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BREEDING BIOLOGY OF GRAY-CROWNED TYRANNULET IN THE MONTE DESERT, ARGENTINA[1]

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Abstract. We present information from 75 nests of Gray-crowned Tyrannulet (*Serpophaga griseiceps*) found in open *Prosopis* woodlands of the central Monte desert between 1995 and 1997 and compare it with information corresponding to other species of the genus. Breeding occurred from October to January. Nests are small open cups. Both parents participated in nest building, which lasted 4–7 days. In the *Prosopis* woodland, 98% of the nests were built in chañar (*Geoffroea decorticans*), which also is commonly used as a nest plant by *S. subcristata* in east-central Argentina. Mean clutch size did not vary among years nor within the breeding season, and it was similar to that observed in other *Serpophaga.* Both male and female shared the 13–15 day incubation period. Hatching was asynchronous. Nestling period lasted 13–14 days, during which both parents reared the chicks. Nesting success (26%) appeared to be less than that previously reported for Nearctic open-nesters (50–60%), and Neotropical open-nesters in dry (50%) and wet tropics (35%). Egg and nestling predation were the main cause of nest failure.

Key words: Gray-crowned Tyrannulet, nest predation, reproductive biology, Serpophaga griseiceps, *South America, Tyrannidae.*

Serpophaga is a genus of tyrant flycatchers that comprises five species, found from Costa Rica to Río Negro, Argentina (Fjeldså and Krabbe 1990). These species have a predominantly or entirely gray plumage, usually with a semi-concealed white coronal patch and dark tail. They occur in a wide variety of habitats (Ridgely and Tudor 1994).

Narosky and Yzurieta (1987) considered that three species are found in Argentina: Sooty (*S. nigricans*), White-crested (*S. subcristata*), and White-bellied Tyrannulet (*S. munda*). However, the taxonomic status of

S. munda in relation with *S. subcristata* is controversial (Zimmer 1955, Bó 1969). Straneck (1993), based on voice analyses, suggested that *S. subcristata* and *S. munda* (sensu Narosky and Yzurieta 1987) should be considered subspecies of *S. subcristata*, and revalidated *S. griseiceps* (Gray-crowned Tyrannulet), a species described by Berlioz in 1959 for Cercado, Cochabamba (Bolivia). Ridgely and Tudor (1994) treated *S. griseiceps* as a synonym of *S. munda* following Zimmer (1955), and *S. subcristata* and *S. munda* as full species, because their sympatry seems to be established and, at least in Bolivia, their voices differ (J. V. Remsen Jr., pers. comm. to Ridgely and Tudor 1994). However, the voice ascribed by J. V. Remsen (Remsen and Traylor 1989) to *S. subcristata* would actually correspond to *S. griseiceps* (Straneck 1993).

Serpophaga species are distributed in Argentina during the breeding season as follows: *S. subcristata subcristata* in the eastern half of the country, from Buenos Aires to Misiones province, while *S. subcristata munda* and *S. griseiceps* occupy the western half from La Pampa and Mendoza to Salta and Jujuy provinces (Straneck 1993). In the Biosphere Reserve of Ñacuñán (Mendoza), Contreras (1979) and Marone (1992) cited *S. munda*, but we observed that *S. griseiceps* is the most abundant species of the genus in the reserve. Therefore, the species referred to by Contreras (1979) and Marone (1992) should be *S. griseiceps*. The identity of this species was confirmed by an analysis of its vocalizations (R. Straneck, pers. comm.). The occasional presence of *S. subcristata munda* also has been established in Ñacuñán (J. Lopez de Casenave and V. Cueto, pers. comm.).

Although the basic breeding biology of *S. subcristata* and *S. nigricans* are partially known (De la Peña 1995, 1997, Narosky and Salvador 1998), that of *S. griseiceps* has not been described. Our objectives are to: (1) describe the breeding biology of *S. griseiceps* in the central Monte desert, (2) compare this information with available data for other species of the genus, and (3) present data about nesting success of *S. griseiceps* in this desert area.

METHODS

This study took place during three breeding seasons (1995–1997), in the Biosphere Reserve of Ñacuñán (34°02'S, 67°58'W; 12,282 ha), which is located in the province of Mendoza, Argentina, at an intermediate latitude of the Monte desert biome (Morello 1958). The predominant habitat is an open *Prosopis flexuosa* woodland with abundant shrub (mainly *Larrea divaricata, Capparis atamisquea, Lycium* spp.) and grass cover (*Pappophorum, Trichloris, Aristida, Digitaria* spp.). The chañar (*Geoffroea decorticans*) makes up small isolated clumps, usually associated with heavy soils (Marone 1992).

Ñacuñán's climate is dry and temperate with cold winters. Rainfall is highly variable from year to year, with most precipitation occurring in spring–summer (October–March). In 1995, both autumn–winter (April–September) and spring (October–December) rainfall were lower than the average. In 1996 and 1997, autumn–winter rainfall was near the average, and spring rainfall surpassed the average. On the other hand, maximum and minimum temperatures were usually higher than the monthly average in the springs of 1995 and 1996, but very close to mean values in 1997.

We located nests by both random searching and pursuing the birds. We started to search for nests in late September. Once a nest was found, we measured a set of nest variables (external and internal diameter, external height, and depth to the nearest 0.1 cm), as well as several microhabitat variables such as the species and height (m) of the plant supporting the nest, the height of the nest's rim above the ground, the distance from nest's rim to the top of the plant directly above the nest, a periphery index (visually calculated as the ratio of trunk to nest distance divided by the canopy radius at nest height; Lazo and Anabalón 1991), and the number and diameter of branches supporting the nest.

We visited nests every 1–3 days, numbered eggs with indelible ink, and measured their maximum length and breadth to the nearest 0.1 mm. Egg and nestling weights were established to the nearest 0.1 g. We observed nests during periods of 30 min to calculate the frequency of visits for nest construction and nestling feeding, and 60-min periods to estimate the proportion of time that adults remained incubating the eggs.

RESULTS

START AND DURATION OF THE BREEDING SEASON

S. griseiceps is a spring–summer dweller in Ñacuñán (mean density $\pm$ SE = 1.6 $\pm$ 0.2 individuals ha^{-1}, n = 10 years), although a few individuals can be occasionally seen in some winters (J. Lopez de Casenave et al., unpubl. data). During this study, bird numbers increased remarkably in September and many birds were singing and some of them paired by early October. On several occasions, we observed one or both members of the pair chasing intruder birds approaching the nest. In all events, the intruders were displaced, supporting the idea that *S. griseiceps* is a territorial species (Straneck 1993).

Nest building started in early October (first observations: 9 October of 1995, and 6 October of 1996 and 1997). The laying of the first egg was observed in late October (20, 17, and 24 October in 1995, 1996, and 1997, respectively). The laying period continued until the end of December and early January, with the last egg of the last nest found on 28 December, 30 December, and 12 January in 1995, 1996, and 1998, respectively. The duration of the breeding season of *S. griseiceps* is quite similar to that of other species of the genus that breed in Argentina (Narosky and Salvador 1998).

COPULATION AND NEST CONSTRUCTION

Courtship behaviors consisted of flutterings, with both individuals pursuing each other. We observed two copulation events of different pairs of *S. griseiceps* on 8 October 1996, between 08:00 and 10:00. In one instance, the pair was beginning nest building, and the female was adding some nest material when the male perched near her and copulation ensued. This copulation occurred 12 days before the laying of the first egg. In the second case, the same copulation behavior was

observed, but the pair had not yet started nest construction.

Nests are small open cups (external diameter: 4.9 ± 0.1 cm, $n = 15$, internal diameter: 3.8 ± 0.1 cm, $n = 24$, external height: 4.4 ± 0.3 cm, $n = 8$, and depth: 3.4 ± 0.1 cm, $n = 26$). Nest size was similar to that of *S. subcristata* and *S. munda* (De la Peña 1995, Narosky and Salvador 1998). The nest was built with grass stems (e.g., *Pappophorum, Diplachne, Trichloris*), lichens, spider oothecas and silk, wool, hairy achenes of Compositae species, and petioles of *Prosopis flexuosa*. The inner side of the cup was lined with feathers (2–4 cm in length). Mean nest weight was 3.2 ± 0.3 g ($n = 6$). Other *Serpophaga* species are also reported to use these materials for building nests (Cruz and Andrews 1989, Narosky and Salvador 1998).

Both parents collaborated in nest building. Mean number of visits during nest construction was 8.3 ± 1.2 visits 30-min^{-1} ($n = 37$ observations in 15 nests, range 2.3–17.0). The mean time the birds remained in the nest was 16.3 ± 4.8 sec ($n = 21$ observations in 6 nests, range 6.6–37.9 sec). During egg laying, parents continued putting material inside the nest (0–5 visits 30-min^{-1}, $n = 4$ observations in 3 nests). Nest construction lasted 4–7 days (5.9 ± 0.3, $n = 12$). Other *Serpophaga* species seem to use longer periods to build nests: *S. subcristata* employs about 8 days, and *S. nigricans* uses 15–16 days to construct its more complex nests (De la Peña 1997).

Out of 75 nests we found in open *P. flexuosa* woodlands of the Reserve of Ñacuñán, 98% were built in chañar trees, 1% in *Condalia microphyla*, and 1% in *Atriplex lampa*. Of these three plant species used as nest sites, chañar trees were used significantly more than expected according to their proportion in random plots (33%, $n = 60$, E. T. Mezquida and F. Milesi, unpubl. data) ($\chi^2_1 = 184.4$, $P < 0.001$), whereas *C. microphyla* and *A. lampa* were underutilized relative to their availability (25% and 42%, respectively in random plots, E. T. Mezquida and F. Milesi, unpubl. data) ($\chi^2_1 = 29.9$ and $\chi^2_1 = 67.1$, $P < 0.001$, respectively).

Mean height of selected chañar trees were 2.80 ± 0.06 m ($n = 72$), whereas nest height in chañar trees averaged 1.91 ± 0.05 m ($n = 71$). The nest to canopy distance was 0.60 ± 0.04 m ($n = 58$), and the periphery index 0.4 ± 0.0 ($n = 68$). Nests were supported by 3.9 ± 0.1 branches ($n = 48$), which had a diameter of 10.0 ± 0.7 mm ($n = 124$ in 31 nests).

EGG STAGE

Eggs of *S. griseiceps* are ovoid, white-creamy colored, and with a smooth and delicate shell (average of maximum length and breadth: 14.4 ± 0.1 and 11.0 ± 0.1 mm, respectively, $n = 94$; mean weight: 1.1 ± 0.0 g, $n = 75$). Maximum egg length and breadth in *S. griseiceps* appear to be smaller than in other *Serpophaga* species (Cruz and Andrews 1989, Narosky and Salvador 1998). Eggs were laid on alternate days (we observed 16 complete laying sequence events). The sequence in *S. subcristata* might be on consecutive as well as alternate days (Mason 1985, Narosky and Salvador 1998; R. Fraga, pers. comm.). De la Peña (1997) reported alternate days in *S. nigricans*.

Mean clutch size in *S. griseiceps* was 2.9 ± 0.1 eggs

($n = 35$, range 2–3), and modal clutch size was 3. A clutch size of 3 eggs also is common among other species of the genus (Narosky and Salvador 1998). In Ñacuñán, mean clutch size did not differ among years (2.7 ± 0.2 eggs, $n = 7$ in 1995, 2.8 ± 0.1 eggs, $n = 14$ in 1996, and 3.0 ± 0.0 eggs, $n = 14$ in 1997; Kruskal-Wallis test, $H_2 = 4.0$, $P > 0.1$); modal clutch size was always 3. In order to test whether clutch size changes during the breeding season, we divided the data into two groups, before and after the mean date of egg laying. Mean clutch size did not differ between the first (2.9 ± 0.1 eggs, $n = 18$ nests) and second half of the season (2.8 ± 0.1 eggs, $n = 17$ nests; Mann-Whitney U-test, $U = 125.5$, $P > 0.1$). Thus, clutch size appeared to remain constant among years as well as throughout the breeding season.

Daytime incubation was performed by both male and female, which is not very common within tyrant flycatchers (Bent 1942, Skutch 1960). Given their similar appearance, we could not distinguish parents in the nest, but we saw them replacing each other during incubation. The proportion of time that parents sat on eggs appears to be related to ambient temperature: when the temperature increased, the adults spent more time incubating (E. T. Mezquida, unpubl. data). This behavior may avoid egg overheating (Walsberg and Voss-Roberts 1983). On the other hand, the incubation period (13.6 ± 0.2 days, $n = 14$, range 13–15) was similar to those observed in *S. subcristata* and *S. nigricans* (De la Peña 1995, 1997; R. Fraga, pers. comm.).

Similar to *S. subcristata*, the last egg of *S. griseiceps* hatched a day later than the previous one (De la Peña 1995). Asynchronous hatching might occur because parents usually sat on eggs for short periods before the "true" incubation (E. T. Mezquida, pers. observ.), perhaps reaching the temperature that allows development (Morton and Pereyra 1985). True incubation appears to start the night before the last egg was laid, as it is usual in other tyrant flycatchers (Morton and Pereyra 1985).

NESTLING AND FLEDGLING STAGE

At hatching (day 0), nestlings showed sparse, yellowish-brown down in the capital, spinal, humeral, alar, femoral, and ventral feather tracts. The bill was yellow, mouth lining orange and surrounded by a yellow rim on the beak, skin grayish in back and yellowish-orange in the ventral area, and legs orange. First sheaths emerged in alar feather tract at 2–3 days of age, all other feather tracts emerged on days 3–4. Feather sheaths ruptured on days 5 and 6 (Table 1). The eyes began to open from day 3, and skin, bill, and leg color darkened from day 2–3 (Table 1). Mean nestling weight on day 0 was 0.99 ± 0.04 g ($n = 11$ nestlings from 6 nests). Because of asynchronous hatching, there was a size hierarchy within a clutch, with earlier-hatched young larger than later-hatched young, which continued the whole nestling period.

Both parents also shared the rearing of nestlings. Daytime brooding decreased as nestlings grew: young nestlings (0–6 days old) were brooded 60–100% of the time, whereas old nestlings (> 6 days) were brooded 0–3% of the time ($n = 3$ and 2 nests, respectively).

TABLE 1. Developmental patterns in young *Serpophaga griseiceps* (. . . . Pin feathers appear, _____ Pin feathers unsheathing, for feathers tracts).

Developmental characteristic	Age (days)												
or feather tract	1	2	3	4	5	6	7	8	9	10	11	12	13

Opening of eyes   Shut   Opening   Fully open

    *************************************** (days 7–13)
    -------------------- (days 4–5)
    ooooooooooooooooooooo (days 1–3)

Color of beak   Yellow Transitional   Grayish

    *** (days 6–13)
    ----------------------- (days 4–5)
    ooooooooooooo (days 1–3)

Color of legs   Orange Transitional   Gray-yellowish

    ** (days 6–13)
    ----------------- (days 4–5)
    ooooooooooooo (days 1–3)

Feather tract

Capital
    _____
    ....

Spinal
    _____
    ....

Alar
    _____
    ....

Humeral
    _____
    ....

Femoral
    _____
    ....

Crural
    _____
    ....

Caudal
    _____
    ....

Ventral
    _____
    ....

TABLE 2. Causes of nesting mortality in *Serpophaga griseiceps*, Reserve of Ñacuñán, 1995–1997. Percentages given in parentheses.

Eggs laid[a]	116	
Losses		
Hatching failure	6	(5.2)
Predation	45	(38.8)
Abandonment	2	(1.7)
Unknown cause	2	(1.7)
Young hatched	61	(52.6)
Nestlings[a]	55	
Losses		
Predation	24	(43.6)
Exposure	0	(0.0)
Starvation	0	(0.0)
Fly infection	2	(3.6)
Unknown cause	2	(3.6)
Young Fledged	27	(49.1)
Overall egg success[b]	0.258	

[a] Include only eggs or nestlings whose fates are known.
[b] [(hatching rate) × (fledging rate), Mayfield 1975].

Both parents shared nestling feeding and fecal removal. The number of feeding visits nestling^{-1} 30-min^{-1} varied between 0 and 2.5, with a mean of 1.0 ± 0.3 visits ($n = 19$ observations in 8 nests). These figures appear to be low considering, for instance, the 4–12 meals nestling^{-1} hr^{-1} suggested by Skutch (1976) as a standard frequency of feeding visits in small passerines.

The 13–14 day nestling-period (13.3 ± 0.2, $n = 8$) in *S. griseiceps* is shorter than that reported for *S. subcristata* (De la Peña 1995; R. Fraga, pers. comm.). After fledging, the chicks continued to depend on both parents for feeding.

EGG AND CHICK MORTALITY

Overall egg success was relatively low in 1995–1997 (0.26, Table 2). Nevertheless, egg success in 1995 was higher than in 1996 and 1997, especially because of lower egg predation and no nestling loss in 1995. Nesting in 1995 was very sparse in the Reserve of Ñacuñán, probably because of dry climatic conditions (see Methods), and nest predation could have been low because of density-dependent reasons (Martin 1988).

DISCUSSION

The reproductive biology of *S. griseiceps* was similar in some respects to that of other *Serpophaga* species inhabiting Argentina, particularly *S. subcristata*. Both male and female *S. griseiceps* share building of the nest, incubation of eggs, and rearing of nestlings. Most tyrant flycatchers are monogamous birds (Fjeldså and Krabbe 1990), in which the male and female usually collaborate in nest building and nestling feeding. However, male incubation is not a common event among tyrant flycatchers (Fjeldså and Krabbe 1990). Within *Serpophaga*, male *S. nigricans* participate in nest building (De la Peña, 1997), and both parents bring food to the nestlings in *S. subcristata* (Narosky and Salvador 1998). Yet, there is no information about the role of males during incubation in these species.

S. griseiceps appeared to strongly select chañar trees to build nests. However, another small tree (*Bulnesia retama*) also was used in those patches where it is present in the central Monte. In La Pampa province, *S. griseiceps* builds nests in chañar trees too, although other thorny plants are used as well (e.g., *C. microphyla, Jodina rhombifolia*) (J. Maceda, pers. comm.). Likewise, out of 19 nests of *S. subcristata* reported by De la Peña (1995) in east-central Argentina, 68% were located in chañar trees. Although the selection of thorny plants for nesting has been suggested as an adaptation to avoid nest predation by small passerines (Lazo and Anabalón 1991), we found that nests located in chañar trees actually suffered more predation than nests located in nonthorny plants in several experiments with artificial nests carried out in the central Monte desert (unpubl. data). Therefore, the selection of chañar trees could be due to these trees providing a suitable structure to support nests, even though they do not reduce predation risk.

Predation was the major factor limiting nesting success in *S. griseiceps*, as it has been reported for many open-nesting passerines (Ricklefs 1969). Birds like *Milvago chimango, Speotyto cunicularia*, and *Pseudoseisura lophotes*, and mammals like *Galictis cuja* have been confirmed as nest predators in the reserve (E. T. Mezquida, pers. observ.), but other potential nest predators include other mammals (*Didelphis albiventris, Conepatus chinga, Dusicyon griseus*) and small snakes.

Mean reproductive success of *S. griseiceps* in the central Monte desert (26%) appeared to be lower, although highly variable from year-to-year, than that reported for Nearctic open nesters (50–60%; Martin 1993), and Neotropical open nesters in both dry (50%; Marchant 1960), and wet tropical habitats (35%; Skutch 1985). However, other Argentinian open nesters also have low nesting success (12–15%; Mermoz and Reboreda, in press). Because predation of eggs and nestlings was the main cause of nesting failure, our results suggest that nest predation might constitute a strong selective pressure on some south temperate birds and, particularly, on some South American desert birds.

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