ornithol Adv.* 2015; 132:206–211.10.1642/AUK-14-158.1
- Paganelli CV, Olszowka A, Ar A. The avian egg: surface area, volume, and density. *Condor.* 1974; 76:319–325.10.2307/1366345
- Pennock, DS. MSc thesis. Department of Zoology, Brigham Young University; Provo, UT, USA: 1990. Seasonal distribution of hatching asynchrony and brood reduction in house wrens.
- Portugal SJ, Hauber ME, Maurer G, Stokke BG, Grim T, Cassey P. Rapid development of brood-parasitic cuckoo embryos cannot be explained by increased gas exchange through the eggshell. *J Zool (Lond).* 2014; 293:219–226.10.1111/jzo.12144
- Ricklefs RE, Smeraski CA. Variation in incubation period within a population of the European Starling. *Auk.* 1983; 100:926–931.
- Robinson WD, Styrsky JD, Payne BJ, Harper RG, Thompson CF. Why are incubation periods longer in the tropics? A common-garden experiment with house wrens reveals it is all in the egg. *Am Nat.* 2008; 171:532–535.10.1086/528964 [PubMed: 18254684]
- Schielzeth H. Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol.* 2010; 1:103–113.10.1111/j.2041-210X.2010.00012.x
- Slagsvold T. Asynchronous versus synchronous hatching in birds: experiments with the pied flycatcher. *J Anim Ecol.* 1986; 55:1115–1134.10.2307/4437
- Slagsvold T, Lifjeld JT. Constraints on hatching asynchrony and egg size in pied flycatchers. *J Anim Ecol.* 1989; 58:837–849.10.2307/5127
- Stein LR, Badyaev AV. Evolution of eggshell structure during rapid range expansion in a passerine bird. *Funct Ecol.* 2011; 25:1215–1222.10.1111/j.1365-2435.2011.01887.x
- Stoleson SH, Beissinger SR. Hatching asynchrony and the onset of incubation in birds, revisited. *Curr Ornithol.* 1995; 12:191–270.10.1007/978-1-4615-1835-8_6
- Vleck, CM.; Bucher, TL. Energy metabolism, gas exchange, and ventilation. In: Stark, JM.; Ricklefs, RE., editors. *Avian growth and development: evolution within the altricial-precocial spectrum.* Oxford University Press; Oxford, UK: 1998. p. 89-116.
- Wang JM, Beissinger SR. Variation in the onset of incubation and its influence on avian hatching success and asynchrony. *Anim Behav.* 2009; 78:601–613.10.1016/j.anbehav.2009.05.022
- Wiebe KL. Intraspecific variation in hatching asynchrony: should birds manipulate hatching patterns according to food supply? *Oikos.* 1995; 74:453–462.10.2307/3545990
- Wiebe KL, Bortolotti GR. Food supply and hatching spans of birds: energy constraints or facultative manipulation? *Ecology.* 1994; 75:813–823.10.2307/1941737
- Wiebe KL, Wiehn J, Korpimäki E. The onset of incubation in birds: can females control hatching patterns? *Anim Behav.* 1998; 55:1043–1052.10.1006/anbe.1997.0660 [PubMed: 9632488]
- Wiehn J, Ilmonen P, Korpimäki E, Pakkala M, Wiebe KL. Hatching asynchrony in the Eurasian kestrel *Falco tinnunculus*: an experimental test of the brood reduction hypothesis. *J Anim Ecol.* 2000; 69:85–95.10.1046/j.1365-2656.2000.00374.x
- Viñuela J. Laying order affects incubation duration in the black kite (*Milvus migrans*): counteracting hatching asynchrony? *Auk.* 1997; 114:192–199.10.2307/4089160
- Zimmermann K, Hipfner JM. Egg size, eggshell porosity, and incubation period in the marine bird family Alcidae. *Auk.* 2007; 124:307–315.10.1642/0004-8038(2007)124[307:ESEPAI]2.0.CO;2

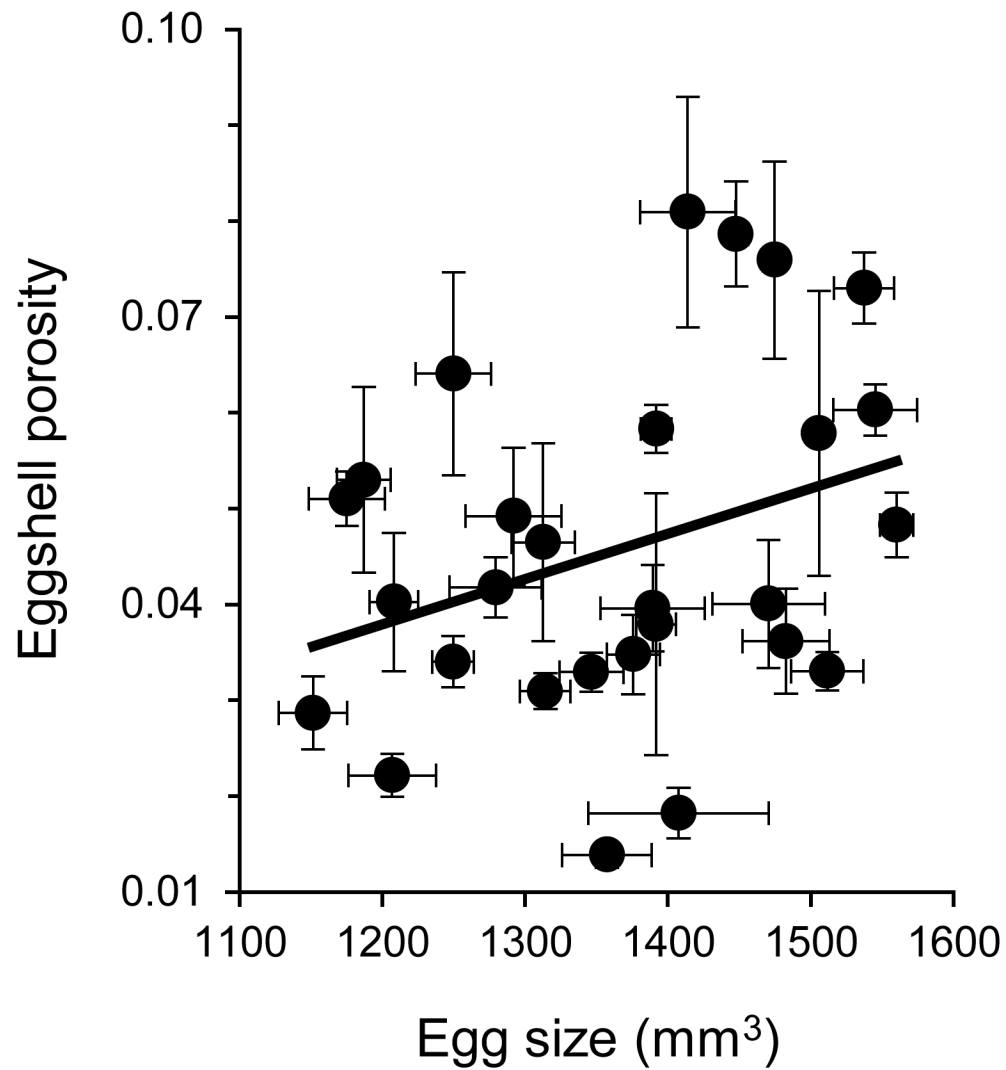


Fig. 1. Among-female variation in eggshell porosity (pore area [mm²] \times eggshell thickness [mm]⁻¹) and egg size in the House Wren (*Troglodytes aedon*). Plotted are bivariate means \pm SE for each clutch ($N = 4$ eggs from each).

Table 1

Results of analyses testing for among- and within-clutch variation in eggshell porosity.

(a) Among-clutch variation.				
	Estimate ± SE	F	df	P
Egg size	0.348 ± 0.162	4.63	1, 23	0.042
Female tarsus length	−0.291 ± 0.168	3.00	1, 23	0.097
Intercept	−0.003 ± 0.165			
(b) Within-clutch variation.				
	Estimate ± SE	F	df	P
Relative laying order	0.206 ± 0.306	0.09	1, 82.2	0.766
Incubation onset (early vs. late)	0.538 ± 0.388	1.92	1, 51.5	0.172
Rel. laying order × Incub. Onset	−0.561 ± 0.367	2.34	1, 81.1	0.130
Relative egg size	0.024 ± 0.080	0.09	1, 83.4	0.766
Intercept	−0.219 ± 0.286			

Note: For incubation onset, females commencing incubation prior to laying the penultimate egg had slightly, but not significantly, increased porosity estimates relative to those that commenced incubation upon laying the penultimate or ultimate egg.