

## Factors affecting the probability of double brooding by Southern House Wrens

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**ABSTRACT.** Seasonal fecundity of birds is influenced by clutch sizes and the number of successful breeding attempts during a breeding season. As such, understanding the factors that determine the decision to initiate multiple broods within a season and the consequences of this reproductive tactic is important. We examined the frequency of double brooding by Southern House Wrens (*Troglodytes aedon musculus*) in eastern Argentina. We analyzed inter- and intraseasonal variation in double brooding and evaluated the effect of weather conditions and laying date on the frequency and occurrence of this behavior. Finally, we assessed the effect of double brooding on the seasonal and lifetime productivity of female Southern House Wrens. During our 8-year study, we found that ~43% (range = 17–83% each year) of breeding pairs attempted a second brood after successfully raising a first brood. The probability of females having a second brood was affected by the laying date of the first nesting attempt, but was independent of the number of young fledged. About 65% of females that started laying eggs before the first quarter of each breeding season produced a second brood, and this percentage decreased to ~40% after this period. In addition, variation in double-brooding frequency among years was related to weather conditions, with the proportion of pairs double brooding increasing with increased precipitation early in the breeding season. More precipitation likely contributed to an increase in insect abundance. Although double brooding increased the seasonal and lifetime productivity of female Southern House Wrens, additional study of the survival and fate of fledglings from first and second broods is needed to assess the importance of multi-brooding in the reproductive success of these wrens.

### **RESUMEN. Factores que afectan la probabilidad de doble puesta en *Troglodytes aedon musculus***

La fecundidad estacional de las aves está influenciada por el número de huevos producidos y por el número de intentos reproductivos exitosos realizados durante una temporada reproductiva. Por lo tanto, es importante entender los factores que determinan la decisión de producir nidadas múltiples dentro de una misma temporada y las consecuencias de esta táctica reproductiva. Examinamos la frecuencia de dobles puestas en la Ratona Común (*Troglodytes aedon musculus*) en el este de Argentina. Además analizamos la variación inter- e intraestacional de las dobles puestas y evaluamos los efectos de las condiciones climáticas y el día en que se inicia la primera nidada, en la ocurrencia y frecuencia de este comportamiento. Finalmente, evaluamos el efecto de la doble puesta sobre la productividad estacional y a lo largo de la vida de las hembras de Ratona. En los 8 años de nuestro estudio encontramos que el ~43% (rango = 17–83% cada año) de las parejas reproductivas intentaron una segunda nidada luego de criar exitosamente la primera. La probabilidad de que las hembras efectuaran un segundo intento de nidificación, fue afectada por la fecha de puesta del primer intento, pero fue independiente del número de volantones producidos. Alrededor del 65% de las hembras que iniciaron su puesta antes del primer cuarto de cada estación reproductiva produjeron una segunda camada, pero este porcentaje se redujo un ~40% luego de este período. Además, la variación de la frecuencia de dobles puestas entre años estuvo relacionada con las condiciones climáticas, incrementándose la proporción de parejas que produjeron una segunda puesta con la precipitación ocurrida al principio de la temporada reproductiva. El incremento en la precipitación puede contribuir al incremento en la disponibilidad de alimento (abundancia de insectos). Aunque la doble puesta incrementó la productividad tanto estacional como a lo largo de la vida de las hembras de Ratona, sería necesario realizar estudios complementarios sobre la probabilidad de supervivencia de los volantones producidos durante la primera y segunda camada para evaluar la importancia de la nidificación múltiple en el éxito reproductivo del ave.

*Key words:* environmental factors, fecundity, lifetime productivity, nesting success, reproductive effort, *Troglodytes aedon musculus*

Life history theory predicts that, given the resources required for reproduction, parents

should have the ability to choose between investing in current or in future reproduction to maximize their fitness (Stearns 1992, Ogden and Stutchbury 1996). According to this theory, short-lived species should favor their current

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fecundity over their own survival whereas long-lived species should instead prioritize their own survival over immediate fecundity and the survival of their offspring (Drent and Daan 1980, Sæther and Baake 2000, Husby et al. 2009). This trade-off between fecundity and survival not only affects the decision to invest in each breeding season, but may also determine the number of reproductive events during each season (Verhulst et al. 1997).

In short-lived passerines, the number of young produced during a breeding season could be maximized by increasing the clutch size in a given nesting attempt or by increasing the number of breeding attempts per season (Nagy and Holmes 2005a). Multiple brooding (i.e., producing more than one brood in a breeding season) is a common reproductive tactic among temperate and tropical passerines (Martin 1987, Holmes et al. 1992, Smith and Marquiss 1995, Ogden and Stutchbury 1996, Jacobs et al. 2013). Multi-brooded females may be able to increase their reproductive success considerably (Smith and Roff 1980, Geupel and DeSante 1990, Nagy and Holmes 2004, 2005a, Weggler 2006, Williams 2012), although raising additional broods might also affect the probability of survival of offspring (Verhulst et al. 1997). However, not all females who produce a successful first brood attempt a second brood (Rodenhouse and Holmes 1992, Smith and Marquiss 1995, Ogden and Stutchbury 1996, Jacobs et al. 2013). Differences among females in the number of broods per breeding season are usually explained by differences in when they initiate first broods (Geupel and DeSante 1990, Holmes et al. 1992, Smith and Marquiss 1995, Verboven and Verhulst 1996, Verhulst et al. 1997) and food availability (Verboven et al. 2001, Brickle and Harper 2002, Morrison and Bolger 2002, Nagy and Holmes 2005a, Husby et al. 2009). Other factors such as age, reproductive experience, and female condition can also affect the likelihood of having a second brood (De Laet and Dhondt 1989, Geupel and DeSante 1990, Whittingham et al. 2002, Nagy and Holmes 2005a, Lohmus and Björklund 2009, Bowers et al. 2012, Jacobs et al. 2013).

Given the recognized importance of the frequency of multiple brooding on annual fecundity and population growth (Martin 1995, Sæther and Baake 2000, Nagy and Holmes 2004, 2005a, Weggler 2006, Williams 2012),

understanding the factors that influence the decision to initiate multiple broods within a season and the consequences of this reproductive tactic is important. We examined the frequency of double brooding by Southern House Wrens (*Troglodytes aedon musculus*) and the factors affecting the probability of such behavior. We also evaluated the consequences of double brooding on the annual and lifetime fecundity of females. Specifically, we assessed the effects of the timing of clutch initiation during the first nesting attempt and weather on the occurrence of double brooding by Southern House Wrens. We hypothesized that early nesting and favorable weather conditions during the rearing of a first brood could increase the probability of attempting a second brood.

## METHODS

**Study site.** Our study was carried out over eight years (2004–2011) on an 8-ha woodland at General Lavalle, Buenos Aires province, Argentina (36°28'S, 56°58'W). At this site, 93 nest boxes are attached to trees, 1.5 m above the ground, and have been used by House Wrens for nesting since 2004. The study area is a temperate grassland in the flooding pampas (Vervoorst 1967). The area is flat, low, and marshy, with little of the land >4 m above sea level. Woodlands are present in a naturally fragmented pattern on the higher areas. The woodlands are composed mainly of *Celtis ehrenbergiana*, *Scutia buxifolia*, and *Schinus longifolius*. In our study area, mean monthly temperatures in mid-summer (January) are ~21°C and drop to ~7°C in mid-winter (July). The average annual rainfall is 1048 mm, and ~70% of the annual rainfall typically occurs during spring and fall (Vervoorst 1967).

**Study species.** Southern House Wrens are short-lived insectivorous passerines that, in our study area, are year-round residents that defend all-purpose territories. Males have a higher survival probability than females (0.53 vs. 0.34, respectively; Cormack–Jolly–Seber models based on marking and resighting birds in our study population from 2004 to 2011; Carro 2012). The predominant social mating system is monogamy (only 1% of males were polygynous; Llambías and Fernández 2009), but females engage in extra-pair copulations (Labarbera et al. 2010). The breeding season extends from

mid-October to mid- to late January, lasting about 80 days (range = 76–85; P. Llambías, unpubl. data). Typical clutch sizes are 4–5 eggs (range = 3–7 eggs), the incubation period lasts 13 or 14 days, and nestlings remain in nests for 16 or 17 days (Llambías and Fernández 2009). Only females incubate, but both males and females feed nestlings. Food items provided to nestlings include spiders and adult and larval insects (M. E. Carro, pers. observ.). After a successful breeding attempt, females may start a second nest (Llambías and Fernández 2009). There is no consistent difference in the number of eggs laid or in the success of first and second nests (Llambías and Fernández 2009).

**Data collection.** Early in the breeding season (early October), we performed regular censuses in the study area to identify individuals and breeding territories. The study site included 30–60 territories defended by males. Each territory had at least one nest box. We checked territories and nest boxes periodically during the breeding season to identify territorial males and determine their social status (single vs. monogamous). We were able to band most adults (87%) for individual recognition with a unique combination of a numbered aluminum band and three plastic color bands. We captured most males (95%) and some females (32%) before first nesting attempts using mist-nets and playback of male song. The rest of the adults were captured at nest boxes using a wig-wag trap when nestlings were 10–12 days old. All captured individuals were sexed using external morphological characteristics (presence of brood patch or cloacal protuberance) and behavior (only males sing). During the breeding season, we visited nest boxes every 3–4 days, recording the laying date (when the first egg was laid), clutch size, brood size, number of young fledged, and nest fate. We considered a nesting attempt successful if at least one nestling fledged. We banded nestlings at nests with a unique numbered aluminum band when they were 10–12 days old.

The nesting attempt of each female was classified as a first attempt when it was the first nest of the season and at least one egg was laid, as a replacement attempt when birds initiated a second or third nest following a failed attempt, and as a double-brood attempt when a female started a second nesting attempt following a successful first attempt. For this study, we limited most

of our analyses to females that fledged young from their first nests, excluding those that failed in their first nesting attempt because only one of 22 first breeding pairs that failed in their first nesting attempt re-nested successfully and attempted a double brood. Therefore, females were classified as either single-brooded if their first nesting attempt was successful and they did not initiate another nest in the same breeding season or as double-brooded if they initiated a second nest after a successful first nesting attempt, independently of the fate of that second nesting attempt. Only nests built by banded females were included into our analyses.

For each nesting attempt, we calculated the relative date when females started laying eggs by considering the time in days since they laid their first egg relative to the date when the first egg in the population was laid in each season (hereafter, laying date). For double brooders, we estimated the interval between broods as the time in days between the date when fledglings left the first nest and the date when a female started laying eggs in the second nest.

**Annual variation of double brooding.**

The frequency of double broods was calculated for each year of our study, and the effect of the median Julian date of the first nesting attempts (the median time in days when females laid their first egg relative to 1 January of each year) and meteorological conditions during October and November on the proportion of double broods were tested using generalized linear models (GLM). Weather conditions were included in our analyses using an aridity index for October and November of each year based on monthly accumulated precipitation and mean temperature. We obtained precipitation data from a station in General Lavalle (5 km from our study area), but temperature data were obtained from Dolores (36°19'S, 57°38'W), located ~60 km from our study area. Given the high correlation between temperatures at General Lavalle and Dolores (correlations between mean monthly temperatures for 1995 and 1996,  $P < 0.01$ ,  $R > 0.99$ ), we assumed that temperatures at Dolores were a reliable estimator of those in General Lavalle. We then estimated the de Martonne's index of aridity  $I$  for October and November of each year as  $P/(T + 10)$ , with  $P$  being the monthly accumulated precipitation and  $T$  the mean monthly temperature (de Martonne 1927). High values of  $I$  indicate wet conditions,

whereas low values reflect dry conditions. This index was estimated for October and November because these months correspond to the start of the breeding season and the peak period of first breeding attempts (Llambías and Fernández 2009).

We constructed different models for the effect of the weather and the temporal factors because some variables were highly correlated. The median laying date was correlated with the index of aridity for October (Spearman rank correlation,  $P = 0.03$ ), and marginally correlated with it for November (Spearman rank correlation,  $P < 0.1$ ). Thus, the effect of weather factors and median laying date of first nesting attempts were tested independently. The number of double broods during each year was included as the response variable in these models, and the total number of first nests was used as a covariate. We assumed a Poisson error distribution and a log link function and we included in the models the single factors as predictive variables. When we tested the effect of more than one single factor on the response variable, we also included the interaction among factors in the model.

#### Individual variation in double brooding.

To assess factors that affected the probability that females would produce a second brood, we used generalized linear mixed models (GLMM), with production of the second brood as a dichotomous response variable (produce/not produce), assuming a binomial distribution of errors and a logit link function. In these models, we included female identity as a random factor because one female could have more than one first breeding attempt in different seasons. Initially, we built a model with the laying date and number of fledglings as predictors nested within season (year).

We also examined the possible effects of weather and the number of fledglings in the first nesting attempt on the interval between nests for double brooders (from fledging of young in the first nest to the start of egg-laying in the second nest). We used a GLMM with the interval between broods as the response variable, and the aridity indices for October and November (see above) and number of fledglings produced during the first nest attempt as predictive factors. Female identity was included as a random factor because a female could be represented more than once in the dataset. We assumed a Poisson

distribution of errors and a log link function, and the single and the interaction effect of predictive factors were tested.

**Effect of double brooding on female survival and productivity.** The potential effect of double brooding on the probability of females surviving to the next breeding season was also tested using a GLMM. We included the survival probability of females as a dichotomous response variable (survive/not survived) in the model, and the age of females and whether or not they were double-brooders as predictors nested in the year. Brood size was included as a covariate and female identity was incorporated as a random factor. For this analysis, we assumed a binomial error distribution and a logit link function.

Finally, we analyzed the effect of double brooding on the productivity of females. For each female, we estimated seasonal productivity, defined as the sum of fledglings produced in the first and second broods each year, and lifetime productivity, defined as the total number of fledglings produced during a female's life (the sum of all fledglings produced during each year the female was alive). Because we never found marked adult females outside our study area, we believe that this constituted a reliable estimate of their lifetime productivity. We used a Poisson regression analysis (GLM) with the number of fledglings produced per season or per lifetime as the response variable, and number of breeding attempts and number of breeding seasons that each female was alive as predictors.

We carried out statistical analyses using GenStat DE3 (VSN International Ltd., Hemel Hempstead, UK). All GLM and GLMM models were tested by searching for the minimal explicative model, removing the non-significant factors first, and then the significant terms while checking for changes in statistical significance (Crawley 2005). All  $P$  values are two-tailed and differences were considered significant at  $P < 0.05$ . Values are presented as means  $\pm$  SE, unless indicated otherwise.

## RESULTS

**Annual variation in frequency of double brooding.** Overall, 43% (71/167) of House Wren pairs produced a second brood after having a successful first nest. The proportion of females with double broods differed significantly among the years, ranging from 17% in 2008 to

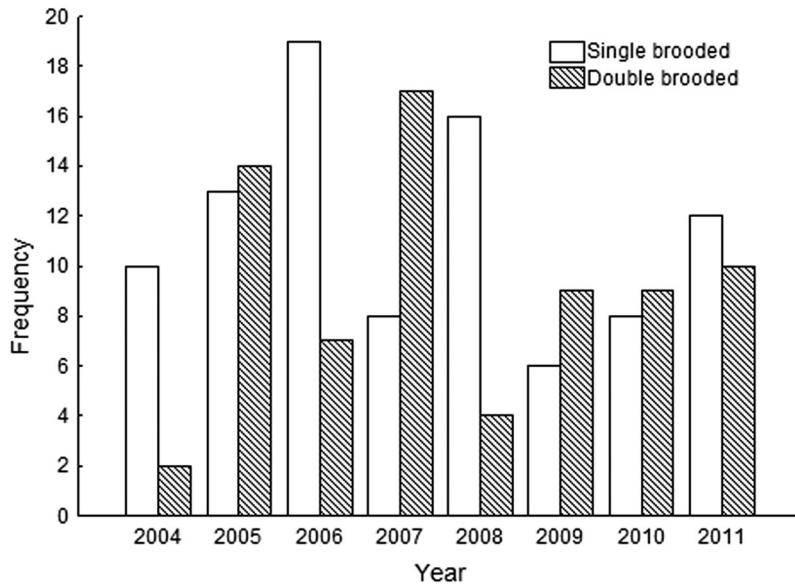


Fig. 1. Annual variation of the frequency of double brooding by Southern House Wrens.

83% in 2009 (Wald  $\chi^2_{7,52.7} = 22.3$ ,  $P = 0.007$ ; Fig. 1). This variation was not explained either by the median date of first nesting attempts or weather conditions during October. Only the aridity index for November explained the annual variation in the number of double broods (Wald  $\chi^2_{1,52.7} = 81.0$ ,  $P < 0.001$ ). We found a positive relationship between the frequency of double broods and the aridity level during November, with the proportion of pairs double brooding increasing with increased precipitation in November (Fig. 2).

#### Individual variation in double brooding.

About 58% (14/24) of females that survived at least one year and reared two broods in the first year also produced two broods in the second year. Similarly, ~43% (10/23) of females that produced a single brood in the first year produced one brood in the second year (Fisher's exact test,  $P = 0.56$ ). Double-brooding females waited, on average,  $14 \pm 5.7$  (SD) days after young fledged from first nests before initiating a second clutch (range = 4–27 days;  $N = 55$ ). About 45% of females that initiated a second brood started it within two weeks (25/55), the presumed time it takes for fledglings to reach independence (P. Llambías, unpubl. data). The time before initiating a second brood was independent of aridity conditions during October

and November ( $P > 0.4$ ), but this time increased with the number of fledglings produced (Wald  $\chi^2_{1,42} = 7.2$ ,  $P = 0.01$ ).

Laying date for first nests was a significant predictor of the occurrence of double brooding (Wald  $\chi^2_{8,53.9} = 84.7$ ,  $P < 0.001$ ). The probability of producing a second brood decreased with later laying dates (Fig. 3). About 76% of females (52/68) that produced a second brood initiated their first clutch during the first quarter of the breeding season (first 20 days after the laying of the first egg in the population), whereas 32.9% of females that started their first clutch later in the season produced a second brood (16/49). Considering the standardized date relative to the date the first clutch was initiated in the population each year, double-brooded females initiated their first clutches an average of  $14.8 \pm 8.3$  days ( $N = 70$ ) after the appearance of the first egg in the season, whereas single-brooded females waited  $28.0 \pm 16.5$  days ( $N = 90$ ).

**Female survival and productivity.** Survival probability of females was not affected either by double brooding (Wald  $\chi^2_{54} = 0.001$ ,  $P = 0.99$ ) or age (Wald  $\chi^2_{139} = 4.7$ ,  $P = 0.67$ ). Fewer than half of banded females survived for more than one year (44.4%, 60/135) and <5% of females survived for more than two

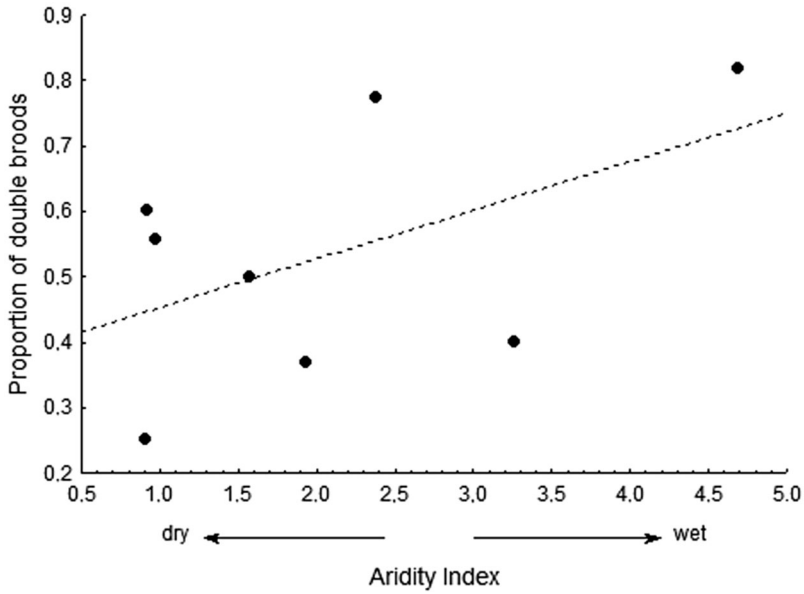


Fig. 2. Relationship between the proportion of double-brooded Southern House Wrens in our study population and weather conditions during November over eight breeding seasons. The Aridity Index represents the relationship between monthly accumulated precipitation and mean monthly temperature + 10 (de Martonne’s index of aridity; de Martonne 1927). High values of the aridity index indicate wetter conditions and low values indicate drier conditions.

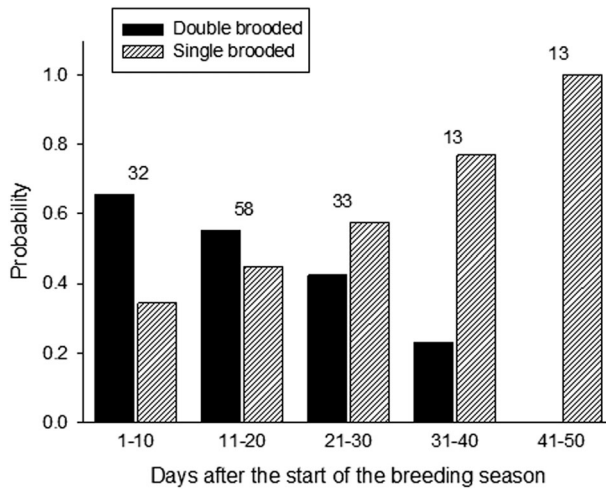


Fig. 3. Effect of egg-laying date on the probability of female Southern House Wrens being double- or single-brooded. All females that started laying eggs for their first nests of the season after day 41 were single-brooded. Numbers above the bars represent the sample sizes.

years (6/136). Double brooding increased the seasonal productivity of females (Wald  $\chi^2_8 = 59.4$ ,  $P < 0.001$ ), almost doubling the mean number of fledglings produced in a season

( $4.2 \pm 0.9$  fledglings for single brooders and  $7.9 \pm 0.8$  fledglings for double brooders). The total number of breeding attempts also affected lifetime productivity of females. The number of

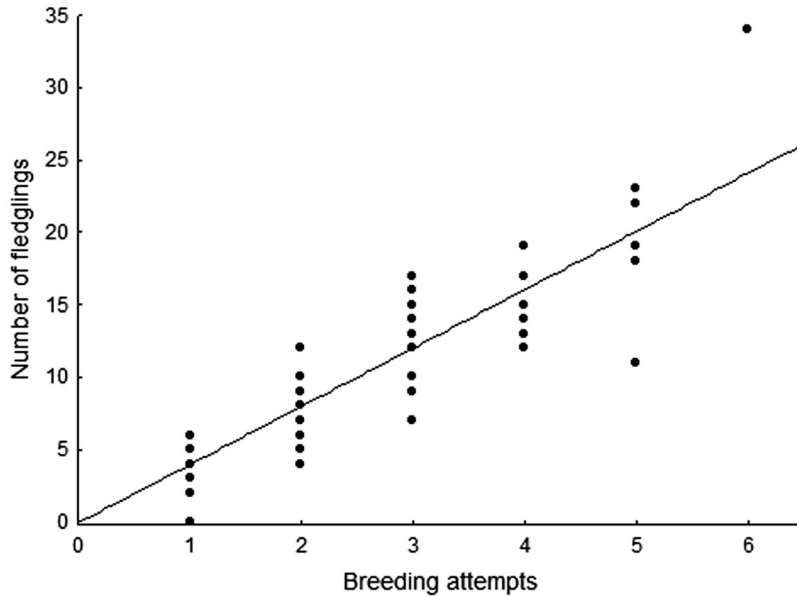


Fig. 4. Variation in the number of fledglings produced by female Southern House Wrens relative to the number of breeding attempts during their lifetimes. Each point represents a single female.

fledglings produced increased with the number of breeding attempts by females after controlling for female age (Wald  $\chi^2_1 = 45.0$ ,  $P < 0.001$ ; Fig. 4).

### DISCUSSION

During our eight-year study, ~43% of Southern House Wrens attempted to raise a second brood after having successfully raised a first brood. Double brooding increased both the annual and lifetime productivity of females. In northern House Wrens (*T. a. aedon*), multi-brooded males (both polygynous and sequentially monogamous males) produced up to twice as many fledglings as single-brooded males regardless of extrapair paternity (Poirier et al. 2004). The fecundity of other short-lived passerines is also influenced by the number of broods females are able to rear successfully (Klomp 1970, Smith and Roff 1980, Geupel and DeSante 1980, Holmes et al. 1992, Morrison and Bolger 2002, Nagy and Holmes 2004, 2005a, Weggler 2006). However, increased fecundity does not necessarily indicate an increase in the reproductive success of individuals that double-breed. For Southern House Wrens, most juveniles (>90%) recruited into the popula-

tion fledged from first broods (Carro 2012) so fledglings from second broods may only provide marginal fitness benefits to parents. Additional studies focusing on the survival and fate of fledglings from first and second broods are needed to assess the importance of multi-brooding in the reproductive success of these wrens.

During our study, the percentage of double-brooded females varied among years from 17 to 83%. This variation was apparently related to the weather conditions experienced during first nesting attempts. The frequency of double broods in our study population decreased with decreasing aridity indices (i.e., drier conditions). House Wrens feed on insects on the ground or on the trunks and branches of trees (M. E. Carro, pers. observ.), and wetter conditions presumably contributed to an increase in insect availability. A relationship between food abundance and frequency of double brooding has also been reported for other passerines (Arcese and Smith 1988, Rodenhouse and Holmes 1992, Nagy and Holmes 2005a,b, Husby et al. 2009, Jacobs et al. 2013).

Within-year variation in the probability of producing a double brood for Southern House Wrens was explained mainly by the date females

began laying eggs. In addition, we detected a decrease in the frequency of double brooding as the season progressed. About 65% of females that started laying eggs during the first quarter of each breeding season were able to produce a second brood, whereas this percentage decreased to about 40% for females that started egg-laying after that time. Early nesting has also been found to be a good predictor for double brooding by northern House Wrens, with pairs more likely to initiate second breeding attempts if females start laying eggs early in the season (Poirier et al. 2004).

Nest predation could also influence the likelihood of double brooding. In our study, only one of 22 females that failed in their first nesting attempt and re-nested also successfully raised a second brood. Southern House Wrens nesting in natural cavities have higher rates of nest failure than those nesting in nest boxes (Llambías and Fernández 2009). As a result, the frequency of double brooding for wren populations nesting in natural cavities could be lower than observed in our study, and nest predation/failure could be the most important factor determining this frequency. However, the effect generated by the loss of a nest could be related to the fact that re-nesting implies a delay in the onset of the reproductive attempt, reducing the temporal window available to initiate a double brood.

Seasonal variation in the probability of producing a second brood is usually explained by differences between early and late breeding pairs in phenotypic or environmental quality (the individual quality hypothesis) or by a seasonal change in environment conditions (e.g., food availability and predation risk) that affect the probability of raising an additional brood (Verhulst and Nilsson 2008). For Southern House Wrens breeding in nest boxes, nest success was found to be similar for early and late nesting attempts (Llambías and Fernández 2009) so predation risk apparently does not vary seasonally. Instead, environmental temperatures increase and precipitation decreases as the season progresses (Vervoort 1967), i.e., environmental conditions deteriorate during the breeding season and likely affect food availability. Therefore, a delay in laying a first clutch could lead to less-favorable late conditions for raising a second brood. In addition to harsher conditions, the decision to start a second brood could also be influenced by the limited fitness benefits

of double brooding. For tropical wrens, Young (1996) suggested that parents should invest more care in offspring, enhancing their probability of survival and recruitment because this might have a greater influence on fitness than maximizing fecundity. If so, having a second brood could reduce the fitness of early offspring and, therefore, affect the reproductive success of parents.

We found that some female Southern House Wrens that initiated egg-laying early in the season did not initiate second broods. This interindividual variation in the decision to start a second brood could be explained by differences in the quality of individuals and territories. Females that produced second broods may be breeding in territories with greater food availability, may be of higher phenotypic quality, or may have higher quality mates that reduce their reproductive costs (Daan et al. 1990, Moreno et al. 1998, Nagy and Holmes 2005a,b, Verhulst and Nilsson 2008, Lömhús and Björklund 2009). In northern House Wrens, females in poor body condition have a lower probability of attempting a second brood than those in better physical condition (Whittingham et al. 2002, Bowers et al. 2012). In Southern House Wrens, these factors remain to be tested.

Costs related to post-fledging care could also affect a female's decision to start a second brood. In northern House Wrens, females were more likely to start a second breeding attempt when males fed fledglings (Bart 1990). Given the low survival of females in both northern and Southern House wrens (0.25 and 0.34, respectively; Carro 2012, Llambías et al., unpubl. data), females may tend to invest less in current broods and increase their reproductive success by attempting a second brood (Verboven et al. 2001, Gruebler and Naef-Daenzer 2008). Accordingly, we found that ~45% of female Southern House Wrens that initiated a second breeding attempt started their nesting attempt <14 days after fledging of the first brood. This suggests that, in these cases, males likely assumed most post-fledging parental care, and that male behavior may affect the ability of females to attempt second broods.

In sum, double brooding by Southern House Wrens may be influenced primarily by environmental conditions, but variation in individual quality/condition may also help explain why some birds initially laid eggs earlier than others.



Moreover, a female's decision could be affected by a trade-off between the costs of reduced parental attention for the first brood and the benefits of a second breeding attempt (Smith et al. 1987). However, assessing the fitness consequences of double brooding will require additional study of the effects of such behavior on the survival of young from first and second broods.

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#### LITERATURE CITED

- ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *Journal of Animal Ecology* 57: 119–136.
- BART, J. 1990. Male care, mate switching, and future reproductive success in a double-brooded passerine. *Behavioral Ecology and Sociobiology* 26: 307–313.
- BOWERS, E. K., S. K. SAKALUK, AND C. F. THOMPSON. 2012. Experimentally increased egg production constrains future reproduction of female House Wrens. *Animal Behaviour* 83: 495–500.
- BRICKLE, N. W., AND D. G. C. HARPER. 2002. Agricultural intensification and the timing of breeding of Corn Buntings *Miliaria calandria*: in an intensively managed agricultural landscape, few females attempted a second brood. *Bird Study* 49: 219–228.
- CARRO, M. E. 2012. *Dispersión natal y reproductiva de la ratona común Troglodytes musculus*. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires, Argentina.
- CRAWLEY, M. J. 2005. *Statistics: an introduction using R*. John Wiley, West Sussex, UK.
- DAAN, S., C. DIJKSTRA, AND J. M. TINBERGEN. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the ultimate control of variation in laying date and clutch size. *Behaviour* 114: 83–116.
- DE LAET, J. F., AND A. A. DHONDT. 1989. Weight loss of the female during the first brood as a factor influencing second brood initiation in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. *Ibis* 131: 281–289.
- DE MARTONNE, E. 1927. Regions of interior basin drainage. *Geographical Review* 17: 397–414.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225–252.
- GEUPEL, G. R., AND D. F. DESANTE. 1990. Incidence and determinants of double brooding in Wrentits. *Condor* 92: 67–75.
- GRÜEBLER, M. U., AND B. NAEF-DAENZER. 2008. Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. *Ecology* 89: 2736–2745.
- HOLMES, R. T., T. W. SHERRY, P. P. MARRA, AND K. E. PETTIT. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler, in an unfragmented temperate forest. *Auk* 109: 321–333.
- HUSBY, A., L. E. B. KRUIK, AND M. E. VISSER. 2009. Decline in the frequency and benefits of multiple brooding in Great Tits as a consequence of a changing environment. *Proceedings of the Royal Society B* 276: 1845–1854.
- JACOBS, A. C., L. L. READER, AND J. M. FAIR. 2013. What determines the rates of double brooding in the Western Bluebird? *Condor* 115: 386–393.
- KLOMP, H. 1970. The determination of clutch-size in birds: a review. *Ardea* 58: 1–124.
- LABARBERA, K., P. E. LLAMBÍAS, E. R. A. CRAMER, T. D. SCHAMING, AND I. J. LOVETTE. 2010. Synchrony does not explain extra-pair paternity rate variation in Northern or Southern House wrens. *Behavioral Ecology* 21: 773–780.
- LLAMBÍAS, P. E., AND G. J. FERNÁNDEZ. 2009. Effects of nestboxes on the breeding biology of Southern House Wrens *Troglodytes aedon bonariae* in the southern temperate zone. *Ibis* 151: 113–121.
- LÖHMUS, M., AND M. BJÖRKLUND. 2009. Leptin affects life history decisions in a passerine bird: a field experiment. *PLoS ONE* 4: e4602.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* 18: 453–487.
- . 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101–127.
- MORENO, J., A. DE LEON, J. A. FARGALLO, AND E. MORENO. 1998. Breeding time, health and immune response in the Chinstrap Penguin *Pygoscelis antarctica*. *Oecologia* 115: 312–319.
- MORRISON, S. A., AND D. T. BOLGER. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia* 133: 315–324.
- NAGY, L. R., AND R. T. HOLMES. 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? *Journal of Avian Biology* 35: 487–491.
- , AND ———. 2005a. To double-brood or not? Individual variation in the reproductive effort in Black-throated Blue Warblers (*Dendroica caerulescens*). *Auk* 122: 902–914.
- , AND ———. 2005b. Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* 86: 675–681.
- OGDEN, L. J. E., AND B. J. M. STUTCHBURY. 1996. Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. *Condor* 98: 736–744.
- POIRIER, N. E., L. A. WHITTINGHAM, AND P. O. DUNN. 2004. Males achieve greater reproductive success

- through multiple broods than through extrapair mating in House Wrens. *Animal Behaviour* 67: 1109–1116.
- RODENHOUSE, N. L., AND R. T. H. HOLMES. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73: 357–372.
- SÆTHER, B. E., AND O. BAKKE. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81: 642–653.
- SMITH, R. D., AND M. MARQUISS. 1995. Production and costs of nesting attempts in Snow Buntings *Plectrophenax nivalis*: why do they attempt second broods? *Ibis* 137: 469–476.
- SMITH, J. N. M., AND D. A. ROFF. 1980. Temporal spacing of broods, brood size, and parental care in Song Sparrows. *Canadian Journal of Zoology* 58: 1007–1015.
- SMITH, H. G., H. KÄLLANDER, AND J.-Å. NILSSON. 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. *Auk* 104: 700–706.
- STEARNS, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- VERBOVEN, N., J. M. TINBERGEN, AND S. VERHULST. 2001. Food, reproductive success and multiple breeding in the Great Tit *Parus major*. *Ardea* 89: 387–406.
- , AND S. VERHULST. 1996. Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. *Journal of Animal Ecology* 65: 264–273.
- VERHULST, S., AND J.-Å. NILSSON. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B* 363: 399–410.
- , J. M. TINBERGEN, AND S. DAAN. 1997. Multiple breeding in the Great Tit; a trade-off between successive reproductive attempts? *Functional Ecology* 11: 714–722.
- VERVOORST, F. 1967. Las comunidades vegetales de la Depresión del Salado (provincia de Buenos Aires). INTA. La vegetación de la República Argentina. Serie Fitogeogeográfica 7: 1–62.
- WEGGLER, M. 2006. Constraints on, and determinants of, the annual number of breeding attempts in the multi-brooded Black Redstart *Phoenicurus ochruros*. *Ibis* 148: 273–284.
- WILLIAMS, T. D. 2012. *Physiological adaptations for breeding in birds*. Princeton University Press, Princeton, NJ.
- WHITTINGHAM, L. A., S. M. VALKENAAR, N. E. POIRIER, AND P. O. DUNN. 2002. Maternal condition and nestling sex ratio in House Wrens. *Auk* 119: 125–131.
- YOUNG, B. E. 1996. An experimental analysis of small clutch size in tropical House Wrens. *Ecology* 77: 472–488.