J Ornithol
DOI 10.1007/s10336-015-1217-2

ORIGINAL ARTICLE

Latitudinal differences in life-history traits and parental care in northern and southern temperate zone House Wrens

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Received: 1 August 2014 / Revised: 10 March 2015 / Accepted: 31 March 2015

Abstract South temperate songbirds differ from north temperate species in life-history traits, having greater adult survival, smaller clutch size, longer developmental periods and extended parental care. Due to its broad distribution, the House Wren, Troglodytes aedon, is an excellent model to evaluate selective pressures that may influence the maintenance of present clutch size. Here we report data on life-history traits and parental care of socially monogamous House Wrens from a north temperate and a south temperate population. Southern House Wrens exhibited smaller clutch sizes and longer developmental periods than Northern House Wrens; however, we did not find significant differences in adult survival probability between populations, contrary to a critical prediction of the cost of reproduction hypothesis. Our data did not support the hypothesis that smaller clutches are the consequence of greater food limitation in the south. Southern wrens have greater adult body mass but smaller territories; southern nestlings reached a greater proportion of adult body mass 6–7 days before fledgling, and provisioning rates to the nest per nestling were greater in the south. We did not find support for the hypothesis that reduced clutch size is a consequence of limited parental activity at the nest as southern wrens did not reduce parental care during the incubation and nestling stage. Our data better supports the offspring quality hypothesis; southern wrens invest more per nestling than northern wrens as provisioning rates per nestling were significantly higher and developmental periods longer in the south. Published results from Tropical House Wrens suggest that neither food limitation nor nest predation can explain reduced clutches in Central America. We suggest that south temperate and tropical wrens may differ in parental investment strategies as tropical wrens seem to invest even less per nestling than north temperate wrens.

Keywords Life-history traits · Breeding biology · Parental care · House wren

Zusammenfassung

Breitengradunterschiede in ‚Life-history traits' und elterlicher Brutpflege bei nördlichen und südlichen Hauszaunkönigen der gemäßigten Zone

Singvögel der südlich gemäßigten Zone unterschieden sich von Arten der nördlich gemäßigten Zone in den sogenannten Life-history traits, indem sie eine höhere Überlebensrate der Adulten, kleinere Gelege, längere Entwicklungsperioden und eine ausgeweitete elterliche Brutpflege haben. Aufgrund seiner weiten Verbreitung ist der Hauszaunkönig (Troglodytes aedon) ein geeigneter Modellorganismus, um den Selektionsdruck, der die Erhaltung der bestehenden Gelegegröße beeinflussen könnte, zu evaluieren. Wir präsentieren Daten zu life-history traits und elterlicher Brutpflege von sozial monogamen Hauszaunkönigen der

Communicated by C. G. Guglielmo.

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Published online: 10 April 2015

nördlich gemäßigten sowie der südlich gemäßigten Population. Südliche Hauszaunkönige haben kleinere Gelege und eine längere Entwicklungsperiode als nördliche Hauszaunkönige. Entgegen der kritischen Prognose zur Reproduktionskosten-Hypothese, fanden wir keine signifikanten Unterschiede in der Überlebenswahrscheinlichkeit der Adulten zwischen den Populationen. Unsere Daten unterstützten nicht die Hypothese, dass kleinere Gelege die Konsequenz aus einer größeren Nahrungsknappheit im Süden sind: südliche adulte Hauszaunkönige sind schwerer, aber haben kleinere Reviere. Die Küken der südlichen Hauszaunkönige erreichen einen größeren Anteil der Adulten-Körpermasse 6–7 Tage vor dem Flüggewerden und die Fütterungsraten pro Nestling waren größer im Süden. Wir konnten keine Hinweise zur Stützung der Hypothese finden, dass eine geringere Gelegegröße die Konsequenz einer begrenzten elterlichen Nestaktivität ist, da südliche Hauszaunkönige während der Bebrütung und der Kükenphase ihre elterliche Brutpflege nicht reduzieren. Deutlich besser stützen unsere Daten die Hypothese zur Qualität der Nachkommen: südliche Hauszaunkönige investieren mehr pro Küken als nördliche Hauszaunkönige, da im Süden die Fütterungsraten pro Nestling signifikant höher waren und die Entwicklung länger dauerte. Publizierte Studien über tropische Hauszaunkönige ergaben, dass weder Nahrungsbegrenzung noch Nestprädation die kleineren Gelege in Zentralamerika erklären können. Wir denken, dass sich südlich gemäßigte und tropische Zaunkönige in ihren elterlichen‘ Investment-Strategien‘unterschieden können, da es scheint, dass tropische Zaunkönige noch weniger investieren pro Küken, als die der nördlich gemäßigten Zone.

Introduction

South temperate birds differ from north temperate species in life-history traits, having greater adult survival, smaller clutch size, longer incubation and nestling periods and extended parental care of juveniles (Moreau 1944; Yom-Tov 1994; Martin 1996; Peach et al. 2001; Russell et al. 2004). Similarities in life-history traits between south temperate and tropical birds are the result of selection from similar ecological pressures (e.g., low seasonality and milder winter conditions; Cody 1966; Stutchbury and Morton 2001). Hence, current life-history theory should be able to explain differences between north temperate and tropical-south temperate species. However, differences in avian life histories between north and south temperate species have not been explored as thoroughly as between north temperate and tropical birds (but see Moreau 1944; Yom-Tov 1994; Martin 1996; Peach et al. 2001; Russell et al. 2004).

Several hypotheses have been proposed to explain the smaller clutch sizes of birds from tropical and south temperate regions. The nest predation hypothesis proposes that high predation rates constrain parental activity at the nest that may attract visual predators, favoring a reduced clutch size relative to north-temperate regions (Skutch 1949, 1985; Martin 1996; Martin et al. 2000). The food limitation hypothesis (Lack 1947; Ashmole 1963; Cody 1966) states that food limitation favors reduced clutch sizes as adults are constrained in the number of nestlings they can raise. The clutch size may not only be constrained by immediate costs, and future cost of survival and fecundity may play a crucial role. The cost of reproduction hypothesis proposes that longer lived adults should reduce clutch size, decreasing investment in present reproduction while investing in future reproduction and survival (Moreau 1944; Ashmole 1963; Williams 1966; Martin et al. 2000; Ghalambor and Martin 2001; Martin 2002). However, the offspring quality hypothesis proposed by Young (1996) assumes that resident tropical birds have similar adult mortality probability to north temperate migratory species. Young (1996) proposes that survival in resident populations is influenced mainly by territory acquisition and intraspecific competition, while migratory species are subject to extrinsic mortality, caused by unpredictable weather conditions during migration. Hence, resident birds should invest more in offspring quality, whereas migratory species should invest in quantity (Young 1996). Badyaev and Ghalambor (2001) reported that along altitudinal gradients, high-elevation species have significantly smaller clutch sizes and provide greater parental care even though adult survival does not differ between high- and low-elevation

and Kuenzler 1955; Barg et al. 2005). We defined the core of the territory as the area surrounding the nest box the male added sticks to. We defined its boundaries using song playback to stimulate aggressive behavior for 2–5 min and observing male's movements during two sessions of 15 min inside its territory and by recording male's location during nest checks. Additional information to complete the polygon was gathered by observing the male while foraging when nestlings were 2–3, 7–8 and 11–12 days old. We followed all birds during the first 5 h after sunrise. To calculate the territory area, we later connected the outermost locations (stored on GPS Garmin e Trex and Vista HCx) using the program Map Source 6.16.3 (Garmin 2010) or the track function on a GPS Garmin Vista HCx.

Breeding biology

Nest boxes were checked every 1–3 days. When possible, we checked nests close to laying, with eggs near hatching or nestlings near fledging every day to record more exact laying, hatching and fledgling day. For each nest we recorded clutch initiation date, clutch size, brood size and fledging number (number of nestlings observed at the last check of successful nests minus the number of dead nestling inside the nest box). We recorded a nest as successful if at least one fledgling was observed in the territory.

For each breeding season we calculated the proportion of females that laid a second brood as the number of females that produced a successful nesting attempt and laid a second clutch divided by the total number of females whose first nesting attempt was successful. We calculated the annual productivity for each female as the total number of fledglings produced from successful nests per season. This measurement provides an estimation of the mean number of nestlings a female can fledge annually since we were unable to calculate an estimate of annual breeding success as nest boxes were protected against predators. We excluded from the analyses years where females from late nests were not identified (Buenos Aires: 2006 and 2008 and New York: 2006 and 2007).

We calculated the inter-brood period as the number of days since the fledging of the first successful brood until the laying of the first egg of a second brood. We calculated the incubation period as the number of days since clutch completion to the hatching of the first nestling and the nestling period as the number of days from the hatching of the first nestling until all nestlings left the nest (fledging is synchronous).

We categorized laying in each nest as early or late. For each year, we designated the day we found the first egg laid as day 1. We then calculated for each site and year the median laying date and defined early nests as those whose eggs were laid on or before the median date, and late nests as those whose eggs were laid after the median date. When either the exact hatch date or fledge date was unknown, the exact date of one of these two variables allowed calculating the other, assuming a length of incubation stage of 14 and 15 days and a length nestling stage of 16 and 17 days (Northern and Southern House Wrens, respectively).

We measured nestlings (mass and tarsus length) when they were 10 days old in 48 Northern and 34 Southern House Wren nests. As adult size differs between populations, we compared the relative mass and tarsus length (average measurement of each brood/average measurement of the adult population) between sites. To evaluate brood reduction during the nestling stage, we calculated the proportion of nestling fledged (fledge number/brood size).

Parental care

We filmed nests with Hi 8 video cameras (Sony Handycam), camouflaged with grass and cloth, placed 5–10 m from the nest. We set cameras 1 h after sunrise and filmed continuously for 4 h during incubation and when nestlings were 2–3, 7–8 and 11–12 days old (we consider day 0 as the day when the majority of the nestlings hatched). We started the video analysis when an adult was observed entering or leaving the nest for the first time. The duration of an incubation on-bout was calculated as the time (mm:ss) that a female remained inside a nest box and of an off-bout as the time (mm:ss) a female spend out of the nest box. For each nest we calculated an average on- and off-bout. We calculated incubation attentiveness (% of time on the nest incubating) as the number of minutes in the nest/total minutes monitored. We evaluated provisioning rate to the nest calculating food deliveries (House Wrens carry only one prey item per visit) per hour/brood and per hour/nestling. When nestlings where 2–3 days old, we calculated the mean duration of the brooding on-bout per brood for the 4-h observation session. For comparisons of provisioning rates between populations we only presented data of nests with biparental care. Following Johnson et al. (1993), we considered an adult as fully aided if her/his mate fed nestlings at a mean rate >1.0 trip/nestling/h.

Statistical analysis

We assessed differences in breeding season length, territory size, females' annual productivity and adult body measurements between Northern and Southern House Wren using Mann-Whitney U tests, and we compared the proportion of females that started a second brood using a chi-square test (SPSS 21.0; IBM Corp. 2010). All tests performed were two-tailed and differences considered significant at $P < 0.05$. We used generalized linear mixed models (GLMMs) to test for differences between Northern

and Southern House Wrens in clutch size, brood size and fledgling number (GenStat DE3; VSN International Ltd.). As clutch size could vary through the breeding season, we included a categorical covariate (early or late nests) in our models. We assumed a Poisson error distribution and a log-link function for these GLMM models. We included female identity as a random variable in these models, and early or late nests, year and population (New York or Buenos Aires) into a hierarchical model (early or late nests were nested into year, while year was nested into population) as predictive variables. When comparing brood sizes we included clutch size as a covariate, while for fledgling number we included brood size as a covariate. When we detected differences between years and/or early or late nest for any response variable, we re-ran the models for each population independently. We obtained minimal models by removing sequentially the model terms and checking the changes of the model fit.

We compared the length of nesting stages (incubation and nestling) and inter-brood interval between Northern and Southern House Wrens using a generalized linear mixed model, assuming a gamma error distribution and a reciprocal link function. We used a hierarchical nested design to test the effect of early or late nests, year and population on the length of nesting stages and inter-brood interval, including female identity as a random variable. We used a similar function to compare nestling relative masses and tarsus length.

We assessed differences in parental effort between populations using GLMMs, comparing nest attentiveness during incubation, mean incubation off- and on-bout, mean brooding time, feeding trips/h and feeding trips/h/nestling. We included population as a predictor factor and year as a random factor into the models. For these models we assumed a gamma error distribution and a reciprocal link function.

We estimated adult survival and recapture probabilities using Cormack-Jolly-Seber models (CJS) based on adult presence or absence in each year. We compiled capture histories for 411 adult birds (92 females and 126 males in the Southern House Wren and 108 females and 85 males in the Northern House Wren). We first built a general global model using the Program MARK that allowed survival (Φ) and recapture/re-sighting (p) to vary with sex, year and site. Then, we compared this model varying Φ and p (and combinations thereof) with models having a constant Φ and p. All models were constructed using the logit-link function (White and Burham 1999). We compared the models using Akaike's criterion (AIC_c), and we estimated the relative likelihood of each model with AIC weights (wi). We selected the model that presented the lower AIC_c and greater wi. We then assessed the goodness-of-fit (GOF) using a bootstrap (n = 500 simulations). This method allowed us to assess whether the data fulfilled the assumptions of the model. From the simulations we estimated c-hat (c-hat = variance of model/variance of the mean of the simulations). This parameter controls for lack of fit to the model caused by extrabinomial variation since it reflects the overdispersion of data. We then used the derived QAIC (Akaike's information criterion adjusted for overdispersion) to make our final choice among competing models.

We excluded from the present analysis all polygynous nests, as breeding success, nestling provisioning and life-history traits may be affected by the social mating system. Socially monogamous males of the two populations do not differ significantly in their contribution to parental care (Llambías et al. 2012), so it is unlikely that differences in the social mating system have biased our results. We also excluded nests that were experimentally manipulated during the study period to induce polygyny (see Llambías 2012).

Results

Adult measurements and survival

Males and females from the northern wren population had a significantly smaller body mass and shorter tarsus than the southern population (Table 1).

We detected evidence of overdispersion (c-hat > 1) with our general global model; survival and recapture/re-sighting varied with year, site and sex (P = 0.41; observed deviance = 36.91; mean simulated deviance = 36.59; c-hat = 1.01). Therefore, we used $QAIC_c$ for model selection. Our best supported model had wi of 0.85 (Table 2). In this model survival differed only by sex but not by site or year, while recapture/re-sighting did not vary by year, sex or site. Our models support the hypothesis that there were significant differences in survival between sexes but not between populations: House Wren males had a higher annual survival than females in both populations (Table 3).

Breeding biology

Across all years in our study, the Northern wren population bred from the beginning of May (first egg laid = May 6th) until the end of July (last egg laid = July 30th) for a breeding season lasting 69.2 days ± 1.6 (mean ± SE; range 63–73). Southern population birds bred from early October (first egg laid = October 7th) until mid-January (last egg laid = January 13th) lasting 80.7 days ± 1.6 (mean ± SE; range 76–85). Although the breeding season length in the north was only 11 days shorter, it was significantly longer in the southern population (Mann-Whitney U test, Z = −2.88, P = 0.004).

Table 1 Adult body mass and tarsus length for Northern and Southern House Wrens

	Mean ± SD (n)		Mann-Whitney U test	
	Northern House Wren	Southern House Wren	Z	P
Male mass	10.87 ± 0.10 (49)	12.27 ± 0.08 (59)	−8.08	<0.001
Female mass	11.12 ± 0.97 (56)	13.14 ± 1.12 (19)	−5.83	<0.001
Male tarsus	16.89 ± 0.07 (55)	18.02 ± 0.08 (68)	−7.75	<0.001
Female tarsus	16.83 ± 0.57 (63)	18.00 ± 0.58 (25)	−6.18	<0.001

Table 2 Models of annual survival (Φ) and recapture (p) probabilities for Northern and Southern House Wrens

Model	$QAIC_c$	Delta $QAIC_c$	$QAIC_c$ weight	Model likelihood	No. of parameters	$Q_{deviance}$
$\Phi_{(sex)}$, p	608.56	0.00	0.91	1.00	5	36.60
$\Phi_{(sex)}$, $p_{(sex)}$	614.74	6.18	0.04	0.05	8	36.60
$\Phi_{(sex)}$, $p_{(site)}$	614.74	6.18	0.04	0.05	8	36.60
$\Phi_{(sex*site)}$, p	618.97	10.41	0.00	0.01	17	21.79
Φ, p	621.97	13.41	0.00	0.00	2	56.11
Φ, $p_{(site)}$	621.97	13.41	0.00	0.00	2	56.11
Φ, $p_{(sex)}$	624.51	15.95	0.00	0.00	5	52.56
$\Phi_{(sex*site)}$, $p_{(sex)}$	625.48	16.92	0.00	0.00	20	21.79
$\Phi_{(sex*site)}$, $p_{(site)}$	625.48	16.92	0.00	0.00	20	21.79
$\Phi_{(site)}$, p	627.57	19.01	0.00	0.00	5	55.61
$\Phi_{(site)}$, $p_{(sex)}$	629.69	21.13	0.00	0.00	8	51.55
$\Phi_{(site)}$, $p_{(site)}$	633.75	25.19	0.00	0.00	8	55.61
$\Phi_{(sex)}$, $p_{(sex*site)}$	639.81	31.25	0.00	0.00	20	36.13
Φ, $p_{(sex*site)}$	647.47	38.91	0.00	0.00	17	50.30
$\Phi_{(site)}$, $p_{(sex*site)}$	650.26	41.70	0.00	0.00	20	46.58
$\Phi_{(sex*site)}$, $p_{(sex*site)}$	652.41	43.85	0.00	0.00	32	21.79

Subscripts give parameterization for Φ and p; subscripts joined by an '*' indicate a factorial model

No subscript constant over group and time variables, sex female and male, site New York and Buenos Aires

Table 3 Averaged estimates of annual survival (Φ) and recapture (p) probabilities, standard errors and profile likelihood 95 % confidence intervals for House Wrens from New York (USA) and Buenos Aires (Argentina)

Location	Φ ± 1 SE (95 % CI)		p ± 1 SE (95 % CI)
	Female	Male	
Buenos Aires	0.29 ± 0.04 (0.21–0.38)	0.47 ± 0.04 (0.40–0.54)	1.00 ± 0.00 (0.99–1.00)
	n = 92	n = 126	
New York	0.25 ± 0.04 (0.18–0.35)	0.48 ± 0.05 (0.38–0.59)	
	n = 108	n = 85	

Territories of northern males were significantly larger than territories of southern males (mean ± SD 1766.50 ± 693.9 m^2, n = 26 vs. 753.71 ± 397.04 m^2, n = 60, respectively, Mann-Whitney U test, Z = −6.44, P < 0.001).

Birds from the northern population had larger clutches and broods sizes, which produced more fledglings than southern wrens (Table 4). While Northern House Wrens laid smaller clutches and produced smaller broods and fewer fledglings in late nests (Wald = 65.51, df = 6, 102.8, P < 0.001 for clutch size; Wald = 41.15, df = 6, 86.2, P < 0.001 for brood size; Wald = 17.85, df = 6, 83.0, P = 0.01 for number of fledglings produced), we did not observe a consistent seasonal reduction in clutch size, brood size and fledgling number across years in Southern House Wrens during the study period (Wald = 11.35, df = 5, 123.3, P = 0.05 for clutch size; Wald = 3.32, df = 5, 68.0, P = 0.65 for brood size; Wald = 3.21,

df = 4, 46.0, P = 0.53 for number of fledglings produced). The proportion of females that produced second broods did not differ significantly between populations (north = 38.82 %, n = 85, south = 39.19 %, n = 74, $x^2 = 0.002$, P = 0.96); however northern females' mean number of nestlings fledged per season from successful nests was greater (mean ± SD north = 7.14 ± 2.75, n = 86, south = 4.01 ± 1.10, n = 76, Mann-Whitney U test, Z = −8.33, P < 0.001).

The northern wren population had shorter incubation periods than the southern population (Table 4) with significant differences between breeding seasons (Wald = 17.98, df = 8, 127.0, P = 0.03). After controlling for inter-annual variation, there was still a significant difference in intra-annual variation (early vs. late nests, Wald = 28.9, df = 10, 127.0, P = 0.003). In both wren populations late nests had shorter incubation periods than early nests (Wald = 18.9, df = 6, 61.2, P = 0.009 for Northern House Wren; Wald = 12.29, df = 4, 52.2, P = 0.02). In contrast, the nestling and the inter-brood period only varied by population, being shorter for northern wrens (Table 4).

Parental care

Northern House Wren females had greater incubation attentiveness and fewer but longer incubation on-bouts than Southern House Wrens (Table 5). However, mean duration of incubation off-bout did not differ between populations.

Mean brooding bouts of Northern and Southern House Wrens with 2–3 days nestlings did not differ significantly (mean ± SD 6.82 ± 1.59 min, n = 34 vs. 7.59 ± 2.26 min, n = 38 respectively; Wald = 2.76, df = 1, 68.5, P = 0.1). Wrens did not significantly differ in the average number of feeding trips to the nest per brood except when nestlings were 2–3 days old (Table 6). However, southern wrens made significantly more trips to the nest per nestling during all three nestling periods measured (Table 6).

Table 4 Life-history traits for Northern and Southern House Wrens

	Mean ± SD (n)		GLMM		
	Northern House Wren	Southern House Wren	Wald	df	P
Clutch size	6.03 ± 0.99 (156)	4.85 ± 0.76 (157)	178.02	1, 280.9	<0.001
Brood size	5.48 ± 1.21 (137)	4.49 ± 1.12 (93)	80.56	1, 117.9	<0.001
Fledgling number	4.41 ± 2.14 (152)	2.90 ± 2.16 (134)	26.27	1, 129.0	<0.001
Incubation period	13.85 ± 0.69 (72)	15.24 ± 1.10 (63)	107.14	1, 127.0	<0.001
Nestling period	15.91 ± 1.25 (58)	17.04 ± 1.09 (27)	14.80	1, 76.0	<0.001
Inter-brood period	44.17 ± 6.03 (24)	52.88 ± 7.18 (16)	11.82	1, 28.0	0.002

Table 5 Attentiveness (% of time on the nest incubating), number of on-bouts per hour, mean incubation on-bout (minutes a female spend inside the nest) and mean off-bout (minutes a female spend outside the nest) for Northern and Southern House Wren females

	Mean ± SD (n)		GLMM		
	Northern House Wren	Southern House Wren	Wald	df	P
Attentiveness	0.72 ± 0.07 (24)	0.60 ± 0.06 (15)	34.60	1	<0.001
On-bouts/h	3.08 ± 0.79 (24)	4.14 ± 0.87 (15)	14.77	1	<0.001
Incubation on-bout	15.32 ± 5.62 (24)	9.00 ± 1.97 (15)	20.90	1	<0.001
Incubation off-bout	5.74 ± 1.62 (24)	6.08 ± 1.32 (15)	0.46	1	0.50

Table 6 Feeding trips to the nest per hour (feeding trips/h) and per nestling (feeding trips/h/nstl) for Northern and Southern House Wren at three nestling stages: 2–3, 7–8 and 11–13 days old

	Mean ± SD (n)			GLMM		
	Age	Northern House Wren	Southern House Wren	Wald	df	P
Feeding trips/h	2–3	19.72 ± 3.76 (34)	17.75 ± 3.77 (38)	4.85	1, 70.0	0.03
	7–8	28.15 ± 7.38 (37)	25.81 ± 7.03 (31)	1.76	1, 66.0	0.19
	11–13	35.95 ± 10.90 (35)	31.60 ± 10.43 (21)	2.16	1, 54.0	0.15
Feeding trips/h/nstl	2–3	3.74 ± 0.86 (34)	4.31 ± 0.67 (38)	9.25	1, 70.0	0.003
	7–8	5.32 ± 1.29 (37)	6.44 ± 1.26 (31)	13.03	1, 66.0	<0.001
	11–13	6.80 ± 1.87 (35)	8.33 ± 2.33 (16)	7.25	1, 34.5	0.01

Relative mass of 10-day-old nestlings was greater in the south than in the north (mean ± SD 0.95 ± 0.06, n = 34 vs. 0.91 ± 0.05 n = 48, respectively, Wald = 13.24, df = 1, P < 0.001). However, tarsus relative size did not differ (mean ± SD south = 0.99 ± 0.03 n = 32, north = 0.99 ± 0.02, n = 41; Wald = 0.03, df = 1, P = 0.86). Nestling success was similar between Northern and Southern Wrens (mean ± SD 0.93 ± 0.34, n = 127, 0.91 ± 0.15, n = 71 respectively, Wald = 0.09, df = 1, 127.8, P = 0.77).

Discussion

Northern and Southern House Wrens at our temperate study sites differed in several life-history traits. The southern population, like many tropical and south temperate species, was characterized by smaller clutches, lower incubation attentiveness and longer incubation, nestling and interbrood periods. Northern House Wrens showed a seasonal decline in clutch size; however, we did not observe a consistent pattern in the Southern House Wren. Seasonal decline in clutch size may be caused by a reduction in food supply (Lack 1966; Lundberg and Alatalo 1992) or an increment in juvenile mortality (Young 1994).

The cost of reproduction hypothesis predicts that reduced clutch size should be correlated with reduced reproductive effort and increased adult survival (Ashmole 1963; Martin et al. 2000; Russell et al. 2004; Ricklefs 2010). Northern and Southern House Wren' females have higher adult mortality than males. However we did not find significant differences in adult survival between populations for either sex. Our results should be taken with caution as survival estimates for the northern population are conservative since wrens may have dispersed outside the study area without been observed (see "Methods"). Similar survival probabilities between populations that differ in clutch size can be expected if the total amount of energy allocated in reproductive effort does not differ (Badyaev and Ghalambor 2001) or if causes of mortality differ between populations (Young 1996). Provisioning rates per brood were lower for southern wrens when nestlings were 2–3 days old, but we did not find significant differences between populations for 7–8- and 11–12-day-old nestlings. Although the developmental periods were significantly longer in the south, they differed by only 2 days. To properly evaluate the cost of reproduction hypothesis, a comparison of reproductive effort between populations considering both physiological measurements (e.g., basal and field metabolic rate, water influx rate, etc.) and maternal effects (e.g., egg quality) will allow assessing whether the lack of differences in adult mortality is due to similarities in parental investment.

Our results seem to support the hypothesis that Southern House Wrens invest more in offspring quality, while Northern House Wrens invest more in offspring quantity. Although in both populations a similar proportion of females started a second brood after a successful nest, northern wrens can produce more fledglings per season as female's annual mean number of nestlings fledged from successful nests was greater in the north. However, wrens breeding in tree cavities may seldom achieve this productivity as successful double brooding maybe be infrequent because of nest predation. In the south, provisioning rates per nestling were significantly higher, and nestling mass 6–7 days before fledgling reached a greater proportion of adult body mass. However, our results should be taken with caution as measurements of nestling development, immune response, post-fledgling parental care and juvenile survival are needed for a proper evaluation of the offspring quality hypothesis. According to the offspring quality hypothesis (Young 1996), survival of resident Southern House Wrens should be influenced by intra-specific competition, while migratory Northern House Wrens should be subject to density-independent mortality during migration. In our south temperate population, juvenile quality may be essential to be able to settle on a territory to breed, as male-male competition for monopolizing female territories is particularly strong (Llambías 2012). Density-independent mortality has been reported in several small migrant passerines and can be caused by adverse weather during migration or atypical cold weather soon after arriving to or before departing from breeding areas (Sillet and Holmes 2002; Butler 2000; Newton 2006). Life-history strategies can deeply affect social mating systems through their effects on parental care patterns. Although House Wrens are predominantly social monogamous, social polygyny rate is higher in Northern than in Southern House Wrens (Johnson et al. 1993; Llambías and Fernández 2009). Differences in polygyny rate may be the consequence of different strategies in male's reproductive effort: while northern wrens may invest more time and energy in mating effort, southern wrens may invest more in parental effort. However, a previous study did not find significant differences in male relative contribution to provisioning nestlings of monogamous pairs in Northern and Southern House Wrens (Llambías 2012).

Another hypothesis proposed to explain the latitudinal differences in life-history traits is related to the availability of food as a constraint to parental investment (the food limitation hypothesis; Ashmole 1963). As predicted, Southern House Wrens have a longer developmental period and smaller clutch size than their northern relative. However, parental care patterns were contrary to the predictions. Provisioning trips per brood were greater in the north only when nestlings were 2–3 days old, and provisioning

rates per nestling were greater in the south for 2–3-, 7–8- and 11–12-day-old nestlings. Furthermore, by day 11 southern nestlings had reached a greater proportion of adult body mass than northern nestlings and brood reduction did not differ between populations, suggesting that nestling starvation was not more frequent in the south. It has been proposed that low food availability should select for smaller body mass to reduce energy expenditure (Katti and Price 2003; Tieleman et al. 2006), and both empirical and experimental studies provide evidence that smaller territories are associated with greater food availability (reviewed by Newton 1998). Adult body mass was greater in the Southern House Wren and territory size was smaller, suggesting that southern wrens can find enough food to support a bigger mass on smaller territories.

Nest predation risk has also been proposed as a selective force molding life-history traits in passerine birds (Skutch 1949). We were not able evaluate nest predation rates in this study as nest boxes that are relatively protected from predators may not reflect the predation rates to which wrens have evolved when breeding in natural cavities (Purcell et al. 1997; Llambías and Fernández 2009). Irrespective of predation rates, the observed pattern of parental visitation activity of Northern and Southern House Wrens is contrary to the predictions for a population with smaller clutch size: incubation on-bouts were shorter and more frequent in the south; provisioning rate per nestling was greater in the south; provisioning rate per brood was similar between populations when nestlings were 7–8 and 11–12 days old, and developmental periods were 2 days longer in the south. These behaviors are likely to increase parental activity, which in turn may attract visual predators during the incubation and nestling stage.

Our results suggest that the cost of reproduction, food limitation and nest predation hypotheses may not be able explain the smaller clutches of Southern Wrens. Are these hypotheses also unable to explain differences in clutch size between Northern and Tropical Wrens? Young (1996) artificially increased the brood size of Tropical House Wrens during three breeding seasons and showed that although both sexes increased the number of feeding trips to the nest, adult survivorship remained unaffected. As tropical House Wrens spend more time in incubation, nestling and post-fledgling stages, Young (1996) proposed that tropical wrens invest more energy in offspring quality than Northern House Wrens without compromising adult survival. However, Tieleman et al. (2006) concluded that the overall investment during the nestling period was lower in Tropical House Wrens as at their tropical study site wrens have a lower provisioning rate to the nest per brood and lower field metabolic and water influx rates than at a north temperate site. Both studies however concluded that food limitation cannot explain smaller clutches of tropical wrens. Young (1996) showed that Tropical House Wrens can increase the feeding effort of artificially enlarged broods and fledge nestlings successfully. Tieleman et al. (2006) suggested that food is not more limiting for Tropical than Northern House Wrens as levels of whole-organism energy expenditure in tropical wrens does not differ from north temperate wrens even though adult body mass of tropical wrens is larger. Nest predation seems not able to explain reduced clutch size in Tropical House Wrens either, as predation is unrelated to brood size and parental activity at the nest (Young 1996).

Southern House Wrens are similar to Tropical Wrens in having a reduced clutch size, extended developmental period, social monogamy and resident lifestyle. In both wrens, it seems unlikely that the food limitation and nest predation hypotheses will be able to explain the observed life-history syndrome. However, parental investment strategies may differ between tropical and south temperate wrens. While the provisioning rate per nestling does not differ between Tropical and Northern House Wrens (Tieleman et al. 2006), our results showed that Southern House Wrens made significant more feeding trips per nestling than Northern House Wrens. These differences in parental invest strategies between south temperate and tropical wrens are particularly interesting, and while most studies have focused on the differences in life-history traits between north temperate and tropical birds, the more subtle differences between tropical and south temperate birds may shed new light on our understanding of the evolution of clutch size.

Acknowledgments We thank David W. Winkler for helpful comments on the manuscript, Valentina Ferretti, Myriam Mermoz and Pablo Rodriguez for help in the field, and Mario Beade and Bob Johnson for logistic support. Economic support was provided to PEL by the Department of Ecology and Evolutionary Biology at Cornell University, the Cornell Laboratory of Ornithology, Mario Einaudi Center for International Studies, Cornell Chapter of Sigma Xi, The Scientific Research Society, American Ornithologist Union and Andrew W. Mellon Student Research Grant. Support to GJF and MEC was provided by the University of Buenos Aires (grant 20020090200117) and CONICET grants (PIP11220090100011). All methods used in the present study meet the ethical requirements for science research and comply with the current laws of the countries in which they were performed. We thank two anonymous reviewers for their helpful comments on an earlier version of this manuscript.

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