Articles

A comparison of life-history and parental care in temperate and tropical wrens

Sharon A. Gill and Thomas M. Haggerty

S. A. Gill (sharon.gill@wmich.edu), Dept of Biological Sciences, Western Michigan Univ., Kalamazoo, MI 49008-5410 USA. – T. M. Haggerty, Dept of Biology, Univ. of North Alabama, Florence, AL 35632, USA.

Comparing closely related species that live in different environments is a powerful way to understand selective pressures that influence life-history evolution. We examined a suite of life-history traits and parental care in neotropical buff-breasted wrens *Cantorchilus leucotis* and north-temperate Carolina wrens *Thryothorus ludovicianus* (Family Troglodytidae), to test hypotheses about life-history evolution. As expected, buff-breasted wrens exhibited smaller clutch sizes and higher annual adult survival than Carolina wrens. We found minimal support for the nest predation hypothesis, as nest survival and age-corrected provisioning rates to whole broods were similar between species, and number of breeding attempts and breeding season length were greater in temperate wrens. Critical predictions of the food limitation hypothesis were not supported; in particular age-corrected provisioning rates per nestling were higher in the tropical than temperate species. The adult survival and offspring quality hypothesis garnered the most support, as buff-breasted wrens exhibited greater age-corrected provisioning rates per nestling, a longer nestling period, longer re-nesting intervals following nest success, and lower annual fecundity than Carolina wrens. Despite similarly prolonged breeding seasons, reproductive strategies differ between species with buff-breasted wrens investing considerably in single broods to optimize first-year survival and Carolina wrens investing in multiple small broods to optimize annual fecundity.

Understanding the selective pressures that favor pace-of-life strategies across environmental gradients has been a central focus of studies of life-history evolution (Williams 1966, Badyaev and Ghalambor 2001, Martin 2004, Robinson et al. 2010). Among songbirds, a general pattern is that species from tropical and south-temperate regions exhibit smaller clutch sizes, higher adult survival, and an overall slower pace-of-life compared with species from more northerly latitudes, which lay larger clutches, have lower survival, and live at the 'fast' end of the life-history continuum (Moreau 1944, Lack 1947, Skutch 1949, Martin 1996, 2004, Ricklefs 2000, Jetz et al. 2008, Robinson et al. 2010). Each of the major hypotheses for life history evolution in birds (Table 1) predicts reductions in clutch size from northerly to southerly latitudes, therefore to advance life-history theory, data on additional traits that comprise relatively smaller proportions of reproductive effort are needed (Martin 1996, 2004, Robinson et al. 2010). Less is known about latitudinal variation in these other life history traits, such as duration of nestling care, nestling feeding rates, and number of breeding attempts per year (Martin 2004, but see Martin 2002, Schaefer et al. 2004, Ferretti et al. 2005, Tarwater and Brawn 2010, Tarwater et al. 2011), but many are predicted to respond differently to selection from food limitation, nest predation, and adult survival (Martin 1996, 2004, Robinson et al. 2010).

In this study, we tested hypotheses for life-history evolution (Table 1) by comparing a suite of life-history traits and parental care strategies of two wren species (family Troglodytidae) that inhabit low- and high-latitude environments. We studied neotropical buff-breasted wrens *Cantorchilus leucotis* in central Panamá and north-temperate Carolina wrens *Thryothorus ludovicianus* in the southeastern United States. These are closely related species that inhabit different latitudes, but they share key intrinsic factors known to influence life-history evolution (Jetz et al. 2008). Both species are small insectivores, which are non-migratory and defend year-round territories (Haggerty and Morton 1995, Gill 2011). Moreover, both species exhibit genetic monogamy combined with long-term partnerships (Haggerty et al. 2001, Gill et al. 2005, Gill and Stutchbury 2006); thus, the influence of sexual selection in shaping their life history traits is similar (Bonduriansky et al. 2008). Differences in life-history traits between the two species should therefore be due primarily to differences in selection pressures between latitudes (Jetz et al. 2008). Few life-history data exist for most tropical wrens (Ahumada 2001, Robinson, T. R. et al. 2000, Marshall-Ball and Slater 2003, Logue 2009, Taylor 2011), and our study presents the first detailed life-history account of a *Cantorchilus* species or any tropical wren formerly placed within *Thryothorus* genus (see below).

Table 1. Summary of alternative hypotheses, predictions and results for differences in life-history traits and parental care between neotropical buff-breasted wrens and north-temperate Carolina wrens (modified from Martin 1996). Positive signs (+) indicate traits predicted to be greater in north-temperate than neotropical wrens, whereas negative signs (−) indicate traits predicted to be greater in neotropical species. Blank cells indicate traits with no predicted difference between species. All traits listed were measured in the present study, with symbols in bold indicating support for specific predictions.

| | Hypotheses | | |
Variable	Nest predation	Food limitation	Adult survival and offspring quality
Adult survival	+	+	−
Reproductive traits			
Clutch size	**+**	**+**	**+**
Nesting cycle	**+**	**−**	**−**
incubation	**+**	**−**	**−**
nestling	**+**	**−**	**−**
Re-nest interval			
after failure	−	−	−
after success		−	−
No. breeding attempts	−	+	+
Breeding season length			
population	−	+	
individual	−	**+**	
Parental care			
Provisioning rates			
per brood	+	+	+
per nestling	+	+	−
Prey size	−	**+**	−
Prey loading	−	+	+
Mass at fledgling	−	+	−
Reproductive success			
Nest survival	+	+	−
Nest failure due to predation	**−**		
Nest failure due to starvation		−	
Fledgling success	+	+	−
Annual fecundity	**+**	+	**+**
Survival to age of first reproduction		+	−

As latitudinal patterns in life history traits other than clutch size and annual adult survival are not well established (Martin 1996, 2004), we present data on these traits, but also brood sizes, duration of nesting cycles and breeding seasons, and re-nesting intervals after both nest failure and success. We compare parental care via overall provisioning rates, per capita provisioning rates, prey loading, prey size, and nestling mass near fledging. Finally, we present data on reproductive success and predation rates, and using data on adult mortality and annual fecundity, we calculate estimates of the survival of offspring to the age of first reproduction (Ricklefs and Bloom 1977). Based on this broad suite of traits (Table 1), we test three main hypotheses for life history evolution in tropical and temperate birds. The nest predation hypothesis proposes that differences in nest predation rates between tropical and temperate regions favor different patterns of investment in individual breeding attempts, parental activity near the nest, and re-nesting (Skutch 1949, Martin 1996). This hypothesis predicts that 1) nest predation is higher in tropical than

temperate birds; 2) nesting cycles, particularly the period of nestling feeding, are shorter in tropical birds to minimize the duration of the life history stage with high mortality risk; and 3) overall and per capita provisioning rates are lower in tropical birds to minimize visits to the nest; however, parents compensate by bringing larger and more prey items per feeding visit. The food limitation hypothesis poses that a combination of density-dependent competition, lower prey productivity and prey diversity decrease prey availability during breeding in tropical compared with temperate regions (Lack 1947, Ashmole 1963, Cody 1966, McNamara et al. 2008, Ricklefs 2010). Key predictions of this hypothesis are that 1) north-temperate birds exhibit higher rates of provisioning per brood and per nestling, and bring more and larger prey per visit than tropical birds, 2) because of greater food availability, nesting cycles and re-nesting intervals are shorter in north-temperate species, resulting in more broods per year than in tropical birds, and 3) nest failure due to nestling starvation occurs more frequently in tropical than temperate birds.

Finally, lower seasonality in tropical environments plus year-round territoriality may lead to higher adult survival and increased density-dependent competition for resources during non-breeding periods compared with north-temperate species. Although higher adult survival favors reduced reproductive effort, parents may increase investment in a smaller number of offspring to enhance their probability of survival (Ashmole 1963, Ricklefs 1980, Martin et al. 2000, McNamara et al. 2008). In other words, tropical birds invest more in offspring quality, whereas temperate birds invest in annual fecundity (Martin 1996, Martin et al. 2000). The adult survival hypothesis predicts that 1) adult annual survival is greater in tropical than temperate species, 2) tropical birds lay fewer clutches with longer intervals between clutches, especially after successfully fledging young, 3) tropical birds provision broods at a lower rate overall, but per nestling provisioning rates and prey loading are higher than for temperate birds, and 4) as a result of greater investment in offspring, tropical birds experience higher probability of survival to the age of first reproduction than temperate birds (Table 1).

Methods

Study species and study areas

Buff-breasted and Carolina wrens until recently were congeners within the *Thryothorus* genus. Based on molecular and behavioral data, the *Thryothorus* genus was recognized as paraphyletic and Mann et al. (2006, 2009) proposed four genera (*Thryothorus*, *Pheugopedius*, *Thryophilus* and *Cantorchilus*), which have been accepted by the South American Classification Committee of the American Ornithologists' Union (Remsen et al. 2010). Carolina wrens are the only species of the original 23 examined that remain within *Thryothorus*, with buff-breasted wrens placed within *Cantorchilus* (Mann et al. 2006, Remsen et al. 2010). The Carolina wren is the only species in these genera that inhabits north-temperate regions and hence is the most appropriate species for the comparison with tropical wrens, despite placement of the two species in different genera.

Buff-breasted wrens are small (mean ± SD, range: females: 17.9 ± 0.8 g, 16–19.5 g; males: 20.2 ± 1.0 g, 18.5–23 g, Gill and Vonhof 2006) insectivores with an entirely neotropical distribution from central Panamá into north-central South America, primarily east of the Andes. Males and females are similar in appearance, but can be reliably sexed by predictable differences in behavior and body size within pairs (Gill and Vonhof 2006, Alessi et al. pers. comm.). Gill studied a color-banded population of buff-breasted wrens in 22-ha secondary forest fragment near Gamboa, Republic of Panamá (9°7′N, 79°42′W; see Gill and Stutchbury 2005 for a description of the study area) between 1997–2000, 2004–2005 and 2009–2011; the data presented here, with the exception of longevity records, derive from observations made during February–May 1997, February–July 1998 and 1999, October 1998, and March 2000. This region shows little seasonality in daily temperatures, with a mean difference in annual daily high temperatures of 1.44°C ± 0.35 (data provided by the Meteorological and Hydrological Branch of the Panama Canal Authority). A pronounced dry season occurs from mid-December to mid- to late-April, with the onset of breeding by buff-breasted wrens coinciding with the onset of the rainy season in April or May. Independent offspring delay dispersal and remain on natal territories for an average of 10 months after fledging; they typically do not stay long enough to overlap with breeding and as a result, cooperative breeding is rare (Gill 2004, Gill and Stutchbury 2010).

Carolina wrens are found in the eastern United States into the Midwest, eastern Texas and northeast Mexico, with several disjunct populations in the Yucatan Peninsula, Guatemala, Belize and Nicaragua (Haggerty and Morton 1995). Carolina wrens are small (mean ± SD, range: females: 18.7 ± 5.1 g, 16.2–21.5 g; males: 21.2 ± 1.3 g, 18.5–27 g, Haggerty 2006) insectivores, which are resident throughout their range. Males and females are also similar in appearance, but can be sexed by body size and behavior (Haggerty 2006). Haggerty studied a color-banded population of Carolina wrens in a 43-ha mixed hardwood forest on the Tennessee Valley Authority Reservation in Muscle Shoals, Colbert County, Alabama, USA (34°49′N, 87°38′W) between 1988 and 2009. Mean difference in annual daily high temperatures at this site was 4.58°C ± 0.44 (NCDC 2011). Pairs begin breeding in March–April (Haggerty and Morton 1995).

Adult survival and longevity

We used maximum-likelihood estimation with modified Cormack–Jolly–Seber (CJS) encounter history models to obtain apparent annual survival probabilities for both species (Lebreton et al. 1992). Data were obtained from the capture and recapture/re-sighting of individually color-marked wrens during breeding. Only territorial adults (i.e. singing and nesting) were included in the analyses. Both species exhibit high site fidelity (Haggerty and Morton 1995, Haggerty et al. 2001, Gill and Stutchbury 2006), with individuals of both species defending the same territories for up to a decade or more (Gill unpubl., Haggerty unpubl.). Since both wren species are sedentary and banded individuals that survived were readily detected, recapture probabilities are high. Survival and recapture estimates for buff-breasted wrens were determined from 72 encounter histories (33 males and 39 females) over a four-year period (1997–2000), whereas Carolina wren estimates were based on 349 encounter histories (180 males and 169 females) over 17 breeding seasons (1992–2008). Longevity records were summarized from re-sightings of color-banded territorial birds between 1997–2011 in Panamá and 1988–2008 in the US.

Candidate models were chosen prior to data analysis and were constructed using the sin link function in the Program MARK (Cooch and White 2012). Models were constructed to examine the effects of sex and year on annual adult survival. We used second-order Akaike's information criteria corrected for small sample sizes (AIC_c) to rank candidate models and the best supported models were those with a $\Delta AIC_c \leq 2$ and comparatively high relative probabilities (AIC_c weights; Burnham and Anderson 1998). If a clear 'best' model (i.e. AIC_c weight ≥ 0.90) was not evident, then survival estimates were obtained by model averaging. The goodness-of-fit of the global model (i.e. model with greatest number of parameters) for each species survival data was verified with RELEASE in MARK (Cooch and White 2012).

Reproductive traits

Buff-breasted and Carolina wrens build domed nests for breeding (Haggerty and Morton 1995, Gill and Stutchbury 2005), and Carolina wrens readily use nest boxes as well. We located buff-breasted wren nests by searching areas from which wrens first sang at dawn (first songs are typically given near to breeding nests) and by following individuals carrying nest materials. Because they are difficult to find, few data exist regarding Carolina wrens nesting in natural cavities. In the only study of Carolina wrens using natural cavities of which we are aware, Jackson et al. (2011) found slightly higher survival for Carolina wren nests placed in natural cavities than artificial ones. We provided nest boxes in late winter (5–6 territory^{-1}) and most data presented here were collected from breeding attempts in the nest boxes. Nest boxes ($13.0 \times 10.5 \times 14.0$ cm) were attached to a 1.5 m section of conduit, which was then positioned on 50 cm pieces of rebar driven into the ground. The entrance to the nest box was a 3.0–4.0 cm slot along one side and near the top of the box. We did not attach anti-predator guards or reinforce the entrances in any way, and have evidence that snakes, birds and mammals depredated nests within boxes (Haggerty unpubl.). The top of the box was hinged to allow researcher access and used boxes (both successful and failed) were typically cleaned out by hand and moved to new locations on territories.

To document date of clutch initiation, clutch and brood size, length of incubation and nestling periods, we checked nests and nest boxes every 1–5 d until nests failed or young fledged and noted the nest contents. When nests were too high for visual inspection, we observed them for 15–45 min to determine nesting stage (females returned to incubate or one or both parents brought food to the nest). Occasionally, nests were found with completed

clutches or with nestlings, and we monitored these nests till hatch or fledging and determined clutch initiation and hatch date by back-dating.

For pairs whose nests had failed, we monitored them for signs of nest building in the week after nest failure. We calculated re-nesting interval after nest failure as the number of days between the day the nest was first recorded to have failed (within 1–4 d) to the day the first egg of the replacement clutch was laid. At nests where the date of predation was not known precisely, we used the midpoint between the last and the next-to-last check to calculate re-nesting interval. We calculated re-nesting interval after nest success as the number of days between fledging of one brood and clutch initiation for the subsequent brood. For both species, > 90% of re-nesting intervals after nest failure came from early breeding attempts (May–July). Re-nesting intervals after success were calculated from second attempts made throughout the season in Carolina wrens, but late in breeding in buff-breasted wrens (August and September). We also quantified the number of breeding attempts initiated per pair.

Finally, we compared estimates of the length of the breeding season between species in two ways. At the population level, we calculated the number of days between laying of the first egg of the first clutch in the population and latest known fledging date in the population. We also calculated an individual-level measure of breeding season length by determining for each pair the number of days between laying of their first egg of their first clutch and latest known fledging of offspring, nest failure, or the end of our field seasons. Fieldwork on buff-breasted wrens ended before breeding ceased; we therefore likely underestimate the number of breeding attempts made by the tropical wrens. Moreover, for both species re-nesting attempts of successful pairs do not include the period of post-fledging care. Juvenile Carolina wrens typically leave natal territories within a month of fledging (Haggerty and Morton 1995), whereas buff-breasted wren parents feed offspring for at least 3 months after fledgling and juveniles may remain on natal territories for more than 1 yr (Gill unpubl., Gill and Stutchbury 2010). Thus, estimates of the duration of breeding for individual pairs are conservative.

Parental care

We examined parental care in buff-breasted and Carolina wrens by comparing provisioning rates of parents feeding nestlings during the second half of the nestling period. This included observations from nests with young between 7–13 d old for Carolina wrens and 9–16 d old for buff-breasted wrens (hatching day = day 0), at which time both parents are actively provisioning food (Haggerty unpubl., Gill and Stutchbury 2005). Buff-breasted wren provisioning data were collected during 58 h of observations at 21 nests of 17 pairs from approximately 10 m, during May–July between 06:00 and 15:00 CST. Carolina wren provisioning data were collected from 61 h of observation at 39 nests of 27 pairs from April to August between 11:00 and 17:00 CST, using concealed video cameras that were positioned 3–4 m from nests. At each nest, we recorded the number of visits by males and females, from which we calculated male, female and total provisioning rate h^{-1} $nest^{-1}$. Clutch size differed between species and among individuals within species; therefore, we also calculated the provisioning rate $nestling^{-1}$ h^{-1} to control for differences in brood sizes. Only visits during which parents carried food to the nest were included in analysis.

During provisioning observations, we also quantified prey loading (defined as the number of prey items brought to the nest $visit^{-1}$) and prey size to evaluate whether these differed between species. We estimated the size of prey in relation to the length of the parent's bill (0.5, 1, 1.5, 2, etc.) and calculated the average relative prey size $observation^{-1}$ for males and females for each species. Estimated prey sizes (mm) were determined by multiplying relative prey size by the length of the parent's bill (mm, measured from bill tip to nares).

To analyze the provisioning data, we used the residual maximum likelihood method (REML) for fitting mixed models (JMP 2007). This method helps control for the nonindependence between observations at the same nests and between observations of the same pair at different nests (Maccoll and Hatchwell 2003). For the analysis, for each provisioning model (Table 2), the subject (i.e. pair provisioning nestlings) was 'nested' within the species variable and had a random effect attribute. We examined the effects of species, nestling age, and their interaction on the provisioning response variables for each sex and total food delivered using F tests.

As a proxy for mass at fledgling, we banded and weighed to the nearest g nestlings of both species when they were 12–14 d old. Buff-breasted wren nestlings may remain in the nest for up to 4 more days on average, whereas most Carolina wren nestlings left the nest within 1–2 d of measurement (Results). Thus, nestling mass at this age may be more likely to reflect actual mass at fledgling in Carolina than buff-breasted wrens.

Reproductive success

Survival-time analysis with Kaplan–Meier estimation was used to compare nest success between wren species where survival 'time' refers to the age of the nesting cycle in days (Nur et al. 2004). Clutch initiation was considered the start of the nesting cycle and nests that fledged young were right censored. When the exact failure date was unknown, we used the midpoint practice for estimating failure date (Nur et al. 2004). Log-ranked tests were performed to compare the nest survival estimate functions between species and we used a Weibull distribution model to obtain estimates for nest success (JMP 2007). We also used the nest survival function in MARK to obtain additional comparative estimates of nest success and assumed a constant daily survival period for both species (Cooch and White 2012). We calculated fledgling success, as the number of nestlings that fledged $nest^{-1}$, and annual fecundity as the number of young fledged $pair^{-1}$ yr^{-1}.

Estimates of survival to the age of first reproduction

Direct estimates of survival from fledging to the onset of the first reproductive attempt are not available for either

Table 2. Models of apparent adult annual survival (φ) and recapture probability (p) for neotropical buff-breasted wrens between 1997 and 2000. 'K' is the number of parameters included in each model.

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	K	Deviance
$\phi.p.$	163.305	0.000	0.527	1	2	10.487
$\phi_{sex}p.$	163.962	0.656	0.379	0.720	2	9.045
$\phi_{year}p.$	168.936	3.634	0.085	0.162	4	9.886
$\phi_{year \times sex}p.$	173.788	8.482	0.008	0.014	7	8.125

Table 3. Models of apparent adult annual survival (φ) and recapture probability (p) of north-temperate Carolina wrens between 1992 and 2008. 'K' is the number of parameters included in each model.

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	K	Deviance
$\phi_{year}p.$	904.700	0.000	0.994	1.000	17	165.848
$\phi_{sex}p.$	916.061	11.361	0.003	0.003	3	206.127
$\phi.p.$	917.245	12.544	0.002	0.002	2	209.329
$\phi_{year \times sex}p.$	920.833	16.133	0.000	0.000	33	147.350

species. Thus, we used the approach of Ricklefs and Bloom (1977) to estimate survival of offspring to the age of first reproduction, S_a. This method assumes that population size and age structure are constant, birds breed in their first year of life, and that sex ratio of fledglings is 1:1 (Ricklefs and Bloom 1977). Limited data are available to address these assumptions, but the density of territories in our study sites remained fairly constant over time, suggesting both populations are stable, and individuals of both species breed in their first year. Underlying this method is the idea that mortality between fledging and the next breeding season reduces the number of potential recruits to adult mortality in a given year, which may or may not reflect actual S_a in the field (Tarwater et al. 2011). We estimated S_a by dividing annual adult mortality ($1-S$, where S is estimated annual adult survival generated by MARK) by the number of young fledged female^{-1} yr^{-1} (that is, annual fecundity divided by 2).

We used JMP (ver. 9 for Windows) to conduct survival time analysis of wren nests and to compare reproductive traits and provisioning rates of buff-breasted and Carolina wrens. Life history trait data that met the assumptions of parametric analyses were analyzed with t-tests, whereas Wilcoxon tests were used when these assumptions were not met. Results were considered significant when $p < 0.05$ and data are reported as means ± 1 standard error (SE) unless otherwise noted.

Results

Adult survival and longevity

Since the global models ($\phi_{year \times sex}$ $p_{year \times sex}$) for both wren species fit the encounter data well, no adjustments for overdispersion were made (buff-breasted wren: $\chi^2 = 4.2$, $p = 0.4$, $DF = 4$; Carolina wren: $\chi^2 = 36.6$, $p = 0.2$, $DF = 30$). For buff-breasted wrens, the survival model with a sex effect ($\phi_{sex}p.$) and the model without any effects ($\phi.p.$) were equally supported and best fit the data ($\Delta AIC_c < 2$; Table 2). The models that included a year effect ($\phi_{year}p.$) and a sex-year interaction ($\phi_{sex \times year}p.$) were not supported and showed relatively low likelihood probabilities of fitting the data (17 and 2%, respectively; Table 2). The apparent annual survival estimate for buff-breasted wrens was 0.67 ± 0.05 SE (95% CI = 0.56–0.76), with males (0.72 ± 0.06; 95% CI = 0.60–0.82) experiencing a higher survival estimate than females (0.62 ± 0.06; 95% CI = 50.0–0.73).

For Carolina wrens, the model with a year influence ($\phi_{year}p.$) clearly fit the data best, while the models examining sex and sex-year interaction had very low likelihood values

(i.e. $> 1\%$; Table 3). The apparent annual survival estimate for Carolina wrens was 0.51 ± 0.08 (95% CI = 0.36–0.67), but survival estimates were considerably lower in some years than others (Fig. 1). For example, in the winter of 1995–1996, a severe ice storm and an extended period of low temperatures were especially devastating to the study population, and survival estimates for that year were $< 15\%$.

Longevity records support findings from the survival analysis, with longer life spans recorded in buff-breasted than Carolina wrens. The minimum oldest age for territorial male and female buff-breasted wrens was 15 and 13 yr (based on 72 banded birds), respectively; the male, banded as a territory holder in 1997, was still alive during a census conducted May 2011 (Alessi et al. pers. comm.). The minimum oldest age recorded for territorial male and female Carolina wrens was 10 and 6 yr, respectively (based on 381 banded birds); both birds were banded as territory holders and disappeared during the study period.

Reproductive traits

Consistent with the well-established latitudinal pattern, buff-breasted wrens had significantly smaller clutch and brood sizes than Carolina wrens (Table 4). Most female buff-breasted wrens laid clutches of three eggs, whereas modal clutch size in Carolina wrens was five eggs (n = 60 clutches). Brood size was variable in Carolina wrens, ranging from 1 to 6 nestlings (mode = 4), with typically four nestlings fledging
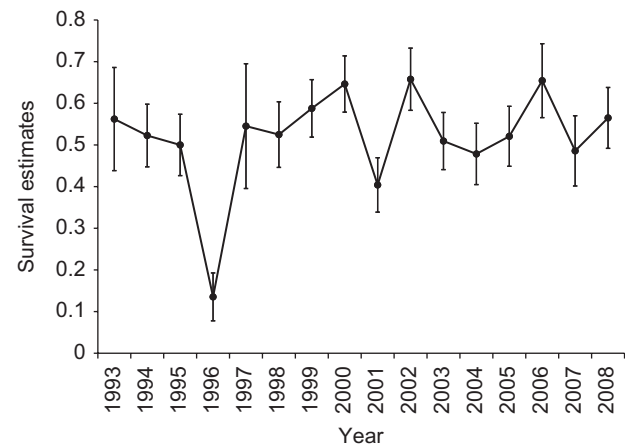

Figure 1. Apparent annual survivorship probabilities ($\pm$ SE) for the Carolina wren based on 180 males and 169 females banded in Muscle Shoals, Alabama, 1992–2008. The best-fit model for annual survival in Carolina wrens included a significant time effect ($\phi_{year}p.$).

Table 4. Reproductive traits of neotropical buff-breasted wrens and north-temperate Carolina wrens, and the results of statistical analyses comparing the species. Data are presented as mean ± SE (n).

Reproductive trait	Buff-breasted wren	Carolina wren	t or Z value	p-value
Clutch size	2.8 ± 0.06 (41)	4.6 ± 0.10 (60)	−8.33	< 0.0001
Brood size	2.6 ± 0.16 (18)	4.1 ± 0.15 (46)	−4.981	< 0.0001
Incubation period (d)	16.3 ± 0.11 (16)	15.8 ± 0.11 (78)	2.33	0.02
Nestling period (d)	16.5 ± 0.30 (19)	13.3 ± 0.35 (26)	4.95	< 0.0001
Nesting cycle (d)	32.3 ± 0.50 (10)	28.5 ± 0.53 (12)	5.13	< 0.0001
Mass (g) of nestlings 12–14 d old	16.3 ± 0.22 (13)	16.4 ± 0.38 (12)	0.11	0.9
Re-nesting interval after nest failure (d)	11.5 ± 0.70 (24)	12.06 ± 1.12 (58)	1.27	0.2
Number of breeding attempts yr^{-1}	2.1 ± 0.17 (38)	3.0 ± 0.17 (37)	4.46	< 0.0001
Individual breeding season length yr^{-1}	61.8 ± 5.0 (33)	113.1 ± 4.4 (41)	7.77	< 0.0001

from successful nests (3.94 ± 0.08, n = 189). Buff-breasted wren parents cared for 1–3 nestlings (mode = 3), of which only two typically fledged from successful nests (1.96 ± 0.12, n = 28).

Incubation and nestling periods were significantly longer in the tropical species, resulting in a nesting cycle that was longer by 4 d on average in buff-breasted than Carolina wrens (Table 4). The length of the incubation period was variable in Carolina wrens, ranging from 13 to 18 d, whereas buff-breasted wren nests always hatched after 16–17 d of incubation. Nestling periods were variable in both species and nestlings fledged up to 3 d earlier than and up to 3 d after the average fledgling age in the population; the causes of this variability are unknown. The nestling period in buff-breasted wrens was on average 3.8 d longer than in Carolina wrens.

On average, Carolina wrens initiated more breeding attempts per year than buff-breasted wrens (Table 4). Re-nesting interval after nest failure did not differ between the two species, and when nests failed, females of both species initiated replacement clutches 11–12 d later on average. We had too few observations in buff-breasted wrens for analysis of re-nesting interval after offspring fledged (n = 3 double-brooded pairs), but our data point to large differences between species. Re-nesting interval after nest success in buff-breasted wrens was 53.3 ± 18.9 d (n = 3) compared with the relatively short interval of 13.8 ± 1.27 (n = 49) in Carolina wrens.

At a population level, breeding seasons for buff-breasted and Carolina wrens spanned 161 d (3 May–11 Oct) and 187 d (8 Mar–10 Sept), respectively. Females of both species initiated most clutches between May and July (Haggerty and Morton 1995, Gill unpubl.). The population estimate for buff-breasted wrens is based on only one breeding season (1998) for which we had the best sampling and maximum breeding season length may be longer in years in which clutches are initiated earlier (e.g. the first clutch in 1999 was 6 April compared with 3 May in 1998). Individual Carolina wren pairs bred over a significantly longer season than buff-breasted wrens (Table 4), commonly initiating second and even third clutches after successfully fledgling young from the first nest.

Parental care

Buff-breasted and Carolina wrens provisioned whole broods similarly. Female wren provisioning visits to nests

h^{-1} did not differ between species ($F_{1,51} = 0.11$, p = 0.74), with nestling age ($F_{1,111} = 0.90$, p = 0.34), or from a species × nestling age interaction ($F_{1,111} = 0.02$, p = 0.90). A similar pattern was found for male feeding visits to nests h^{-1} (species: $F_{1,41} = 0.55$, p = 0.46; nestling age: $F_{1,114} = 0.46$, p = 0.50; species × nestling age: $F_{1,114} = 0.58$, p = 0.45) and for the total number of visits to nests h^{-1} (species: $F_{1,51} = 1.92$, p = 0.17; nestling age: $F_{1,112} = 0.66$, p = 0.50; species × nestling age: $F_{1,112} = 0.01$, p = 0.91). By contrast, a significant species effect existed for male, female and total feeding visits $nestling^{-1}$ h^{-1} models (Table 5). In all models, buff-breasted wren parents provisioned individual nestlings more than Carolina wrens (Fig. 2). The other independent variables in the models had no effect (Table 5).

Prey loading did not differ between species, as buff-breasted and Carolina wren parents only brought one prey item to the nest at a time. However, there was a species effect for the prey size h^{-1} models for both sexes (female: $F_{1,53} = 7.04$, p = 0.01; male: $F_{1,48} = 11.8$, p = 0.001). Carolina wrens delivered significantly larger prey than buff-breasted wrens (Fig. 2). The other independent variables in the models had no effect (p > 0.05). The mass of 12–14 d nestlings old did not differ between species (Table 4).

Reproductive success

No difference in survival functions was detected between buff-breasted and Carolina wren nests using survival analysis (log-ranks test, $\chi^2 = 0.91$, DF = 1, p > 0.3) or MARK (Fig. 3, Table 6). In the early portion of the nesting period (day 1–20), survival of Carolina wren nests appeared higher than for buff-breasted wren nests, but this

Table 5. Results from fixed effect tests of mixed models (REML) on provisioning rates for neotropical buff-breasted wrens and north-temperate Carolina wrens during the second half of their nestling periods.

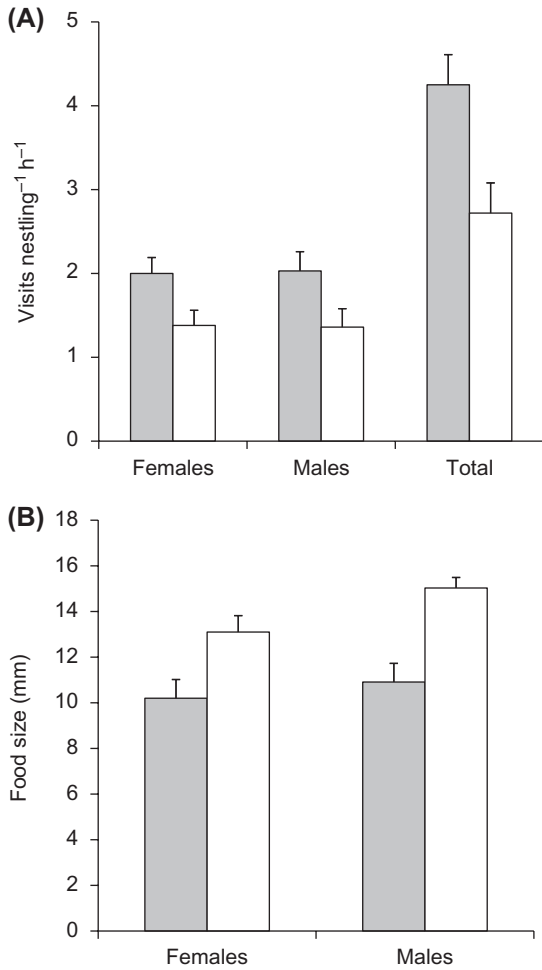| Response variable	Effect	DF	F ratio	p > F
Female visits/ nestling/h	Species	1,55	5.15	0.027
	Nestling age	1,112	0.36	0.547
	Species × nestling age	1,112	0.01	0.908
Male visits/nestling/h	Species	1,48	4.39	0.042
	Nestling age	1,113	0.01	0.925
	Species × nestling age	1,113	0.21	0.648
Total visits/nestling/h	Species	1,55	8.80	0.005
	Nestling age	1,112	0.30	0.585
	Species × nestling age	1,112	0.00	0.986

(A)

(B)

Figure 2. Provisioning of nestlings during the second half of the nestling period by adult buff-breasted (n = 17 pairs, gray bars) and Carolina (n = 27, white bars) wrens. (A) Least squares mean (± SE) number of visits nestling⁻¹ h⁻¹ by females and males, plus the combined total visits. (B) Least squares mean (± SE) of prey size (mm) delivered by female and males.
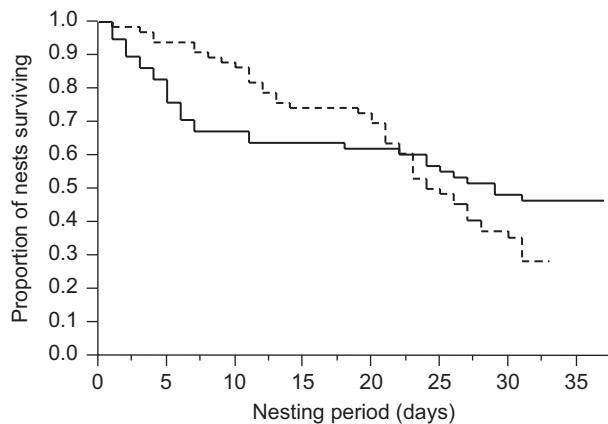

Figure 3. Cumulative survival functions for nests of neotropical buff-breasted wrens (solid line) and north-temperate Carolina wrens (hatched line) showing the proportion of nests of each species surviving in relation to nest age. Survival functions did not differ between species (p > 0.3).

Table 6. Measures of reproductive success for neotropical buff-breasted wrens and north-temperate Carolina wrens.

Measure of reproductive success	Buff-breasted wrens	Carolina wrens
Success estimate – Survival Analysis (95% CI, n)[a]	0.455 (0.333–0.584, 57)	0.369 (0.254–0.471, 66)
Success estimate – MARK (95% CI, n)[a]	0.440 (0.310–0.564, 57)	0.391 (0.283–0.499, 66)
Fledgling success[b]	0.75 ± 0.12 (78)	1.42 ± 0.19 (104)
Annual fecundity[c]	1.8 ± 0.98 (31)	4.8 ± 3.64 (38)

[a]Success estimates were based on nest survival to fledging, which occurred on day 32 of the nesting cycle for buff-breasted wrens and day 29 for Carolina wrens.
[b]Fledging success was defined as the number of nestlings that fledged nest⁻¹.
[c]Annual fecundity was defined as the number of fledglings pair⁻¹ yr⁻¹.

pattern reversed during the latter portion of the nesting cycle (day 20–30; Fig. 3). Indeed, more buff-breasted wren nests failed during the egg than nestling stages (72 vs 28% of failed nests) and more Carolina wren nests failed during the period of nestling care (39 vs 61%, $\chi^2 = 6.88$, DF = 1, p = 0.009). Most failures were due to predation in both species (93.5% of 31 failed buff-breasted wren nests and 70% of 44 failed Carolina wren nests; $\chi^2 = 6.06$, DF = 1, p = 0.015), but buff-breasted wren nests also failed due to infertility (3.2%) and undetermined reasons (3.2%), and Carolina wren nests failed following abandonment (23%), brood parasitism (5%), and inclement weather (2%).

Using MARK, the daily survival rates for buff-breasted wrens and Carolina wrens were 0.975 ± 0.004 and 0.968 ± 0.004, respectively, and these estimates yielded similar nest success values to those obtained through survival analysis methods (Table 6). Fledging success did not differ between species (Wilcoxon two-sample test, Z = 1.27, p = 0.20). However, Carolina wrens experienced significantly higher annual fecundity than the tropical wren (Wilcoxon two-sample test, Z = 3.96, p < 0.001), fledging more than twice the number of offspring yr⁻¹ than buff-breasted wrens (Table 6).

Estimates of survival to age of first reproduction

Survival to age of first reproduction (S_a) was estimated based on annual adult mortality (0.35 for female buff-breasted wrens, 0.49 for Carolina wrens) and annual fecundity per female (0.9 for buff-breasted wrens, 2.4 for Carolina wrens). S_a was 0.389 and 0.204 for the tropical and temperate wrens, corresponding to 58 and 40% of mean adult survival values in buff-breasted and Carolina wrens, respectively. Annual adult survival for Carolina wrens varied among years from 0.14–0.67, and this range of survival estimates generated values of S_a ranging from 0.058 to 0.279 for first-year Carolina wrens.

Discussion

Comparisons of a broad suite of life-history traits from closely related species living at different latitudes may provide novel insights into life-history evolution. Our study

revealed a striking similarity between neotropical and north-temperate wrens in the overall duration of their breeding seasons, but with clear differences in reproductive strategies. Carolina wrens laid multiple clutches of five eggs with relatively short periods of parental care over an extended season. With this strategy, Carolina wrens had more than double the annual fecundity of buff-breasted wrens. By contrast, buff-breasted wrens typically focused on a single small brood over a similar period of time, provisioning individual nestlings at higher rates as well as providing extended periods of post-fledgling care (Gill and Stutchbury 2010, Gill unpubl.). With this strategy, buff-breasted wrens appear to optimize first-year survival, which we estimated as almost twice that of Carolina wrens. Below, we discuss what these and other findings from our study of a phylogenetically matched pair of wrens reveal about hypotheses for life-history evolution in birds.

Nest predation

High nest predation selects for a life history characterized by small clutches, many reproductive attempts per season, reduced activity around nests, and shorter nesting cycles (Table 1). We found little evidence that nest predation influenced life history differences between buff-breasted and Carolina wrens, as key predictions of this hypothesis were not supported. Nest survival and fledgling success (number of fledglings nest^{-1}) were similar between low- and high-latitude species, results consistent with previous multi-species studies that find limited evidence for latitudinal differences in nest predation (Robinson, W. D. et al. 2000, Martin et al. 2006, Brawn et al. 2011). In addition, buff-breasted wrens displayed a longer nesting cycle than Carolina wrens, mostly due to a longer period of nestling care, rather than incubation period which was similar between species. Finally, contrary to expectations, parents of the two species showed similar age-corrected provisioning rates and prey loading to whole broods and temperate Carolina wrens brought larger prey items to nestlings than did the tropical wrens. Thus, despite a longer time in the nest and greater accumulation of mortality risk, buff-breasted wren parents did not compensate by feeding less often or by bringing more and larger prey items per feeding visit. Nest predation appears to be the key reason for nest failure in both species, with over 90 and 70% of nest failures in buff-breasted and Carolina wrens, respectively. However, nest predation does not appear to be a main driver of life history differences between these species.

One caveat to our results is that data on Carolina wrens were collected from nest boxes. Whether nest boxes positively or negatively affect nest success is unclear, as comparisons of nest success in boxes and natural nests from the same population are limited and contradictory (Lambrechts et al. 2010). Carolina wren nests are very difficult to find, and we are aware of only one study that monitored nest success in a robust sample of natural nests in comparison with artificial nests (Jackson et al. 2011). Jackson et al. (2011) found slightly higher nest success in natural nests than the artificial ones, and an overall higher nest success than detected in our study. The latter finding might suggest that predators may have developed search

images for our nest boxes, resulting in predation rates that could be elevated relative to natural nests. If so, then our comparison of nest success may be compromised, which is a possibility that we unfortunately cannot test. However, nest success results are not the only findings that are inconsistent with the nest predation hypothesis (see above). Therefore, we suggest that nest success should be viewed carefully, but that this result is consistent with findings from the broader suite of traits considered.

Food limitation

Food limitation and adult survival hypotheses share a number of predictions (Table 1), most of which were supported in the current study, but the critical prediction of the food-limitation hypothesis was not. Although parents of the tropical species provisioned whole broods at a lower rate than temperate parents, consistent with food limitation, per capita provisioning is also predicted to be lower in the tropical wrens, but the opposite pattern was observed for female, male and total visits per nestling. Moreover, although likely at different developmental stages, mass of 12–14 d old nestlings was similar between species, which suggests that food was not limited and that more feeding visits did not translate into faster growth in buff-breasted wrens (Ricklefs 1976).

Unexpectedly, brood reduction appeared to occur in buff-breasted wrens, which may support the idea of food limitation (Ricklefs 1976). Starvation of entire broods was never recorded in either species, but most pairs of the tropical wren failed to fledge their entire broods: 85% of females laid three eggs, but 82% of pairs fledged only 1 or 2 offspring. This did not appear to occur as consistently in Carolina wrens. Our findings contrast with those of an experimental manipulation of clutch size in neotropical spotted antbirds *Hylophylax naevioides*. Styrsky et al. (2005) found that the number of young fledged was equivalent to clutch sizes in almost all cases, even when clutches were made larger than naturally occurs in the species. Thus, spotted antbirds, which never lay three egg clutches, are capable of fledging all of them, whereas buff-breasted wrens, which typically lay a larger clutch, seems able to fledge only two young. Further study is needed to better understand brood reduction in buff-breasted wrens, as well as to determine whether it occurs in other tropical wren species, many of which lay more than the two eggs so characteristic of tropical passerines.

Adult survival and offspring quality

Evidence for differences in adult annual survival across latitudes has been contradictory (Karr et al. 1990, Johnston et al. 1997, Sandercock et al. 2000, Blake and Loiselle 2008), possibly because of methodological differences among studies, in particular the use of banding versus banding-resighting data (Ghalambor and Martin 2001). Our survival estimates, based on multiple resightings of banded individuals, revealed mean annual survival of adults to be approximately 16% higher in buff-breasted (0.67) than Carolina wrens (0.51). In years with severe winters, Carolina wren annual survival was extremely low

(< 15%), and approximately one-fifth of those for buff-breasted wrens on average, as well as for Carolina wrens during more benign years. These results provide evidence for latitudinal differences in adult survival, which is expected to lead to latitudinal differences in reproductive effort and parental care (Ashmole 1963, Ricklefs 1980, Martin et al. 2000).

Our results support the hypothesis that tropical wrens invest more in offspring quality and temperate wrens invest in offspring quantity. Buff-breasted and Carolina wrens re-nested after a similar number of days after nests failed, but buff-breasted wrens did not appear to commonly attempt second broods after successfully fledging young. When pairs did so, the interval between fledgling of the first brood and initiation of the second clutch was prolonged relative to re-nesting intervals in successful Carolina wrens. Overall age-corrected provisioning rates to the entire brood did not differ between species, but per capita age-corrected provisioning rates in the tropical wrens were higher than for the temperate wrens and both males and females made more provisioning visits per nestling in buff-breasted than Carolina wrens. This difference in per capita provisioning may be compounded over the nestling period, as nestlings of the tropical species stay on average 3 d longer in the nest than do temperate offspring. The higher investment in offspring in buff-breasted wrens continues through an extended post-fledging period (Russell 2000, Tarwater and Brawn 2010), as parents continue to provision offspring well past the age at which juveniles of most temperate birds, including Carolina wrens, disperse (Haggerty and Morton 1995, Gill unpubl.) and nutritionally independent juveniles delay natal dispersal for 10 months on average (Gill and Stutchbury 2010). Our estimates of offspring survival are consistent with these observations, as survival to the age of first reproduction is higher in buff-breasted (~40%) than Carolina wrens (~20%; Tarwater and Brawn 2010, Tarwater et al. 2011).

Conclusion

Our comparison of a suite of life history traits in phylogenetically matched species that breed at different latitudes finds most support for the hypothesis that differences in adult survival and reproductive effort between tropical and north-temperate species select for different life history strategies. Despite similarly prolonged breeding seasons, buff-breasted wrens invest in single broods thereby optimizing first-year survival, whereas Carolina wrens invest in multiple small broods thereby optimizing annual fecundity. Given some conflicting findings regarding food limitation, future work on these species should examine further the influence of food limitation, in particular by measuring incubation attentiveness and nestling growth rates in both species, and identifying potential mechanisms of brood reduction in buff-breasted wrens.

References

Ahumada, J. A. 2001. Comparison of the reproductive biology of two neotropical wrens in an unpredictable environment in northeastern Colombia. – Auk 118: 191–210.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. – Ibis 103: 458–473.

Badyaev, A. and Ghalambor, C. 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. – Ecology 82: 2948–2960.

Blake, J. G. and Loiselle, B. A. 2008. Estimates of apparent survival rates for forest birds in eastern Ecuador. – Biotropica 40: 485–493.

Bonduriansky, R., Maklakov, A., Zajitschek, F. and Brooks, R. 2008. Sexual selection, sexual conflict and the evolution of ageing and life span. – Funct. Ecol. 22: 443–453.

Brawn, J. D., Angehr, G., Davros, N., Robinson, W. D., Styrsky, J. N. and Tarwater, C. E. 2011. Sources of variation in the nesting success of understory tropical birds. – J. Avian Biol. 42: 61–68.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach, 2nd ed. – Springer.

Cody, M. L. 1966. A general theory of clutch size. – Evolution 20: 174–184.

Cooch, E. G. and White, G. C. (eds) 2012. Program MARK: a gentle introduction, 11th ed. – < www.phidot.org/software/mark/docs/index.html >.

Ferretti, V., Llambias, P. E. and Martin, T. E. 2005. Life-history variation of a neotropical thrush challenges food limitation theory. – Proc. R. Soc. B 272: 769–773.

Ghalambor, C. K. and Martin, T. E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. – Science 292: 494–497.

Gill, S. A. 2004. First record of cooperative breeding in a *Thryothorus* wren. – Wilson Bull. 116: 337–341.

Gill, S. A. 2011. Buff-breasted wren (*Cantorchilus leucotis*). – In: Schulenberg, T. S. (ed.), Neotropical birds online. Cornell Lab of Ornithology, Ithaca, < http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp = 535596 >.

Gill, S. A. and Stutchbury, B. J. M. 2005. Nest building is an indicator of parental quality in the monogamous neotropical buff-breasted wren (*Thryothorus leucotis*). – Auk 122: 1169–1181.

Gill, S. A. and Stutchbury, B. J. M. 2006. Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). – Behav. Ecol. Sociobiol. 61: 245–261.

Gill, S. A. and Vonhof, M. J. 2006. Sexing monochromatic birds in the field: cryptic sexual size dimorphism in buff-breasted wrens (*Thryothorus leucotis*). – Ornitol. Neotrop. 17: 409–419.

Gill, S. A. and Stutchbury, B. J. M. 2010. Delayed dispersal and territory acquisition in neotropical buff-breasted wrens (*Thryothorus leucotis*). – Auk 117: 372–378.

Gill, S. A., Vonhof, M. J., Stutchbury, B. J. M., Morton, E. S. and Quinn, J. S. 2005. No evidence for acoustic mate guarding in duetting buff-breasted wrens (*Thryothorus leucotis*). – Behav. Ecol. Sociobiol. 57: 557–565.

Haggerty, T. M. 2006. Sexual size dimorphism and assortative mating in Carolina wrens. – J. Field Ornithol. 77: 259–265.

Haggerty, T. M. and Morton, E. S. 1995. Carolina wren (*Thryothorus ludovicianus*). – In: Poole, A. and Gill, F. (eds), The birds of North America, no. 188. Academy of Natural Sciences, Philadephia, and American Ornithologists' Union, Washington, DC.

Haggerty, T. M., Morton, E. S. and Fleischer, R. C. 2001. Genetic monogamy in Carolina wrens (*Thryothorus ludovicianus*). – Auk 118: 215–219.

Jackson, A. K., Evers, D. C., Etterson, M. A., Condon, A. M., Folsom, S. B., Detweiler, J., Schmerfeld, J. and Cristol, D. A. 2011. Mercury exposure affects the reproductive success of a free-living terrestrial songbird, the Carolina wren (*Thryothorus ludovicianus*). – Auk 128: 759–769.

Jetz, W., Sekercioglu, C. H. and Böhning-Gaese, K. 2008. The world-wide variation in avian clutch size across species and space. – PLoS Biol. 6: 2650–2657.

JMP 2007. Statistics and graphics guide. – SAS Inst., Cary, NC, USA.

Johnston, J. P., Peach, W. J., Gregory, R. D. and White, S. A. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. – Am. Nat. 150: 771–789.

Karr, J. R., Nichols, J. D., Klimkiewicz, M. K. and Brawn, J. D. 1990. Survival rates of tropical and temperate forests: will the dogma survive? – Am. Nat. 136: 277–291.

Lack, D. 1947. The significance of clutch-size. – Ibis 89: 302–352.

Lambrechts, M. M., Adriaensen, F., Ardia, D. R., Artemyev, A. V., Atiénzar, F., Bańbura, J., Barba, E., Bouvier, J.-C., Camprodon, J., Cooper, C. B., Dawson, R. D., Eens, M., Eeva, T., Faivre, B., Garamszegi, L. Z., Goodenough, A. E., Gosler, A. G., Grégoire, A., Griffith, S. C., Gustafsson, L., Johnson, L. S., Kania, W., Keišs, O., Llambias, P. E., Mainwaring, M. C., Mänd, R., Massa, B., Mazgajski, T. D., Møller, A. P., Moreno, J., Naef-Daenzer, B., Nilsson, J.-Å., Norte, A. C., Orell, M., Otter, K. A., Park, C. R., Perrins, C. M., Pinowski, J., Porkert, J., Potti, J., Remes, V., Richner, H., Rytkönen, S., Shiao, M.-T., Silverin, B., Slagsvold, T., Smith, H. G., Sorace, A., Stenning, M. J., Stewart, I., Thompson, C. F., Török, J., Tryjanowski, P., van Noordwijk, A. J., Winkler, D. W. and Ziane, N. 2010. The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. – Acta Ornithol. 45: 1–26.

Lebreton, J.-D., Burnham, K. P., Clobert, J. and Anderson, D. R. 1992. Modeling survival and testing hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.

Logue, D. 2009. Black-bellied wren (*Thryothorus fasciatoventris*). – In: Schulenberg, T. S. (ed.), Neotropical birds online. Cornell Lab of Ornithology, Ithaca, <http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp = 33086>.

Maccoll, A. D. C. and Hatchwell, B. J. 2003. Sharing of caring: nestling provisioning behavior of long-tailed tit, *Aegithalos caudatus*, parents and helpers. – Anim. Behav. 66: 955–964.

Mann, N. I., Barker, F. K., Graves, J. A., Dingess-Mann, K. A. and Slater, P. J. B. 2006. Molecular data delineate four genera of "*Thryothorus*" wrens. – Mol. Phylogenet. Evol. 40: 750–759.

Mann, N. I., Dingess, K. A., Barker, F. K., Graves, J. A. and Slater, P. J. B. 2009. A comparative study of song form and duetting in neotropical *Thryothorus* wrens. – Behaviour 146: 1–43.

Marshall-Ball, L. and Slater, P. J. B. 2003. Nesting and breeding biology of the plain wren (*Thryothorus modestus zeledoni*). – Ornitol. Neotrop. 14: 339–343.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? – J. Avian Biol. 27: 263–272.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. – Proc. R. Soc. B 269: 309–316.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? – Auk 121: 289–301.

Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J. and Fontaine, J. J. 2000. Parental care and clutch sizes in North and South American birds. – Science 287: 1482–1485.

Martin, T. E., Bassar, R. D., Bassar, S. K., Fontaine, J. J., Lloyd, P., Mathewson, H. A., Niklison, A. M. and Chalfoun, A. 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. – Evolution 60: 390–398.

McNamara, J. M., Barta, Z., Wikelski, M. and Houston, A. I. 2008. A theoretical investigation of the effect of latitude on avian life histories. – Am. Nat. 172: 331–345.

Moreau, R. E. 1944. Clutch size: a comparative study, with reference to African birds. – Ibis 86: 286–347.

NCDC 2011. National Climatic Data Center. – <www.ncdc.noaa.gov/oa/ncdc.html>.

Nur, N., Holmes, A. L. and Geupel, G. R. 2004. Use of survival time analysis to analyze nesting success in birds: an example using loggerhead shrikes. – Condor 106: 457–471.

Remsen, J. V. Jr, Cadena, C. D., Jaramillo, A., Nores, M., Pacheco, J. F., Robbins, M. B., Schulenberg, T. S., Stiles, F. G., Stotz, D. F. and Zimmer, K. J. 2010. A classification of the bird species of South America. – American Ornithologists' Union, <www.museum.lsu.edu/~Remsen/SACCBaseline.html>.

Ricklefs, R. E. 1976. Growth rates of birds in the humid New World tropics. – Ibis 118: 179–207.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. – Auk 97: 38–49.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. – Condor 102: 9–22.

Ricklefs, R. E. 2010. Parental investment and avian reproductive rate: Williams's principle reconsidered. – Am. Nat. 175: 350–361.

Ricklefs, R. E. and Bloom, G. 1977. Components of avian breeding productivity. – Auk 94: 86–96.

Robinson, T. R., Robinson, W. D. and Edwards, E. C. 2000. Breeding ecology and nest-site selection of song wrens in central Panama. – Auk 117: 345–354.

Robinson, W. D., Robinson, T. R., Robinson, S. K. and Brawn, J. D. 2000. Nesting success of understory forest birds in central Panama. – J. Avian Biol. 31: 151–164.

Robinson, W. D., Hau, M., Klasing, K. C., Wikelski, M., Brawn, J. D., Austin, S. H., Tarwater, C. E. and Ricklefs, R. E. 2010. Diversification of life histories in New World birds. – Auk 127: 253–262.

Russell, E. 2000. Avian life histories: is extended parental care the southern secret? – Emu 100: 377–399.

Sandercock, B. K., Beissinger, S. R., Stoleson, S. H., Melland, R. R. and Hughes, C. R. 2000. Survival rates of a neotropical parrot: implications for latitudinal comparisons of avian demography. – Ecology 81: 1351–1370.

Schaefer, H.-C., Eshiamwata, G. W., Munyekenye, F. B. and Böhning-Gaese, K. 2004. Life-history of two African *Sylvia* warblers: low annual fecundity and long post-fledging care. – Ibis 146: 427–437.

Skutch, A. F. 1949. Do tropical birds rate as many young as they can nourish? – Ibis 91: 430–455.

Styrsky, J. N., Brawn, J. D. and Robinson, S. K. 2005. Juvenile mortality increases with clutch size in a neotropical bird. – Ecology 86: 3238–3244.

Tarwater, C. E. and Brawn, J. D. 2010. The post-fledging period in a tropical bird: patterns of parental care and survival. – J. Avian Biol. 41: 479–487.

Tarwater, C. E., Ricklefs, R. E., Maddox, J. D. and Brawn, J. D. 2011. Pre-reproductive survival in a tropical bird and its implications for avian life histories. – Ecology 92: 1271–1281.

Taylor, J. 2011. Bay wren (*Cantorchilus nigricapillus*). – In: Schulenberg, T. S. (ed.), Neotropical birds online. Cornell Lab of Ornithology, Ithaca, <http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp = 533516>.

Williams, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. – Am. Nat. 100: 687–690.