Natural History Note

Why Are Incubation Periods Longer in the Tropics? A Common-Garden Experiment with House Wrens Reveals It Is All in the Egg

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ABSTRACT: Incubation periods of Neotropical birds are often longer than those of related species at temperate latitudes. We conducted a common-garden experiment to test the hypothesis that longer tropical incubation periods result from longer embryo development times rather than from different patterns of parental incubation behavior. House wrens, one of few species whose geographic range includes tropical equatorial and temperate high latitudes, have incubation periods averaging 1.2 days longer at tropical latitudes. We incubated eggs of house wrens in Illinois and Panama under identical conditions in mechanical incubators. Even after factoring out differences in egg size, tropical house wrens still required 1.33 days longer, on average, to hatch. We conclude that parental attendance patterns do not account for latitudinal differences in incubation period but that some other as yet unmeasured factor intrinsic to the egg or embryo, or both, extends development time in the tropics.

Keywords: avian incubation period, life-history evolution, maternal effects, Panama, house wren, *Troglodytes aedon*.

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Tropical birds have incubation periods that average about 10% longer than those of their temperate relatives (Ricklefs 1969*b*). These longer tropical incubation periods are surprising because time-dependent mortality of eggs tends to be higher in tropical settings (Ricklefs 1969*a*; Robinson et al. 2000), which should select for faster rather than slower development (Ricklefs 1993; Bosque and Bosque 1995). A potential explanation for extended incubation periods is that tropical parents reduce nest attendance to decrease activities that might attract the attention of predators (Skutch 1949; Martin 2002). Reduced parental attendance could lower egg temperatures and extend incubation (Drent 1975; Boersma 1982; Martin 2002). Alternatively, eggs of tropical birds may simply require longer incubation periods to complete embryonic development. One way to determine whether eggs of tropical birds do, in fact, require a longer amount of time to incubate is to control for possible differences in parental nest attendance by removing eggs from nests as they are produced and artificially incubating them under identical environmental conditions.

We tested the hypothesis that incubation periods of tropical birds are longer than those of temperate birds because their embryos develop more slowly by conducting a common-garden experiment that exposed freshly laid house wren (*Troglodytes aedon*) eggs from Panama and Illinois to identical environmental conditions in incubators. This eliminated any potential geographic differences in parental incubation behavior. Under natural conditions, temperate house wrens have an incubation period of 12.8 ± 0.1 (SD) days in early-season clutches and 12.2 ± 0.1 days in late-season clutches (Dobbs et al. 2006), whereas tropical house wrens in Panama hatch in 14 days (Tieleman et al. 2006). By standardizing the incubation environment, we removed possible effects of parental attendance patterns and could thus compare the time required to incubate eggs to hatching.

Table 1: Results of a two-way ANCOVA for the effect of latitude, laying order, and egg size on incubation periods of house wren eggs

Source	df	Sum of squares	Mean square	*F* ratio	*P* (>*F*)
Model	3	21.931	7.310	128.74	<.0001
Error	46	2.612	.057		
Total	49	24.543			
Effect tests:					
Site	1	5.905	5.905	103.98	<.0001
Laying order	1	.013	.013	.23	.6334
Egg mass	1	.109	.109	1.92	.1729

Note: Two- and three-way interaction terms were all nonsignificant; thus, the effects of site, laying order, and egg mass from the ANCOVA with the interaction terms removed are presented here. Tropical house wren eggs had significantly longer incubation periods than temperate house wren eggs exposed to identical conditions in mechanical incubators. Laying order had no effect on incubation period, and egg mass was a nonsignificant covariate in the analysis.

Methods

House wrens occur throughout the New World from Alaska to Argentina (AOU 1998). Ornithologists have variously considered the mainland forms to be members of as few as one species to perhaps three or more (Brumfield and Capparella 1996), but currently they remain officially recognized as a single species (AOU 1998).

We studied temperate house wrens (*Troglodytes aedon aedon*) at the Mackinaw Study Area, McLean County, Illinois (41°N, 89°W), in 2001 and tropical house wrens (*Troglodytes aedon musculus*) in Gamboa, Republic of Panama (9°N, 79°W), in 2000. Nest boxes were placed in the study areas to attract wrens. Boxes were monitored every 3 days throughout the breeding seasons until nests were lined; then nests were checked every day for eggs. Eggs were collected within 1–3 h of being laid, numbered with a fine-tip permanent marker, weighed to the nearest 0.001 g on Acculab PocketPro 2060D portable electronic balances (Acculab, Edgewood, NY), and transported for immediate placement in incubators. We removed the second- and third-laid eggs from Illinois June–July clutches and the first-, second-, and third-laid eggs from Panama late April–June clutches, substituting artificial eggs to reduce the chances of nest abandonment.

Tropical eggs were placed in a Brinsea Mark III Octagon 20 incubator (Brinsea Products, Titusville, FL) and temperate eggs in a comparable Grumbach 8014 compact S84 incubator (Grumbach, Asslar, Germany). At both sites, eggs were incubated at 38°C and 85%–90% relative humidity. Temperature and humidity were measured in the incubators twice daily in both Illinois and Panama. Temperature and humidity ranged from 37.8° to 38.0°C and from 85% to 90%, respectively, in the Grumbach incubator used in Illinois. Temperature and humidity ranged from 37.9° to 38.2°C and from 85% to 90%, respectively, in the Brinsea incubator used in Panama. Field measurements of egg temperatures under natural conditions in Panama were unavailable until after our study (Tieleman et al. 2004) and indicate eggs average 35.3°C and reach maximum temperatures of 35.9°C. Relative humidity measurements in nests have not been made but average 85%–90% during the breeding season in habitats around nest boxes (W. D. Robinson, unpublished data). In temperate settings, house wren egg temperatures average 35.1°C (Tieleman et al. 2004). Humidity at the Illinois site during the summer is also high but has not been measured within nest boxes. Eggs were turned by the incubators through one-half to three-quarters of a full rotation every hour.

Beginning 11 days after the start of incubation in Illinois and 13 days after the start of incubation in Panama, we monitored eggs for signs of hatching. In Illinois, eggs were monitored by video; Panama eggs were visually checked every hour. Once hatchlings emerged, they were collected or returned to their nest for brooding, and the artificial eggs were removed. Length of incubation period was measured to the nearest 15 min (Illinois) or 30 min (Panama).

We used ANCOVA to compare incubation periods of temperate and tropical wrens because egg mass is positively correlated with incubation period (Rahn and Ar 1974) and eggs of tropical house wrens were heavier than those of temperate house wrens (table 1). Therefore, we used egg mass as a covariate when evaluating latitudinal differences in incubation periods. Because first-laid eggs were collected in addition to eggs 2 and 3 from some nests in Panama, we also included clutch position in the analysis to test for an effect of laying order. All analyses were performed with SAS software, version 9.1 (SAS 2002); we considered $\alpha \leq .05$ to be statistically significant.

Results

We measured mass and incubation period of 27 temperate and 23 tropical house wren eggs. Even when controlling for egg mass, incubation periods of tropical wrens were significantly longer than those of temperate wrens (table 1), by an average of 1.33 days (table 2). Although eggs laid by house wrens in Panama were 27.7% heavier than those laid by house wrens in Illinois ($t = -9.77$, df = 48, $P < .0001$; table 2), egg size had no effect on incubation period (table 1). Similarly, incubation periods did not increase significantly with egg size within regions (temperate: $r^2 = 0.021$, $P > .48$; tropical: $r^2 = 0.032$, $P > .42$). Laying order also had no measurable effect on incubation period (table 1).

Results are the same based on an analysis of clutch means rather than individual eggs (overall model $F = 92.54$, df = 2, 22, $P < .0001$): mean incubation time to hatch was significantly greater for tropical house wren eggs than for temperate house wren eggs ($F = 51.27$, df = 1, $P < .0001$), and mean egg mass had no effect on mean incubation time ($F = 0.38$, df = 1, $P = .54$).

Table 2: Comparison of egg size and incubation period between temperate and tropical house wren eggs reared in mechanical incubators

	Temperate	Tropical
No. clutches	17	8
No. eggs	27	23
Egg mass (g):		
Mean ± SD	1.432 ± .138	1.828 ± .148
95% CI	1.378–1.487	1.763–1.892
Minimum–maximum	1.229–1.786	1.554–2.106
Incubation (days):		
Mean ± SD	13.61 ± .24	14.94 ± .23
95% CI	13.51–13.70	14.84–15.04
Minimum–maximum	13.23–14.01	14.63–15.68

Note: Eggs of house wrens in tropical Panama were on average 0.4 g heavier than those in temperate Illinois and required on average 1.33 days more incubation time under standardized environmental conditions. CI = confidence interval.

Discussion

Incubation periods of Panama house wrens were longer than those of Illinois house wrens, but the 28% greater mass of tropical house wren eggs did not account for this difference. Similarly, laying order had no effect on incubation period, indicating that the inclusion of first-laid eggs from Panama clutches but not Illinois clutches did not bias the results. Having eliminated possible differences in parental attendance from the comparisons by standardizing incubation environments in mechanical incubators, we conclude that the eggs of tropical house wrens require a longer period of incubation than do eggs of temperate house wrens. Our experiment demonstrates for the first time that geographic differences in embryonic development time cannot be explained by differences in parental incubation behavior.

Our experiment did not accelerate development time. Even under constant application of heat and removing cooling that occurs naturally during the time parents spend off the nest, eggs in incubators took the same amount of time or slightly longer than naturally incubated eggs to hatch. Because we used only one combination of temperature and humidity conditions, we cannot eliminate the possibility that other conditions might accelerate development. Nevertheless, the lack of acceleration here suggests that natural incubation speed is as fast as it might be. Chemical processes that drive the metabolic engine building embryos may require fluctuations in temperature caused naturally by parents spending time off the nest. Such needs for temperature cycling may not allow acceleration of development time under the constant conditions of mechanical incubators. Given that cross-fostering experiments designed to partition genetic and environmental components of incubation time have revealed minor variation from genetic components (Crittenden and Bohren 1961; Ricklefs and Smeraski 1983), we hypothesize that even in tropical species, incubation periods are as short as they can be. Why then are tropical incubation periods longer than those of birds breeding at temperate latitudes?

Tropical organisms may simply take longer to grow. In addition to longer incubation and nestling periods, many tropical birds, including the house wren (see Tieleman et al. 2006), receive considerably longer periods of postfledging parental care than related temperate species (Skutch 1949; Fogden 1972; Russell et al. 2004). Such longer periods of parental investment might be required for acquisition of specialized foraging skills or increased abilities to compete successfully for limited territorial vacancies in tropical bird populations (Ashmole 1963; Kokko and Lundberg 2001). The demands of living in environments with more pests and pathogens may require more time to create highly functioning immune systems. Ricklefs (1992) found a negative correlation between developmental period and prevalence of hematozoan blood parasites in birds, suggesting that longer developmental periods allow for construction of better immune systems. Thus, several lines of evidence link slower development of tropical birds to the demands of life in tropical environments. Even if the pace of life is slower in the tropics (Ricklefs and Wikelski 2002), it may be slower because of strong selection for investment in developing high-quality individuals that can attain long life spans.

Although differences in incubation behavior may have some influence on the length of incubation periods, our results suggest that the next stage of investigation should focus primarily on differences in the morphological, physiological, and immunological components among temperate and tropical bird eggs so that we may understand why it takes longer to grow a tropical bird.

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