

BREEDING BIOLOGY OF THE MANY-COLORED RUSH-TYRANT (*TACHURIS RUBRIGASTRA*) IN A NATURAL LAGOON IN THE ÑUBLE REGION, SOUTH-CENTRAL CHILE

Biología reproductiva del siete colores (*Tachuris rubrigastra*) en una laguna natural de la región del Ñuble, centro-sur de Chile

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ABSTRACT.- Between 2005 and 2009, we studied the breeding biology of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) in a 2-ha tall-rush patch in south-central Chile. We monitored the nesting activity by visiting 59 active nests at 2-3 days intervals. Nesting was markedly seasonal, concentrating during spring months. Tyrants built pensile, conical open-cup nests with tall-rush fibers and firmly attached them to live tall-rush stems or other plants. Pairs nested clumped (distance among nests = 4.7 ± 3.1 m [mean $\pm$ SD]) in well-protected vegetation bands (distance from shore-line = 101.2 ± 162.3 m, tall-rush density = 237.2 ± 100.6 m²). The mean clutch size was 2.7 ± 0.5 eggs. Eggs were oval-shaped (16 ± 1.3 mm x 12 ± 0.9 mm) and white-colored. Incubation lasted 16.1 ± 1.4 days. Nestlings left the nest at 15.1 ± 2.9 days old and when fully feathered. Parents fed nestlings mostly with aquatic insects (92.5% of all prey individuals), with dragonflies being the primary prey (55.2%). By the Mayfield method, the overall nesting success was 0.47. We hope our findings will guide future conservation actions for this rush-specialist tyrant species.

KEY WORDS: Chick growth, clumped nesting, clutch size, nesting success, nestling feeding, territorial tolerance.

RESUMEN.- Entre 2005 y 2009 estudiamos la biología reproductiva del sietecolores (*Tachuris rubrigastra*) en un juncal de 2 ha en el centro-sur de Chile. Monitoreamos la actividad de nidificación visitando 59 nidos activos a intervalos de 2-3 días. La nidificación fue marcadamente estacional, concentrándose durante los meses de primavera. Los sietecolores construyeron nidos cónicos con copa abierta usando fibras de juncos, sujetándolos firmemente a tallos vivos de juncos. Las parejas anidaron agrupadas (distancia entre nidos = $4,7 \pm 3,1$ m [media $\pm$ DE]) en sitios bien protegidos (distancia desde la playa = $101,2 \pm 162,3$ m; densidad de tallos = $237,2 \pm 100,6$ m²). El tamaño de la puesta fue de $2,7 \pm 0,5$ huevos. Los huevos fueron ovalados ($16 \pm 1,3$ mm x $12 \pm 0,9$ mm) y blancos. La incubación duró $16,1 \pm 1,4$ días. Los polluelos dejaron el nido a los $15,1 \pm 2,9$ días, cuando estaban completamente emplumados. Los padres alimentaron a los polluelos con insectos acuáticos (92,5% de todas las presas), siendo las libélulas las presas principales (55,2%). El éxito global de nidificación medido por el método Mayfield fue de 0,47. Esperamos que nuestros hallazgos orienten futuras acciones de conservación de este tiránido dependiente de juncuales.

PALABRAS CLAVES: Alimentación de los polluelos, desarrollo de los polluelos, éxito de nidificación, nidificación agrupada, tamaño de puesta, tolerancia territorial.

INTRODUCCIÓN

Knowing the natural history of water birds is pivotal to understanding their adaptation and tolerance to human activities and mitigating the negative impacts of humans on freshwater ecosystems (Kushlan 1993, Weller 1994, 1999). Specific information about the breeding habits and habitats of water birds facilitates the necessary actions for eventual habitat management or restoration.

Many-colored Rush-tyrants (*Tachuris rubrigastra*) are endemic to southern South American wetlands, mainly inhabiting lentic water systems (*e.g.*, lakes, lagoons, ponds, marshes, and swamps) with dense and extensive emerging vegetation (Ridgely & Tudor 1994, Figueroa *et al.* 2001, Fitzpatrick 2004, Tejeda *et al.* 2020). The breeding biology of Many-colored Rush-tyrants is scarcely known (Clock 2020). Much of the available information consists of short descriptive reports and occasional observations on nest building, egg features, and reproductive behavior (*e.g.*, Housse 1945, Goodall *et al.* 1957, Narosky *et al.* 1983, de la Peña 2005, Fitzpatrick 2004).

So far, Barrionuevo & Montes (2015) and Reynoso *et al.* (2023) have provided the most complete descriptions of the breeding habits of Many-colored Rush-tyrants. Together, these authors provided information on nest and egg characteristics, incubation period, nesting microhabitat, reproductive success, and some observations on parental behavior and nestling size in Peruvian wetlands. However, Barrionuevo & Montes (2015) and Reynoso *et al.* (2023) restricted their study to only one breeding period. To our knowledge, there are no studies based on successive reproductive periods. Therefore, we do not know how phenology and reproductive success change over several

years. Moreover, there are only occasional observations on the feeding and development of nestlings.

Here, we report the results of a long-term study on the breeding biology of Many-colored Rush-tyrants in an agricultural area of south-central Chile. Our objectives were to gather fundamental information about nesting activity, describe reproductive phenology, and detect eventual temporal variations in breeding success. Knowing all these aspects is essential for future conservation and management actions of Many-colored Rush-tyrant populations and their habitats.

MATERIAL AND METHODS

Study area

We conducted our study in Laguna Santa Elena (36°48'S, 72°23'W, 77 m a.s.l.), Ñuble region, south-central Chile. This lagoon is a small body of water (160 ha) located in an agricultural area (Fig. 1) with sugar beet (*Beta vulgaris*), wheat (*Triticum* spp.), and blackberry (*Rubus ulmifolius*) crops, and exotic tree plantations (Monterrey pine [*Pinus radiata*] and eucalyptus [*Eucalyptus* spp.]). On the lagoon edge is a vegetation strip composed of native and introduced plants, including wild herbs, shrubs, and trees. The composition of the shrub layer includes yellow bush lupine (*Lupinus arboreus*) and romerillo (*Baccharis racemosa*) thickets. The tree layer comprises native species such as myrtle (*Luma apiculata*), boldo (*Peumus boldus*), roman cassie (*Acacia caven*), litre (*Lithraea caustica*), maqui (*Aristotelia chilensis*), and patagua (*Crinodendron patagua*), and introduced species such as Monterrey pine, Australian blackwood (*Acacia melanoxylon*), silver wattle (*A. dealbata*), Simon's poplar (*Populus simonii*), Hum-



Figure 1. Aerial view of the laguna Santa Elena, Bulnes, Ñuble region, south-central Chile. The study of the breeding biology of Many-colored Rush-tyrants was within the area demarcated in red. Photograph: Fernando González S.

boldt's willow (*Salix humboldtiana*), Babylon willow (*S. babylonica*), and basket willow (*S. viminalis*). The aquatic vegetation covering the lagoon edges is composed of tall-rush (*Juncus procerus*), common water hyacinth (*Eichhornia crassipes*), water fern (*Azolla filiculoides*), and parrot's feather (*Myriophyllum aquaticum*). The climate is Mediterranean humid, with cool, rainy winters and hot summers (di Castri & Hajek 1976).

Field procedures

We monitored the breeding activity of Many-colored Rush-tyrants in an extensive patch of tall rush (≈ 2 ha) in the central part of the lagoon's western edge. We searched for and surveyed nests during four breeding seasons (2005-2009) from early August to late January at intervals of 2-3 days. Two to three observers participated in the field work with each visit. At each visit, the nest location and monitoring were between 07:00 and 19:00 h. Thus, we completed 320 days per 12 h in the field for combined breeding periods (total sampling effort = 3840 h).

We searched for nests using a rowboat, moving slowly throughout the vegetation to avoid habitat damage and minimize the disturbance of nesting pairs. Before entering the tall-rush patch, we observed the patch edge from almost 10 m using binoculars to locate any nest present. Within the patch, we searched for nests by moving slowly through the vegetation, stopping every 5 to 10 m to observe the vegetation around us. After finding one nest, we slowly walked among the tall-rush and tied a colored flag in the upper part of one or several tall-rush stems just above the nest to facilitate its later location. We checked active nests every time we visited the study site. To avoid stressing nesting pairs, we decided not to capture adult individuals. In addition, investing time in capturing breeding individuals would have considerably limited our time to evaluate the nesting activity. Capturing adult individuals by boat involves a much greater logistical deployment than by foot.

During each breeding season, we registered the following life history traits for each monitored breeding pair: (1) reproductive phenology, (2) nest morphometrics, (3) nest location, (4) clutch size (*i.e.*, number of eggs at the incubation onset), (5) egg characteristics, (6) nestling growth, (7) nestling feeding, and (8) breeding success and nest failure.

We evaluated reproductive phenology by registering dates of courtship (*i.e.*, from the first date we registered prey offer, mutual grooming, or copulation until egg laying), egg-laying (*i.e.*, the day when tyrants laid first eggs), incubation (*i.e.*, the time between laying and hatching of first egg), and chick-rearing or nestling period (*i.e.*, the time between hatching and fledging). To detect

nesting activity peaks along the breeding period, we divided each breeding season into three stages: early season (September-October), mid-season (November), and late season (December-January). Among nests detected, we distinguished old and new nests. An old nest was a nest that tyrants built during a previous breeding season, and a new nest was a nest that tyrants built during the current breeding season. Among these, we considered a nest active when it contained newly laid eggs, an incubating adult, or nestlings. When any breeding pair occupied an old nest, we classified it as a reused nest.

Nest characteristics we measured included the (i) nest shape and size, (ii) nest material, and (iii) number of tall-rush stems supporting nests. We only measured nests when the nesting pairs were no longer attending them (*i.e.*, without eggs or nestlings). Spatial variables included: (i) nest height above water (from water surface to lower edge of the nest); (ii) the distance from the nest to the nearest borderline between the tall-rush patch and open water; (iii) nest distance to shoreline (from nest center to shoreline); (iv) distance to the nearest conspecific nest measured from center to center of the cup; (v) distance to nearest nest of other co-nesting passerine species located during our surveys (see Lara *et al.* 2011); and (vi) tall-rush density around nests. To measure distances and heights, we use a metric tape measure (± 1 mm). We measured the tall-rush density around nests by counting the number of stems within a 2-m radius circle.

After hatching, we measured the chick growth each time we visited the study area. We banded 96 newly hatched chicks (2-3 days) throughout the four breeding seasons. However, we could follow the growth of fewer than a third of the banded chicks due to nestling loss by depredation or other causes. We established three age categories: 1-3 days, 6-9 days, and 12-15 days. In each, we measured the body mass, tarsus length, bill length, wing-chord length, tail length, and total length. We measured these variables following Eck *et al.* (2011; details in Fig. 4). We measured nests, eggs, and nestlings using a digital caliper (± 0.01 mm) and weighed eggs and nestlings using a digital balance (± 0.1 g). Handling and banding of nestlings followed the ethical guidelines of animal welfare of the Faculty of Veterinary Sciences of the Universidad de Concepción.

We evaluated the nestling diet by recording the prey offered to nestlings by parents in 16 nests during the breeding period 2005-2006. We took the photos from the boat while stopping 5-10 m from the nest. When a parent arrived with prey to the nest, we photographed it using a digital camera (magnification = 200 mm, lens aperture = 2.8). We quantified the nestling diet on 1350 high-resolution images taken on different days. An entomologist

assisted us in the prey identification.

We evaluated the reproductive success for all nests combined and for individual nests. For individual nests, we measured the (i) mean clutch size per nests, (ii) mean number of hatched eggs per nest, and (iii) mean number of fledglings per nest. For the nests combined, we measured four variables: (i) proportion of hatched eggs (number of eggs hatched/number of eggs laid); (ii) proportion of fledged young following hatching (number of young fledged/number of hatched eggs); (iii) proportion of young that fledged following laying (number of fledged young/number of eggs laid) (Martin-Vivaldi *et al.* 1999); and (iv) proportion of successful nests (number of nests that fledge at least one fledgling/total number of monitored active nests). We considered that a nestling fledged when it moved between the nest and the surrounding vegetation or between the vegetation close to the nest. If a nest was empty after it had nestlings on a previous visit, we searched for fledglings around the nest, identifying them by the band color. We also evaluated productivity based on the number of chicks produced over the entire breeding season (Martin-Vivaldi *et al.* 1999).

Complementarily, we estimated nesting success using the Mayfield (1975) method. This method requires calculating the daily nest loss rate, the probability of daily survival for a nest, and the survival probability for one nest throughout each breeding stage or the entire breeding period. We obtained the daily nest loss rate by dividing the number of nests lost by the exposure time (*i.e.*, the time each nest is under observation) measured in nest-days. We measured the exposure time for incubation by counting the number of nest-days between the first egg-laying date or when we found a nest with eggs for the first time until the day the eggs hatched. For the nestling stage, we counted the number of nest-days between the first egg-hatching date or when we found a nest with nestlings for the first time until the day when the nestlings left or were no lon-

ger in the nest. If a nest failed between two visits with a 2-day interval, we assumed that failure occurred the day after the last visit. If a nest failed between two visits with a 3-day interval, we assumed that failure occurred in the middle of the interval.

The daily nest survival probability results by subtracting the daily nest loss rate from the probability that all nests survive (*i.e.*, 1 minus daily nest loss rate). We calculated the standard error for each daily nest survival value following Johnson (1979). We calculated the probability of overall nest survival separately for the incubation and nestling stages. In each case, we calculated the overall nest survival by raising the daily nest survival probability to a power equal to the mean duration of each breeding stage. Finally, we calculated the nesting success by multiplying the daily nest survival probabilities generated for the incubation and nestling stages.

Statistical procedures

We analyzed our results using descriptive statistics including the arithmetic mean, standard deviation (SD), median and range. For the height and distance measurements, we also included modal values because it allows better detecting typical values. We avoid the use of inferential procedures because our study was essentially descriptive.

RESULTS

Breeding phenology

During our study, we located 75 nests (Table 1). Ten nests were old, and 65 nests were fresh. We found active nests during all breeding stages (Fig. 2, Table 1). Excepting the breeding season 2007-2008, the number of nests located was similar among years (Table 1). Among the nests located, 68 were active, including three reused and 65 new (Table 1). The number of active nests varied over the years (Table 1). Because of the loss of some active nests during the early breeding season, we could not follow all active

Table 1. Number of nests used to evaluate the nesting activity of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. Detected nests included both old and new nests. Old nests correspond to those that remained from the previous breeding season, and new nests correspond to those built during the current breeding season. Active nests included nests under construction, nests with eggs, or nests with nestlings. Reused nests were old nests occupied by any tyrant pair during the current breeding season. Monitored nests were those followed to evaluate the fate of eggs and nestlings.

Breeding season	Detected nests	Old/new nests	Active nests	Reused/new nests	Monitored nests
2005-2006	22	7/15	16	1/15	13
2006-2007	22	3/19	21	2/19	19
2007-2008	8	0/8	8	0/8	8 ^a
2008-2009	23	0/23	23	0/23	19
Total	75	10/65	68	3/65	59

^a All nests failed during the nestling stage due to flooding after of heavy rain.

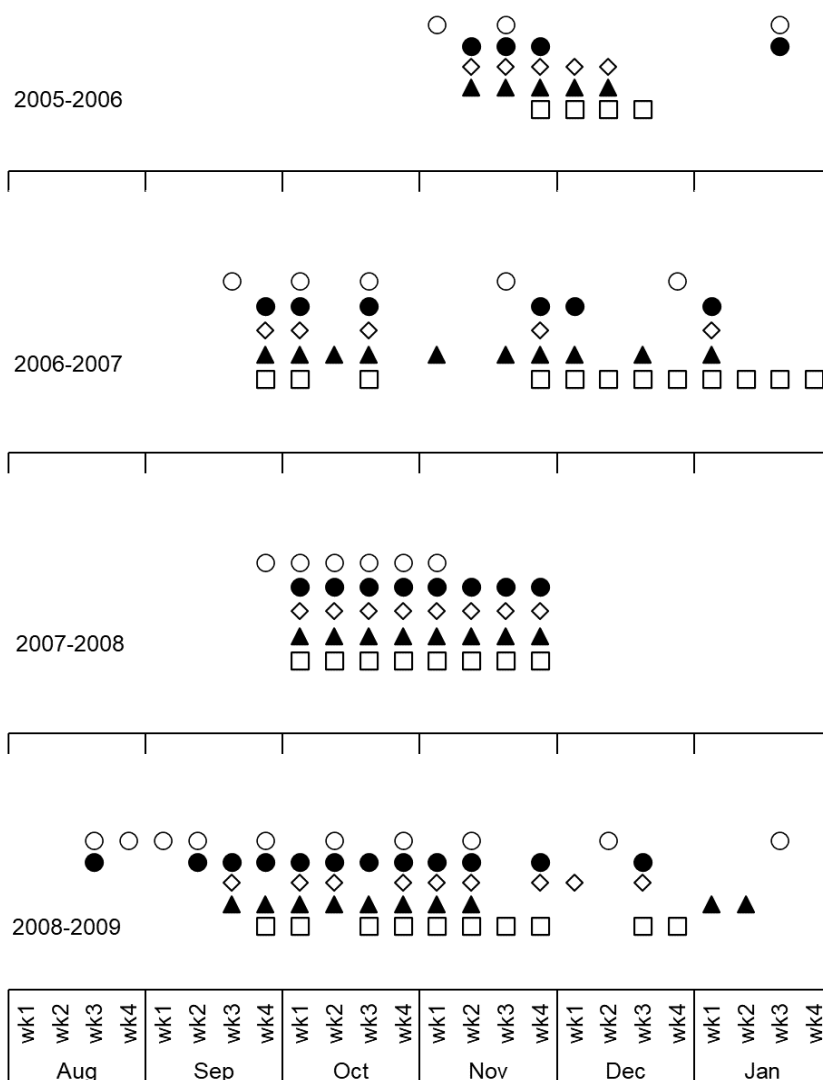


Figure 2. Breeding phenology of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. Month names abbreviated with the three first letter; the letters wk represents weeks. White circles = courtship, black circles = nest building, diamonds = egg laying, black triangles = incubation, white squares = nestlings.

nests to evaluate the fate of eggs and nestlings (Table 1). The maximum length of the breeding season of Many-colored Rush-tyrants was about six months (August-January, Fig. 2), with most nests active from October to December (Fig. 2, Table 2).

Courtship period.- We observed the earliest courtship displays on 17 August 2008 and the latest on 18 January 2006 (Fig. 2). The starting of the breeding activity of each tyrant pair was evidenced by the following events: (i) an increase in plumage color expression; (ii) a courtship ritual in which males made successive leaps over plants around females, often lifting tuft feathers, moving the tail, and repeatedly uttering a monotonous *fuitiu, fuitiu*; (iii) females were more restless and responded to male call's by uttering paused and regular tweets; and (iv) an increased aggressiveness towards conspecific individuals or indi-

viduals of co-nesting species (e.g., Wren-like Rushbird [*Phleocryptes melanops*], Warbling Doradito [*Pseudocolopteryx flaviventris*]).

Nest building.- The earliest nest-building activity we observed was on 20 August 2008 and the latest on 21 January 2005 (Fig. 2). After courtship displays, both pair members often engaged in nest building ($n = 65$ pairs) or repairing old nests ($n = 3$ pairs). Due to the absence of an evident difference in the plumage coloration and naked parts between both sexes, we could not determine which individual was female or male while building the nest. However, we were sure both pair members participated in the nest building as we observed them simultaneously carrying nest material or molding the nest.

To initiate the nest building, the tyrants collected long, fresh strips of tall-rush and elaborated a crown-like

Table 2. Nesting phenology of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. Early season = September-October, mid-season = November, late season = December-January, % = percentage of nests, n = number of nests.

Season	Nests with eggs laid			Total nests
	Early season % (n)	Mid-season % (n)	Late season % (n)	
2005-2006	0 (0)	62.5 (10)	18.8 (3)	13
2006-2007	38.1 (8)	14.3 (3)	38.1 (8)	19
2007-2008	0 (0)	100 (8)	- ^a	8
2008-2009	43.5 (10)	13.0 (3)	26.1 (6)	19
Mean % ± SD	20.4 ± 23.6	47.4 ± 41.9	20.7 ± 15.9	

Season	Nests with eggs hatched			Total nests
	Early season % (n)	Mid-season % (n)	Late season % (n)	
2005-2006	0 (0)	37.5 (6)	18.8 (3)	9
2006-2007	28.6 (6)	14.3 (3)	33.3 (7)	16
2007-2008	0 (0)	25.0 (2)	- ^a	2
2008-2009	26.1 (6)	8.7 (2)	17.4 (4)	12
Mean % ± SD	13.7 ± 15.8	21.4 ± 12.7	17.4 ± 13.6	

Season	Nests with nestlings			Total nests
	Early season % (n)	Mid-season % (n)	Late season % (n)	
2005-2006	0 (0)	25 (4)	18.8 (3)	7
2006-2007	19 (4)	4.8 (1)	28.6 (6)	11
2007-2008	- ^a	- ^a	- ^a	0
2008-2009	21.7 (5)	8.7 (2)	17.4 (4)	11
Mean % ± SD	10.2 ± 11.8	9.6 ± 10.8	16.2 ± 11.9	

^a All nests failed due to flooding after of heavy rain.

circular structure by firmly intertwining the vegetal material. Then, they continued weaving the nest downwards, progressively reducing the structure diameter. The Many-colored Rush-tyrant pairs filled the cup bottom with thin plant fibers until forming a soft lining cup. Tyrants attached nests to live stems of tall-rush (n = 57 nests) or built them on tree branches located in the lagoon border (n = 6 nests). The tyrants took 3–6 days to build nests (mean ± SD = 4 ± 1.1, n = 8 pairs). Although some tyrant pairs nested in old nests after repairing them (Table 1), only two fledged young chicks; the remaining nests failed during egg laying, incubation, or hatching stages.

Egg laying and incubation period.– The earliest egg-laid record was on 14 September 2008, and the latest on 4 January 2006. The female immediately began laying eggs after the plant material composing the nests was dry (plant material turned and straw-colored). By our recording calendar, females laid eggs at 1-day intervals (n = 32

nests). Over the four years of study, the highest proportion of nests with newly laid eggs occurred in the middle of the breeding season (Table 2). Tyrants started incubation after the female laid the first egg, so hatching was asynchronous. Since the plumage coloration patterns are similar for both sexes, we could not determine if both parents participated in the incubation. The average incubation period was 16 days (range = 14–19 days, Table 3).

Egg hatching and nestling period.– Overall, the proportion of hatched eggs was higher in the middle of the breeding season (Table 3). The earliest egg hatching occurred on 2 October 2008, and the latest on 19 January 2005. Nestlings remained on nests for two to three weeks after hatching (mean ± SD = 15.1 ± 2.9 days, range = 11–22 days; Table 4). The earliest record of nestlings leaving the nest was on 5 October 2008, and the latest on 24 January 2005.

Table 3. Incubation period of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) and nestlings period during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. n = number of nests surveyed.

Season	Incubation length			Days at which nestlings leave nest		
	Mean $\pm$ SD	Range	n	Mean $\pm$ SD	Range	n
2005-2006	16.2 $\pm$ 1.5	14-18	4	16.6 $\pm$ 1.1	15-18	5
2006-2007	16.5 $\pm$ 2.1	14-19	11	14.1 $\pm$ 2.8	11-18	8
2007-2008	15.5 $\pm$ 0.7	15-16	7	..a	..a	..a
2008-2009	15.5 $\pm$ 1.0	15-17	6	15.1 $\pm$ 3.9	11-22	11
Total	16.1 $\pm$ 1.4	14-19	28	15.1 $\pm$ 2.9	11-22	24

^a All nests failed due to flooding after of heavy rain.

Table 4. Structural and spatial nest characteristics of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons (2005-2009) in Laguna Santa Elena, Ñuble province, south-central Chile. Measurements included to both old and new nests.

Nest characteristics	N° Nests	Mean $\pm$ SD	Range	Mode
Structure variables				
Nest height (cm) ^a	63	11.4 $\pm$ 2.3	6.5-19.5	12
Maximum nest width (cm) ^b	63	4.7 $\pm$ 0.9	4.2-8	5.5
Maximum diameter of nest entrance (cm)	63	4.4 $\pm$ 1.1	3.5-10.9	4
Minimum diameter of nest entrance (cm)	63	4.0 $\pm$ 0.4	3.3-5	4.1
Cup depth (cm) ^c	63	3.9 $\pm$ 0.7	2.8-4.4	3.9
Number of tall-rush supporting nest	57	1.3 $\pm$ 0.7	1.0-4	1
Diameter of tall-rush supporting nest (cm)	57	2.7 $\pm$ 1.2	0.6-6.2	0.9
Spatial variables				
Height of nest above water surface (cm) ^d	63	48.1 $\pm$ 19.5	17.2-84	46
Nest distance from tall-rush/water borderline (m) ^e	63	20.7 $\pm$ 24.5	0.5-97	0.5
Nest distance from firm ground (m) ^f	63	101.2 $\pm$ 162.3	2-500	100
Linear distance to the nearest tyrant nest (m) ^g	8	4.7 $\pm$ 3.1	1.6-10.4	-
Linear distance to the nearest rushbird nest (m) ^g	16	5.4 $\pm$ 4.2	1.4-15.8	-
Tall-rush density (m ²) ^h	63	237.2 $\pm$ 100.6	95-428	-

Measurement criteria: ^a From the upper edge to the outer lower edge. ^b At the level of the upper edge. ^c From the upper edge to the cup bottom.

^d From the outer bottom edge to the water surface. ^e From nest center to borderline between tall-rush patch and water mirror. ^f From nest center to shoreline. ^g Between nest centers. ^h Within a 2-m radius circle.

Nest morphometrics and location

All nests were pensile conical open-cups (Fig. 3A). The building material included mostly fibers of tall-rush. We only found one nest structure composed of tall-rush fibers intertwined with horsehair. Overall, nests had an open circular entrance and a shallow cup (Fig. 3A, Table 4). Of all measured nests, 57 were on tall-rush stems, four on willow branches, and two on a tall-rush stem plus a willow branch. Among nests attached to tall-rush, 45 wrapped only one stem, 7 to two stems, 4 to three stems, and 1 to four stems. The diameter of tall-rush stems was variable but tended to be relatively stiff and thick (Table 4).

Although ranges were broad, many nests were placed at a low elevation from the water surface, near tall-rush /water borderline, distant from the shoreline, and to a short distance between them (Table 4). Regarding the distance between the nests of tyrants and those of Wren-

like Rushbirds, some were relatively close, and others at farther distances (Table 4). Most tyrant pairs located their nests in sites with high plant density (Table 4).

Clutch size and egg characteristics

The clutch size was uniform over the four years of study (Table 5), reaching a modal value of three eggs (43 of 59 nests). Only a pair laid a maximum of four eggs. Eggs were elliptical (oval-shaped) and small-sized (< 20 mm in length, Table 5). Coloration varied from white to light pinkish, becoming opaque as the incubation progressed. We observed no streaking or spotting on eggshells (Fig. 3B)

Nestling growth

The chicks were born almost entirely naked with closed eyes, strong-yellow lip edges, light pinkish skin, and head,



Figure 3. Nest and eggs of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) in Laguna Santa Elena, Ñuble province, south-central Chile. **A.** Many-colored Rush-Tyrant pairs build a nest pensile conical open-cups, which they weave with fibers of tall-rush and attach to 1-4 tall-rush stems. **B.** Nests have an open circular entrance and a shallow cup. Eggs are oval-shaped, small-sized (length < 20 mm), and white to light pinkish. Photographs. A. Daniel González-Acuña. B. Carlos O. Barrientos.

back, and wings covered with lemon-yellow down (Fig. 4A). Most chicks opened their eyes between 5-8 days old ($n = 84$). At this age, down profusely covered their bodies, and the first feathers had already emerged (Fig. 4B). When 12 days old, nestlings were almost fully feathered but with patches of down on the head and neck ($n = 27$, Fig. 4C). At 15 days old they had their whole body covered with feathers, but with traces of down on the head and neck ($n = 26$). The plumage at that age was pale yellow on the belly and face and dark brown on the back, wings, tail, and nape. Young of 15-days also had a black eye mask, white chin, dark bill with heavy-yellow edges, and pinkish legs. In addition, a thin white line corresponding to the external vexillum was visible upon the wings.

The mass, total length, wing chord length, and tail length of nestlings increased markedly from hatching until fledging (Fig. 5). The growth of tarsi and bill steadied within a few days, after which these slightly increased in size (Fig. 5). Thus, tarsus and bills were the first to reach nearly-adult size.

Nestling feeding

Both parents fed nestlings. Although we did not band adult tyrants and sexes are undistinguishable by plumage coloration, we observed simultaneously both parents delivering prey to nestlings. Most prey delivered to nestlings were aquatic insects (92.5% of all prey individuals), including dragonflies, damselflies, dipterans, scorpion flies, stone-

Table 5. Clutch size and egg size of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. n = number of eggs measured.

Season	Eggs laid	N° Nests	Mean $\pm$ SD (range)					
			Clutch size	Egg length (mm)	Egg width (mm)	n	Egg mass (g)	n
2005-2006	36	13	2.8 $\pm$ 0.6 (1-3)	16 $\pm$ 0.9 (13-17)	12 $\pm$ 1.4 (10-16)	16	1.4 $\pm$ 0.2 (0.8-1.6)	20
2006-2007	51	18	2.7 $\pm$ 0.7 (1-4)	15 $\pm$ 1.6 (12-18)	12 $\pm$ 1.2 (9-15)	30	1.3 $\pm$ 0.2 (0.8-1.6)	33
2007-2008	24	8	3.0 $\pm$ 0.0 (3)	16 $\pm$ 1.4 (15-19)	12 $\pm$ 1.0 (11-13)	24	1.4 $\pm$ 0.4 (0.9-2.1)	24
2008-2009	50	19	2.6 $\pm$ 0.5 (2-3)	16 $\pm$ 1.3 (12-18)	12 $\pm$ 0.6 (11-13)	40	1.2 $\pm$ 0.1 (1.0-1.6)	43
Total	161	59	2.7 $\pm$ 0.5 (1-4)	16 $\pm$ 1.3 (12-19)	12 $\pm$ 0.9 (9-16)	110	1.3 $\pm$ 0.3 (0.8-2.1)	120

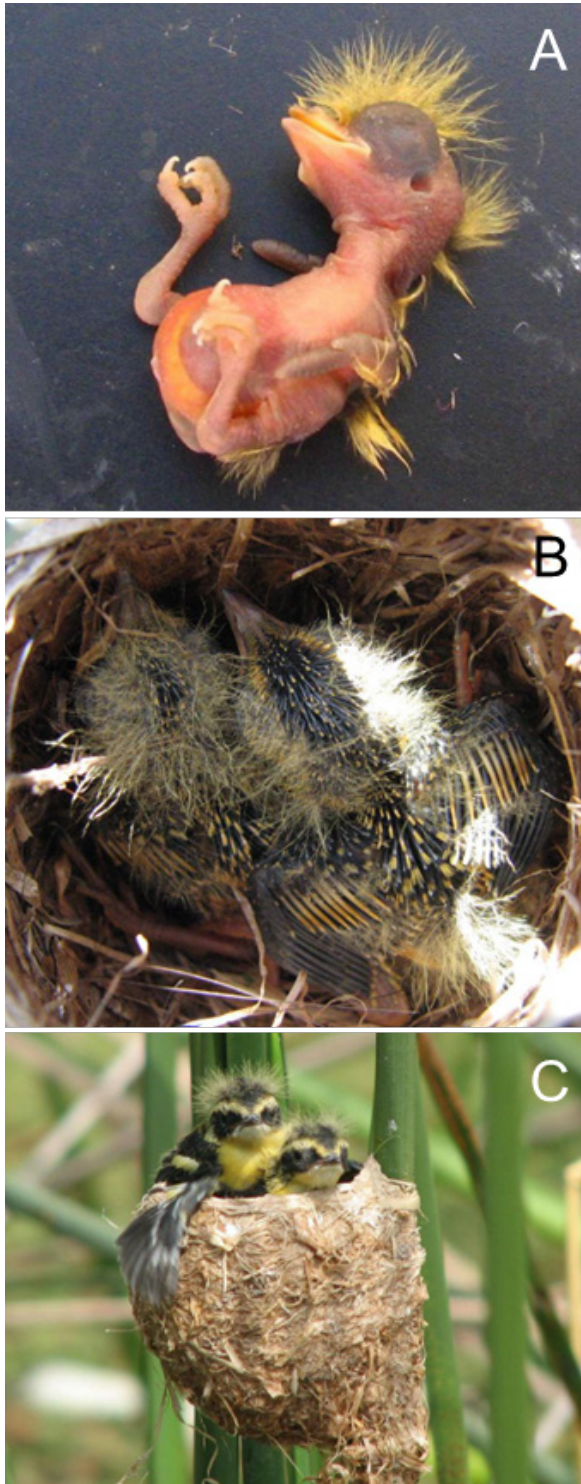


Figure 4. Growth of nestling Many-colored Rush-Tyrants (*Tachuris rubrigastra*) at three age categories from young banded in Laguna Santa Elena, Ñuble Province, south-central Chile. **A.** Newly hatched chicks are entirely naked with closed eyes. In addition, they have strong-yellow lip edges, light pinkish skin, and head, back, and wings covered with lemon-yellow down. **B.** At 6-9 days, they are covered profusely with down, and the first feathers have already emerged. **C.** When 12 days old, nestlings are fully feathered, but with patches of down on the head and neck. Photographs: Carlos O. Barrientos.

flies, and mayflies (Table 6, Fig. 6). Among these, the dragonfly *Oxyagrion rubidium* and crane flies of the genus *Tipula* (Fig. 6A, 6B) together accounted for two-thirds of all prey items (Table 6). Moths, lacewings, locusts, true bugs, ants, and spiders were occasional prey. While fed, the nestlings produced a fecal sac (*i.e.*, excrement encased in a mucous membrane), which the parents immediately removed from the nest.

Reproductive success

Nest failure.- During the breeding season 2007-2008, the early nests ($n = 5$) failed because of unusual and intense spring rains and the breakage of a nearby irrigation channel. The abrupt rise of the water level caused detachment of the nest structure from tall-rush stems. We found a nest floating with two 5-day-old nestlings dead in its interior. From there on, we did not register more nesting events throughout the reproductive season. Other known causes of nest failure included entrance obstruction by nests of the Wren-like Rush-bird ($n = 2$), predation ($n = 1$), and destruction by coypu (*Myocastor coypus*; $n = 2$). Another 26 nests failed due to unknown causes. Throughout the four reproductive periods, 29 nests failed during incubation and 10 during the nestling stage.

Breeding success of combined nests.- Excepting the breeding season 2007-2008, the proportion of hatched eggs and fledged young following hatching was high ($> 60\%$, Table 7). The proportion of fledged young regarding the number of eggs laid reached values around 50% (Table 7). About half of the nests monitored annually fledged at least one young (Table 7). Productivity was similar among breeding seasons: 20 fledglings in 2005-2006, 29 fledglings in 2006-2007, and 28 fledglings in 2008-2009.

Breeding success per nest.- The mean number of eggs hatched per nest was similar between the 2005-2006 and 2006-2007 breeding seasons (Table 8). The mean number of eggs hatched was somewhat lower in the two subsequent breeding seasons. This decrease was most noticeable during the 2007-2008 breeding season (Table 8). The mean number of fledglings per nest was similar between breeding seasons, except for the 2007-2008 season (Table 8). In this latter season, none of the monitored pairs produced fledglings due to the loss of nests by flooding, as mentioned above.

Nesting success measured by the Mayfield method.-

The daily nest survival probability during the incubation and nestling stages was similarly high ($> 90\%$) among breeding seasons (Table 9). However, the nest survival probability during each entire stage varied markedly.

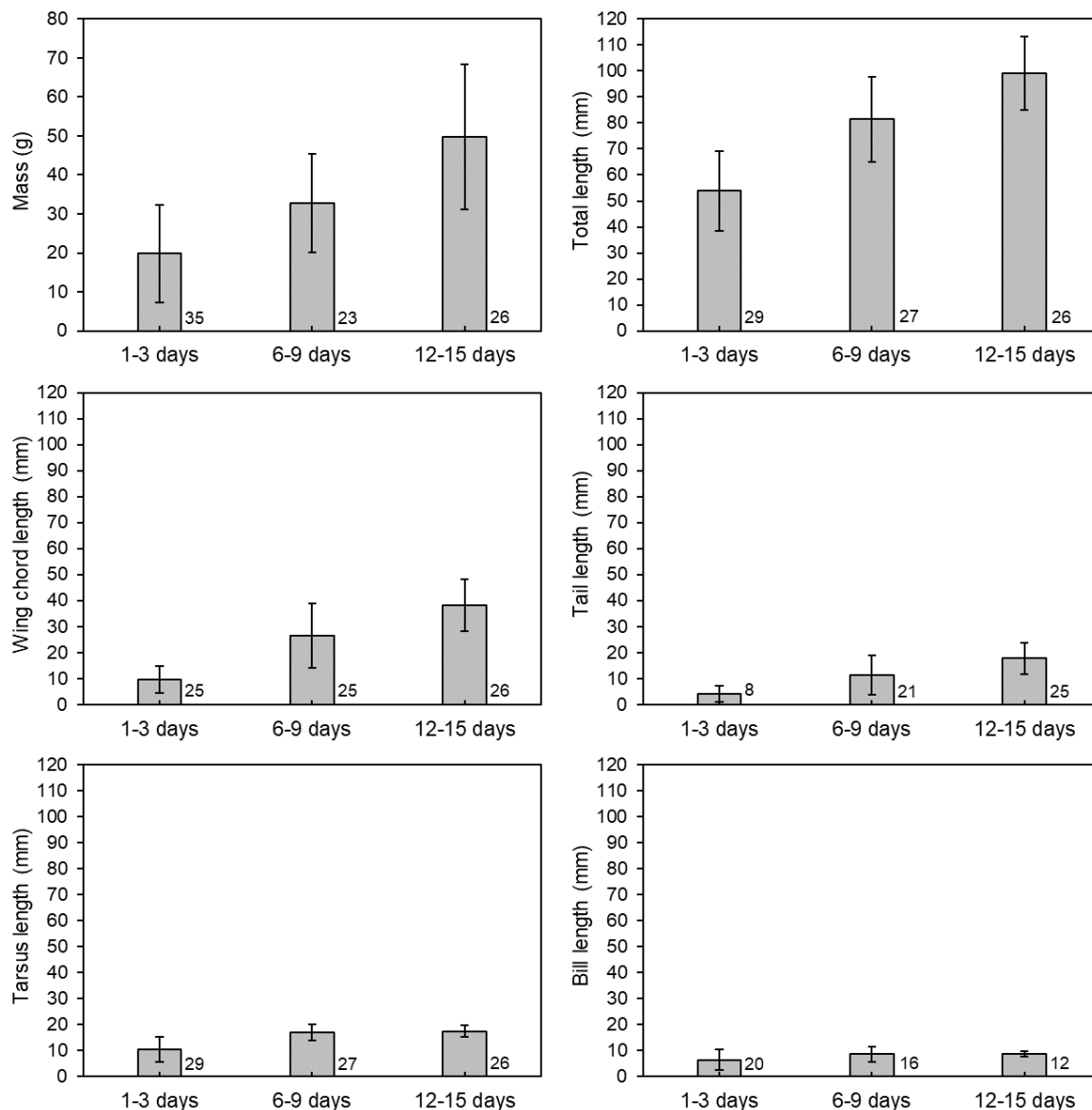


Figure 5. Body size of nestling Many-colored Rush-Tyrants (*Tachuris rubrigastra*) at three age categories from young banded in Laguna Santa Elena, Ñuble Province, south-central Chile. Measurements according to Eck *et al.* (2011). Total length: measured from bill tip to the tip of the longest tail feather. Wing-chord length: measured from carpal joint to the tip of the longest primary feather. Tail length: measured from the base of the innermost rectrices to the tip of the longest tail feather. Tarsus length: measured from the joint between tarsus and toes to the inter-tarsal joint. Bill length: measured from the tip to the proximal edge of the nostrils. Grey bars represent the mean, and error bars are standard deviations. Numbers on the bar side indicate nestlings measured.

During the incubation, the survival probability varied from 0.25 to 0.89, and during the nestling stage varied from 0.62 to 0.88 (Table 9). The nesting success during each entire breeding period ranged from 0.52 to 0.56, with an overall nesting success of 0.44 (Table 9).

DISCUSSION

Breeding phenology and behavior

The breeding activity of the Many-colored Rush-tyrant in Laguna Santa Elena was markedly seasonal, which agrees

with observations in Peruvian wetlands (Barrionuevo & Montes 2015, Reynoso *et al.* 2023). Like in Peruvian mangroves (Reynoso *et al.* 2023), the nest-building and egg-laying in Laguna Santa Elena concentrated particularly during the spring months. Although previous observations in other localities suggest a shorter (3-4 months) or earlier breeding period (Nores & Yzurieta 1980, de la Peña 1987, Rottmann 1995, Barrionuevo & Montes 2015), the reported dates fall within the range dates we registered in our study site. Despite the strong seasonality of the Ma-

Table 6. Invertebrate prey delivered by adult Many-colored Rush-tyrants (*Tachuris rubrigastra*) to nestlings during breeding season 2005-2006 in Laguna Santa Elena, Nuble province, south-central Chile. Authors identified prey based on 1350 digital photographs of parents arriving with food at the nest.

Prey taxa	N° individuals	%
Insects		
Odonata (dragonflies)		
<i>Oxyagrion rubidum</i>	231	36.2
Unidentified imagoes ^a	120	18.7
Unidentified larvae	2	0.3
Diptera (Crane flies, hoverflies)		
<i>Tipula</i> imagoes	166	26
<i>Eristalis</i> larvae	2	0.3
Unidentified imagoes	4	0.6
Mecoptera (scorpionflies)		
Unidentified imagoes	31	5
Plecoptera (stoneflies)		
Unidentified imagoes	29	4.5
Ephemeroptera (mayflies)		
Unidentified imagoes	14	2.2
Lepidoptera (moths)		
Noctuidae imagoes	8	1.3
Neuroptera (lacewings)		
Unidentified imagoes	7	1.1
Orthoptera (grasshoppers)		
Acrididae imagoes	3	0.5
Unidentified imagoes	1	0.1
Hemiptera (bugs)		
Unidentified imagoes	1	0.1
Hymenoptera (ants)		
Formicidae imagoes	2	0.3
Arachnida (spiders)		
Araneae adults	17	2.7
Hirudinea (leeches)		
Unidentified leech	1	0.1
Total individual prey	639	100

^aImagoes = insect adult stage.

ny-colored Rush-tyrant's breeding period, we observed a high nesting asynchrony among pairs during each breeding season. Possibly, this was because of differences in sexual maturity or breeding experience of tyrants (Sargent 1965, Collias & Collias 1984) or some unknown factor.

As in other localities, in our study site some breeding pairs occupied old nests. In Argentina, de la Peña (1983) observed some breeding pairs repairing or reconditioning old nests with fresh plant material or building a

second nest after the loss of the first one. Rottmann (1995) affirms that Many-colored Rush-Tyrants in central Chile may build several nests within the same breeding season. Although we suspected some pairs in Laguna Santa Elena built a new nest during the same season, we could not confirm this as we did not band adult tyrants. Different studies show that nest reuse and construction of more than one nest is common to several Neotropical passerine species inhabiting wetlands (de la Peña 1983, Lara *et al.* 2011, Pretelli & Isacch 2013, Chiaradia *et al.* 2017).

The duration of the laying time in Laguna Santa Elena agrees with some previous reports. In Argentina, de la Peña (2005) found that Many-colored Rush-Tyrants laid the first eggs during mid-September (early spring) and the last ones during early January (early summer). Although in some Peruvian wetlands, the breeding period of Many-colored Rush-Tyrants begins much earlier than in Laguna Santa Elena, the females also lay their eggs over five months (Reynoso *et al.* 2023). The incubation periods of Many-colored Rush-Tyrants in Laguna Santa Elena were within the ranges observed in Peruvian wetlands (11-16 days; Barrionuevo & Montes 2015, Reynoso *et al.* 2023). Thus, the duration of the incubation stage of this tyrant species falls within those of many other open-cup passerine species of southern South America (11-17 days; de la Peña 2013).

The nestling period of Many-colored Rush-Tyrants in our study site also was like that found in some Peruvian wetlands (7-12 days, Reynoso *et al.* 2023). Nonetheless, during some breeding seasons, we detected differences among pairs regarding the age at which nestlings left the nest (11-22 days). We do not know what factors could cause these differences. It is possible that certain ecological (*e.g.*, microclimate, food availability), physiological (*e.g.*, nutritional condition), or behavioral (*e.g.*, parents' experience, variation in parents' dependence) factors were involved (Drent & Daan 1980, Martin 1987, Naef-Daenzer & Keller 1997).

Nest characteristics

The structural characteristics of Many-colored Rush-Tyrant nests in our study site are closely like those observed in other wetlands of southern South America. The nests consist of well-elaborated pensile semi-conical open cups composed exclusively of strips of emergent vegetation (Housse 1945, de la Peña 1983, 1987, Sick 1985, Canevari *et al.* 1991, Narosky & Salvador 1998, Fitzpatrick 2004, Kovacs *et al.* 2006, Barrionuevo & Montes 2015, Reynoso *et al.* 2023). These nest structure characteristics are common to many marshland-specialist passerine species (Collias & Collias 1984). The nest size of Many-colored Rush-Tyrants in our study site was within ranges observed

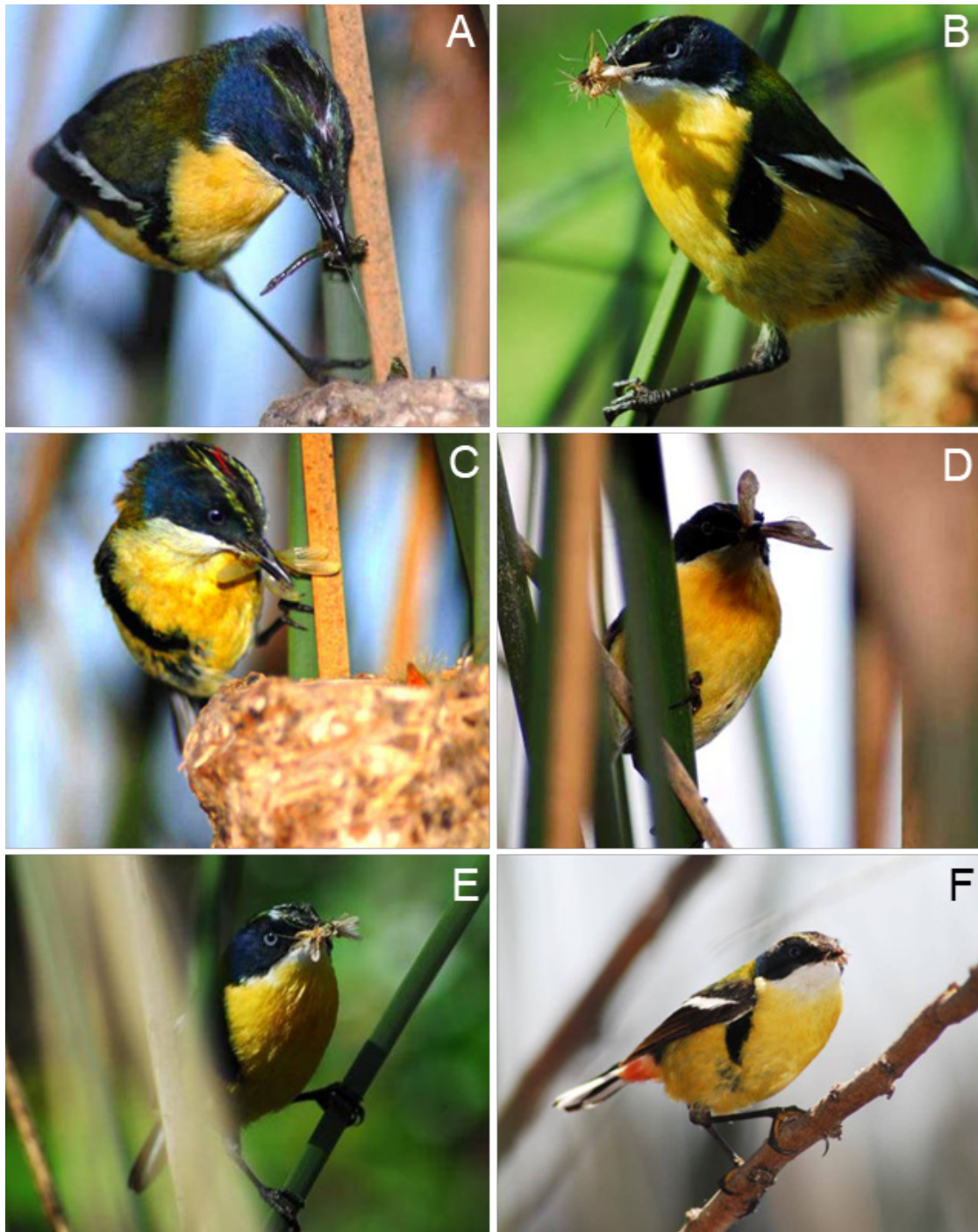


Figure 6. Some invertebrate prey delivered by parent Many-colored Rush-Tyrants to nestlings during breeding season 2005-2006 in Laguna Santa Elena, Ñuble Province, south-central Chile. A. Delivery of an adult dragonfly (*Oxyagrion rubidum*) on 15 November 2006. B. Delivery of an adult crane fly (*Tipula* spp.) on 18 November 2006. C. Delivery of an adult scorpionfly (Mecoptera) on 5 December 2005. D. Delivery of an adult stonefly (Plecoptera) on 12 October 2005. E. Delivery of an adult moth (Lepidoptera) on 11 November 2006. F. Delivery of an adult spider (Aranea) on 20 December 2006. Photographs: Daniel González-Acuña.

in other wetlands (nest height = 3–11 cm, nest width = 3–7 cm, cup deep = 2.5–4.5 cm; Narosky & Salvador 1998, de la Peña 2005, Barrionuevo & Montes 2015, Reynoso *et al.* 2023).

Like in Laguna Santa Elena, the tyrants from oth-

er localities tie their nests mostly on rush stems (Housse 1945, Sick 1985, Canevari *et al.* 1991, Narosky & Salvador 1998, Kovacs *et al.* 2006, de la Peña 2013, Reynoso *et al.* 2023), and rarely on other substrate types (*e.g.*, bulrush, herbs; de la Peña 2013). Although the number of tall-rush

Table 7. Breeding success of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. Percentage of hatched eggs = (n° hatched eggs/n° eggs laid) x 100. Percentage of fledged young following hatching = (n° fledglings/n° hatched eggs) x 100. Percentage of fledged young following laying = (n° fledglings/n° eggs laid) x 100. Nests success = (n° nests that fledged at least one fledgling/n° nests monitored to know the fate of eggs and nestlings) x 100.

Season	% Hatched eggs	% Fledglings follow- ing hatching	% Fledglings follow- ing laying	Nests success
2005-2006	75.0 (27/36)	74.1 (20/27)	55.6 (20/36)	53.8 (7/13)
2006-2007	76.5 (39/51)	74.4 (29/39)	56.9 (29/51)	57.9 (11/19)
2007-2008	25.0 (6/24)	- ^a	- ^a	- ^a
2008-2009	64.0 (32/50)	87.5 (28/32)	56.0 (28/50)	57.9 (11/19)
Total	64.6 (104/161)	74.0 (77/104)	47.8 (77/161)	49.1 (29/59)

^a All nests failed due to flooding after heavy rain.

Table 8. Average hatching and fledging success per nest of Many-colored Rush-Tyrants (*Tachuris rubrigastra*) during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. Hatching success corresponds to a mean number of hatched eggs per nest according to nests monitored from the egg laying. Fledging success is the mean number of fledglings per nest according to nests monitored from egg hatching. n = number of nests monitored.

Season	Mean ± SD (range)			
	Hatched eggs per nest	n	Fledglings per nest	n
2005-2006	2.1 ± 1.4 (0-3)	13	2.2 ± 1.3 (0-3)	9
2006-2007	2.1 ± 1.2 (0-4)	19	1.9 ± 1.3 (0-3)	16
2007-2008	1.4 ± 0.8 (0-3)	8	- ^a	-
2008-2009	1.7 ± 1.4 (0-3)	19	2.3 ± 1.0 (0-3)	12
Total	1.9 ± 1.3 (0-4)	59	2.2 ± 1.2 (0-3)	37

^a All nests failed due to flooding after heavy rain.

Table 9. Nesting success of the Many-colored Rush-Tyrant (*Tachuris rubrigastra*) as estimated by the Mayfield method during four breeding seasons in Laguna Santa Elena, Ñuble province, south-central Chile. n = number of nests included in calculations.

Season	Incubation stage					Nestling stage					
	Daily nest loss rate	Daily survival probability for a nest	Survival probability for one nest during the entire stage	Nest-days	n	Daily nest loss rate	Daily survival probability for a nest	Survival probability for one nest during the entire stage	Nest-days	n	Nesting success during the entire breeding period
2005-2006	0.011	0.989 ± 0.011	0.839	92	7	0.031	0.969 ± 0.021	0.621	64	6	0.521
2006-2007	0.007	0.993 ± 0.007	0.895	145	15	0.031	0.969 ± 0.015	0.628	131	14	0.562
2007-2008	0.082	0.918 ± 0.035	0.255	61	7	- ^a	- ^a	- ^a	- ^a	- ^a	- ^a
2008-2009	0.029	0.971 ± 0.013	0.622	171	17	0.008	0.992 ± 0.008	0.888	127	12	0.552
Overall	0.026	0.974 ± 0.007	0.660	469	46	0.022	0.978 ± 0.008	0.719	322	32	0.475

^a All nests failed due to flooding after heavy rain.

stems supporting the nest tends to be variable within and among localities (some pairs use up to six stems; House 1945), most pairs tie their nests to only one stem (Nores & Yzurieta 1980, Rottmann 1995, Reynoso *et al.* 2023 this study). Possibly, that depends on the stem thickness,

as thicker stems are more resistant to gravity, wind, and water flow. Like other marsh-nesting passerine species (Burger 1985), the Many-colored Rush-Tyrant would attach its nest to more than one stem when one is not strong enough to support a nest. Microclimate factors (*e.g.*, wind,

rain, sun) and resistance of building material can strongly influence how passerines build their nests (Collias & Collias 1984, Bailey *et al.* 2014).

Previous reports indicate that Many-colored Rush-Tyrants locate nests at 30–165 cm above the water surface (Housse 1945, de la Peña 2013, Reynoso *et al.* 2023), which matches our results. Interestingly, the average height from the water surface of the nests measured by de la Peña (2013; mean = 47.8 ± 17.4 cm, mode = 40 cm; $n = 16$) is closely like ours. Thus, tyrants would prefer to build nests at an intermediate height from the water surface. That would simultaneously avoid immediate contact with water and diminish exposure to wind or aerial predators (Collias & Collias 1984, Burger 1985). The location of much of the nest near the tall-rush/open water borderline but distant from the shoreline could be related to mammalian anti-predation tactics (Burger 1985, Picman *et al.* 1988, 1993, 2002).

The proximity among the nests of Many-colored Rush-Tyrants indicates that this species may nest clumped, which implies a high territorial tolerance among nesting pairs after the courtship period. Interestingly, Many-colored Rush-Tyrant pairs were also tolerant toward nearby Wren-like Rushbird nesting pairs. In other wetlands, Many-colored Rush-Tyrants and Wren-like Rushbirds breed clumped within the densest vegetation bands (Burger 1985, Favretto *et al.* 2017, 2022). Similarly, in our study site, both species placed their nests where the tall-rush tended to be densest (Lara *et al.* 2011, this study). Possibly, this clumped nesting resulted from the microhabitat structure, food availability, nest defense, or a combination of them.

Perhaps the nest clumping in denser vegetation bands could provide immediate protection against sun, rain, wind, and predators (Burger 1985, Stewart 1999, Eastman 1999, Weller 1999, Picman *et al.* 2002). Another explanation is that denser vegetation bands had provided Many-colored Rush-Tyrants a high and renewed availability of insect prey (see discussion below). Often, marsh-grassland passerines forage primarily in patches of emergent vegetation (Brush *et al.* 1986, Pretelli *et al.* 2014). The clumped nesting could also eventually have social advantages, such as rapid warning about predators and mutual nest defense (Picman *et al.* 1988, 2002) or facilitate information transfer regarding productive foraging areas by following neighbors on foraging trips (Gori 1988).

Egg characteristics

The Many-colored Rush-Tyrant females laid white eggs that tended to be elliptical. That is something typical in passerine birds (Stoddard *et al.* 2017). The characteristics

of these eggs were like those eggs previously described by other authors (Nores & Yzurieta 1980, Canevari *et al.* 1991, de la Peña 1992, 2005, 2006, Narosky & Salvador 1998, Barrionuevo & Montes 2015, Reynoso *et al.* 2023). Unlike Narosky & Salvador (1998), we did not find eggs with brown spots towards the narrow pole (pointed end). That suggests that eggs in our study site were well calcified as eggshell pigmentation indicates calcium deficiency (Gosler *et al.* 2005).

According to our observations, the pinkish eggshells appear to be related to egg age, being that coloration is typical of eggs laid a few hours earlier. The conservative egg size over the four breeding seasons was likely due to temporally stable nutritional conditions (*e.g.*, invariable availability of food), similarity in physiological traits, or similarity in diet quality of the females (Christians 2002, Figuerola & Green 2005). The conservative egg size could also be a fixed life history trait within the studied population (Christians 2002, Figuerola & Green 2005).

Hatching asynchrony

Asynchronous hatching is usual among altricial birds (Clark & Wilson 1981, Magrath 1990, Stoleson & Beissinger 1995), and it is supposedly a parental strategy for matching offspring number with food availability (*i.e.*, brood-reduction hypothesis; Lack 1947). With asynchronous hatching, the last hatched nestling will be the smallest, and parents could sacrifice it when food availability is scarce. As far as we could observe in our study, none of the smaller nestlings was left to die. That is consistent with our visual perception that the abundance of insect prey was high during each breeding season. It will be necessary to wait for a decline in food availability to verify if Many-colored Rush-Tyrants reduce the number of offspring in such a situation.

Alternative explanations about the role of asynchronous hatching are that it favors earlier fledging of nestlings for increasing brood survival, decreases nestling predation, increases eggs viability, allows taking advantage of a food availability seasonally limited, or decreases the timing of hatching (Perrins 1965, Bryant 1975, Clark & Wilson 1981, Cooke *et al.* 1984, Arnold *et al.* 1987, Watson *et al.* 1993). Some of these hypotheses are relevant in the case of Many-colored Rush-Tyrant pairs, which strongly depend on the availability of ephemeral insects to feed nestlings.

Clutch size

The number of eggs laid by Many-colored Rush-Tyrants in Laguna Santa Elena was like that observed for this species in other wetlands (range = 1–4 eggs; de la Peña 2005, Barrionuevo & Montes 2015, Reynoso *et al.* 2023). How-

ever, in our study site, more than 70% of nesting pairs (43 out of 59) laid three eggs, resulting in a higher mean clutch size (2.7 ± 0.5 eggs [mean $\pm$ SD]) compared to pairs from other wetlands (de la Peña 2005: 2.4 eggs; Barrionuevo & Montes 2015: 2.4 ± 0.5 , Reynoso *et al.* 2023: 2.0 ± 0.0). Despite this geographical difference in the clutch size, it is clear enough that the clutch size of the Many-colored Rush-Tyrant typically ranges from 2 to 3 eggs, as happens with more than half of all bird species (Jetz *et al.* 2008). The mean clutch size of the Many-colored Rush-Tyrant in our study site was closely like that documented by Yom-Tov *et al.* (1994) for the Tyrannidae family in southern South America (2.69 ± 0.55 eggs). That corroborates that Deutero-Oscines passerines have clutch sizes smaller than Oscines passerines in that region (Yom-Tov *et al.* 1994).

Although multiple environmental factors influence the clutch size within bird populations (Wiebe *et al.* 2006, Ricklefs & Wikelski 2002), prevalent explanations are food limitation (Lack 1947, Ashmole 1963, Drent & Daan 1980) and predation risk (Slagsvold 1982, Martin 1993a, 1995, Eggers *et al.* 2006). Since predation upon tyrant nests in Laguna Santa Elena was minimal, we think a more probable reason for the constant clutch size was equitable food availability for the most pairs in each breeding season. According to Ashmole's hypothesis, there should be substantial uniformity of clutch size within a habitat patch since the seasonal productivity of food affects all birds within that habitat patch (Ashmole 1963). Lazo (1996) demonstrated that differential availability of food caused by differences in habitat characteristics influence the clutch size in some species of Chilean passerines.

Growth and feeding of the nestlings

As far as we know, there is minimal information about the growth of Many-colored Rush-Tyrant nestlings. Reynoso *et al.* (2023) measured nestlings at two days old, and their measurements coincided with ours for that age category. Like many altricial birds (Ricklefs 1968, Case 1978), the Many-colored Rush-Tyrant nestlings in our study site exhibited rapid growth, attaining the adult size within 15-17 days from hatching, just when their bodies were fully feathered. That suggests most nestlings left the nest when they were close to achieving the adult mass (7.6-8.8 g; Salvador 2014). Consistently, total and wing length markedly increased as body mass increased.

The insectivorous diet of nestling Many-colored Rush-Tyrants in our study site agrees with previous occasional observations from other localities where tyrant adults hunted insects and other invertebrates (Olrog 1984, Canevari *et al.* 1991, Rottmann 1995, de la Peña 2005, Favretto *et al.* 2022). The high proportion of flying insects captured by adult Many-colored Rush-Tyrants in Laguna

Santa Elena is striking because they are not specialist aerial hunters. Possibly, adult Many-colored Rush-Tyrants captured those prey insects while posing on the rush stems (e.g., dragonflies) and water surfaces (e.g., dipterans) or moving among vegetation.

The preeminence of dragonflies among the food offered to nestlings could be because these insects are generally plentiful in marshlands, and their large body size and striking coloration make them vulnerable prey. We did not measure the prey availability, but dragonflies were regular, active, and conspicuous insects within the tall-rush patch we studied. Moreover, compared to other insect taxa in our study area, the larger body size of dragonflies would give them a higher nutritional value. The high proportion of dragonflies in the nestling diet of other passerine species inhabiting South American wetlands (e.g., Wren-like Rushbirds, Spectacled Tyrant; Lara *et al.* 2011, Pretelli *et al.* 2014) reinforce such presumptions.

Even though Many-colored Rush-Tyrants and Wren-like Rushbirds co-nested in Laguna Santa Elena, the latter offered fewer dragonflies and dipterans (40% and 11.4% of all individuals prey, respectively) and many more spiders (20%) to chicks compared to the first one. Moreover, adult Wren-like Rushbirds fed their nestlings with earthworms (11%; Lara *et al.* 2011), a prey item we did not register in the case of the tyrants. That suggests that both species used the available prey resources differently. Unlike the Wren-like Rushbirds, adult tyrants seemingly did not look for prey on the ground.

Nest loss and breeding success

The negligible predation rate of Many-colored Rush-Tyrants nests we witnessed in our study site (1.5%) is striking as predation is one of the more determining factors of nest failure in marsh-dweller passerines (e.g., Martin 1993b, Pretelli & Isacch 2013, Chiaradia *et al.* 2017). Perhaps we underestimated the nest predation rate since those nests we considered lost by unknown causes suffered possibly predation. If so, the nest predation becomes relatively high (37.7% of all nests). A high predation of nests in our study site is feasible as there are several potential avian and mammalian predators. Among these are Chimango Caracaras (*Milvago chimango*), Cooi Herons (*Ardea cooi*), Great Egrets (*Ardea alba*), long-tailed rice rats (*Oligoryzomys longicaudatus*), domestic cats (*Felis catus*), and dogs (*Canis vulgaris*) (Lara *et al.* 2011).

Commonly, water overflow and the activity of other animal species can cause the loss of a few nests of passerine species that breed in wetlands (Burger 1985, Chiaradia *et al.* 2017). However, the impact of the flood in our study site was far beyond a few lost nests. Although the flooding occurred only at the start of the breeding sea-

son 2007-2008, it was enough to inhibit the Many-colored Rush-Tyrant's breeding activity during the rest of the season. Thus, when they occur, floods can have a negative impact superior to predation on the breeding success of marsh-dwelling passerines. The capacity of Many-colored Rush-Tyrants to successfully resume breeding activity during the following years after flood indicates this species can rapidly overcome catastrophic circumstances.

Considering nests combined, Many-colored Rush-Tyrants in Laguna Santa Elena exhibited a breeding success similar to co-nesting Wren-like Rushbird pairs (hatching success = 60%, fledgling success following laying = 46%; Lara *et al.* 2011). The breeding success of these two species in our study site was as high as that observed in Peruvian wetlands (Barrionuevo & Montes 2015, Reynoso *et al.* 2023). However, the breeding success of Many-colored Rush-Tyrants and Wren-like Rushbirds in Laguna Santa Elena considerably differs from those reported for some marsh-dweller passerine species in Argentinean wetlands. In marshlands of the Pampa region, Argentina, Chiaradia *et al.* (2017) found that fledgling success and nest success of Wren-like Rushbirds was only 29% (69 fledglings/235 eggs laid), and 14% (33 out 245 nests produced fledglings), respectively. In the same region, Pretelli & Isacch (2013) observed that the breeding success of Spectacled Tyrants was only 28% (15 out of 54 nests produced fledglings).

In our study site, the survival probability for one tyrant nest during the entire nesting period was also high compared with those of Wren-like Rushbirds and Spectacled Tyrants in some Argentinean wetlands. Pretelli & Isacch (2013) and Chiaradia *et al.* (2017) found the survival probability for one nest of these two species throughout the entire nesting period varied between 0.21 and 0.25. Thus, the values of nesting success of Many-colored Rush-Tyrants in Laguna Santa Elena are closer to those of several Nearctic passerine species that nest in marshes (Martin 1993b). As already discussed, local-specific factors could explain the variations observed in nesting success among passerine species breeds in wetlands (Chiaradia *et al.* 2017).

Advancing the natural history of the Many-colored Rush-Tyrant

Our study reveals remarkable aspects of the natural history and breeding biology of the Many-colored Rush-Tyrant, which have implications for conservation and management both at the species and habitat levels. First, many pairs nested in well-protected and densest vegetation bands using almost exclusively tall-rush to build their nest and fed nestlings mostly with aquatic insects. Such findings indicate that Many-colored Rush-Tyrants are

strongly habitat-dependent. Second, the clumped nesting of tyrant pairs reflects they are spatially tolerant of conspecific individuals. That fact merits much more attention as this could have social implications (*e.g.*, nest defense, information transfer). Third, the small clutch size of Many-colored Rush-Tyrants indicates that this species tends to be a K-type breeder (Yom-Tov *et al.* 1994). That implies its population will remain small among populations of passerine species with larger clutch sizes. Finally, Many-colored Rush-Tyrants recuperated their breeding success after suffering an almost total nest failure due to a catastrophic climate event. This capacity could be fundamental for an eventual population recovery.

Some limitations of our study (*e.g.*, not identifying adult tyrants by some marking method) prevented us from knowing much more about the breeding biology of the Many-colored Rush-Tyrant. Nevertheless, we hope our findings will allow ornithologists to understand more deeply the natural history and fundamental ecology of an eye-catching little-studied passerine.

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