



Neither paternity loss nor perceived threat of cuckoldry affects male nestling provisioning in grass wrens

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Abstract

Extra-pair paternity (EPP) is frequent in socially monogamous birds with biparental care. However, males should avoid providing care to unrelated offspring. In this study, we first analyzed the relationship between parental care and paternity loss, and secondly, we evaluated if males adjust parental care to a perceived threat of cuckoldry. Over three breeding seasons, we intensively studied a color-banded population of south temperate grass wrens *Cistothorus platensis*. We monitored nests attended by socially monogamous males, collected blood samples from adults and nestlings, and recorded male provisioning rates to the nestlings. Paternity was assigned genetically using SNP markers. We simulated territorial intrusions during the female fertile period (egg-laying) to manipulate males' perceived threat of cuckoldry. Neither the proportion of extra-pair offspring nor the presence/absence of extra-pair offspring in the nest affected male provisioning rates, suggesting that males did not adjust parental effort to actual paternity loss. Simulated territorial intrusions revealed that males were more likely to approach and attack a conspecific than a heterospecific stuffed decoy. However, experimental and control males provided food to their nestlings at similar rates. Retaliatory reduction of paternal care might not have evolved in grass wrens given the low frequency of extra-pair paternity (23%). Alternatively, males may rely predominately on precopulatory strategies (e.g., territoriality and mate guarding) to prevent females from obtaining extra-pair fertilizations.

Significance statement

A central tenet in the study of extra-pair behavior in birds is that males should reduce their parental contribution when females engage in extra-pair copulations. Males are thought to use indirect clues (female absences, male intrusions) and direct clues (observation of copulations) to gauge paternity loss. We studied the relationship between extra-pair behavior and male contribution to feeding nestlings in a Neotropical population of grass wrens. We found that males did not adjust their contribution to paternal care based on actual paternity loss. Moreover, simulated male intrusions during the female fertile period, which influence a male's perceived threat of cuckoldry, did not affect paternal care. Our results suggest that male grass wrens do not indirectly retaliate against females who engage in extra-pair behavior by reducing parental care.

Keywords *Cistothorus platensis* · Extra-pair paternity · Neotropic · Paternal care

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Introduction

Extra-pair paternity (EPP)—the siring of offspring by a male other than the female's social partner—occurs in 76% of socially monogamous birds with biparental care (Brouwer and Griffith 2019). Males engaging in extra-pair copulations might increase their reproductive output by producing more offspring without the costs of parental care (Westneat et al. 1990; Birkhead and Møller 1992). Females seeking extra-pair copulations might gain both indirect and direct benefits, such as improving the genetic quality or diversity of their offspring (Hamilton 1990; Westneat et al. 1990; Birkhead

and Møller 1992), assuring fertility (Wetton and Parkin 1991), maximizing genetic compatibility between themselves and the father of the offspring (Kempnaers et al. 1999), and accessing resources on the extra-pair male's territory (Gray 1997). This creates a conflict between the sexes as males should avoid providing care to unrelated offspring (Trivers 1972; Westneat and Sherman 1993; Houston 1995; Kokko 1999; Sheldon 2002). Hence, it is expected that females seeking extra-pair copulations might suffer retaliation in the form of reduced parental care from their social partners (Arnold and Owens 2002; Westneat and Stewart 2003).

Several studies have analyzed how birds adjust paternal care (e.g., nest defense and nestling provisioning) to paternity loss. Studies evaluating the correlation between male parental contribution and paternity loss have reported a positive (e.g., Lubjuhn et al. 1993; Dixon et al. 1994), negative (e.g., Freeman-Gallant 1997), or a lack of relationship (e.g., Whittingham and Lifjeld 1995; Wagner et al. 1996; Yezerinac et al. 1996; Bouwman et al. 2005; Poblete et al. 2021). Correlational studies have been criticized, as confounding factors such as male or territory quality may covary with paternity loss and paternal care, complicating the interpretation of results (Kempnaers and Sheldon 1997; Sheldon 2002; Alonzo and Klug 2012). For example, low-quality males may provide overall less parental care and achieve lower paternity than high-quality males (Kempnaers and Sheldon 1997).

Since birds are not able to distinguish between kin and non-kin (Leonard et al. 1995; Westneat et al. 1995; Kempnaers and Sheldon 1996; Lattore et al. 2019), experimental studies have focused on manipulating indirect cues related to how males perceive the threat of cuckoldry (Kempnaers and Sheldon 1997; Wright 1998). There is evidence suggesting that females visit males in neighboring territories to engage in extra-pair copulations (Kempnaers et al. 1992; Sheldon 1994). Assuming that the female's absence during her fertile period (i.e., egg-laying stage) increases how her social mate perceives the threat of cuckoldry, researchers conducted temporary removal experiments evaluating whether males adjust their parental contribution accordingly. While some temporal removal studies have reported that experimental males reduce their provisioning to the offspring (e.g., Wright and Cotton 1994; Sheldon et al. 1997), others showed no effect (e.g., Kempnaers et al. 1998). An alternative approach consists of temporarily removing the male during the female fertile period. However, these studies produced mixed results as well (e.g., Whittingham et al. 1993; Lifjeld et al. 1998; Sheldon and Ellegren 1998; Dickinson 2003).

A third approach consists of increasing a male's perceived threat of cuckoldry by simulating the intrusion of a

second male into its territory during the fertile period of the resident female. For instance, Hoi et al. (2013) conducted a confrontation experiment in reed warblers *Acrocephalus scirpaceus* by exposing the territorial male to a conspecific "intruder" male in a cage together with a loudspeaker placed on top of the cage. During two 20-min exposures, a song of a male was broadcasted while recording the territorial male's behavior (e.g., attacks on the caged male). Similarly, in the house wren *Troglodytes aedon*, a mount made from a taxidermized male skin was used to manipulate the male's perceived threat of cuckoldry (DiSciullo et al. 2019). While in both studies the resident male recognized and attacked the intruder, only experimental male house wrens were less likely to provision the young.

Temporal removal of individuals or simulated intrusions might not always affect the male's perceived threat of cuckoldry, since it may depend on the natural history and habitat characteristics of the focal species. For instance, extra-pair copulations may occur in complex habitats that are visually occluded, which makes monitoring the activities of social mates more difficult (Sherman and Morton 1988; Mays and Ritchison 2004; Brouwer and Griffith 2019). Additionally, the temporary removal of breeding individuals during the egg-laying stage may induce nest desertion (Howes and Frei 2014). Hence, experimental studies should also evaluate the relationship between EPP and male provisioning of non-experimental individuals in the population. Although either approach (experimental or observational) may provide a weak result on its own, together they may provide insights into the relationship between paternal care and paternity loss (e.g., Dickinson 2003; Hoi et al. 2013).

Further studies on a diverse array of environments and species that differ in life history traits are needed to draw general conclusions about the relationship between paternity loss and paternal care in birds (Brouwer and Griffith 2019). Most studies have focused on north temperate passerines, characterized by high adult mortality (Macedo et al. 2008). However, in such species, males are less likely to reduce parental care to retaliate against females due to the uncertainty of surviving until the next breeding event (Mauck et al. 1999; Arnold and Owens 2002).

Over three breeding seasons, we intensively studied the parental behavior and genetic mating system of grass wrens *Cistothorus platensis* in south temperate Argentina. We first analyzed whether male grass wrens adjust their contribution to parental care with paternity loss, expressed as (1) the proportion of extra-pair offspring in the nest and (2) the presence of extra-pair offspring in the nest. We examined both measures of paternity loss because they may affect a male's behavior differently. For instance, a male might reduce provisioning only if his social mate engages frequently (rather than occasionally) in extra-pair copulations. Second, we simulated territorial intrusions by presenting stuffed decoys

close to the nest of the focal male during the female fertile period. Assuming that the intrusion increased the perceived threat of cuckoldry in experimental males, we evaluated whether male provisioning was reduced accordingly.

Methods

Study site

We studied a resident population of grass wrens in the flood plain of the Uspallata stream and Mendoza River (32° 38' S, 69° 22' W, 1800 m.a.s.l.) in Mendoza Province, Argentina. Our study site spanned approximately 120 ha and consisted of pockets of riparian grasslands and small swamps dominated by pampa grass *Cortaderia selloana* (Martínez Carretero 2000). Seasonality is pronounced, with low temperatures and occasional snowfall during the austral winter and warmer temperatures and milder conditions in the austral summer (Martínez Carretero 2000).

Study species

The grass wren is a small (10 g), insectivorous passerine that inhabits grasslands and wet meadows from Cape Horn (Argentina) to Mesoamerica (Zarco and Llambías 2018; Remsen et al. 2022). At our study site, grass wrens are territorial year-round and predominantly socially monogamous, with very rare instances of polygynous males (3%, Llambías et al. 2018). Grass wrens showed low to moderate rates of extra-pair paternity (8–27%, Arrieta et al. 2022) and low rates of conspecific brood parasitism (0–10%, Arrieta et al. 2020). Nests are dome-shaped structures, constructed mainly with dry grasses (Llambías et al. 2020). Grass wrens frequently lay two successive clutches of 4–6 eggs per breeding season and the incubation period lasts 14–18 days. The nestling period ranges from 12 to 19 days (Llambías et al. 2019). Both sexes provide food to nestlings in similar proportions, but only females incubate the eggs and brood the young (Llambías et al. 2019).

General fieldwork procedures

We carried out intensive fieldwork during three breeding seasons (October to February, 2015–2017). Early in the breeding season (mid-October), we mapped the breeding territories and captured adults using mist-nets. We captured focal males before nest-building commenced by using song playback. Females were caught by herding them to the mist-net or by setting the mist-net close to the nest while they fed the nestlings (11–12 days old). We marked individuals with a unique combination of three colored leg bands and an

aluminum band for identification. We also collected a blood sample (20–50 µL) for paternity analysis. Blood samples were collected from the brachial vein and stored in lysis buffer until DNA extraction.

Each year, we monitored 21–25 territories periodically to determine social interactions and find active nests by using parental behavioral cues and systematic searching. The locations of nests were recorded using a GPS (Garmin Etrex 20, Olathe, KS, USA) and marked with plastic tape. During egg-laying and incubation, we counted the eggs by introducing two fingers inside the nest. When eggs were close to hatching or nestlings were close to fledging, we checked nests daily to record more exact hatching and fledging dates. Otherwise, nest contents were checked every 2–3 days. We assumed a length of the incubation period of 14–15 days and a length of nestling period of 16–17 days to calculate an estimated hatch or fledge date when the exact date was unknown (Llambías et al. 2018). We counted the nestlings by extracting them from the nest during the hatching stage and before recording parental care (see below). When nestlings were 7–10 days old, we banded them with aluminum rings and collected blood samples for paternity analyses. For those pairs that raised more than one brood per season, we chose randomly which one (first or second) to include for paternity analyses. Recording data blind was not possible as our study involved focal animals in the field.

Parental care recording

To assess male provisioning effort to the offspring, we filmed nests when nestlings were 2–3, 7–8, and 11–12 days old for at least 4 h continuously. We defined “day 0” as the day when the majority of nestlings in a nest had hatched. Nests were filmed using micro-cameras (Mini 550 resolution button screw microcamera) connected to a portable mini DVR (PV500 LITE). Micro-cameras were installed between 0700 and 0730 h and placed 15–20 cm from the nests, concealed with small pieces of camouflaged netting and stems. We recounted nestlings at different ages (2–3, 7–8, and 10 days old) to adjust male provisioning by brood size in the statistical analysis.

The total time of video recordings consisted of 128 h in 2015 ($N=11$), 324 h in 2016 ($N=28$), and 360 h in 2017 ($N=30$). Four members of our research team analyzed each video recording to confirm the identity of the parents and determine the male provisioning rate (number of male provisioning trips per hour) using VLC media player (v. 3.0.13). Average male and female provisioning rates in relation to the nestling age are shown (Fig. 1). Video analysis was done blind concerning the presence of extra-pair offspring in the nest to avoid observer bias. Based on detailed field observations and parental care videos, males were classified as socially monogamous or polygynous.

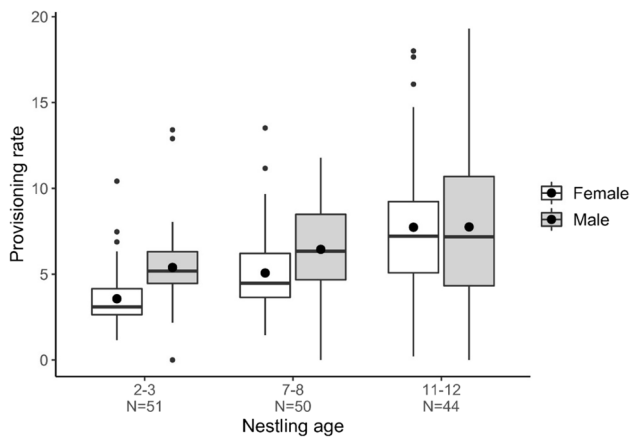


Fig. 1 Average male and female provisioning rates (number of provisioning trips per h) in relation to the nestling age (days old) in south temperate grass wrens. Box plots show mean (point in the middle), median (line in the middle), 25% and 75% percentiles (lower and upper end of the box), 10% and 90% percentiles (whiskers), and all data points falling outside the 5% and 95% percentiles. Numbers indicate sample sizes for each category

We considered a male to be socially polygynous if two females nested within his territory and their incubation or nestling periods overlapped. Only broods belonging to socially monogamous males were considered in our study.

ddRAD sequencing and SNP data analysis

We extracted DNA from blood samples following a standard protocol of dehydration and precipitation with ethanol and NaCl (Miller et al. 1988). We performed double-digest restriction site-associated DNA sequencing (ddRAD) for single-nucleotide polymorphism (SNP) discovery. The ddRAD sequencing protocol together with the SNP data analysis was described in Arrieta et al. (2020). This procedure resulted in 762 SNPs for the 2015 season, 906 SNPs for 2016, and 855 SNPs for 2017.

Parentage analysis

We conducted paternity analyses using CERVUS 3.0.7 (Kalinowski et al. 2007) and calculated the proportion of extra-pair offspring in each brood. CERVUS assigns paternity using the natural logarithm of the likelihood ratio (LOD score), which provides the likelihood of paternity of each candidate male relative to a random male in the population. We accepted the CERVUS assignment when the highest-ranked male showed a positive (or slightly negative) pair LOD score and the number

of genotype mismatches between the assigned male and the offspring was ≤ 8 (see Arrieta et al. 2022 for more details).

Experimental intrusion

We used a standardized method to experimentally manipulate the perceived threat of cuckoldry in resident males (modified from Hoi et al. 2013; DiSciullo et al. 2019). We exposed socially monogamous male grass wrens ($N = 48$) to simulated territorial intrusions during the female fertile period (i.e., laying of the second or third egg) by using stuffed decoys in concert with playback of male song. A grass wren (experimental) or rufous-collared sparrow *Zonotrichia capensis* (control) decoy was mounted on a stick and placed about 1 m from the nest. A speaker (Philips BT50B) connected to an MP3 player (SanDisk Sansa m230) was concealed with camouflage and located behind the decoy. Based on recordings conducted in the field, we set the speaker to broadcast song samples at approximately 42 dB by using a CEM DT-85A mini sound level meter. Due to the lack of mounted specimens, we only used one decoy for each treatment category, leading to pseudoreplication of the visual stimulus (Milinski 1997). However, both treatment categories included five song samples, each recorded from different individuals on our study site. Thus, we avoided testing for the effect of the song from a given individual (Kroodsma 1990). None of the recorded males were neighbors of focal males in the experiments described here.

After focal males were located visually, we placed the decoy and song playback equipment about 1 m from the nest. All song samples began with 2 min of silence followed by 10 min of grass wren or rufous-collared sparrow song. During the first 2-min period of silence, we hid among vegetation about 10–15 m away from the decoy and observed the behavior of the focal male with 10×42 binoculars. Then, the song playback track was broadcasted for the next 10 min. On each trial, we recorded the behavior of the focal male during the first 5 min of the intrusions beginning when the focal male first moved within 5 m of the decoy. We registered two behavioral parameters: (1) the number of approaches to the decoy and (2) whether the focal male attacked the decoy. While an “attack” involved physical contact (e.g., the focal male landing on the decoy’s back and pecking vigorously and repeatedly on the head), an “approach” consisted of the focal male perching close (less than 1 m) to the decoy. Since 10 nests were predated before nestlings were 2 days old, we were able to record male provisioning from 38 nests (18 experimental and 20 control).

The nests of the experimental and control males were filmed during the nestling stage as described above to assess differences in provisioning effort to the nestlings.

Statistical analyses

We evaluated the association between male provisioning and paternity loss using linear mixed-effects models (LMM) with a Gaussian error distribution and log-link function. Male provisioning rate (expressed as number of male provisioning trips per hour) was set as the response variable. We built separate models that included the proportion of extra-pair offspring (model A) and the presence/absence of extra-pair offspring in the nest (model B) as explanatory variables. Both models included an interaction term between the explanatory variable and nestling age. Both models also included other variables that might affect male provisioning such as brood size and timing of breeding. Timing of breeding was defined as the difference between the date the first egg was laid and the date when the first egg in the population was laid and standardized using the mean value and standard deviation for each year. As male provisioning might be affected by female provisioning (Wright and Cuthill 1990), male proportion of provisioning trips (i.e., the number of male provisioning trips divided by the total number of trips for the male and female combined) was set as a covariate too. Male body size might also influence provisioning (DeMory et al. 2010); however, a preliminary analysis did not find a significant association between these variables (Table S2). Thus, male body size was not included as a predictor in the full models. Both social father/mother identities were set as random effects as approximately 17% of males and 13% of females were recorded in more than one breeding attempt. We also set year as random effect to account for between-year variations.

Male agonistic behavior when exposed to a grass wren (experimental) or rufous-collared sparrow (control) stuffed decoy was evaluated by using generalized linear models (GLM). The number of approaches to the decoy was analyzed with a GLM using a negative binomial error distribution. As “attack” was included as a binary response variable (yes vs. no), we used a GLM based on a binomial distribution. Territorial intrusion (experimental vs. control) was set as the explanatory variable in both models. Thus, we assessed whether the territorial intrusions were perceived as a threat of cuckoldry by experimental males.

We then used a LMM to assess whether males adjusted their provisioning rates accordingly to their perceived threat of cuckoldry by comparing male provisioning rates between experimental and control groups. Territorial

intrusion (experimental vs. control) was set as the explanatory variable. Fixed effects included brood size, timing of breeding, and male proportion of provisioning trips. We also included the interaction between territorial intrusion and nestling age. Year and both social father/mother identities were set as random effects.

All the analyses were performed in R (R Core Team 2019). LMMs were fitted using package lme4 (Bates et al. 2015) and figures were generated in the R-package ggplot2 (Wickham 2009). All continuous predictors were standardized to facilitate interpretation and improve model convergence (Gelman 2008). We conducted backward stepwise elimination of non-significant predictors ($p > 0.05$) by comparing full model to each of the reduced models through chi-squared likelihood ratio tests. For each analysis, we used residual and normal probability plots to check the assumptions of the models.

Results

Over three breeding seasons, we genotyped 81 adults (40 males, 41 females) and 221 nestlings from 52 broods. On average, a clutch consisted of 4.3 ± 0.1 eggs (mean \pm SE; $N = 259$ nests, range 1–6). This resulted in broods containing an average of 3.9 ± 0.1 nestlings (mean \pm SE; $N = 161$ nests, range 1–6).

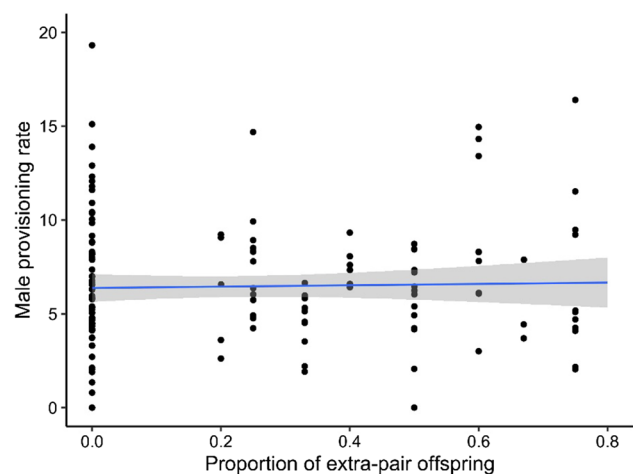


Fig. 2 Relationship between male provisioning rate (number of provisioning trips per hour) and the proportion of extra-pair offspring in the nest in south temperate grass wrens. The raw data (points) and model predictions with 95% confidence intervals (blue line and shaded area) are shown

Table 1 Results from a linear mixed-effects model analyzing the male provisioning rate in relation to the proportion of extra-pair offspring (EPO) in the nest in south temperate grass wrens ($N=52$ nests, 145 total observations)

Model A	Estimate (SE)	df	χ^2	p
Intercept	6.48 (0.22)	-	-	-
Proportion of EPO \times nestling age	-0.12 (0.16)	1	0.54	0.46
Proportion of EPO	0.06 (0.20)	1	0.10	0.75
Nestling age	1.53 (0.16)	1	65.94	<0.001
Timing of breeding	-1.09 (0.19)	1	27.32	<0.001
Brood size	0.53 (0.18)	1	6.87	0.01
Male proportion of provisioning trips	2.38 (0.19)	1	104.10	<0.001
Random effect	σ^2			
Year	0.03			
Social mother identity	0.64			
Social father identity	<0.001			

Parameter estimates with standard errors (in parentheses), degrees of freedom, χ^2 values, and p values of likelihood ratio tests are given

Estimates are for standardized predictors

Significant p values are indicated in bold (significance level considered: $p < 0.05$)

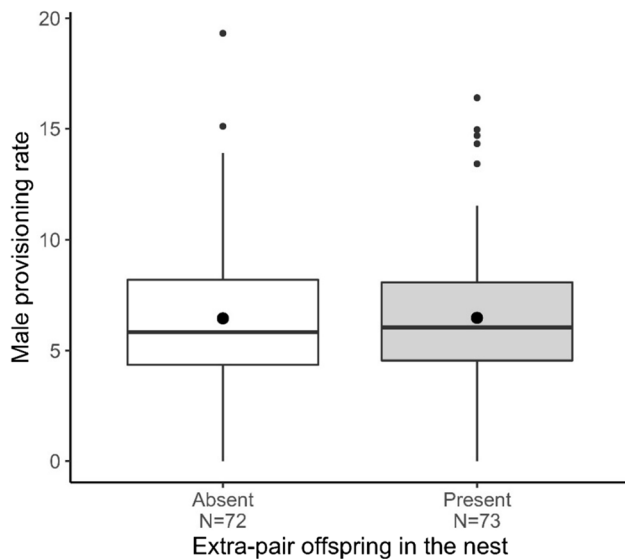


Fig. 3 Average male provisioning rate (number of provisioning trips per hour) in relation to the presence of extra-pair offspring in the nest in south temperate grass wrens. Box plots show mean (point in the middle), median (line in the middle), 25% and 75% percentiles (lower and upper end of the box), 10% and 90% percentiles (whiskers), and all data points falling outside the 5% and 95% percentiles. Numbers indicate sample sizes for each category

Prevalence of extra-pair offspring did not affect male provisioning rates

More than half of the sampled broods (52%, 27/52) contained at least one extra-pair offspring. Fifty-one out of 221 nestlings (23%) were sired by extra-pair males. We did not find a relationship between the proportion of extra-pair offspring in the nest and male provisioning rate (Fig. 2, Table 1). Nor did males seem to adjust their provisioning

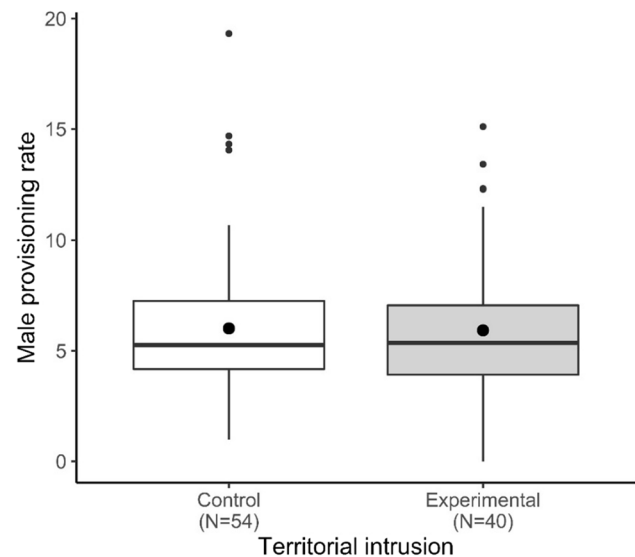


Fig. 4 Average provisioning rates (number of provisioning trips per hour) of male grass wrens in relation to the presence of a heterospecific (control: male rufous-collared sparrow stuffed decoy) or conspecific (experimental: male grass wren stuffed decoy) intruder during the female fertile period (egg-laying stage). Box plots show mean (point in the middle), median (line in the middle), 25% and 75% percentiles (lower and upper end of the box), 10% and 90% percentiles (whiskers), and all data points falling outside the 5% and 95% percentiles. Numbers indicate sample sizes for each category

according to the presence or absence of extra-pair offspring in the nest (Fig. 3, Table S1).

Experimental intrusions did not influence male provisioning rates

During the simulated territorial intrusions, experimental males were more likely to approach ($N_{\text{control}} = 20$,

Table 2 Results from a linear mixed-effects model analyzing the male provisioning in relation to the perceived threat of cuckoldry in south temperate grass wrens ($N=38$ nests, 94 total observations)

	Estimate (SE)	df	χ^2	p
Intercept	5.08 (0.93)	-	-	-
Territorial intrusion \times nestling age	-0.01 (0.35)	1	0.001	0.97
Territorial intrusion (experimental)*	0.32 (0.40)	1	0.61	0.43
Nestling age	1.75 (0.18)	1	60.97	<0.001
Timing of breeding	-0.24 (0.21)	1	1.26	0.26
Brood size	1.03 (0.20)	1	22.14	<0.001
Male proportion of provisioning trips	2.37 (0.21)	1	82.26	<0.001
Random effect	σ^2			
Year	2.22			
Social mother identity	0.65			
Social father identity	0			

Parameter estimates with standard errors (in parentheses), degrees of freedom, χ^2 values, and p values of likelihood ratio tests are given

Estimates are for standardized predictors

Significant p values are indicated in bold (significance level considered: $p < 0.05$)

*Categorical predictor with two levels (reference category: control)

$N_{\text{experimental}} = 18$, $\chi^2 = 28.64$, $p < 0.001$) and attack ($N_{\text{control}} = 20$, $N_{\text{experimental}} = 18$, $\chi^2 = -6.50$, $p = 0.01$) the decoy than control males. However, the male provisioning rate between experimental and control groups did not differ significantly (Fig. 4, Table 2).

Discussion

In this study, we found that male grass wrens did not adjust their food provisioning effort to actual paternity loss. Additionally, we did not find experimental evidence that a perceived threat of cuckoldry affects male provisioning. Together, these results suggest that female grass wrens that gained extra-pair fertilizations (or may be perceived to have gained such fertilizations) were not indirectly retaliated by males by reducing food provisioning to the nestling.

We provide further evidence for the general pattern that males do not adjust their provisioning rate to actual paternity loss (e.g., Wagner et al. 1996; Yezerinac et al. 1996; Bouwman et al. 2005). South temperate birds provide a unique opportunity for studying EPP as they are thought to have greater adult survival than north temperate species (Robinson 1990; Martin 1996; Magrath et al. 2000; Russell 2000; but see Llambías et al. 2012). Having greater adult survival, males are expected to reduce parental care when females obtain extra-pair fertilizations (Wright 1998). Even

though recently there has been an increase in research on EPP in Neotropical birds, only one other study has evaluated the relationship between EPP and paternal care in temperate South America. Similarly to our results, Poblete et al. (2021) found that male thorn-tailed rayaditos (*Aprastura spinicauda*) do not adjust parental care to the proportion of extra-pair offspring in the nest. However, further studies conducted on south temperate birds are needed to draw general conclusions.

Evidence suggests that territorial intrusions using conspecific stuffed decoys during the female fertile period increase males' perceived threat of cuckoldry (Mougeot et al. 2001; DiSciullo et al. 2019). In grass wrens, males were more likely to attack and approach a conspecific than an heterospecific male decoy, suggesting that conspecifics were considered a threat. Furthermore, in one instance, we observed a resident female soliciting copulations to the decoy by shaking her wings and cocking the tail. However, experimental males did not adjust their provisioning accordingly. Our result is consistent with what has been found in previous studies in north temperate passerines (e.g., Whittingham et al. 1993; Kempenaers et al. 1998; MacDougall-Shackleton and Robertson 1998; Dickinson 2003). As far as we know, ours is the first experimental study of this type conducted on a Neotropical bird. Negative results are frequently criticized as it is not possible to ascertain whether experimental manipulations have successfully influenced perceived paternity (Wright 1998). However, our experimental results are supported by observational data as males also did not adjust their provisioning to actual paternity loss.

A lack of relationship between male parental contribution and paternity loss may be explained by several factors. First, low EPP rates found in our grass wren population might increase the cost of retaliation for males (McNamara et al. 2002). Even though more than half of the sampled broods contained at least one extra-pair offspring, cuckolded males sired most of the offspring in their broods. As birds are not able to discriminate between intra- and extra-pair offspring (Leonard et al. 1995; Westneat et al. 1995; Kempenaers and Sheldon 1996; Lattore et al. 2019), cuckolded males reducing their provisioning might also reduce the survival of their offspring (Dickinson 2003). Although our result suggests that males might not be under strong selection pressure to adjust their provisioning according to females' extra-pair behavior, both the costs of parental care and male desertion remain to be evaluated.

Second, male grass wrens may also rely on precopulatory strategies like mate guarding and territoriality rather than on female retaliation to reduce paternity loss. Male grass wrens are strongly territorial during the breeding season and frequently engage in song duels to settle territorial disputes (Garrido Coria et al. 2021). Males also seem to closely guard

their mates during the egg-laying stage (1.0–3.0 m; Arrieta personal observations).

Third, we assumed that provisioning food to unrelated offspring should have a cost for males (Trivers 1972). However, males may gain indirect benefits from parental care. For example, parental performance might be a sexually selected character in birds, offering a reliable index by which females could measure male quality and select mates (Wagner 1992; Wagner et al. 1996). Freeman-Gallant (1997) found that male provisioning rate to the first brood determines a male's subsequent mating success in savannah sparrows *Passerculus sandwichensis*. From this perspective, cuckolded male grass wrens might still provide care to unrelated offspring to obtain extra-pair copulations from neighboring females and assure higher paternity in future breeding attempts with the current mate.

To conclude, our results provide compelling evidence against male provisioning adjustment to paternity loss and perceived threat of cuckoldry in a south temperate passerine. In grass wrens, females seeking extra-pair fertilizations might not suffer the costs associated with retaliation (e.g., aggression and/or reduced paternal care). However, males may have effective precopulatory strategies to reduce extra-pair fertilizations. Indirect retaliation may be prominent in species with high rates of EPP where selection should favor males to invest less in parental care and more in seeking extra-pair fertilizations (Westneat and Sherman 1993). We did not evaluate other aspects of paternal behavior such as nest defense and nestling provisioning under the risk of predation, which should be considered in future studies. Further studies in other south temperate passerines will provide greater insight into the relationship between female extra-pair behavior and male facultative responses.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03253-y>.

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Author contribution Conceptualization (RSA, PEL, BM); data curation (RSA, PEL); formal analysis and investigation (RSA); funding acquisition (RSA, PEL, BM, LC); methodology (RSA, PEL, BM, LC); project administration (RSA); resources (RSA, PEL, BM, LC); software (RSA, LC); visualization (RSA); writing—original draft preparation (RSA, PEL, BM, LC).

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Data availability All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Declarations

Ethics approval Fieldwork permits (resolution 459 and 1564) were provided by the Secretaría de Ambiente y Desarrollo Sustentable, Dirección de Recursos Naturales Renovables, Mendoza, Argentina. During the study period (2015–2017), procedures involving live birds did not require ethical approval from the Animal Care Committee. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Competing interests The authors declare no competing interests.

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