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BREEDING BIOLOGY OF THE SOUTHERN HOUSE WREN ON CHILOÉ ISLAND, SOUTHERN CHILE

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ABSTRACT.—We studied the breeding biology of a Southern House Wren (*Troglodytes aedon chilensis*) population using nest boxes on Chiloé Island, southern Chile (41° S) to make latitudinal comparisons at the intraspecific level. There were no significant differences in body size between adult males and females, although wings were significantly longer in males. Clutch size averaged 4.3 eggs per nest, and brood size was 3.9 nestlings. Egg size averaged 17.3 mm in length and 13.2 mm in width. Incubation and nestling periods averaged 16 days each. The Southern House Wren on Chiloé Island has a larger clutch size than in the tropics, but a smaller clutch size than populations at the same latitude in the Northern Hemisphere. The Southern House Wren has larger eggs and a longer incubation period but a similar nestling period as House Wrens in the Northern Hemisphere. Received 23 August 2011. Accepted 29 January 2012.

Studies of species with a broad distributional range are valuable to gain information on the latitudinal effects on physiology and morphology as well as behavior and life history traits. Knowledge of breeding biology is useful for testing hypotheses about effects of latitude on clutch size, parental care, and breeding phenology (Geffen and Yom-Tov 2000). However, in comparison with Northern Hemisphere species, few studies have been conducted on the breeding biology of South American species, where information about natural history of numerous species is lacking (Geffen and Yom-Tov 2000, Russell et al. 2004).

The House Wren (*Troglodytes aedon*; Troglodytidae) has a distribution from southern Canada to southern Chile, encompassing one of the largest latitudinal distributions for any native passerine species (Johnson 1998). Brumfield and Caparella (1996) recommended re-elevating the three main recognized taxonomic groups to species level: *T. aedon* (Northern House Wren), *T. brunneicollis* (Brown-throated House Wren), and *T. musculus* (Southern House Wren). The House Wren is currently considered a single species (Johnson 1998, Bird Life International 2011, Gill and Donsker 2012) and we use the common name Southern

House Wren for the subspecies *T. a. chilensis* in our study.

The Southern House Wren inhabits the austral extreme of Chile and Argentina. It is a small insectivorous bird and a secondary cavity nester (Johnson and Goodall 1967, Grigera 1982, Kroodsma and Brewer 2005). It typically inhabits scrublands and secondary or marginal forests on the island of Chiloé (41° S) (Rozzi et al. 1996, Díaz et al. 2005) and is also common in urban areas (Díaz and Armesto 2003); it is similar to populations of the Northern Hemisphere House Wren (Johnson 1998). The Southern House Wren is considered a year-round resident on Chiloé Island (Jaramillo et al. 2003), but detection during autumn and winter is difficult, suggesting partial migration (S. Ippi, unpub. data). The House Wren is an ideal species model, because of its extensive geographic range, for assessing the effects of latitude on intraspecific variation of breeding biology (e.g., Young 1994). Comparisons of life-history traits with the Northern House Wren, would be informative due to the large amount of information available about the ecology and breeding biology of the species in the Northern Hemisphere (e.g., Kendeigh 1941; Kendeigh et al. 1956; Drilling and Thompson 1988; Johnson and Searcy 1993, 1996; Johnson 1996; Johnson et al. 2001; Janota et al. 2002; Johnson et al. 2008, 2009). Several ecological and reproductive studies have recently been conducted in South America, mainly in Argentina (e.g., Tuero et al. 2007, Fasanella and Fernández 2009, Llambías and Fernández 2009, Labarbera et al. 2010, Serra and Fernández 2011). The objective of our study was to describe the breeding biology of the Southern House Wren in a southern Chilean population and to compare our

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results with studies of House Wrens from North America, Central America, and other localities in South America. We predicted smaller reproductive investments (e.g., smaller clutch size) by the Southern House Wren compared to House Wrens in the Northern Hemisphere.

METHODS

Study Area.—The study was conducted on Chiloé Island, southern Chile (41° 52' S, 73° 39' W) at 50–100 m asl in the austral spring (Oct–Jan) of 2002–2005. Chiloé Island is <10 km from the mainland and supports similar forest bird communities (Johnson and Goodall 1967, Fjeldså and Krabbe 1990). The continuous distribution of temperate rainforests as experienced by Charles Darwin in 1834–1835 have been cleared in large areas of northern Chiloé Island with remaining fragments embedded in an agricultural landscape (Willson and Armesto 1996).

Field Procedures.—Three hundred nest boxes were placed in scrublands and forest edges in Senda Darwin Biological Station (described by Carmona et al. 2010) and 50 at Fundo 'Los Cisnes' at the northern tip of the island close to mainland Chile (nest boxes are described in Moreno et al. 2005, 2007). Both study sites included large fragments of regenerating evergreen forests of *Drimys winteri*, *Nothofagus nitida*, *Weinmannia trichosperma*, several myrtaceous species, and the conifer *Podocarpus nubigena* (Veblen et al. 1996, Aravena et al. 2002). Nest boxes were suspended from tree branches or fastened to tree trunks or shrub branches 150 cm above the ground in scrublands and forest edges with some up to 100 m within the forest. The mean distance $\pm$ SD between nest boxes was 34.0 $\pm$ 25.2 m as measured with a Global Positioning System (GPS) (Garmin e-TREX; Olathe, KS, USA); the mean distance among active nests (i.e., nest boxes actually used) was 117.1 $\pm$ 79.3 m.

Nest Monitoring.—Nest boxes were checked for occupation on a weekly basis beginning in October each year. Nest boxes occupied by Southern House Wrens were frequently checked to detect laying dates (date of first egg), hatching dates (first visit when eggs were observed to hatch), and fledging dates (empty nest box). Nests were checked on a daily basis 2 weeks after laying of the last egg to record the exact date of hatching. Some nests were visited daily 10 days after hatching to record fledging date. Egg length and breadth were measured for all eggs in the clutch to the nearest 0.1 mm with a digital caliper (Model

101-7015, Z&Y Tool Supply Co. Ltd., Guangxi, China). Egg volume was estimated when clutch size was also assessed using Hoyt's (1979) equation for egg volume: volume = $0.51 \times (\text{length} \times \text{breadth}^2)$. Nests that were depredated or abandoned before incubation were excluded from clutch and egg size analyses.

Adults were captured with nest-box traps when chicks were 10–13 days of age (hatching day = day 0) and marked with metal leg bands (Model 1242–3, National Band and Tag Co., Newport, KY, USA) under the authority of Servicio Agrícola y Ganadero, Chile. We measured tarsus length and beak length to the nearest 0.1 mm using digital calipers, wing length (mm) as flattened wing chord, and tail (mm) following Svensson (1984). Adult males and females were classified using morphology as only females have a brood patch (Johnson 1998). Mass was recorded to the nearest 0.1 g with a Pesola spring balance (Baar, Switzerland). We also weighed nestlings on the day of adult trapping, and measured their tarsus, beak (from tip to skull), and wing length using the same technique as for adults.

Statistical Analyses.—We checked for normality of data and homogeneity of variance with Kolmogorov-Smirnov and Levene tests, respectively. We used non-parametric statistics when these assumptions were violated. We addressed variation in clutch size within the breeding season and among years using non-parametric correlation analysis and Kruskal-Wallis tests, respectively (Siegel and Castellan 1988). Differences in body size between males and females were evaluated using a one-way MANOVA. We conducted this analysis although not all variables were normal, but all variances were homogeneous among the groups. This analysis is considered robust to violation of the assumption of normality (Sokal and Rohlf 1995). We also conducted *a posteriori* univariate analyses, correcting the significance value with a sequential Bonferroni correction (Quinn and Keough 2002). Nested ANOVA was used to analyze clutch size and egg volume, and to investigate differences in body size of nestlings measured at 10 to 13 days of age. All analyses were conducted with STATISTICA 6.0 (StatSoft Inc. 2001) and were considered significant at $P < 0.05$. Values reported are means $\pm$ SD.

RESULTS

Breeding Phenology.—Laying dates of the Southern House Wren on Chiloé Island ranged

TABLE 1. Dates for first and last laying, hatching, and fledging of the Southern House Wren during three breeding seasons (2002–2004) on Chiloé Island, Chile.

Season	Laying date	n	Hatching date	n	Fledging date	n
2002–2003	8 Nov to 2 Jan	7	27 Nov to 1 Jan	5	13 Dec to 4 Jan	3
2003–2004	28 Oct to 3 Dec	18	24 Nov to 20 Dec	15	30 Nov to 18 Dec	3
2004–2005	19 Oct to 8 Jan	16	5 Nov to 15 Jan	16	8 Jan to 26 Jan	3

from mid October to January, while hatching dates were from November to January (Table 1). Fledging occurred from the end of November to January (Table 1). Wrens were not color banded and we have no information about polygyny in our population. One female reared a second brood in a neighboring nest box, ~60 m distant, but we have no information about the success of its first clutch. Two males and one female bred in our study site for two consecutive breeding seasons, and one male for three consecutive seasons. All bred in nest boxes that were nearby in the previous year.

Clutch and Brood Size.—Clutch size in nests with at least one hatched egg was two and five eggs with an average of 4.3 ± 0.7 eggs ($n = 59$) (Table 2). The modal clutch size was four eggs. There was no seasonal trend in clutch size within year (Spearman correlation coefficient, $r_s = 0.18$; $P = 0.24$), and there were no differences in clutch size among years (Kruskal Wallis; $H = 1.2$; $P = 0.75$; $n = 59$). The mean brood size was 3.9 ± 1.1 chicks (range = 1 to 5, $n = 27$).

Egg Size.—Southern House Wren females laid eggs measuring 17.3 ± 0.7 mm in length and 13.2 ± 0.3 mm in width ($n = 66$) in 15 nests monitored during the 2003 breeding season. Egg volume was $1,532.8 \pm 103.8$ mm³ ($n = 66$). Mean egg volume decreased with clutch size ($F_{1,50} = 20.4$, $P < 0.001$) if only four- and five-egg clutches are considered. The number of successful clutches with two and three eggs was small; they were excluded from the analysis.

Incubation and Nestling Period.—The incubation stage, the period between the last laid egg and first hatched egg, ranged between 14 and 19 days (16.0 ± 1.0 day; $n = 32$ nests). There was no seasonal trend in incubation period within year ($r_s = 0.14$; $P = 0.45$). All eggs in the clutch hatched within 1 day. The nestling period was 16.0 ± 1.0 days ($n = 5$ nests) and was 33.8 ± 1.6 days ($n = 5$) from laying to fledging.

Chick and Adult Body Size.—Chicks were measured between days 10 and 13 (11.4 ± 1.1) in 24 nests (Table 3). Significant morphological differences occurred between nestlings measured in different days (10 to 13; $F_{12,164} = 29.2$; $P < 0.001$; $n = 88$). Univariate results revealed length of wing ($F_{3,61} = 133.1$; $P < 0.001$), beak ($F_{3,61} = 41.9$; $P < 0.001$), and tarsus ($F_{3,61} = 23.2$; $P < 0.001$) differed, while mass of nestlings at 10, 11, 12, and 13 days did not ($F_{3,61} = 0.7$; $P = 0.54$). Mean tarsus length did not differ between adults and nestlings measured after 10 days of age ($F_{1,126} = 0.3$; $P = 0.61$; $n = 128$).

We measured 38 adults (21 females and 17 males) (Table 3). There were no significant differences in morphological measurements between males and females ($F_{5,30} = 2.4$, $P = 0.064$). No difference was detected in body mass ($F_{1,36} = 0.004$; $P = 0.95$), tarsus length ($F_{1,36} = 0.1$; $P = 0.78$), tail length ($F_{1,34} = 0.01$; $P = 0.92$), and beak length ($F_{1,36} = 0.04$; $P = 0.84$) between males and females. However, wing length was significantly longer for males than for females, after sequential Bonferroni correction ($F_{1,36} = 8.7$; $P = 0.006$).

DISCUSSION

Clutch Size.—The mean clutch size of the Southern House Wren in our study was comparable to that observed by Young (1994; 4.5 eggs in Nahuel Huapi National Park in Argentina vs. 4.3 at Chiloé Island) at a similar southern latitude, although the Argentina data were obtained from museum samples of natural nests. Artificial nest boxes did not appear to have a major influence on

TABLE 2. Mean $\pm$ SD clutch and brood size of the Southern House Wren during four breeding seasons (2002–2005) on Chiloé Island, Chile.

Year	Clutch $\pm$ SD	n	Brood size $\pm$ SD	n
2002–2003	4.2 ± 0.6	11	No data	No data
2003–2004	4.4 ± 0.7	21	3.9 ± 1.2	14
2004–2005	4.3 ± 0.7	19	3.9 ± 1	10
2005	4.2 ± 0.7	8	4.3 ± 0.6	3

TABLE 3. Morphological measures (mean $\pm$ SD) of adult and nestling Southern House Wrens on Chiloé Island, Chile.

	Mass (g)	Wing (mm)	Tarsus (mm)	Tail (mm)	Beak (mm)	n
Adult females	10.0 $\pm$ 0.5	50.1 $\pm$ 1.5	17.9 $\pm$ 0.9	43.7 $\pm$ 2.6	13.9 $\pm$ 1.3	21
Adult males	10.0 $\pm$ 0.5	51.5 $\pm$ 1.5	17.8 $\pm$ 0.6	43.7 $\pm$ 1.8	14.0 $\pm$ 1.1	17
Nestlings	9.8 $\pm$ 0.6	33.7 $\pm$ 4.2	17.8 $\pm$ 0.8		9.7 $\pm$ 1.1	24

clutch size, which agrees with Llambías and Fernández (2009). In contrast, Northern House Wrens have larger clutches, and more nestlings and fledglings in artificial nest boxes compared to natural tree cavities (Purcell et al. 1997).

The Southern House Wren on Chiloé Island has a smaller clutch size (mean = 4.3; range = 2–5 eggs) compared to populations at the same latitude in the Northern Hemisphere (range of reported means = 6.0–6.5 eggs/clutch; Robinson and Rotenberry 1991, Quinn and Holroyd 1992, Elliot et al. 1994, Young 1994, Johnson 1998). This is still larger than in tropical (means between 3.3 and 3.9 eggs/clutch; Freed 1987, Young 1994) and subtropical latitudes (3.5 eggs/clutch in natural tree cavities; Auer et al. 2007), although some authors have recorded as many as five eggs for tropical populations (Skutch 1953) and 4.7–5.2 eggs/clutch at 35–36° S (Mason 1985, Tuero et al. 2007, Llambías and Fernández 2009). We did not detect any seasonal decline in clutch size (Finke et al. 1987, Robinson and Rotenberry 1991, Johnson et al. 2001), in contrast to Northern House Wrens. However, we had insufficient detailed data about possible second broods. There were positive associations between latitude and clutch size for both Northern and Southern House wrens, although clutch size and the range of latitudinal variation are smaller in the Southern Hemisphere (3.3 to 5.0 eggs vs. 3.3 to 7.1 eggs in the Northern Hemisphere; Young 1994).

Egg and Nestling Size.—Mean egg size for the same clutch size is slightly larger on Chiloé Island than in the Northern Hemisphere (Kendeigh et al. 1956; Table 4). The width and length of eggs of

Southern House Wrens from Chiloé Island (13.2 and 17.3 mm, width and length, respectively) are slightly greater than those in the Northern Hemisphere (12.7 and 16.6 mm; Johnson et al. 2001, Styrsky et al. 2002), and similar to egg dimensions from Central America (13.4 and 17.8 mm; Skutch 1953), subtropical Argentina (13.4 and 17.0 mm; Auer et al. 2007), and southern Argentina (13.1 and 17.5 mm; Tuero et al. 2007).

Southern House Wren nestlings reach an asymptotic growth after 10 days of age, similar to wrens in Canada and Colombia (Zach 1982, Kattan 1996). No differences were found between mass of nestlings at 11 and 13 days in our population and mean weights were similar to those of Northern House Wrens from Manitoba, Canada (mean weights within 9.8–10 g; Zach 1982); these weights differed in comparison to House Wrens from Valle del Cauca, Colombia (mean weight within 14.5–15.5 g; Kattan 1996). However, tarsus, beak, and wing length differed between 10 and 13 days, suggesting they were still growing at this time. The adult body mass of House Wrens from Colombia recorded by Kattan (1996) is striking as House Wrens at this location have a much larger body size compared to other low latitude populations, contradictory to general predictions about increasing body size with latitude (Blackburn et al. 1999).

Incubation and Fledging Period.—The incubation period is slightly longer for Southern House Wrens on Chiloé Island (14 to 19 days; mean = 16) compared to Northern House Wrens from North America (9 to 16 days, mean = 12.6;

TABLE 4. Mean $\pm$ SD width and length of eggs of Southern House Wrens from Chiloé Island, Chile vs. Northern House Wrens from Ohio (40° N, Kendeigh et al. 1956) in nests of four and five eggs.

	Mean width (mm)		Mean length (mm)	
	Clutch size		Clutch size	
	4	5	4	5
Kendeigh et al. 1956	12.9	12.8	16.8	16.6
Present study	13.3 $\pm$ 0.3	13.1 $\pm$ 0.2	17.5 $\pm$ 0.8	17.5 $\pm$ 0.6

Johnson 1998, Johnson et al. 2001). Skutch (1953) reported a 15-day incubation period for a resident population of House Wrens in Central America, similar to resident populations at 26° S (15.8 days; Auer et al. 2007) and 35° S latitude (14.8 days; Tuero et al. 2007). Fledging at our study site occurred at a mean of 16 days of age, within the range reported for different populations of Northern House Wrens (14 to 20 days; Kendeigh 1941, Skutch 1953, Johnson 1998, Johnson et al. 2004), and slightly longer than the 14.8 days recorded for a subtropical population (Auer et al. 2007). This period is shorter than the 18–20 days described for Central American populations of House Wren (Skutch 1953, Freed 1987).

Adult Body Size.—The Southern House Wren had little differentiation in body size between males and females. However, males had longer wings than females, similar to populations in the Northern Hemisphere, although beak and tail length are also greater in males in those populations (Johnson 1998). The Southern House Wren appears to be slightly larger, particularly considering that females (F) and males (M) have longer beak length (F: M = 13.9; 14.0 mm in Chiloé vs. 11.8; 12.7 mm in Northern Hemisphere populations), tarsus (F: M = 17.8; 17.9 mm vs. 16.8; 17.5 mm), and tails (F: M = 43.7; 43.7 mm vs. 40.8; 42.1 mm) (Johnson 1998).

The Southern House Wren population on Chiloé Island has smaller clutch size, larger eggs, and a longer incubation period than populations of the Northern House Wren at similar latitudes in the Northern Hemisphere. Some hypotheses have invoked predation pressure, winter mortality, and migration to explain smaller clutch sizes in South American species (Ricklefs 1980, Martin et al. 2000, Yom-Tov and Geffen 2002, Griebeler and Bohning-Gaese 2004). Martin (2002) proposed the low rate of adult mortality in southern compared to northern passerines can explain smaller reproductive investment, such as reduced nest care, which results in a longer incubation period and smaller clutch size (see also Ghalambor and Martin 2001, and Robinson et al. 2008). Nest attentiveness during incubation is lower, the incubation period is longer, and the total period of parental care is longer for tropical and south temperate species than for their northern counterparts (Russell et al. 2004, Chalfoun and Martin 2007). In contrast, the fledging period is similar in Northern and Southern House wrens, but it is longer in Central America. The results of our

study suggest that duration of the fledging period decreases with latitude. Short nestling periods could be adaptive in high latitudes to synchronize brood rearing with maximum food availability (Lack 1947, Siikamäki 1998), improve survival rate of fledglings (Naef-Daenzer et al. 2001, Moreno et al. 2005), and/or avoid molting during breeding (Svensson and Nilsson 1997). Our study highlights the effects that latitude can have on a species' breeding biology and the large geographic variation that can occur in the breeding strategies between populations of a single species. Data on variation in reproductive traits over the entire distributional range of the species are incomplete, because the Southern House Wren inhabits regions ranging to the southern extreme of South America.

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