

Social mating system, male parental care contribution and life history traits of a southern Sedge Wren (*Cistothorus platensis platensis*) population: a comparison with northern Sedge Wrens (*Cistothorus platensis stellaris*)

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Abstract The study of geographic variation of social mating systems can shed new light on our understanding of how ecological variables shape extant mating associations. We report data on the social mating system, parental care and life history traits of a temperate population of southern Sedge Wrens (*Cistothorus platensis platensis*) in South America. We compared our results with published records of two temperate populations of northern Sedge Wren (*Cistothorus platensis stellaris*) in North America. The southern temperate population had a lower social polygyny rate, greater male contribution to feeding nestlings and smaller clutch sizes than northern temperate populations. A similar pattern of low rates of social polygyny and smaller clutch sizes in the south versus moderate rates of social polygyny and bigger clutch sizes in the north has been reported for the House Wren (*Troglodytes aedon*). This suggests that different selective forces may be operating in northern and southern wren populations. Future work in additional study populations is essential to establishing the generality of our results.

Keywords Breeding biology · Clutch size · Social monogamy · Paternal care · Social polygyny

Zusammenfassung

Das Paarungssystem, der Beitrag der Männchen zur Brutpflege und life history-Merkmale in einer südlichen Population des Seggenzaunkönigs (*Cistothorus platensis platensis*) im Vergleich zu einer nördlichen (*Cistothorus platensis stellaris*)

Die geographischen Variationen von Paarungssystemen zu untersuchen kann zu neuen Erkenntnissen darüber führen, wie ökologische Gegebenheiten bestehende Paar-Verbindungen gestalten. Wir präsentieren hier Daten zum sozialen Paarungssystem, zur Brutpflege und zu charakteristischen Merkmalen im Leben einer in gemäßigten Breiten lebenden Population des südlichen Seggenzaunkönigs (*Cistothorus platensis platensis*) in Südamerika. Unsere Ergebnisse vergleichen wir mit entsprechenden, bereits publizierten Ergebnissen für zwei nördliche Populationen (*Cistothorus platensis stellaris*) in Nordamerika. Die südliche Population zeigte weniger Polygynie, einen größeren Beitrag der Männchen am Füttern der Brut sowie kleinere Gelegegrößen als die nördlichen Populationen. Über ein ähnliches Muster für geringere Polygynie und Gelegegrößen wurde bereits für südliche versus nördliche Populationen des Hauszaunkönigs (*Troglodytes aedon*) berichtet. Dies lässt vermuten, dass in nördlichen und südlichen Zaunkönig-Populationen ein unterschiedlicher Selektionsdruck zum Zug kommt. Weitere Untersuchungen anderer Populationen sind unerlässlich, um die generelle Aussagekraft unserer Ergebnisse zu untermauern.

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Introduction

The study of intraspecific variation in social mating systems can shed new light on our understanding of how ecological variables shape extant mating associations (Lott 1991; Halupka et al. 2014; Remes et al. 2015). While entire avian lineages are predisposed to particular social mating systems by traits that evolved millions of years ago, present ecological conditions facilitate differences in social mating systems between closely related species or between populations of the same species (Owens and Bennett 1997; Bennett and Owens 2002). However, studies of intraspecific variation in social mating systems are scarce as they require detailed information on partnerships between banded individuals in different populations across a broad geographic scale (see Dunn and Robertson 1992; Llambías et al. 2012; Halupka et al. 2014).

Differences in social mating systems are often associated with differences in parental care patterns, which in turn are thought to be related to food availability (Silver et al. 1985; Mock and Fujioka 1990; Webster 1991; Székely et al. 2000). Monogamy is generally associated with food limitation and biparental care (Silver et al. 1985; Mock and Fujioka 1990; Ligon 1999). In contrast, social polygyny is often associated with greater food abundance and less male contribution to parental care (Webster 1991; Slagsvold and Lifjeld 1994; Gowaty 1996; Olson et al. 2008). Differences in food availability between populations can explain differences in polygyny rates as documented for Reed Warblers (*Acrocephalus scirpaceus*) (Halupka et al. 2014). However, the importance of male parental care does not always explain differences in social mating systems between populations. In Tree Swallows (*Tachycineta bicolor*) the frequency of polygyny did not significantly differ between two populations that greatly differed in food abundance and in the importance of biparental care (Dunn and Robertson 1992). Indeed, variation in social mating systems can also arise through differences in adult sex ratio, and temporal and/or spatial distribution of mates and other resources (Emlen and Oring 1977; Wittenberger and Tilson 1980; Reichard 2003; Kokko and Jennions 2008; Liker et al. 2013; Székely et al. 2014).

The House Wren (*Troglodytes aedon*) and the Sedge Wren (*Cistothorus platensis*) are excellent models for the study of geographic variation in social mating systems. Both species are distributed from southern Canada to Tierra del Fuego (Argentina and Chile), and are found in both tropical and temperate environments (Brewer 2001). While House Wrens inhabit woodlands and forest edges, Sedge Wrens inhabit grasslands and marshlands (Kroodsma and Brewer 2005), providing an opportunity to evaluate the importance of ecological conditions in shaping

the social mating system. Previously we have shown that differences in polygyny rate between northern and southern House Wrens are not associated with differences in the importance of male parental care in feeding the young (Llambías 2012; Llambías et al. 2012, 2015). Here we present a complementary study on the social mating system, parental care and life history traits of a southern Sedge Wren population in temperate South America and compare our results with published data from two northern Sedge Wren populations in temperate North America (Crawford 1977; Burns 1982). This represents the first detailed description of the social mating system for southern Sedge Wrens and is the first step towards evaluating broad patterns of geographic variation in social mating systems along the species range.

Methods

Study species

The Sedge Wren is a small insectivorous passerine that inhabits grasslands and marshes from southern Canada to southern Tierra del Fuego in Argentina and Chile (Brewer 2001; Kroodsma and Brewer 2005). Although several genetic lineages have been described (Campagna et al. 2012; Robbins and Nyári 2014), the Sedge Wren is considered a single species (Remsen et al. 2017).

Northern Sedge Wrens are migratory, breeding in north-central North America and wintering along the Atlantic coast of the southeastern USA and northeastern Mexico (Schramm et al. 1986; Bedell 1996; Kroodsma et al. 1999a, b; Herkert et al. 2001; Hobson and Robbins 2009). During the breeding season, northern Sedge Wrens are highly nomadic with little site fidelity, producing first broods and second broods in different areas of their breeding range (Bedell 1996; Kroodsma et al. 1999a, b; Hobson and Robbins 2009). In contrast, southern Sedge Wrens in Central and South America are year-round residents (Brewer 2001; Kroodsma and Brewer 2005).

Sedge Wren males sing and defend multipurpose territories; only females incubate the eggs and brood the nestlings (Herkert et al. 2001). During the breeding season, Sedge Wrens frequently build three different nest structures: incomplete nests, non-breeding nests and breeding nests (Kroodsma and Brewer 2005). Incomplete nests are rudimentary spheroid structures of entangled grasses (Burns 1982). Non-breeding and breeding nests are dome-shaped structures, constructed mainly with dry grasses (Burns 1982). In southern Sedge Wrens we have observed both sexes adding material to incomplete, non-breeding and breeding nests. In contrast, Burns (1982) observed that in northern Sedge Wrens, the male builds the three nest

types and the female only adds lining to the breeding nest. Non-breeding and breeding nests have a similar structural layer; however, non-breeding nests generally lack an inner cup of lining (Burns 1982; P. Llambías, unpublished data). Non-breeding nests have often been associated with courtship behavior and female attraction, but may also be used as dormitories or decoys for predators (Burns 1982). The possible function of multiple nest-building in southern Sedge Wrens is currently under study.

Study populations

We studied a resident population of southern Sedge Wrens in the flood plain of the Uspallata stream (32°38'S, 69°22'W, 1800 m a.s.l.) in Mendoza Province, Argentina. Although mean annual precipitation is low (100 mm), the riparian grasslands and small swamps are irrigated by the Uspallata and San Alberto streams and form a fertile corridor that extends into the Mendoza River (Carretero 2000). Several bird species associated with humid grasslands are present in the area (e.g., Many-colored Rush-Tyrant *Tachuris rubigastria*; Spectacled Tyrant *Hymenops perspicillatus*; Wren-like Rushbird *Phleocryptes melanops*). Seasonality is pronounced, with low temperatures and occasional snowfall during the austral winter and warmer temperatures and milder conditions in the austral summer (Carretero 2000). Most breeding occurs between September and March.

We compared the breeding biology of Sedge Wrens in our study population with published data from two temperate northern Sedge Wrens populations from Iowa [Dewey's Pasture, 43°11'N, 94°55'W, 410 m a.s.l. (Crawford 1977)] and Minnesota [Crookston, 47°40'N, 96°21'W, 270 m a.s.l. (Burns 1982)].

General field procedures

During five breeding seasons (October–February, 2010–2014) we carried out intensive fieldwork and searched for nests in 99 territories (14–26 territories per year). The number of territories varied between years because we expanded the study area in 2011 and 2012, and because some were lost to river flooding. We used behavioral observations of males during nest-searching and nest-monitoring to determine the boundaries of territories. In each visit, we opportunistically recorded singing perches, agonistic behavior and resighted males while foraging and nest-building to define the territories. We later transcribed our field observations to satellite images to delineate approximate territorial boundaries. We visited the site briefly during the austral winter (April–August) to confirm the presence of banded pairs in the territories.

We captured 72 males and 42 females with mist nets and banded them with a combination of one aluminum and three color bands. We banded both adults in 60.6% of the territories, the male in 92.9% and the female in 62.6%.

Using both behavioral observations and systematic searching, we located 92 incomplete, 76 non-breeding and 196 breeding nests. To compare the frequency of nest types (incomplete nests, non-breeding nests and breeding nests) between southern and northern Sedge Wrens, we calculated the mean number of nest types per male territory per breeding season for our study population and the Minnesota population.

We checked breeding nests every 2–3 days, and on a daily basis close to hatching and fledging to record more exactly hatching and fledging date. During egg-laying and incubation, we counted the eggs by introducing two fingers inside the nest. We counted the nestlings by extracting them from the nest during the hatching stage (day 0 up to and including day 2) and when setting a camera to film parental care (see below). We banded nestlings with an aluminum band when they were 10 days old.

We observed Shiny Cowbird (*Molothrus bonariensis*) eggs in 64 (32.7%) breeding nests ($n = 196$) and removed them as part of a cowbird control project. Hence, our estimates of breeding success did not consider the costs of incubating a cowbird egg and raising a cowbird chick. We determined clutch size only for nests that survived throughout the egg-laying stage and where there was no evidence of cowbird interference (e.g., pecked eggs, cowbird eggs, enlarged dome entrance).

To facilitate comparisons with the northern Sedge Wren, we calculated the incubation period as the number of days from clutch completion to hatching of the last nestling; and the nestling period, as the number of days from hatching of the first nestlings until fledging.

We recorded a nest as “successful” if at least one nestling fledged from the nest. We considered a nest to be “preyed upon” if eggs or young disappeared before fledging and as “deserted” if both adults were observed alive and eggs were cold or nestlings were dead. We assumed “weather-caused desertion” if breeding nests were deserted the day after heavy rains or river flooding. We assumed that “nest failure” was caused by Shiny Cowbirds if the breeding nest was deserted after we had observed evidence of cowbird interference. We recorded a “Sedge Wren takeover” if eggs were pecked or nestlings were killed after a male had taken over part of the territory.

To compare breeding success between southern and northern Sedge Wrens, we calculated the proportion of successful breeding nests from a subset of 130 breeding nests that we found during egg-laying and for which final outcome was known. We excluded from the analysis three nests that failed due to human disturbance (horse

trampling, desertion after accidental female capture and egg fracture during nest check). We calculated the proportion of females that laid a second brood after a successful first nesting attempt per season for both southern and northern Sedge Wrens.

Parental care

We filmed breeding nests for at least 4 h continuously with micro-cameras (Mini 550 resolution button screw micro-camera) connected to a portable mini DVR (PV500 LITE) located 15–20 cm from the nests, disguised with small pieces of camouflaged netting and stems. We set cameras within the first hour after sunrise. To assess male parental care participation in feeding nestlings of southern Sedge Wrens, we filmed nests when nestlings were 2–4, 7–8 and 11–12 days (day 0 = day the majority of nestlings in a nest had hatched) for approximately 4 h (mean \pm SD; 2–4 days, 268.52 \pm 34.87 min; 7–8 days, 264.92 \pm 40.65 min; 11–12 days, 273.64 \pm 43.31 min). During video analysis, we determined the number of male and female trips to feed the nestlings.

To assess male participation in feeding nestlings in northern Sedge Wrens, we used the number of male and female trips of 14 nests with 4- to 10-day-old nestlings reported for Minnesota [98 h of observation from blinds (Burns 1982)]. To compare male contribution to feeding nestlings between northern and southern Sedge Wrens, we re-calculated male participation in the southern Sedge Wrens by lumping video sessions when nests were filmed more than once.

Social mating systems

We used territorial maps to determine the sociospatial association of males and females. Similar techniques were used to monitor the territories of ten males in Minnesota and 26 males in Iowa. We used data reported from the territorial maps to calculate the polygyny rate (polygynous males/total breeding males) for the three populations. We considered a male to be socially polygynous if it was associated with more than one female with overlapping reproductive activity. We did not observe polygynous males associated with more than two females in any of the populations. We considered social polygyny to be usurpation (*sensu* Freed 1986) when a paired male whose social partner was breeding expanded its territory, displaced a neighboring male and initiated a clutch with the resident female. We considered that social polygyny was the result of mate attraction when a secondary female initiated a clutch on the male's territory while the primary female was breeding or feeding fledglings.

Statistical analyses

We report means with \pm SE for all data. We analyzed life history variables, male parental care contribution and social polygyny rate using general linear modeling (GLM) and generalized linear mixed modeling (GLMM) in the R language and environment (version 3.3.0; R Core Team 2016). For these analyses we used the lme4 (Bates et al. 2015) and glmmADMB (Bolker et al. 2012) packages. We performed a post hoc Tukey honest significant difference (HSD) test comparisons with the multcomp R package (Hothorn et al. 2008).

We tested for differences in the mean number of nest types per territory between populations. We used GLMMs for each nest type and included nest type as response variable, population (Uspallata or Minnesota) as predictor and male identity as a random variable. When evaluating differences between populations in non-breeding and incomplete nests we used zero-inflated GLMMs with a quasi-Poisson error distribution (nbinom1) due to the high number of zero values in the data set. We used GLMM with a Poisson error distribution for evaluating differences between populations in the number of breeding nests per territory. In all these models we used a log link function.

We tested temporal variation in clutch size of southern Sedge Wrens using a GLMM, including breeding season (study year), laying date and their interaction as the predictors. We included a linear and quadratic terms for laying dates as clutch size seemed to have a non-linear relation with lay date. We considered lay day = 1 as the date when the first egg was laid in a given breeding season, and sequentially assigned laying dates for the rest of the clutches each season. We standardized linear and quadratic values of laying dates to facilitate the comparison of coefficients (Schielzeth 2010). We included clutch size as the response variable and female identity as a random factor. We assumed a Poisson error distribution and used a log link function. We assessed differences in clutch size between southern and northern Sedge Wrens using a GLM, including clutch size as the response variable and population as a predictor factor. To avoid pseudoreplication in the southern population, we used the modal clutch sizes for nests of the same female. We assumed a Poisson distribution of errors and used a log link function.

We compared breeding success of southern and northern Sedge Wren populations and the proportion of females that initiated a second brood after successfully producing a first brood in a given season using GLMs. We used a dichotomous response variable (success/non-success or double brooded/single brooded) and population as the predictor variable. We assumed a binomial error distribution with a logit link function.

We used GLMMs to evaluate whether southern Sedge Wren's male feeding contribution varied with nestling age. To account for multiple measurements of the same individual and temporal heterogeneity, we included the number of male feeding trips recorded at each nest as response variable and we fitted male identity and year as random terms. We initially explored if variation in male parental effort could be explained by the linear effects of nestling age. Potential variation of parental care over nestling age may be caused by both within-individual changes and between-individual variability (van de Pol and Verhulst 2006). Hence, we applied a within-subject centering method (van de Pol and Wright 2009) where nestling age was decomposed in within- and between-individual components. To estimate the within-individual component we calculated the difference between nestling age of each nest and the mean nestling age of nests attended by each male ($Age_{dif} = A_{ij} - \bar{A}_j$). To estimate the between-individual component, we calculated the mean nestling age of nests attended by the male j ($Male_{dif} = \bar{A}_j$). For the analysis of variation of male contribution, we included $(A_{ij} - \bar{A}_j)$ and \bar{A}_j as predictors. We also included the log of total number of feeding trips recorded (male + female feeding trips) and the number of nestlings as fixed covariates. For these models we assumed a Poisson error distribution with log link function.

We also evaluated the differences in male contribution to feeding nestlings of socially monogamous pairs between southern and northern Sedge Wrens using a GLM with a negative binomial error distribution with a log link function. We included in the model the total number of trips performed by males and females as a covariate.

We compared social polygyny rates between southern and northern Sedge Wrens using a GLM. We assumed a quasi-binomial distribution of errors and a logit link function. We included in the model the occurrence of polygyny as a dichotomous response variable and population as the predictor.

For each analysis, we used residual and normal probability plots to check the assumptions of the models. We tested the global contribution of the predictor factors explaining variation in the response variables by comparing the deviance of nested models (i.e., with and without the predictor) with the likelihood ratio test. All quoted P -values are two-tailed and differences were considered significant at $P < 0.05$.

Results

Life history traits

Southern Sedge Wrens remained on their territories year-round. Color-banded individuals were resighted in their

territories during both the austral winter and breeding season. In contrast, northern Sedge Wrens are migratory during the breeding season (Table 1).

During the study period, we located 367 southern Sedge Wren nests: 92 incomplete (25.1%), 76 non-breeding (20.7%) and 196 breeding nests (53.4%). We were unable to classify the status of three nests (0.8%). Once the female laid the first egg, no additional nests were built until the nestlings fledged or the breeding nest failed. Northern Sedge Wrens also build three nest types; however, in Minnesota, males continue nest building through the nestling period. As a consequence, northern Sedge Wrens build significantly more non-breeding nests than southern Sedge Wrens ($z = -9.59$; $P < 0.01$; Tables 1, 2). However, southern and northern Sedge Wrens did not differ significantly in the number of incomplete and breeding nests built ($z = 0.22$, $P = 0.82$ and $z = -0.43$, $P = 0.67$, respectively; Tables 1, 2).

We removed Shiny Cowbird eggs from 64 (32.6%) of 196 breeding nests. We could determine the fate of 130 breeding nests found during nest building. The main causes of nest failure were predation (49 nests, 37.7%), Shiny Cowbird interference (29 nests, 22.3%) and nest desertion (nine nests, 6.9%). In one nest (0.8%), eggs were pecked during incubation, presumably by a neighboring male that expanded its territory. Other causes of failure were nest collapse (one nest, 0.8%) and weather-related nest desertion (seven nests, 5.4%). Breeding success (number of breeding nests producing at least one fledgling) differed between populations (Tables 1, 2). Breeding success at our study population was lower than in Iowa and Minnesota (post hoc Tukey HSD test, $z = 4.11$, $P < 0.01$ and $z = 3.94$, $P < 0.01$, respectively), but it did not differ significantly between northern populations (post hoc Tukey HSD test, $z = 0.12$, $P = 0.99$; Tables 1, 2).

The proportion of females that successfully fledged at least one young and initiated a second brood differed between populations (Tables 1, 2). In our study population, a greater proportion of females started a second brood than in Iowa (post hoc Tukey HSD test, $z = 3.92$, $P < 0.01$). However, we did not detect a significant difference between our study population and the Minnesota one (post hoc Tukey HSD test, $z = 1.72$, $P = 0.19$; Table 1).

Southern Sedge Wrens laid smaller clutches than northern Sedge Wrens in Iowa ($z = 4.27$, $P < 0.001$; Tables 1, 2). We did not observe variation in clutch size throughout the breeding season (Fig. 1) nor between seasons in our study population (Table 3).

The southern Sedge Wrens' incubation period (days from clutch completion to the hatching of the last nestling) was 15.54 ± 0.13 d ($n = 41$). The nestlings remained in the nest for 15.82 ± 0.20 days ($n = 45$). The data ranges of the observed incubation and nestling periods overlapped

Table 1 Breeding variables of southern Sedge Wrens (*Cistothorus platensis platensis*) in Argentina (Mendoza) and northern Sedge Wrens (*Cistothorus platensis stellaris*) in the USA (Iowa and Minnesota)

Population	Southern Sedge Wren	Northern Sedge Wren	
	Uspallata, Argentina Non-migratory	Iowa, USA ^a Migratory	Minnesota, USA ^b Migratory
Migration			
Incomplete nests/territory [mean ± SE (<i>n</i>)]	0.93 ± 0.13 (99)		0.75 ± 0.35 (12)
Non-breeding nests/territory [mean ± SE (<i>n</i>)]	0.77 ± 0.11 (99)		5.17 ± 0.72 (12)
Breeding nests/territory [mean ± SE (<i>n</i>)]	1.98 ± 0.12 (99)		2.17 ± 0.17 (12)
Breeding success ^c	0.26 (130)	0.68 (31)	0.69 (26)
Proportion of double brooding ^d	0.77 (22)	0.00 (21)	0.44 (9)
Clutch size [mean ± SE (<i>n</i>)]	4.75 ± 0.08 (103)	6.87 ± 0.19 (31)	6.28 (18)
Incubation period (max.–min.)	14–18 days (41)	13–16 days (21)	
Nestling period (max.–min.)	12–19 days (45)	11–16 days (31)	
Male contribution to parental care [mean ± SE (<i>n</i>)]	0.50 ± 0.02 (72)		0.11 ± 0.04 (12)
Polygyny rate	0.03 (65)	0.19 (26)	0.20 (10)
Polygyny type	Usurpation (2)	Female attraction (5)	Female attraction (2)

Max. Maximum, min. minimum

^a Crawford (1977)

^b Burns (1982)

^c Breeding success was calculated as the number of successful nests/total number of breeding nests

^d Proportion of double brooding was calculated as the number of females that started a second brood after a successful first breeding attempt/total number of females that produced a successful first breeding attempt

between the northern and southern populations (Table 1). We were unable to compare statistically the developmental periods between populations as only the range or the means were reported for northern Sedge Wrens.

Parental care patterns

First, a mixed modeling approach using nestling age as a single factor showed a reduction of relative male contribution to feeding nestling with nestling age (Table 4; Fig. 2). The within-subject centering method revealed a significant effect of Age_{dir}. This method allowed us to confirm that males reduced their contribution relative to the total number of parental feeding visits, and was not caused by between-individual effects (Table 4).

The comparison of male contribution to feeding 3- to 11-day-old nestlings between populations revealed that monogamous male southern Sedge Wrens contributed more than monogamous male northern Sedge Wrens in Minnesota ($z = 7.37$, $P < 0.001$; Tables 1, 2).

Social mating systems

Social polygyny was rare in the southern Sedge Wren and significantly lower than in northern populations (Tables 1, 2).

Southern Sedge Wren males achieved polygyny by taking over the territory of a neighbor and its resident female ($n = 2$; Table 1). During the usurpation, females present in the usurped territory were building nests, which were eventually deserted. The resident males were displaced completely from their territories and established new territories in the following days. The nests of both secondary females were predated (during the egg stage and when nestlings were 1 day old). After failure, the territories were usurped by bachelor males that displaced the intruding males back to their original territories.

According to the sociospatial patterns provided by territory maps, all the polygynous northern Sedge Wren males attracted secondary females to their territories ($n = 7$); no instances of territorial takeover were recorded (Table 1).

Discussion

The Southern Sedge Wren population that we studied in central Argentina differs in life history traits, parental care patterns and social mating system from two northern Sedge Wren populations in North America. At our study population, Sedge Wrens were characterized by smaller clutches, greater male contribution to parental care and lower rates of social polygyny.

Table 2 Summary of statistical comparison of life history traits and reproductive behavior between southern and northern Sedge Wren populations

Variable	Coefficient	SE	χ^2	<i>P</i>
Incomplete nests/territory ^a			0.05	0.823
Uspallata	0.398	0.196		
Minnesota	0.291	0.444		
Non-breeding nests/territory ^a			48.66	<0.01
Uspallata	-0.273	0.136		
Minnesota	1.653	0.148		
Breeding nests/territory ^b			0.18	0.67
Uspallata	0.683	0.071		
Minnesota	0.773	0.196		
Breeding success ^c			29.68	<0.01
Uspallata	-1.038	0.199		
Iowa	0.742	0.384		
Minnesota	0.811	0.424		
Double brooding ^c			23.19	<0.01
Uspallata	1.224	0.509		
Iowa	-2.302	0.741		
Minnesota	-0.223	0.671		
Clutch size ^d			17.96	<0.01
Uspallata	1.528	0.06		
Iowa	1.927	0.071		
Male contribution to parental care ^a			-7.37	<0.03
Uspallata	-0.687	0.071		
Minnesota	-2.199	0.189		
Polygyny rate ^e			6.1	0.03
Uspallata	-3.45	0.729		
Iowa	-1.435	0.505		
Minnesota	-1.386	0.803		

^a Derived from zero-inflated generalized linear mixed modeling (GLMM) assuming a quasi-Poisson (nbinom1) error distribution and using a log link function

^b Derived from GLMM assuming a Poisson error distribution and using a log link function

^c Derived from general linear modeling (GLM) assuming Poisson error distribution and using a log link function

^d Derived from GLM assuming a binomial error distribution and using a logit link function

^e Derived from GLM assuming a quasi-binomial error distribution and using a logit link function

South temperate zone species often have smaller clutch sizes, longer developmental periods, lower breeding success, greater frequency of double brooding, sedentary lifestyle and greater adult survival than species in the north temperate zone (Yom-Tov 1994; Martin 1996; Peach et al. 2001; Stutchbury and Morton 2001; Russell et al. 2004; Macedo et al. 2008; Boyce and Martin 2017). Accordingly, our resident southern Sedge Wren population exhibited smaller clutch sizes and lower breeding success than migratory populations in Iowa and Minnesota (Tables 1, 2). We did not observe significant differences between our study population and the Minnesota population in the proportion of females that successfully fledged at least one young and initiated a second brood. The lack of double

brooding in Iowa should be taken with caution as some populations of northern Sedge Wrens may produce first and second broods in different regions of North America within the same breeding season (Bedell 1996; Kroodsmas et al. 1999a, b; Hobson and Robbins 2009). Also, we were unable to statistically test for differences in developmental periods between populations as only means or ranges were reported for northern Sedge Wrens (Table 1). However, differences in clutch sizes suggest different life history strategies that may also relate to parental investment and social mating systems (Russell et al. 2004; Martin 2014, 2015; Lloyd and Martin 2016).

Similarly to the pattern that we observed between Sedge Wren populations, temperate southern House Wrens lay

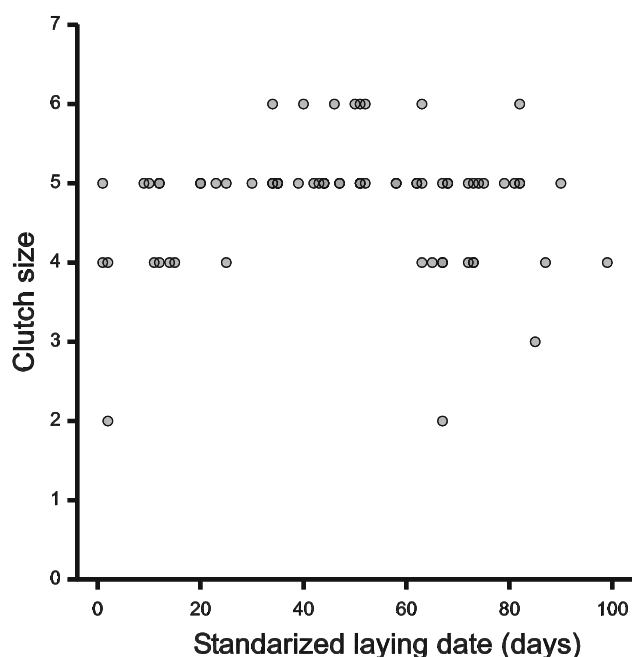


Fig. 1 Distribution of southern Sedge Wren clutch sizes vs. standardized laying date (day 1 = laying date of the first egg laid in a given season) of 103 nests for five breeding seasons in Mendoza province, Argentina

Table 3 Summary of the GLMM assessing linear and quadratic effects of laying dates and the breeding season on clutch size in southern Sedge Wrens

Variables	Coefficient	SE	z value	P
Breeding season	0.003	0.046	0.06	0.96
Laying date	1.098	2.066	0.53	0.60
Laying date ²	-1.047	2.082	-0.50	0.62
Breeding season: laying date	-0.067	0.165	-0.41	0.68
Breeding season: laying date ²	0.063	0.165	0.38	0.70

Linear and quadratic terms for laying date were standardized to facilitate the comparison of the regression coefficients

smaller clutches than northern House Wrens (Tuero et al. 2007; Ippi et al. 2012; Llambías et al. 2015). Also, seasonal declines in clutch size have been reported in northern House Wrens (Llambías et al. 2015) and northern Sedge Wrens (Burns 1982), but there is no consistent pattern in southern House Wrens (Llambías et al. 2015) nor in southern Sedge Wrens. Seasonal decline in clutch size of north temperate populations may be caused by a reduction in food supply (Lack 1966; Lundberg and Alatalo 1992) or an increment in juvenile mortality (Young 1994).

Parental care patterns also differed between northern and southern Sedge Wrens. While low male participation in feeding nestlings has been reported in two other North

Table 4 Summary of GLMM results for the assessment of the effect of nestling age on the relative male contribution to feeding nestlings

Variable	Coefficient	SE	χ^2	P
Simple model				
Nestling age	-0.013	0.005	6.94	<0.01
Within-individual centered model				
Male _{dif}	-0.004	0.026	0.03	0.87
Age _{dif}	-0.013	0.005	7.03	<0.01

To estimate the within-individual component we calculated the difference between nestling age of each nest and the mean nestling age of nests attended by each male ($Age_{dif} = A_{ij} - \bar{A}_j$). To estimate the between-individual component, we calculated the mean nestling age of nests attended by the male j ($Male_{dif} = \bar{A}_j$)

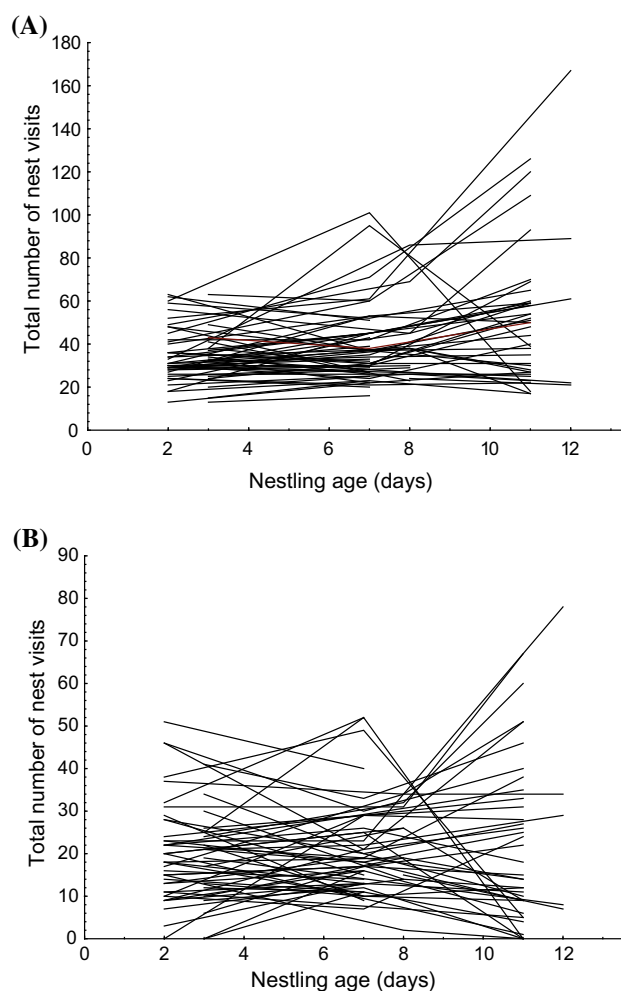


Fig. 2a, b Variation in male parental care contribution to feeding nestlings with nestling age. **a** Total feeding trips to the nest performed by both parents during nestling rearing stage. **b** Number of male provisioning trips during the nestling rearing stage. Lines represent the parental activity at each nest

American populations [Montreal (Mousley 1934); Michigan (Walkinshaw 1935)], biparental care was observed in three other south temperate populations in Argentina [Córdoba (Salvador 2012); Jujuy (Salvador 2015); Buenos Aires (Llambías, unpublished data)]. In socially polygynous species, males provide little parental care and often desert the brood (Searcy and Yasukawa 1995; Gowaty 1996; Olson et al. 2008; Reichard 2003; Leisler and Schulze-Hagen 2011). Males may reduce parental care in a particular nest to provide assistance to the primary female and/or to allocate time and energy to attract additional mates (Clutton-Brock 1991; Slagsvold and Lifjeld 1994; Gowaty 1996; Ligon 1999). Accordingly, males contributed less to feeding nestlings in Minnesota, where social polygyny was moderate, than at our study population, where social polygyny was rare (Tables 1, 2). The fact that northern males in monogamous associations provide little assistance in feeding the brood suggests a tradeoff between male parental care and female attraction. Indeed, Burns (1982) suggests that in Minnesota northern Sedge Wren males continue building incomplete and non-breeding nests to attract secondary females while their social partners are feeding nestlings. However, at our study population, we did not observe multiple nest building during the incubation and nestling stages (see below). In Costa Rica, Kroodsma et al. (1999a, b) also failed to find evidence of social polygyny and observed that both sexes cooperate in nest building and feeding the nestlings.

In House Wrens, social polygyny is rare in south temperate and tropical populations but moderate in north temperate populations (Freed 1986; Llambías et al. 2012; Johnson 2014). However, the male contribution to feeding nestlings is similar between south temperate and north temperate populations [46–56% and 43–58% (Llambías et al. 2012)]. Although the southern Sedge Wren male contribution to feeding nestlings was similar to those reported for monogamous male House Wrens, monogamous northern Sedge Wren males contribute less than 11% of all feeding visits to the nestlings. Differences in parental care patterns between northern House Wren and northern Sedge Wren populations may be related to differences in food availability between different ecosystems, which in turn may affect the costs of male desertion (Verner and Willson 1966; Møller 1985; Leisler and Schulze-Hagen 2011).

In southern House Wrens social polygyny is the consequence of territorial takeover (Freed 1986; Llambías 2012), while in northern House Wrens it is mainly achieved by female attraction (Dubois et al. 2006; Eckerle and Thompson 2006; Demory et al. 2010; Johnson 2014). Similarly, we observed territorial takeover in our southern Sedge Wren population and female attraction in northern Sedge Wrens (Table 1). However, this result should be

taken with caution due to the small sample of polygynous males in southern and northern populations.

Multiple nest-building has been associated with mate attraction (Evans and Burns 1996; Friedl and Klump 1999), post-pairing displays (Gill and Stutchbury 2005), providing shelter for adults and fledglings (Verner 1965) or decoys to reduce nest predation (Leonard and Picman 1987). In Minnesota, non-breeding nests seem to be related to mate attraction as northern males continue building incomplete and non-breeding nests after the eggs of their social partner have hatched [i.e., during attraction of secondary females (Burns 1982)]. As a consequence, northern males build more non-breeding nests than southern males (Tables 1, 2). In contrast, multiple nest-building in our population is likely to have a different function as nest building behavior ceases after the female initiates egg-laying.

Conclusion

Our results suggest a divergence in the social mating system between northern and southern Sedge Wrens, similar to that observed in northern and southern House Wrens. They also suggest a convergence in the social mating system between northern Sedge Wrens and northern House Wrens, and between southern Sedge Wrens and southern House Wrens. This pattern may be caused by differences in ecological conditions between the hemispheres that could facilitate or constrain social polygyny. To establish the generality of our results, much more work on the social mating system and life history strategies of Sedge Wrens is needed. Future efforts should also try to quantify and compare several variables that may explain differences in polygyny rates between northern and southern wrens (e.g., operational sex ratio, frequency of extra-pair fertilizations, female–female aggression, distribution of resources, and importance of paternal care) that still have not been evaluated.

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Compliance with ethical standards

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. Fieldwork permits were granted by the Secretaría de Ambiente y

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