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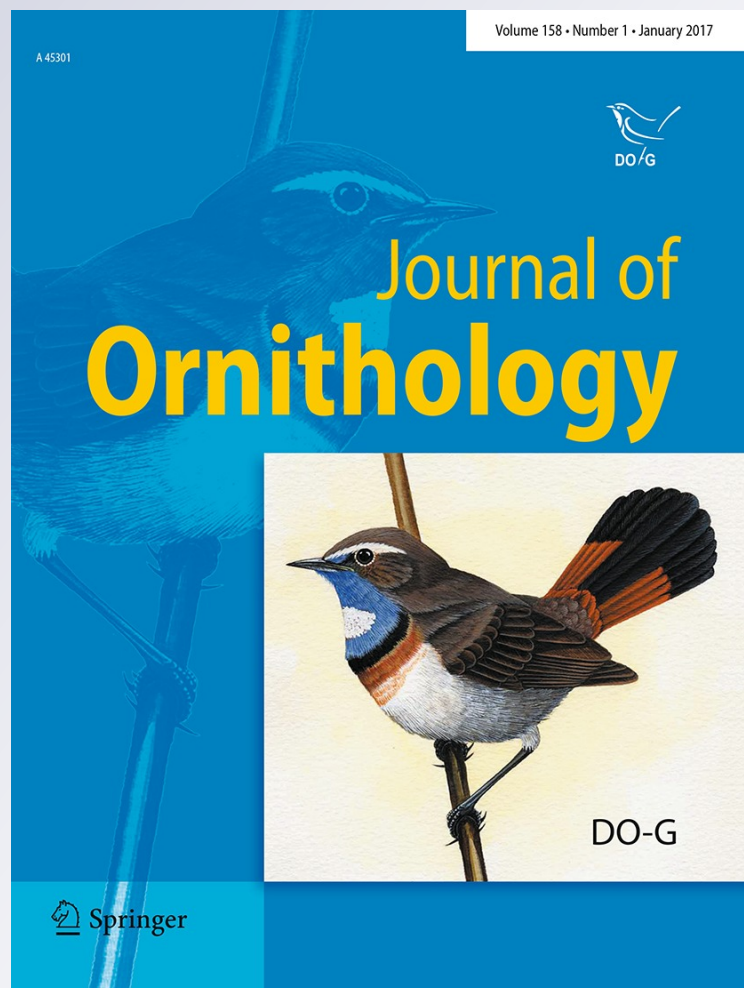
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Parental care and external sexual characters in the Warbling Doradito (*Pseudocolopteryx flaviventris*)

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Abstract Biparental care is the dominant (81 %) form of parental care in birds. The degree of sexual selection and the resulting mating system and parental care type have been determined, in many cases, by inference from external characters of sexual dimorphism. The lack of information and the biological attributes of the tyrant flycatchers (e.g., low sexual dimorphism) make it difficult to determinate the parental care roles in most species. Tyrant flycatchers comprise a diverse bird family, but information on the reproductive behavior of many Tyrannid species is lacking. Our aim was to describe external sexual characters (morphology and coloration) and determine the parental care behavior at the nest in the Warbling Doradito (*Pseudocolopteryx flaviventris*), especially considering the potential role of sexual differences in relation to parental roles at nest. We studied the parental care behavior during two breeding seasons. Parents were captured to take morphological measurements and a blood sample for molecular sex determination. We found that parental care in the Warbling Doradito was biparental biased toward females, where the incubation was performed exclusively by females and the 74 % of activities of nestling brooding and feeding was performed by females. We also found sexual differences, slight in size and plumage, but more conspicuous in bill color. Despite the relatively slight sexual

dichromatism of the Warbling Doradito, the parental care behavior in the nest was biased towards females, and the assistance of males to nestlings was highly variable and was not correlated with either clutch size or increasing nestling mass. Therefore, the evidence presented here suggest that *Pseudocolopteryx* genus may have an unusual social system, otherwise uncommon in tyrannids.

Keywords Tyrannidae · Morphology · Nestling feeding · Pampas · Grasslands · Dichromatism · Argentina

Zusammenfassung

Brutpflege und äußere Geschlechtsmerkmale beim Braunrücken-Sumpftyrann (*Pseudocolopteryx flaviventris*)

Bei Vögeln ist die Brutpflege durch beide Elternteile die vorherrschende (81 %) Form der Brutpflege. Die Ausprägung der sexuellen Selektion und das daraus resultierende System von Balz und Brutpflege wurde sehr häufig nur durch das Schließen von äußeren Merkmalen auf einen Geschlechtsdimorphismus bestimmt. Zu wenig Informationen sowie die biologischen Eigenheiten wie z.B. ein schwach ausgeprägter Geschlechtsdimorphismus bei den Schreivögeln (*Tyrannides*), machen es bei den meisten Arten schwierig, die tatsächliche Rolle der beiden Elternteile in der Brutpflege festzustellen. Die Schreivögel stellen eine große, recht uneinheitliche Familie dar, aber über das Fortpflanzungsverhalten vieler ihrer Arten liegt nur wenig Information vor. Ziel dieser Studie war es, für den Braunrücken-Sumpftyrann (*Pseudocolopteryx flaviventris*) äußere Geschlechtsmerkmale (Morphologie, Färbung) zu beschreiben und das Brutpflegeverhalten am Nest zu bestimmen. Dabei wurde besonderes Augenmerk auf

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mögliche Geschlechtsunterschiede in der Brutpflege durch die beiden Eltern am Nest gelegt. Das Brutpflegeverhalten wurde über zwei Brutzeiten hinweg beobachtet und die Elterntiere gefangen, um ihre Körpermaße zu bestimmen und Blutproben für eine molekulare Geschlechtsbestimmung zu entnehmen. Wir fanden heraus, dass beim Braunrücken-Sumpftyrann die Brutpflege eher von den Weibchen übernommen wurde: das Brüten selbst lag ausschließlich bei den Weibchen, und 74 % aller Aktivitäten ums Brüten und Füttern herum wurden ebenfalls von den Weibchen durchgeführt. Ferner fanden wir äußere Geschlechtsunterschiede: für Größe und Gefieder waren sie eher kleiner, deutlich auffälliger jedoch in der Schnabelfärbung. Trotz der relativ kleinen Geschlechtsunterschiede war das Brutpflegeverhalten am Nest bei den Weibchen stärker ausgeprägt; die Unterstützung durch die Männchen war sehr unterschiedlich und korrelierte nicht mit der Gelegegröße. Diese Ergebnisse legen nahe, dass das soziale System der Gattung *Pseudocolopteryx* möglicherweise anders und unüblich für die übrigen Tyranni ist.

Introduction

Biparental care is the dominant form of parental care in about 81 % birds, but the quality and quantity of the parental care contribution by each gender varies substantially among species (Cockburn 2006). As a consequence, this variation has been considered a major source of conflict between provisioning parents (Trivers 1972). This sexual conflict arises because each parent will benefit from an investment in its offspring, but it should pay a cost of providing that care in terms of reduced survival or fecundity (Clutton-Brock 1991). Generally, the division of parental duties within the pair has been explained by mating system and sexual selection (Lack 1968; Székely et al. 2000; Cockburn 2006). Increased male parental care tends to co-occur with monogamy and sexual monomorphism, whereas reduced or lack of male care has been correlated with polygyny and sexual dimorphism (Lack 1968; Verner and Willson 1969; Trivers 1972; Silver et al. 1985; Ketterson and Nolan 1994).

The degree of sexual selection and the resulting mating system and parental care type have been determined, in many cases, by inference from external characters of sexual dimorphism. However, for species with no conspicuous sexual differences, such inferences may have led to misinterpretations (Ismar et al. 2011). For instance, molecular techniques and more detailed studies have revealed previously uncertain sex differences. However, advances in techniques in determining sex differences, for instance, plumage coloration UV reflectance (perceived by the eye

of birds and not by human; Andersson et al. 1998; Hunt et al. 2001; Ismar et al. 2011), have allowed determination of dichromatisms in species considered monochromatic (no difference in plumage coloration). That suggests that previous interpretations of avian plumage coloration may be misleading (Cuthill et al. 1999). Specifically, large numbers of species appearing sexually monochromatic to the humans may in fact be perceived as sexually dichromatic by birds (Eaton 2005). Therefore, there may be a high degree of sexual selection in certain species that appear monomorphic to the human eye, because of differences perceived only by birds.

Tyrant flycatchers (Family: Tyrannidae) comprise one of the largest and most diverse bird families in the world (Traylor 1977; Fitzpatrick 2004). Most Tyrannid species show little sexual dimorphism, and are mostly socially monogamous (Ridgely and Tudor 1994; Fitzpatrick 2004). The mode of parental care prevailing in tyrant flycatchers is biparental (93 %; Cockburn 2006), and, to a lesser extent, female only care (5 %) and cooperative breeding (2 %; Cockburn 2006). However, there are also many gaps in the knowledge of the breeding and nesting behavior of many Tyrannid species (Fitzpatrick 2004). The lack of information and the biological attributes of the tyrant flycatchers (e.g., low sexual dimorphism, small–medium size; Fitzpatrick 2004) make it difficult to determine the parental care roles in most species.

Pseudocolopteryx is a genus of tyrannids endemic to South America (Ridgely and Tudor 1994; Fitzpatrick 2004) with five species all occurring in Argentina (Narosky and Yzurieta 2010). Apart from occasional good nest descriptions (Dinelli 1933; Ortiz et al. 2006; Ábalos and Areta 2009; Roesler 2009), little is known about the natural history of *Pseudocolopteryx* species. Sexual dimorphism has been reported for some *Pseudocolopteryx* species, for example, in the Crested Doradito (*P. sclateri*) females have a smaller and duller crest (Bostwick and Zyskowski 2001; Fitzpatrick 2004), and males of Crested Doradito, Subtropical Doradito (*P. acutipennis*), and Dinelli's Doradito (*P. dinellianus*) have the sixth and seventh primary feathers modified (Hellmayr 1927; Meyer de Schauensee 1970; Bostwick and Zyskowski 2001). The Warbling Doradito (*P. flaviventris*) is the species with the least difference in external sexual characters of the genus. In this species, females have a flesh-colored lower mandible whereas it is black in males (Fitzpatrick 2004), and males have the chestnut crown more clearly marked and darker than in females (Ábalos and Areta 2009). The Warbling Doradito breeds from southern Brazil and Uruguay to central Argentina in reeds and grasslands flooded or near water bodies (Narosky and Salvador 1998; Roesler 2009; Pretelli et al. 2013; Cardoni et al., under review). The nest of the Warbling Doradito consists of a small and compact open

cup with a globular appearance fixed to grass leaves. The mean clutch ranges between 1 and 3 eggs, and the incubation period extends over approximately 17 days. Chicks remain on average 13 days in the nest (Cardoni et al., under review).

Our aim was to perform a thorough description of the external sexual characters of the Warbling Doradito by using molecular techniques and morphometric measurements, and to study the parental care behavior, especially considering the potential role of sexual differences in relation to parental roles at nest. We predicted that considering the low external sexual differences in the Warbling Doradito, parental care may be slightly skewed to females.

Methods

Study area and nest search

Our study area comprised the Mar Chiquita coastal lagoon (37°40'S, 57°23'W), a MAB-UNESCO Biosphere Reserve located in southeastern Buenos Aires Province, Argentina. The main habitats around the lagoon are grassland communities dominated by *Spartina densiflora* in lowland areas, and by grasslands dominated by *Cortaderia selloana* and *Juncus acutus* in upper zones (Isacch et al. 2006). We studied the nesting behavior of Warbling Doraditos in tall-grasslands dominated by *C. selloana*.

We systematically searched for nests of the Warbling Doraditos during two consecutive breeding seasons (October 2012–January 2013; October 2013–January 2014). We marked the nests we found, recorded their coordinates with GPS, and visited them at intervals of 2–4 days recording the number of eggs, hatching and fledging dates, and instances of predation. We used standard procedures to avoid attracting predators to the nests (Martin and Geupel 1993).

External sexual characters

Individuals of Warbling Doradito were captured using a mist-net (12 × 2.5 m, 20-mm mesh size) placed near nests to ensure we caught both of the pair. Each captured individual was measured and banded. We recorded seven morphological measurements for each bird: bill length, taken from the anterior point of the nostril to the tip of the bill; bill width, taken across the base of the bill under the proximal point of the nostrils; bill depth, taken at the anterior point of the nostrils; tarsus length, taken from the joint of the tibiotarsus and tarsometatarsus to the distal edge of the most distal unbroken scute overlying the middle toe; tail length, taken between the two middle tail feathers, from the base of the

feathers to the end of the longest feather; wing chord, taken from the carpal joint to tip of the longest primary; and body mass. We used a digital calliper (± 0.01 mm) for bill and tarsus measurements, a ruler (± 1 mm) for tail and wing measurements and a digital balance (accurate to 0.1 g) to record the body mass. Additionally, we took photographs (saved in JPEG format) of captured individuals using a digital camera to adequately describe plumage and bill coloration patterns. All the captured individuals were banded with a unique combination of two colors of plastic bands. The research complied with the requirements of our animal ethics system.

Blood sampling and molecular sexing

We took a blood sample to each individual captured. Blood samples (100–200 μ l) were collected during the breeding season from the brachial vein of the adults using a syringe. Samples were transferred to a tube and preserved in absolute ethanol until analysis. DNA was extracted from blood cells using Chelex 100 resin (BioRad, Hercules, CA, USA) (Walsh et al. 1991).

Bird sex DNA marker amplification was performed in a PCR (Bioer Life Express Thermal Cycler, China) using specific oligonucleotide primers 2550F and 2718R (manufactured by Invitrogen Life Technologies) (Fridolfsson and Ellegren 1999). Polymerase Chain Reaction (PCR) amplification was performed in a reaction volume of 12.5 μ l, containing 20–40 ng of DNA, 1 μ M of each primer, 1 U of Taq DNA Polymerase (Promega, Madison, WI, USA), 1× PCR buffer, 1.5 mM MgCl₂ and 0.4 mM of dNTPs. The thermocycling profile included an initial denaturing at 94 °C (4 min), followed by 30–35 cycles of denaturing at 94 °C (30 s) an annealing step at 52 °C (45 s), extension at 72 °C (45 s) and a final extension at 72 °C (5 min). PCR products were separated by electrophoresis in 1× TBE buffer (TrisHCl-boric acid-EDTA) in a 1.5 % (w/v) agarose gel. Gels were stained with SYBR Gold (Invitrogen) and visualized under UV in a transilluminator. PCR products were compared to a 100-bp DNA ladder. Males were recognized as displaying a single PCR product (from CHD 1Z, 600 bp) whereas females showed two PCR products (from CHD 1 W, 450 bp, and from CHD 1 Z) (Fridolfsson and Ellegren 1999).

Parental care

We recorded the parental care behavior at the nest using a digital mini-video recorder (DV-200, resolution: 640 × 480, 30 fps). This camera (8 × 3 × 1 cm in length, width and height, respectively) allows the filming of hidden nests within tussocks of grass without the need to modify the conditions and structure of the plants. The camera has battery autonomy of 4 h and the information is stored in a

micro-SD memory of 16 GB. Cameras were installed between 0800 and 0900 hours Argentina Time (ART), and maintained in the nest for 3 h, 30 min. The first 20 min of each recording was excluded from the analyses to reduce the effect of the camera and our presence at the nest. Video monitoring was carried out on different days with similar weather conditions, avoiding windy ($>20 \text{ km}^{-1}$), rainy and extremely hot conditions ($>30^\circ \text{ C}$). We subsequently analyzed the video samples in the laboratory by recording the several parental care behaviors. During the incubation period, parental care behavior at the nest was categorized into two activities: (1) *incubation* (when a parent is sitting on the eggs) and (2) *nest assistance* (activities related to nest arrangement, e.g., fixing the structure of the nest, incorporating more materials, and nest vigilance within the nest, e.g., when a parent is sitting on the nest or staying very close to it). During the nestling period, three behavioral categories were used: (1) *nestling feeding* (when a parent feeds a nestling), (2) *nestling assistance* (fixing the structure of the nest, when a parent observing the nestlings close to the nest or chick grooming) and (3) *fecal sac removal* (when parents remove or eat the fecal sacs). Each behavior was estimated in time (minutes) and rate (trips) per hour for each sex separately. When comparing the behavior between parents during the nestling period, we standardized the data per grams of nestlings at the nest. Nestling mass was recorded after the end of each videotaping, using a digital balance (accurate to 0.1 g).

Statistical analyses

Morphology We used a simple *t* test to evaluate the null hypothesis of no differences in morphologic characters between the sexes of the Warbling Doradito (Zar 2010). Moreover, we developed a forwards stepwise discriminant function analysis (DFA) on the morphological measurements of Warbling Doraditos to search sexual differences. The performance of each DFA was evaluated through the Wilk's Lambda statistic, which decreases as its discriminatory power increases (Hair et al. 1995). The combination

of measurements that best discriminated between sexes was selected. A significance level of $P = 0.15$ was selected for entry into the model and variables were retained in the stepwise model at the $P = 0.05$ level of significance.

Parental care We used a paired *t* test (by nest) to assess the null hypothesis of no differences in the reproductive investment between parental pairs during the nesting stage. In some cases, we recorded nests attended only by the female, despite the fact that the male was captured, banded and later observed in the nest surroundings. We compared care behavior between these females and females helped by males using a *t* test (Zar 2010). Finally, to assess whether the male increases its effort to feeding the nestlings in relationship to food demand, we plotted the relationship between the nestling feeding rate (trips per hour) and the total nestling biomass in the nest, distinguishing between nests attended by a single female and by both parents; for the latter, we included the relative percentage of nestling feeding trips by the male.

Results

External sexual characters

A total of 66 adult individuals were captured (35 in 2012–13 and 31 in 2013–14) associated with 39 nests. We were able to determine the sex of all individuals, 34 females and 32 males, using molecular techniques. The morphological measures that showed significant differences between sexes were the tail length and wing chord, both longer in males than females (Table 1). The stepwise DFA selected two of the seven variables in the model: tail and wing length (Wilks' Lambda: 0.69, $F_{2,61} = 13.2$, $P < 0.0001$). This function correctly determined the sex of 69 % of the overall individuals, with a correct identification of 61 and 76 % of cases for males and females, respectively.

We found differences in both plumage and bill coloration between the sexes. The coloration of the face

Table 1 Morphological measurements (mean; and SD standard deviation) in individuals of Warbling Doraditos (*Pseudocolopteryx flaviventris*) breeding in *Cortaderia selloana* grasslands at the Mar Chiquita Reserve, Argentina

Character	Female			Male			<i>t</i> test	
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>t</i>	<i>P</i>
Bill length (mm)	34	8.18	0.42	32	8.20	0.37	0.01	0.937
Bill width (mm)	34	3.83	0.18	32	3.83	0.26	0.05	0.831
Bill depth (mm)	34	2.77	0.17	32	2.78	0.17	0.06	0.800
Wing chord (cm)	34	4.61	0.16	32	4.77	0.23	10.42	0.002
Tail length (cm)	33	4.09	0.15	31	4.27	0.15	23.92	0.000
Tarsus length (mm)	34	20.37	3.03	32	20.68	0.78	0.75	0.389
Body mass (g)	33	8.03	0.59	30	7.92	0.28	0.23	0.635

Significant differences ($P < 0.05$) in the *t* test and *P* values are in bold

presented differences between the sexes since in males the lorum and eyebrow have gray and black stripes, whereas in females these parts are less conspicuous, with gray and brown plumage (Fig. 1). The most conspicuous difference

was in the color of the bill which was completely black in the male, whereas the female's bill was black externally with a mostly orange interior, and with a flesh-colored line bordering both the upper and lower mandibles (Fig. 1).

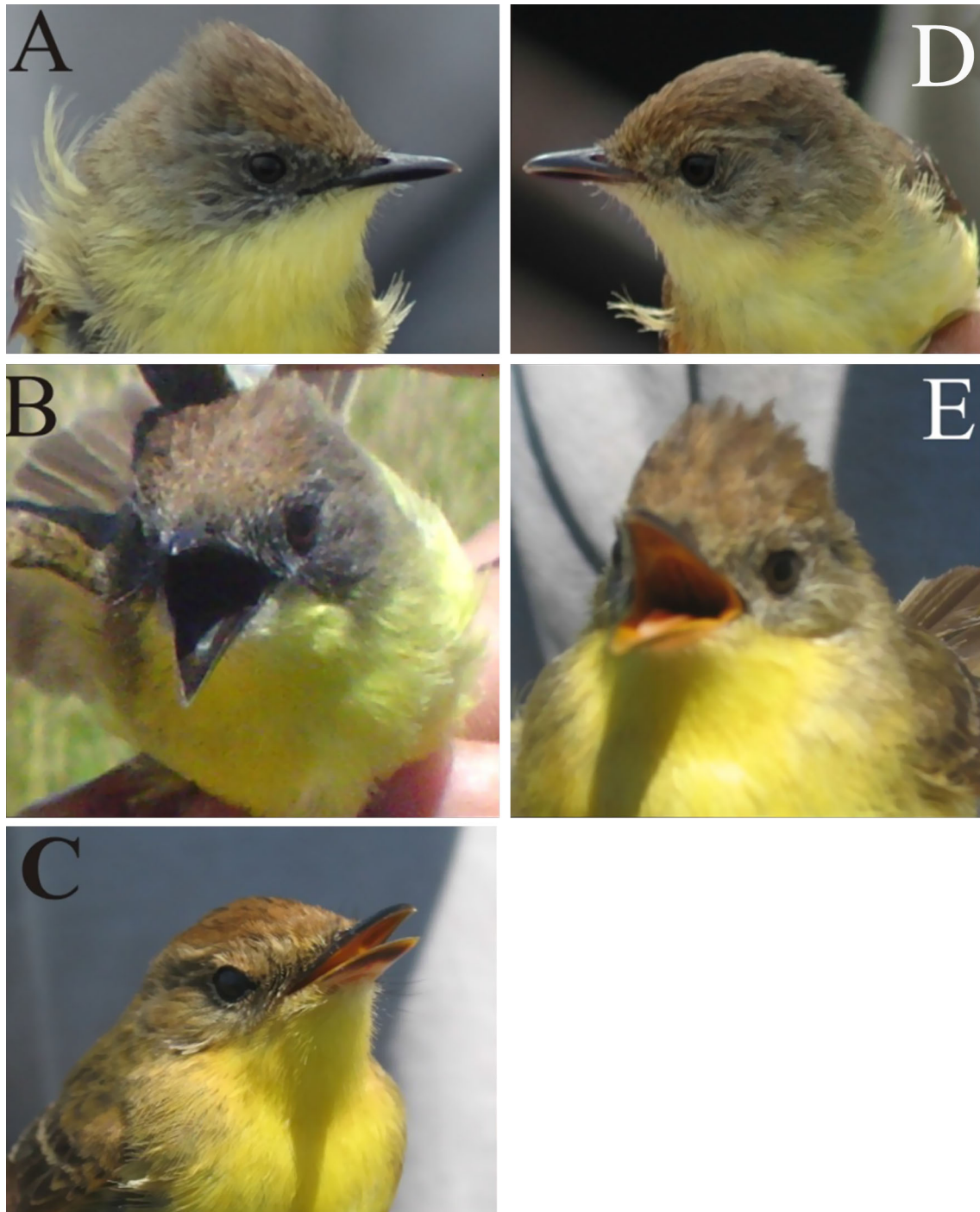


Fig. 1 Male (a, b), female (d, e) and juvenile (c) individuals of the Warbling Doradito (*Pseudocolopteryx flaviventris*) breeding in *Cortaderia selloana* grasslands at the Mar Chiquita Reserve, Argentina

Parental care

We filmed the parental care behavior in 27 nests; 6 during the incubation period and 21 during the nestling period. In total, we recorded 86 h from which we could determine 1149 activities of parental care, including 59 egg incubation events, 704 feeding trips, 183 assistance events, 100 chick brood events, and 103 fecal sac removal events.

Parental care during the incubation period was conducted almost exclusively by females, since in only one nest of six did a male perform assistance tasks (arranging the nest structure and watching over the eggs; average 5 min h^{-1} , 2 trips h^{-1}). Incubation was performed only by females ($n = 6$), incubating on average 12.8 min h^{-1} ($\text{SD} = 4.7$, $n = 6$) interspersed with 4.8 trips h^{-1} ($\text{SD} = 2.2$, $n = 6$). In addition, females devoted on average 0.6 min h^{-1} in assistance activities ($\text{SD} = 0.2$, $n = 6$). The clutch size ranged between 1 and 3 eggs ($n_{1 \text{ egg}} = 5$, $n_{2 \text{ eggs}} = 4$, $n_{3 \text{ eggs}} = 12$).

The total feeding rate of the nestlings at the nest averaged $14.7 \text{ trips h}^{-1}$ ($\text{SD} = 4.7$, nest = 21). The total assistance rate was 3.6 trips h^{-1} ($\text{SD} = 2.8$, nest = 21). The rate of fecal sac removal was 2.4 trips h^{-1} ($\text{SD} = 1.1$, nest = 21). These activities relating to the nestling care were developed more frequently by females (76 % of total activities). In addition, we found that 11 nests were assisted by both parents and 10 nests were attended only by the female. In nests with shared care, both parents attended the nest equally (Fig. 2). The investment of time for such activities showed the same pattern (Table 2).

The frequency of nest visitation to attend the nest by females was higher in nests with a single female (F_{alone}) than in nests where the female was helped by the male (F_{male} ; Fig. 2). The time spent on feeding the nestling and removing fecal sacs was higher for F_{alone} than F_{male} (Table 2). The time devoted to nestling assistance was similar between F_{alone} and F_{male} nests (Table 2).

The parental investment in nestling feeding activity was positively correlated with the chick biomass in the nest ($r^2 = 0.72$, $P < 0.001$; Fig. 3). However, increments in nestling biomass were not associated with increased male proportional participation in assistance. Nests were attended only by females or by both parents with varying percentages of participation regardless of nestling biomass and the number of chicks (Fig. 3).

Discussion

Our results show that the Warbling Doradito exhibits a differential parental care investment due to greater involvement of females, and also that it shows slight sexual

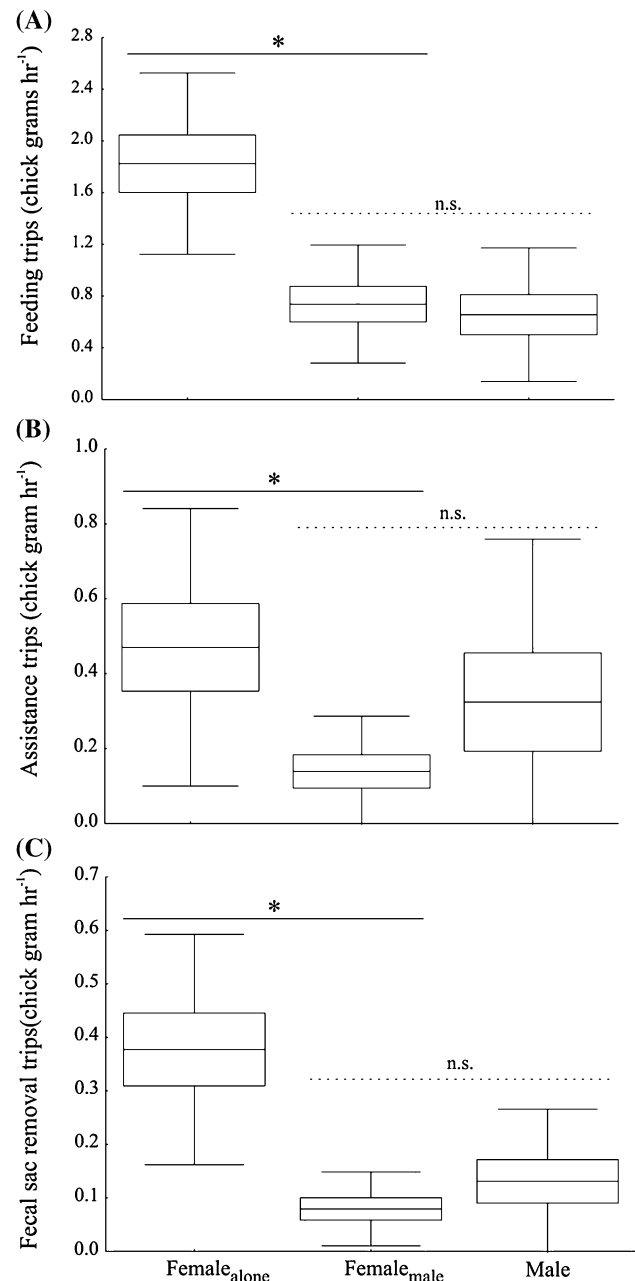


Fig. 2 Frequency of nestling feeding (a), assistance (b) and fecal sacs removals (c) performed by the Warbling Doradito breeding in *Cortaderia selloana* grasslands at the Mar Chiquita Reserve, Argentina. Solid line denotes the statistical comparison (t test) between the female attending nestlings alone (F_{alone}) and the female helped by the male to attend the nests (F_{male}). Dotted line denotes the statistical comparison (paired t test) in nests with biparental care (F_{male} vs. male). * $P < 0.05$; n.s. $P > 0.05$

differences in size and plumage but conspicuously in bill color.

We found a conspicuous diagnostic character to separate the sexes of the Warbling Doradito. In every case, females had orange inside the bill, whereas males had all black bills

Table 2 Parental activities during nestling period performed by Warbling Doraditos breeding in *Cortaderia selloana* grasslands at the Mar Chiquita Reserve, Argentina

	F_{alone}		F_{male}		Male		t test		Paired t test	
	Mean	SD	Mean	SD	Mean	SD	t value	P	t value	P
Time										
Feeding	8.6	3.2	2.2	2.3	3.4	4.4	5.27	0.000	-0.60	0.564
Assistance	14.4	13	6.2	8.7	8.0	12.5	1.72	0.011	-0.35	0.734
Fecal sac removal	2.3	2.5	0.2	0.2	0.7	0.9	2.69	0.014	-1.33	0.215

Shown are the time spent on each activity ($\text{seg} \times \text{h}^{-1}$ by nestling mass). Statistical comparisons between female alone (F_{alone}) and female helped by the male to attend the nest (F_{male}) were developed by using a t test. Statistical comparisons in nest with biparental care (F_{male} vs. male) were developed by using a paired t test

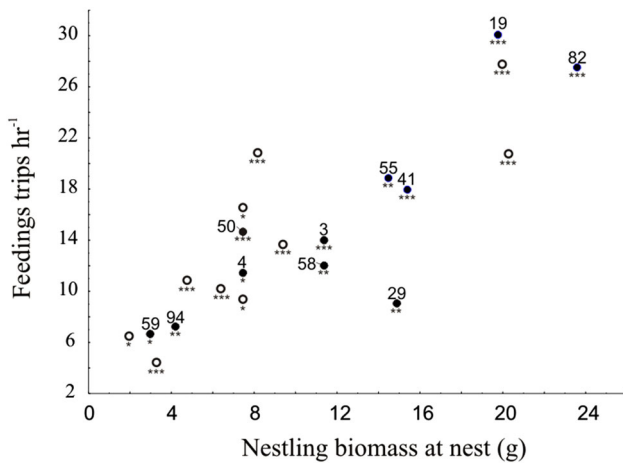


Fig. 3 Relationship between nestling feeding activity ($\text{trips} \times \text{h}^{-1}$) and total nestling biomass (g) at nests of the Warbling Doradito breeding in *Cortaderia selloana* grasslands at the Mar Chiquita Reserve, Argentina. Open circles represent nest attended only by a female and solid circles represents nests attended by both parents. Numbers over solid circles denote the relative percentage of contribution by the male. Asterisks denote the number of nestling (* = 1, ** = 2, *** = 3)

inside and outside. The face of the males was relatively darker than in the females, which can also be considered a diagnostic character, though it is not as evident as the bill coloration. To our knowledge, no other Tyranid has bill differences between the sexes. Diagnostic female characters of the Warbling Doradito resemble those of juveniles (Fig. 1). This is a common pattern in many birds (Lawton and Lawton 1986; Muehter et al. 1997), which has been explained as an adaptive advantage to avoid erroneous conflicts between adult males and juveniles during mate searching (delayed maturation of secondary sexual traits; after Beauchamp 2003). Moreover, we found that the tail and wings were longer in males than in females. These differences have not been reported for other species of *Pseudocolopteryx*. However, other *Pseudocolopteryx* species (Crested, Subtropical, and Dinelli's Doradito) exhibit a

peculiar sexual dimorphism in their wing feathers. In those species, the sixth and seventh primaries of the males are miniaturized and attenuated, and are substantially shorter and narrower than adjacent primaries (Hellmayr 1927; Meyer de Schauensee 1970; Bostwick and Zyskowski 2001). Bostwick and Zyskowski (2001) argued that these features were associated with the production of mechanical sounds (wing-snaps) during display flights. They suggested that the *Pseudocolopteryx* genus may have an unusual social system promoting the evolution of some of these characteristics, otherwise uncommon in tyrannids. The difference in the morphology of the primary feathers is not present in the Warbling Doradito (Wetmore 1926; Bostwick and Zyskowski 2001; this study), nor in the Ticking Doradito (*P. cf. citreola*; Ábalos and Areta 2009). Alternatively, differences in the tail and wing lengths between males and females of Warbling Doradito could be associated with competitive advantages of males during reproductive displays (Székely et al. 2007). Although this was not systematically assessed during our fieldwork, we observed that, in the pre-nesting period, pairs of Warbling Doraditos performed energetic circular flights in the area close to the nest prior to nesting (Cardoni, personal observation).

The mode of parental care in the Warbling Doradito was biparental but biased towards females. The incubation was performed exclusively by females and 74 % of the activities of nestling care (e.g., feeding, assistance, fecal sac removal) were performed by females. The mode of parental care has not been studied for other *Pseudocolopteryx*, which prevents us from making comparisons within the same genus. However, there is information for the congener Gray-backed Tachuri (*Polystictus superciliaris*, clade *elaeniine*; Chaves et al. 2008), which indicates that both parents feed and brood chicks but only the female incubates (Hoffmann and Rodriguez 2011). Beyond the groups related to *Pseudocolopteryx*, the pattern that the incubation duty is performed only by females is common in altricial birds (Silver et al. 1985).

Sexual division of labor during the nesting period observed in birds is generally discussed in terms of sexual selection even in monogamous, monomorphic birds (Trivers 1972). Sexual dichromatisms often associated with a non-monogamous mating system (e.g., polygamy). So, when the sexes are dichromatic, the duller sex is usually responsible for incubation and brooding; when the sexes are alike, the male and female participate more equally in nesting duties (Kendeigh 1952; Silver et al. 1985; Massoni et al. 2012). For instance, in the Spectacled Tyrant (*Hymenops perspicillatus*), a Tyrannid species that exhibits an extreme sexual dichromatism (Fitzpatrick 2004) and breeds in the same grassland habitats as the Warbling Doradito in our study system, the incubation, brooding and feeding of the nestlings is exclusively carried out by the female, and the male only defends the territory (Pretelli 2015; Pretelli et al. 2016). Under this argument, for the Vermilion Flycatcher (*Pyrocephalus rubinus*), a Tyrannid with conspicuous sexual dichromatism, it would be expected that only females perform the nesting duties. However, the nestling care is biparental with females performing the tasks of egg incubation and nestling brooding, while both parents feed the nestlings, and, in turn, the male feeds the female and defends the territory (Fiorini and Rabuffetti 2003). Accordingly, sexual selection and the consequent external sexual differences could not completely explain the division of roles in nestling care (Silver et al. 1985). Other factors could determine the magnitude of the male parental investment, such as ecological factors (e.g., food distribution: Emlen and Oring 1977; Silver et al. 1985; Sejberg et al. 2000; or nest predation risk: Fontaine and Martin 2006; Ghalambor et al. 2013). Moreover, males provided relatively less parental care in species with a higher frequency of extra-pair paternity (Møller 2000), and nowadays, it clear that many apparently monogamous systems involve a high degree of extra-pair mating (Birkhead and Møller 1992; Møller 2000; Griffith et al. 2002).

Despite the relatively slight sexual dichromatism of the Warbling Doradito as compared with other flycatchers (e.g., Vermilion Flycatcher, Spectacled Tyrant), the parental care behavior in the nest was biased towards the females, with half of the nests studied being attended only by females. In addition, the proportional assistance of males to the nestlings was highly variable and was not correlated with clutch size or nestling mass. Therefore, the evidence presented here and in a previous study (Bostwick and Zyskowski 2001) suggest that the *Pseudocolopteryx* genus may have an unusual social system, otherwise uncommon in tyrannids.

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