SIMILAR PATTERNS OF PARENTAL PROVISIONING IN A MONOGAMOUS AND A POLYGYNOUS POPULATION OF THE HOUSE WREN

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Abstract.   In the House Wren (*Troglodytes aedon*), polygyny is characterized by males' partial desertion, males providing little or no help in feeding the nestlings of one of their mates. We evaluated whether contributions to feeding nestlings and patterns of provisioning by partially deserted females can explain geographic variation in the species' rate of polygyny. From 2003 to 2007, we studied two populations differing in polygyny rate (U.S., 40%; Argentina, 2%). We induced polygyny in the monogamous population by removing males from their territories before the onset of egg laying. We predicted that if patterns of parental care are related to variation in the social mating system, monogamous males should contribute more in the monogamous population than in the polygynous population, in the monogamous population partially deserted females should not compensate for the lack of help by feeding at rates higher than do aided females, and partial desertion should be more costly in the monogamous population. Monogamous males of the two populations did not differ significantly in their contribution to provisioning. Females' pattern of provisioning was also similar; partially deserted females fed nestlings at a rate higher than did aided females but did not fully compensate for the lack of help. Furthermore, the cost of male desertion seems greater in the polygynous population, as the breeding and fledging success of poorly aided females were lower. We suggest that the male's contributions to parental care and the patterns of unaided females' feeding cannot explain the geographic variation in the House Wren's mating systems.

Key words: *House Wren,* Troglodytes aedon*, parental care, provisioning rate, social mating system.*

Patrones Similares de Provisión Parental en una Población Monógama y una Polígina de *Troglodytes aedon*

Resumen.   La poliginia social en *Troglodytes aedon* se caracteriza por la deserción parcial de la nidada por parte del macho, con machos que proporcionan poca o ninguna ayuda durante la alimentación de los pichones en uno de sus nidos. Evaluamos si la contribución de los machos durante la alimentación de los pichones y el patrón de provisión de alimento puede explicar la variación geográfica en la tasa de poliginia dentro del rango de distribución de la especie. Del 2003 al 2007 estudiamos dos poblaciones de *Troglodytes aedon* que difieren en la tasa de poliginia (EEUU, 40% vs. Argentina, 2%). Indujimos poliginia en la población monógama mediante la remoción de machos territoriales antes del comienzo de la puesta. Predecimos que si los patrones de cuidado parental están asociados a la variación en el sistema social, (1) los machos monógamos de la población monógama deberían contribuir más a la alimentación de los pichones que los machos monógamos de la población polígina, (2) las hembras desertadas parcialmente en la población monógama no deberían incrementar la tasa de entrega de alimento a los pichones para compensar la falta de cuidado paterno, y (3) la deserción parcial debería ser más costosa en la población monógama. Los machos monógamos de la población polígina y monógama no difirieron significativamente en la provisión de alimento a los pichones. La provisión de alimento de las hembras también mostró un patrón similar en ambas poblaciones; si bien las hembras parcialmente desertadas alimentaron los pichones a tasas mayores que las hembras que contaron con ayuda del macho, no compensaron totalmente la falta de ayuda. Aún más, el costo de la deserción de los machos parece ser mayor en la población polígina, debido a que las hembras parcialmente desertadas produjeron menos pichones y volantones. Sugerimos que la contribución del macho al cuidado parental y los patrones de provisión de alimento de las hembras parcialmente desertadas no pueden explicar la variación geográfica en el sistema de apareamiento social en *Troglodytes aedon*.

INTRODUCTION

Parental care is any form of parental behavior that increases an offspring's fitness (Clutton-Brock 1991, Gowaty 1996a, Cézilly and Danchin 2008). In birds, parental care encompasses a broad range of behaviors: nest building, nest defense, incubation, and brooding and feeding of nestlings (Clutton-Brock 1991, Gill 2007). Differences in how social mates share parental care are generally associated with differences in social mating systems (Mock and Fujioka 1990,

Davies 1991, Ligon 1999, Cézilly and Danchin 2008). Biparental care typifies 81% of all bird species (Cockburn 2006) and is generally associated with social monogamy (Lack 1968, Gowaty 1996a, Ligon 1999, Bennett and Owens 2002, Reichard 2003). In social monogamy, a male and a female form a pair bond and both take care of the young, while in territorial polygyny, a male pairs with more than one female and secondary females often receive less help from the male in raising the brood (Wittenberger 1980, Wittenberger and Tilson 1980, Searcy and Yasukawa 1989, Clutton-Brock 1991, Johnson et al. 1993, Pribil and Searcy 2001).

The need for biparental care can greatly affect mating systems and vice versa (Gowaty 1996b, Møller 2000, Székely et al. 2000). If a single adult cannot raise any young, monogamy is obligatory: it maximizes both the male's and female's fitness (Lack 1968, Bart and Tornes 1989, Ligon 1999, Reichard 2003). In populations where food is abundant and biparental care is less important to offspring production, polygyny should be more frequent since females can breed successfully without a social mate (Dunn and Robertson 1992, Gowaty 1996a, Bennett and Owens 2002). Searcy and Yasukawa (1995) found that for eight species of polygynous passerines the degree of polygyny increases as the male's contribution to provisioning decreases. They proposed that polygyny should predominate only in species in which the male's contribution is low (<25%) and nonessential to offspring production. Indeed, the male's contributions to parental care can influence the evolution and maintenance of avian breeding systems greatly (Bennett and Owens 2002, Olson et al. 2008, Webb et al. 2010). Ultimately, the capacity or disposition of deserted females to compensate for the lack of male help by increasing provisioning rates should be related to the level of male contribution and should affect the ability of males to become polygynous. Hence the male's percentage of contribution to parental care and the patterns of provisioning by deserted females can predispose species to particular mating systems.

The importance of male parental care does not always explain differences in mating systems. Dunn and Robertson (1992) carried out male-removal experiments and studied natural cases of polygyny in two populations of the Tree Swallow (*Tachycineta bicolor*) in Canada. They found that although females without male help produce fewer offspring where food is less abundant, the frequency of polygyny is not greater where food is less limiting. Indeed, other factors, including mate and/or territory quality and the spatial and temporal distributions of resources and mates, have been proposed as determinants of the mating system (Orians 1969, Wittenberger and Tilson 1980, Emlen and Oring 1977, Searcy and Yasukawa 1989). The polygyny-threshold model proposes that if a female's breeding success is determined by the quality of her mate's territory, then a female will breed with an already mated male if the reduction in male help is compensated for by the high quality of the territory (Verner and Wilson 1966, Orians 1969). Similarly, the sexy-son hypothesis proposes that females will accept polygyny if the increase in offspring fitness through the inheritance of their father's attractiveness compensates for the loss of male parental care (Weatherhead and Robertson 1979).

The classic approach to evaluating how parental care can constrain social mating systems has been to remove males during different stages of the nesting period to quantify the cost of the loss of male help on the growth and survival of chicks (see review by Bart and Tornes 1989). But a male-removal experiment does not necessarily mimic polygyny. First, polygyny does not always mean total desertion of one of the broods. In several bird species, secondary females receive some male help in raising the brood (Nolan 1978, Wittenberger 1980, Temrin and Jakobsson 1988, Leonard 1990, Johnson et al. 1993). Second, males may not feed the brood of a secondary female but still defend the nest against predators or conspecifics (Johnson and Albrecht 1993, Searcy and Yasukawa 1995). The main drawback of male-removal experiments is that they assume that primary and secondary females share no components of the male's parental behavior. Although feeding behavior is a form of nonshareable male parental contribution (Wittenberger 1980, Alatalo and Lundberg 1990, Leonard 1990, Johnson et al. 1993), nest defense is often thought to be shareable because a male can defend more than one nest if the nests are not threatened by a predator at the same time (Weatherhead 1990, Johnson and Albrecht 1993, Searcy and Yasukawa 1995, but see Trnka and Prokop 2010). An alternative method of evaluating the costs of polygyny in monogamous populations that more closely mimics the natural effects of polygyny is to induce polygyny in an otherwise monogamous species (e.g., Smith et al. 1982, Greenlaw and Post 1985, Veiga 1992).

In the House Wren (*Troglodytes aedon*), polygyny is characterized by the male's partial desertion: secondary females receive little or no help in feeding the brood for at least some part of the nestling stage but may still be assisted during nest defense or if the primary female's nest fails (Johnson and Kermott 1993, Johnson and Albrecht 1993). To evaluate whether geographic variation in the House Wren's social mating system could be related to the need for biparental care, we studied two populations that differ in polygyny rate (13–40% in the U.S. vs. 0–2% in Argentina). To increase the number of poorly aided and secondary females in Argentina we induced polygyny by removing males before the onset of egg laying. If the observed variation in social mating system is related to the level of male care required to raise offspring and the capacity of females to compensate for male desertion in each population, then (1) monogamous males in the monogamous population should make a greater contribution to provisioning nestlings than do monogamous males in the polygynous population, (2) partially deserted females in the monogamous

population should not fully compensate for the lack of male help, resulting in fewer total trips to provision chicks than to nests of females aided by males, and (3) the cost of male desertion should be higher in the monogamous population.

METHODS

STUDY SPECIES
The House Wren is a small (10–12 g), sexually monomorphic, insectivorous, territorial passerine (biology summarized in Johnson 1998). It breeds in tree cavities, old holes excavated by other species, nest boxes, and other man-made structures (Brewer 2001). It is currently considered one species (Remsen et al. 2012) with a breeding distribution ranging from Canada to Tierra del Fuego, although Brumfield and Capparella (1996) suggested it should be split into three species.

In the subspecies of eastern North America (*Troglodytes aedon aedon*), polygyny occurs most commonly when monogamous males advertise from a secondary nest site in their territory, thus attracting a secondary female (Johnson 1998). In contrast, in *T. a. bonariae* at our study site in Argentina, we have observed polygyny only rarely despite the presence of multiple nest boxes per territory; apparently it occurs only when a monogamous male either evicts the owner of a neighboring territory or replaces it after its death, taking over the resident female and its territory (Llambías 2012). In the northern population 54% of the broods and 25% of the offspring are extra-pair (not sired by the social mate), while in the southern population 33% of the broods and 16% of the young are extra-pair (LaBarbera et al. 2010). Hence both populations differ in their rates of both social and genetic polygyny.

Parental roles are similar in both populations: the male builds the nest structure with sticks and adds spider cocoons and snake skin after which the female constructs the nest cup of grasses, feathers, and animal hair. Only the female incubates the eggs and broods the nestlings, and mate feeding during incubation has not been observed (24 North American and 23 South American nests, each filmed for 4 hr). In both populations both sexes feed the young, but males adjust their provisioning rate in response to their mates' provisioning (LaBarbera et al 2012). Secondary females usually receive little or no male help during feeding (Johnson, and Albrecht 1993, Llambías 2012).

STUDY SITES
We studied two populations of House Wrens breeding in wooden nest boxes, near Ithaca, New York (42° 28′ N, 76° 29′ W), June–August 2003–2008, and near General Lavalle, Buenos Aires province, Argentina (36° 26′ S, 56° 25′ W), October–January, 2003–2007. The northern study area comprised two patches of mixed deciduous forest separated by 3 km. Prior to the first breeding season we erected nest boxes on greased poles, 1.5 m high and 25–50 m apart (two or three boxes per male's territory). The southern study site, described by Llambías and Fernández (2009), was in coastal woodland at a private cattle ranch, Los Zorzales. There we attached two boxes per territory to *Celtis tala* trees. At both sites the boxes measured 30.5 × 16.5 × 12.7 cm with an entrance hole 38 mm in diameter, but materials differed (pine in New York and eucalyptus and pine in Buenos Aires). In Argentina, after the first egg was laid, we reduced the entrance hole's diameter to 27 mm to prevent parasitism by Shiny Cowbirds (*Molothrus bonariensis*).

FIELD DATA COLLECTION
Each year we color-banded 77–80% of the breeding adults for individual identification. We attracted males with recordings and trapped them with mist nets before the start of egg laying; we trapped females inside nest boxes when they were feeding young at least 8 days old. We checked nest boxes every other day between 06:00 and 11:00 and recorded date of laying, clutch size, brood size (number of nestlings hatched), and number of nestlings fledged. We weighed nestlings with a 10-g spring scale ± 0.1 g by day 10 (we considered day 0 as the day the majority of the eggs in the clutch hatched). We classified nest failure as (1) predation when nestlings or eggs were missing and nest material was disturbed, (2) conspecific nest destruction when eggs had small holes pecked in them or we found dead nestlings near or inside the nest box with marks of pecking on the head, or (3) desertion when we found nestlings dead inside the nest and both adults were still alive. We classified a nest as successful if at least one nestling fledged.

We categorized laying in each nest as early or late. Each year, we designated the day we found the first egg laid as day 1, with the laying period consisting of day 1 through the day the last egg was laid. We calculated for each year and site the median date of laying and defined early nests as those whose eggs were laid on or before the median date, late nests as those whose eggs were laid after the median date. When we did not determine the date of laying directly, we calculated it on the basis of the length of the average incubation period (days between the laying of the last egg and the hatching of the last nestling) plus the clutch size (one egg laid every day until clutch was completed). On the basis of observations of monogamous pairs we used an incubation period of 14 days (13.94 ± 0.09, $n = 34$ nests) for New York and 15 days (15.27 ± 0.15, $n = 49$ nests) for Argentina.

EXPERIMENTAL INDUCTION OF POLYGYNY IN THE SOUTHERN HOUSE WREN
In Argentina, natural polygyny occurs at a very low rate, when a paired territorial male is replaced by a previously monogamous neighbor (Llambías and Fernández 2009, Llambías 2012). We induced polygyny by removing males in 2004, 2005, and 2007. Six to eight days before any eggs had been laid, we captured with mist nets 30 territorial males

(9 bachelors, 21 monogamously mated) and translocated them 50 km away, keeping them in individual cardboard boxes and released them within 2 hr of capture. If a nonterritorial male (floater) occupied an open territory, we removed this male as well. We excluded from the analyses males that after translocation returned to their territories. Male-removal experiments and procedures were approved by the Institutional Animal Care and Use Committee (protocol 20576-EM) of Cornell University and meet the ethical guidelines, including adherence to the legal requirements of Argentina. Removal of males caused eight females to breed as a secondary female of eight neighboring previously monogamous males, each of whom expanded its territory to incorporate the "widowed" female. Females were not forced into polygyny, since each year three to seven territorial males were unpaired and defending territories within the 4.1-ha patch of forest where we carried out the experiment, and females could have paired monogamously with them.

PARENTAL-CARE ASSESSMENT

We used video cameras to record parental behavior. We filmed nest boxes continuously for 4 h r when nestlings were 2–3, 7–8 and 11–12 days old (we defined day 0 as the day the majority of the eggs in the clutch hatched). Cameras were camouflaged and placed 5–10 m from the nests 1 hr after sunrise. Later analysis of videotapes enabled us to identify the color-banded adults and quantify the number of trips the male and female made to provision the young. We defined a provisioning trip as an adult entering the nest box with food in its bill and emerging without the food. We considered females to be brooding young if they remained inside the nest box for more than 60 sec. We calculated the mean duration and the mean number of bouts of brooding per 4-hr observation session when nestlings were 2–3 days old (brooding after day 7 is uncommon). We excluded from analyses four Northern and three Southern House Wren nests where adults did not resume provisioning during the first 15 min of recording, as this delay suggested that the placement of the camera was disturbing the birds. We also excluded data from six observation sessions in which it was not possible to identify the adults by color bands.

STATISTICAL ANALYSIS

Parental care. We used a Mann–Whitney test to evaluate (1) whether monogamous male Northern and Southern House Wrens differed in contribution to feeding (male provisioning trips/total provisioning trips), (2) within each population, whether the provisioning rate (feedings per nestling per hour) of females with and without male help differed, and (3), within each population, whether total provisioning rates (male + female) were lower at nests where the male was not feeding. All three analyses were done at each of the three stages (nestlings 2–3, 7–8, and 11–12 days old.). For each population we also compared, with a general

linear model (GLM), the mean duration of bouts of brooding and number of bouts of brooding of females with and without male help when nestlings were 2–3 days old, with male help/no help and number of nestlings as fixed factors.

Costs of male partial desertion. To determine the effects of males' parental care on females' breeding success, we compared several reproductive variables for fully and poorly aided nests. As did Johnson and Kermott (1993) for Northern House Wrens, we considered a nest to be poorly aided if the male was not observed feeding the nestlings during the first half (nestling age 0–9 days) of the nestling stage. Male parental care may be most critical during the first half of the nestling stage, since nestlings cannot fully thermoregulate and females may be unable to increase rates of feeding while still brooding the nestlings for the normal amount of time (Johnson et al. 1992). Sample sizes for these and previously described analyses differ because we here included only nests for which we were able to evaluate the male's contribution at least when nestlings were 2–3 and 7–8 old. We modeled clutch size with a generalized linear mixed-effects model fit by the Laplace approximation (function glmer from the package lme4; Bates and Maechler 2009) with a Poisson distribution, with population, period of laying (early or late), and level of aid (full or poor) as fixed effects and year as a random effect. To test for differences in hatching success (nestlings hatched per egg), fledging success (fledglings produced per nestling), and breeding success (nestlings fledged per egg), we used a generalized linear mixed-effects model with a binomial distribution, with population, period of laying, level of aid, and the interactions of population with period of laying and population with level of aid as fixed effects and with year as a random effect. We were not able to test the interaction of period of laying with level of aid in the full model because we did not have any poorly aided late nests in the southern population; we did test this interaction in a reduced model for the northern population. In cases where an interaction was significant, we ran additional models to determine the direction of the interaction. Because of the distance between our populations, we assumed that year at one site was independent of year at the other and coded year as a categorical variable with different values for each site.

To further examine the effects of lack of male care, we ran a linear mixed-effects model (function lmer from the package lme4; Bates and Maechler 2009), with nestling mass as the response and population, level of aid, and the interaction term as fixed effects, after first determining, using maximum likelihood, the best hierarchical random-effects structure (including the following effects: year, population, and period of laying). We omitted nonsignificant interaction terms from the final models.

Males may contribute not only to nestling provisioning but also to tasks such as nest defense against conspecifics. To evaluate whether poorly aided females suffer a cost due to reduced nest defense, we compared the frequency of egg destruction in nests of secondary and monogamous females.

Except where noted we report means ± SE. We generated mixed-effects models in R version 2.9.2 (R Development Core

Team 2009); for all other statistical analyses we used SPSS version 14.0 (SPSS 2005).

RESULTS

SOCIAL MATING SYSTEM

The social polygyny rate (percentage of males' breeding attempts that were polygynous) was significantly higher in Northern House Wren nests than in control nests of the Southern House Wren (northern: 20%, $n = 142$, annual range 13–40% vs. southern: 1%, $n = 201$, annual range 0–2%; Fisher's exact test, $\chi^2 = 16.36$, $P < 0.001$).

MALES' CONTRIBUTION TO PARENTAL CARE

Monogamous males of the two populations did not differ significantly in their contribution to parental care (proportion of feeding trips, Fig. 1). The contributions of males ranged from 60 to 40%, reaching its maximum when nestlings were 2–3 days old and needed to be brooded by the female (Fig. 1).

PATTERN OF PARENTAL CARE OF PARTIALLY DESERTED FEMALES

At both study sites, some females did not receive male help in feeding the young for at least part of the nestling cycle (Fig. 2). Still, we observed males defending females' territory from other males, responding aggressively to playback, and making alarm calls during nest checks, suggesting that desertion was not complete. Partially deserted females (females with
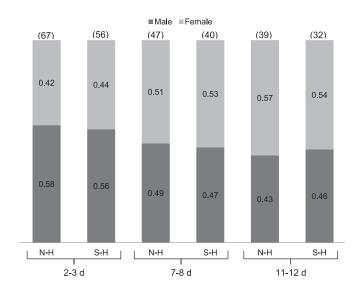

FIGURE 1.   Proportion of feeding trips to nests of monogamous pairs (biparental care—male contribution) of northern (New York; N-H) and southern (Argentina; S-H) populations of the House Wren when nestlings were 2–3, 7–8, and 11–12 days old. The male's contribution did not differ significantly at any of the three ages of nestlings (Mann–Whitney test; $P > 0.40$).

no male help in provisioning nestlings for at least part of the nestling stage) fed nestlings at rates significantly higher than did females with male help when nestlings were 2–3, 7–8, and 11–12 days old (Fig. 2). In both populations, the higher rates of provisioning by unaided females did not fully compensate for the lack of male help when nestlings were 2–3 and 11–12 days old; during these stages total feeding rates (the male's and female's provisioning trips combined) were significantly lower at nests without male help (Fig. 3). Total feeding rates at nests with or without male help did not differ significantly when nestlings were 7–8 days old (Fig. 3) although for the Southern House Wrens there was a trend suggesting that full compensation was still not achieved.

Northern females without male help during feeding spent significantly less time brooding 2- to 3-day-old nestlings over the 4 hr of observation than did aided females (unaided: 350 ± 41 sec, $n = 14$ vs. aided: 489 ± 23 sec, $n = 63$; $F_{1,75} = 103$; $P = 0.01$), but they did not differ significantly in the number of bouts of brooding (unaided: 20.4 ± 1.7, $n = 14$ vs. aided: 18.4 ± 0.6, $n = 63$; $F_{1,75} = 1.8$; $P = 0.18$). Southern females without male help also spent significantly less total time brooding than did aided females (unaided: 366 ± 27 sec, $n = 15$ vs. aided: 457 ± 19 sec, $n = 50$; $F_{1,63} = 5.98$; $P = 0.02$). However, unaided southern females brooded significantly more often (unaided: 24.2 ± 1.1, $n = 15$ vs. aided: 19.8 ± 0.6, $n = 50$; $F_{1,63} = 14.2$; $P = 0.001$).

COSTS OF LOSS OF MALE PARENTAL CARE DURING FEEDING OF NESTLINGS

In New York, poorly aided females (received no male help in feeding 0- to 9–day-old nestlings; $n = 13$) included 10 secondary, one primary, and two monogamous females; fully aided females (received male help in feeding 0- to 9–day-old nestlings; $n = 36$) included 27 monogamous, two secondary, and seven primary females. In Argentina, poorly aided females ($n = 10$) included four monogamous and six secondary females; fully aided females consisted of 30 monogamous and five primary females ($n = 35$).

Poorly aided females of the two populations did not differ from fully aided females in the probability of fledging at least one nestling (successful/successful + unsuccessful nests; northern: 92% poorly aided, $n = 13$; 100% fully aided, $n = 36$, Fisher's exact test, $\chi^2 = 0.31$, $P = 0.26$; southern: 90%, $n = 10$ vs. 94%, $n = 35$; Fisher's exact test, $\chi^2 = 0.00$, $P = 0.54$). Also, the level of male aid received by the female was not significantly related to clutch size or hatching success in either population, nor, in Argentina, was the level of aid related to fledging success or breeding success (Tables 1–3). In the northern population, however, the fledging success and breeding success of fully aided females was significantly higher than that of poorly aided females (Table 3). Period of laying was not related to clutch size, hatching success, fledging success, or breeding success in either population (Table 2). Clutch sizes were significantly greater in the northern population, but in no measure of breeding success
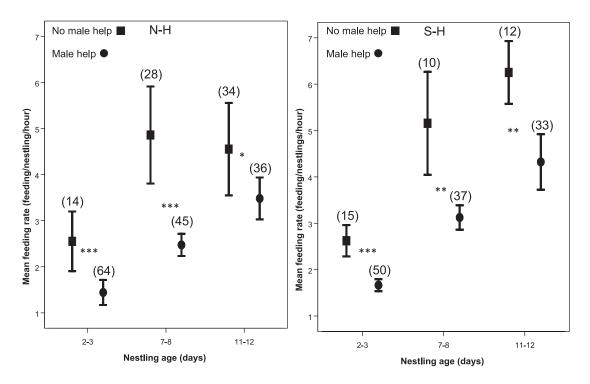
FIGURE 2.   Mean (± SE) rates of provisioning by females of northern (New York; N-H) and southern (Argentina; S-H) populations of the House Wren with and without male help when nestlings were 2–3, 7–8, and 11–12 days old. Asterisks (*) represent groups that are significantly different (* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$) according to a Mann–Whitney test. Sample sizes are in parentheses.
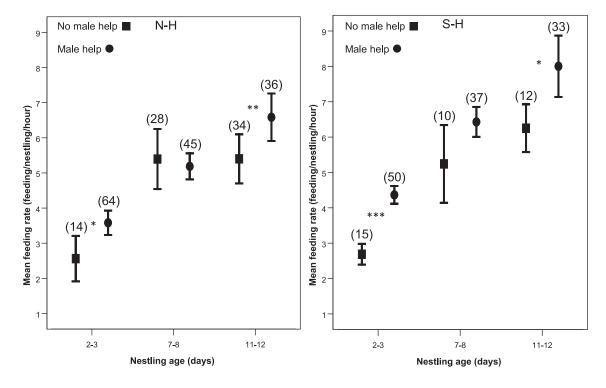

FIGURE 3.   Mean (± SE) combined rates of provisioning by males and females of northern (New York; N-H) and southern (Argentina; S-H) populations of the House Wren with and without male help when nestlings were 2–3, 7–8, and 11–12 days old. Asterisks (*) represent groups that are significantly different (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) according to a Mann–Whitney test. Sample sizes are in parentheses.

TABLE 1.   Means and standard errors for several measures of breeding (clutch size = number of eggs laid, hatching success = number of nestlings hatched/clutch size, fledgling success = number of fledglings/number of nestlings hatched, breeding success = number of fledglings/clutch size) partitioned by population and level of male aid (poorly aided females did not receive male help provisioning 0- 9-day-old nestlings, fully aided females received male help provisioning 0- 9-day-old nestlings).

| | Mean ± SE (n) | | | |
| | Northern House Wren | | Southern House Wren | |
Response	Poorly aided	Fully aided	Poorly aided	Fully aided
Clutch size	6.31 ± 0.21 (13)	6.06 ± 0.14 (36)	4.80 ± 0.13 (10)	4.74 ± 0.09 (35)
Hatching success	0.92 ± 0.05 (13)	0.93 ± 0.02 (36)	0.92 ± 0.04 (10)	0.91 ± 0.02 (35)
Fledging success	0.80 ± 0.08 (13)	0.94 ± 0.02 (36)	0.85 ± 0.10 (10)	0.87 ± 0.04 (35)
Breeding success	0.72 ± 0.08 (13)	0.88 ± 0.03 (36)	0.80 ± 0.10 (10)	0.78 ± 0.04 (36)
Nestling mass	9.57 ± 0.23 (10)	9.95 ± 0.11 (29)	11.52 ± 0.26 (8)	11.95 ± 0.16 (22)

did the two populations differ significantly (Table 2). By day 10 nestlings raised by fully aided females of both populations had greater mass than did those raised by poorly aided females (Table 1 and 2). Masses of southern nestlings were greater than those of northern nestlings, probably because adult southern wrens average 1 g heavier than northern wrens (southern:

$12.48 ± 0.12$ g, $n = 78$ vs. northern: $11.00 ± 0.08$ g, $n = 105$). The interaction of population with level of aid was not significantly related to nestling mass.

In neither population did secondary females lose significantly more nests to conspecific nest destruction than did monogamous females (northern: 4%, $n = 25$ vs. 1%, $n = 134$, Fisher's exact test, $\chi^2 = 0.11$, $P = 0.30$; southern: 20%, $n = 8$ vs. 5%, $n = 126$, Fisher's exact test, $\chi^2 = 1.62$, $P = 0.11$).

DISCUSSION

Although the two populations studied differed in rates of social polygyny (this study) and extra-pair paternity (LaBarbera et al. 2010), our results suggest that variation in House

TABLE 2.   Results of generalized linear mixed-effects models (statistic = z) and linear mixed-effects models (statistic = t) examining the effects of population, period of laying, and level of male aid for Northern and Southern House Wrens on several measures of breeding (clutch size = number of eggs laid, hatching success = number of nestlings hatched/clutch size, fledgling success = number of fledglings/number of nestlings hatched, breeding success = number of fledglings/clutch size). Coefficients shown are in comparison to the following baseline groups: population = southern; period of laying = early; level of aid = poor. Only significant interactions are shown. Asterisks highlight values of $P < 0.05$.

Response and variable	Effect ± SE	Statistic	P
Clutch size			
Population	0.28 ± 0.09	$z = 3.01$	0.003*
Lay period	−0.11 ± 0.10	$z = -1.12$	0.262
Level of aid	−0.01 ± 0.10	$z = -0.09$	0.928
Hatching success			
Population	0.08 ± 0.68	$z = 0.11$	0.911
Lay period	−0.11 ± 0.55	$z = -0.20$	0.838
Level of aid	−0.08 ± 0.59	$z = -0.14$	0.891
Fledging success			
Population	−0.16 ± 0.65	$z = -0.25$	0.804
Lay period	0.73 ± 0.57	$z = 1.26$	0.205
Level of aid	−0.09 ± 0.50	$z = -0.18$	0.856
Population × level of aid	1.88 ± 0.68	$z = 2.41$	0.005*
Breeding success			
Population	−0.15 ± 0.51	$z = -0.29$	0.771
Lay period	0.40 ± 0.42	$z = 0.95$	0.340
Level of aid	−0.13 ± 0.41	$z = -0.32$	0.749
Population × level of aid	1.42 ± 0.53	$z = 2.65$	0.008*
Nestling mass			
Population	−1.98 ± 0.16	$t_{66} = -12.2$	<0.001*
Level of aid	0.40 ± 0.18	$t_{66} = 2.19$	0.032*

TABLE 3.   Results of generalized linear mixed-effects models (statistic = z) examining the effects of period of laying and level of male aid on fledgling success (number of fledglings/number of nestlings hatched) and breeding success (number of fledglings/clutch size) within two populations of the House Wren. Coefficients shown are in comparison to the following baseline groups: period of laying = early; level of aid = poor. Asterisks highlight values of $P < 0.05$.

Response, population, and variable	Effect ± SE	Statistic	P
Fledging success			
Southern			
Lay period	0.73 ± 0.58	$z = 1.26$	0.207
Level of aid	−0.09 ± 0.50	$z = -0.18$	0.859
Northern			
Lay period	−0.44 ± 0.63	$z = -0.69$	0.488
Level of aid	1.87 ± 0.63	$z = 2.99$	0.003*
Breeding success			
Southern			
Lay period	0.40 ± 0.42	$z = 0.95$	0.340
Level of aid	−0.13 ± 0.40	$z = -0.32$	0.753
Northern			
Lay period	−0.43 ± 0.56	$z = -0.77$	0.441
Level of aid	1.42 ± 0.47	$z = 3.03$	0.002*

Wren mating systems is likely not the consequence of variation in requirements of parental care for raising offspring. First, in both populations monogamous males made a similar contribution to provisioning nestlings (Fig. 1). Second, in both populations, females without male help were unable to fully compensate for the lack of male help when feeding nestlings, suggesting similar patterns of compensation of partially deserted females (Fig. 2 and 3). Third, in both populations, nestlings of poorly aided females fledged with smaller body mass and only in the polygynous population did poorly aided females fledge fewer offspring (Table 2 and 3), contrary to what would be expected if the costs of male desertion were responsible for the maintenance of social monogamy. Since nestling mass has been related to fledgling survival in other passerines (Tinbergen and Boerlijst 1990, Hochachka and Smith 1991), poorly aided females may also suffer fledgling survival reduced from that of fully aided females. The reduction in mass of nestlings raised by poorly aided females was not different in the two populations.

Both our study and Johnson and Kermott's (1993) of the Northern House Wren found that unaided females feeding 2- to 3-day-old nestlings reduce brooding time, probably to increase feeding rates, but this increment is not enough to fully compensate for the lack of help. We found that females without male help were also unable to compensate for the lack of male help when nestlings were close to fledging. This lack of compensation toward the end of the nestling period is not caused by a requirement for brooding since brooding is uncommon after nestlings are 7 days old. Rather, it seems that unaided females reach the maximum feeding rate by day 7 and are unable or unwilling to increase feeding rates later in the nestling stage (Fig. 2 and 3). These results suggest that nestling requirements and the adult's ability to compensate vary through the nestling cycle.

The fact that the male's contribution to feeding nestlings is similar in both populations is striking since rates of social polygyny and extra-pair fertilization are higher in the north. This pattern of social and genetic polygyny should produce stronger intersexual selection and sexual conflict in the north. Since selection should favor males that increase their fitness by seeking additional opportunities to mate over those that provide parental care (Maynard Smith 1977, Arnqvist and Rowe 2005, Houston et al. 2005, Olson et al. 2008), we expected northern males to contribute less parental care than did southern males.

Other components of parental care not considered in this study may be important, particularly the male's nest defense against predators. At our study sites wrens bred in nest boxes, which are likely less vulnerable to predation than are natural cavities (Llambías and Fernández 2009), and the level of predation of nests in natural cavities of our northern population is unknown. If predation on nests in natural cavities is higher in Argentina and males are effective in deterring nest predators

from one nest but are unable to defend multiple nests, the breeding success of polygynous females might be lower than that of monogamous females, resulting in selection against polygyny. In the Northern House Wren, however, experimental evidence suggests that in defending the nest from model snakes, secondary females do not receive less help than do females mated to monogamous males (Johnson and Albrecht 1993), suggesting that males can defend multiple nests from attempts at predation.

On both continents male House Wrens usurp territories by evicting the resident male and removing eggs or killing the nestlings (Freed 1986, Johnson and Kermott 1990). Males' defense of the nest against conspecifics might thus have major implications for the maintenance of monogamy. The nest-defense hypothesis proposes that secondary females obtain less help from mates in defending offspring from conspecifics (Johnson and Kermott 1993), so higher rates of destruction of nests of secondary females or poorly aided females can be expected. Although we did not find significant differences between secondary and monogamous females in the proportion of nests destroyed by conspecifics, our sample was small and secondary females tended to lose a higher proportion of nests to nest destruction. Future research should determine whether the male's defense against predators and conspecifics is a shareable form of parental care in both populations.

In both populations partially deserted females fed nestlings at rates significantly higher than did fully aided females (Fig. 2), and they spent less time brooding the young. Life-history theory predicts that increased parental care reduces both survival and future reproduction (Williams 1966, Clutton-Brock 1991). Indeed, the lack of male help during feeding of nestlings can reduce the survival and lifetime reproductive success of females mated to polygynous males (Kempenaers 1995, Wheelwright et al. 1992, Both 2002, Arnqvist and Rowe 2005, but see Bensch 1996, Garamszegi et al. 2004). Hence the difference between the Northern and Southern House Wrens in the rate of social polygyny may be due to differences in the fitness costs of polygyny and their interaction with life-history traits (e.g., if adult survival is greater in the south and the lack of male help reduces lifetime reproductive success, females may delay breeding rather than accept polygyny).

In the polygynous Northern House Wren, the cost of male desertion varies by site and by season at the same site. In a 2-year study in Ohio, Bart and Tornes (1989) removed males when nestlings were 4–5 days old and found that nestling survival was reduced only during hard weather when food was scarce. In Wyoming, Johnson et al. (1992) removed males much earlier, during the second half of the incubation stage, and reported that widowed females produced 32% fewer fledglings per egg laid than did control females. In a later study of the same population, Johnson and Kermott (1993) showed that poorly aided females fledge fewer and lighter nestlings than do fully aided females. In Alberta, Canada,

however, Quinn and Holroyd (1992) did not find secondary and monogamous females to differ significantly in the number of nestlings fledged. In our polygynous Northern House Wren population the cost of male desertion seems to be greater than in our monogamous Southern House Wren population. However, females' patterns of compensation when deserted were similar, and monogamous males made similar contribution to provisioning nestlings. Hence geographic variation in the House Wren's mating systems may be a consequence of variation in other variables such as territory quality, temporal and spatial variation in resources and mates, and intrasexual competition. Still other components of parental care (male defense against conspecifics and predator) remain to be evaluated.

ACKNOWLEDGMENTS

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