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NESTING AND NATURAL HISTORY OF THE CHESTNUT-BELLIED EUPHONIA (*EUPHONIA PECTORALIS*) IN MISIONES, ARGENTINA, AND COMPARISON WITH OTHER SPECIES IN THE GENUS

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Abstract · The genus *Euphonia* includes 28 species that present high levels of specialization on a frugivorous diet, with emphasis on the consumption of mistletoes of the order Santalales. For the Chestnut-bellied Euphonia (*Euphonia pectoralis*), endemic to the Atlantic Forest of South America, nests and eggs have been described, but other aspects of natural history and reproductive biology are unknown. Here we report observations on foraging and ten reproductive events in eight nests between 2003 and 2018 in Misiones, Argentina. We observed a primarily frugivorous diet in adults and nestlings, although adults occasionally consumed insects when they foraged in mixed species flocks. In contrast to other species of *Euphonia*, we observed low frequencies of consumption of Santalales fruits. Nests were globular structures of plant material, supported on epiphytic plants, tree trunks, tree ferns, or thin branches 0.93–5.30 m above the ground. Clutch size was 2–3 eggs (n = 6), smaller than for species of *Euphonia* inhabiting tropical regions, supporting the idea that this genus departs from the general pattern in birds, in which clutch size increases with latitude. The incubation period lasted 16 days and the nestlings fledged when 17–21 days old (n = 2). Both parents participated in nest construction but only the female incubated, brooded, and took care of nest hygiene, ingesting the gelatinous fecal mass directly from the cloaca of her offspring. We observed the male (once) and the female (eight times) feeding the nestlings with regurgitated fruit. Future studies on nesting in the genus *Euphonia* could help to understand evolution of nesting behaviors in the family, resolve its complex phylogenetic situation, and test hypotheses about the factors influencing clutch size in birds.

Resumen · Nidificación e historia natural del Tangará Alcalde (*Euphonia pectoralis*) en Misiones, Argentina, y comparación con otras especies del género

El género *Euphonia* incluye 28 especies que presentan una alta especialización a la dieta frugívora, con énfasis en el consumo de ligas del orden Santalales. Para el Tangará Alcalde (*Euphonia pectoralis*), endémico de la selva Atlántica de Sudamérica, se han descripto nidos y huevos, pero se desconocen otros aspectos de la historia natural y biología reproductiva. Aquí reportamos observaciones de forrajeo y diez eventos de reproducción en ocho nidos entre 2003 y 2018 en Misiones, Argentina. Observamos una dieta mayormente frugívora en adultos y pichones, aunque adultos ocasionalmente consumieron insectos cuando forrajearon en bandadas mixtas. A diferencia de otras especies de *Euphonia*, observamos escasa frecuencia de consumo de frutos de Santalales. Los nidos eran estructuras globulares de material vegetal, apoyados sobre plantas epífitas, troncos de árboles, helechos arborescentes o ramas finas a unos 0.93–5.30 m del suelo. El tamaño de puesta fue de 2–3 huevos (n = 6), menor a las especies de *Euphonia* que habitan zonas tropicales, apoyando la idea de que este género representa una excepción al patrón general en las aves, donde el tamaño de puesta aumenta con la latitud. El período de incubación duró 16 días y los pichones abandonaron el nido a los 17–21 días (n = 2). Ambos padres participaron en la construcción de los nidos pero solo la hembra incubó, empolló y se ocupó de la higiene, tomando la masa gelatinosa fecal directamente de la cloaca de sus pichones. Observamos una vez al macho y ocho veces a la hembra alimentando a los pichones con regurgitaciones de frutas. Futuros estudios sobre la nidificación del género *Euphonia* podrían ayudar a determinar tendencias evolutivas dentro del género, resolver su situación filogenética compleja, y testear hipótesis sobre los factores que influyen en el tamaño de puesta de las aves.

Key words: Atlantic forest · Clutch size · *Euphonia* · Frugivory · Nest · Parental care

INTRODUCTION

The genus *Euphonia* includes 28 Neotropical species with marked sexual dichromatism (Remsen et al. 2017, Collar et al. 2018). Traditionally, the genus was included in the family Thraupidae because of the bright colours of the plumage (Paynter & Storer 1970). Later, based on molecular biology, anatomy, and behavior, *Euphonia* was grouped, together with *Chlorophonia*, in the

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subfamily Euphoniinae, family Fringillidae (Zuccon et al. 2012, Payevsky 2015). The genus *Euphonia* presents a high level of specialization to a frugivorous diet, with a particular specialization on the fruits of parasitic or semiparasitic mistletoes (order Santalales; Skutch 1954, Snow 1981, Blendinger et al. 2016), which is associated with the absence of a gizzard in its digestive system (Clark 1913, Wetmore 1914). However, some *Euphonia* individuals have been observed consuming fruits of other plant orders, and even insects (Pérez-Rivera 1991), and little is known about the diet of nestlings.

Species of the genus *Euphonia* build globular nests of plant material and lay white eggs with chestnut and/or black spots of various sizes, concentrated at the major pole (Isler & Isler 1999, Collar et al. 2018). Both sexes contribute to nest building in *E. luteicapilla*, *E. laniirostris*, *E. hirundinacea*, *E. imitans*, *E. minuta*, *and E. chlorotica*; only the female incubates in *E. luteicapilla*, *E. hirundinacea*, *E. imitans*, *E. minuta*, *and E. chlorotica*; and both sexes feed the nestlings in *E. luteicapilla*, *E. laniirostris*, *E. minuta*, *E. chlorotica*, and *E. cyanocephala* (Barnard 1954, Skutch 1954, 1972, Morton 1973, Sargent 1993, Di Giacomo 2005, Perella et al. 2017, Wright et al. 2017). These aspects of reproduction are still unknown for the remaining species of the genus.

The Chestnut-bellied Euphonia (*Euphonia pectoralis*) is a monotypic species, endemic to the Atlantic Forest, inhabiting humid forests in east-southeast Brazil, eastern Paraguay and northeast Argentina (Hilty 2018). The species feeds on small fruits (melastomes, epiphytes, epiphytic cacti, *Cecropia*, *Solanum*, and palms), flower nectar, and small arthropods (Hilty 2018). Knowledge of their nesting comes from observations and descriptions in Paraguay (Bertoni 1919), southeast Brazil (Snethlage & Schreiner 1929, dos Anjos & Schuchmann 1999, Pizo 2000), and northeast Argentina (Castelino & Saibene 1989). The nests described were closed spheres made of mosses and ferns, with a lateral entrance, placed less than 2 m high and hidden on the surface of a trunk, supported by epiphytic ferns, or in hollows in rocky walls of rivers or streams (Bertoni 1919, Castelino & Saibene 1989, Pizo 2000, Hilty 2018). Other basic details of their reproductive biology (e.g., nesting period and nestling development) remain unknown.

Here we provide information on the diet of *E. pectoralis* and describe ten nesting events. We present information about the incubation period, the permanence of chicks in the nest, and the behavior and roles of parents. Also, we compare these reproductive parameters with the other species of the genus *Euphonia* for which information is available.

METHODS

We observed *Euphonia pectoralis* while living and studying birds in the province of Misiones, Argentina (2003–2018). Nests were found in Cruce Caballero Provincial Park (San Pedro department; 26°31´S, 54°00´W; 550–600 m a.s.l.) and in the Apepú section of Iguazú National Park (Iguazú department; 25°38´S, 54°21´W; 250 m a.s.l.). Cruce Caballero Provincial Park is located in the district of mixed forest with laurel (*Nectandra* spp. and *Ocotea* spp., Lauraceae), guatambú (*Balfourodendron riedelianum*, Rutaceae), and Paraná pine (*Araucaria angustifolia*, Araucariaceae), and Iguazú National Park in mixed forest with laurel, guatambú, and palo rosa (*Aspidosperma polyneuron*, Apocynaceae), with palmito (*Euterpe edulis*, Palmae) associations (Cabrera 1976). *Euphonia pectoralis* is considered a common breeding resident at both sites (Saibene et al. 1996, Bodrati et al. 2010).

Foraging observations were made opportunistically, mostly while we conducted surveys walking slowly along trails, detecting birds by sound or sight, throughout the year (Bodrati & Cockle 2006; Bodrati et al. 2010, 2018). Other observations were made while we searched for nests of cavity-nesting birds each September–December from 2006 to 2018 (Bonaparte & Cockle 2017).

For nest descriptions we follow the classification proposed by Simon & Pacheco (2005). We assigned a number to each nest, and a letter to each nesting attempt in the case of nests used more than once. Nest measurements were made with a measuring tape (0.1 cm). We measured eggs and nestlings with a caliper (0.1 mm) and mass with a digital scale (0.1 g). In order to differentiate the two nestlings in nest 4a, one was marked with a small piece of tape on one of its legs. We observed the behavior of the adults through direct observations using binoculars at 10–25 m from the nest, while remaining hidden in the vegetation, and through video recordings (with a Panasonic DMC-FZ30 camera placed 2 m from the nest and camouflaged with the environment, or with a Samsung Galaxy 7 Cell Phone coupled to a Celestron 80 mm spotting scope). Using both techniques, we made 27 min of observations during construction (at nest 8), 3 h 6 min during incubation (1 h 6 min at nest 4a and 2 h at nest 4b, in 2 sessions of 60 min each), and 6 h 38 min during the nestling period (2 h 20 min at nest 4a, 2 sessions of 60 and 80 min each; and 4 h 18 min at nest 4b, in 4 sessions of 25, 60, 79, and 94 minutes each). We visited nest 4 (a and b) every 2–5 days, making a total of 32 visits over two nesting events in the same breeding season. Nests 5 and 8 were seen daily from our camp kitchen.

RESULTS AND DISCUSSION

Diet. Most of our foraging observations were made on fruit trees. We observed different individuals of *Euphonia pectoralis* feeding on fruits of plants in the families Myrtaceae (*Plinia trunciflora*, *Eugenia involucrata*, *E. uniflora*, *Myrciaria rivularis*, *Hexachlamys edulis*), Primulaceae (*Rapanea acuminata*), Cannabaceae (*Trema micrantha*), Sapindaceae (*Allophylus edulis*), Sapotaceae (*Pouteria gardneriana*), Rubiaceae (*Psychotria carthaginensis*), and Moraceae (*Ficus luschnathiana*), some of which we have already mentioned (Bodrati & Haene 2006, Bodrati 2006). We did not observe *E. pectoralis* consuming mistletoe fruits, even though we observed other species of *Euphonia* consuming mistletoe fruits during our surveys (Areta & Bodrati 2010). Thus, unlike other euphonias (Skutch 1954, Snow 1981, Blendinger et al. 2016) *E. pectoralis* does not appear to be a mistletoe specialist.

During autumn–winter we observed *E. pectoralis* in mixed flocks with up to 50 species of birds (Tyrannidae, Furnariidae, Thamnophilidae, Thraupidae, etc.), where it consumed larvae and adults of small insects. In the same seasons, but less frequently, we observed *E. pectoralis* feeding on fruits in flocks of Euphoniinae dominated by *E. cyanocephala* and also including *E. violacea*, *E. chlorotica*, and *Chlorophonia cyanea*. Areta & Bodrati (2010) mentioned such flocks of Euphoniinae in the Atlantic Forest of Argentina

Table 1. Details of the nests of Chestnut-bellied Euphonia (*Euphonia pectoralis*) found in Iguazú National Park (nest 1) and Cruce Caballero Provincial Park (nests 2–8), Misiones, Argentina. Nests 4, 6, and 7 were within 30 cm of one another, supported by the same epiphytic bromeliad and the trunk of a *Peltophorum dubium*. Nests 4a–c represent multiple breeding events in the same nest structure. Stage found: C = construction, I = incubation, N = nestlings.

Nest	Height (m)	Substrate support	Day found (stage)	Clutch	Fate
1	2.4	*Rhipsalis* sp., bromeliad on *Cupania vernalis* trunk	29 Nov 2007 (I)		unknown
2	3	branching on *Ocotea* sp. trunk	18 Oct 2009 (N)		unknown
3	5.3	bromeliad on *Holocalyx balansae* trunk	19 Sep 2010 (I)	3	2 fledglings
4a	0.9	bromeliad (*Aechmea* sp.) on *Peltophorum dubium* trunk	10 Sep 2015 (I)	2	2 fledglings
4b		same as 4a	24 Oct 2015 (I)	3	1 fledgling
4c		same as 4a	25 Sep 2016 (I)	3	unknown
5	4.2	below bromeliad on tree fern (*Alsophila setosa*) stem	31 Oct 2017 (C)		destroyed
6		same as 4a	19 Aug 2018 (C)	3	destroyed
7		same as 4a	16 Nov 2018 (I)		3 fledglings
8	1.8	tree fern (*A. setosa*) stem	27 Nov 2018 (C)	3	unknown

during autumn–winter, but *E. pectoralis* is represented by few individuals in these flocks.

Nests. We found eight nests of *E. pectoralis* in areas of well-conserved forest: one nest at Apepú, Iguazú National Park (nest 1), and seven nests at Cruce Caballero Provincial Park (nests 2–8; Table 1). Nest 4 was used for three clutches (4a, 4b, and 4c) in two successive breeding seasons (Table 1).

Breeding season. Nesting activity was observed between 19 August (nest 5; in construction) and 17 December (nest 8; eggs). Published nests for *E. pectoralis* were found in late August (construction in Paraguay; Bertoni 1919), October (nestlings in southeast Brazil; Pizo 2000), November (a nest with eggs and another with nestlings in Argentina; Castelino & Saibene 1989), and January (with eggs in southeast Brazil; Snethlage & Schreiner 1929). A possible nest was found in March in southeastern Brazil (dos Anjos & Schuchmann 1999), but no eggs or chicks were observed and nesting was inferred because the male remained inside the nest for 12 minutes, much longer than has otherwise been observed for male euphonias (Bernard 1954; Skutch 1954, 1972; Sargent 1993, Cisneros-Heredia 2006, Solano-Ugalde 2007, Perella et al. 2017). We consider that the breeding period of *E. pectoralis* is likely to run from August to January in Misiones, coinciding with most bird species in the region (Bodrati et al. 2010, 2015; Bonaparte & Cockle 2017).

Nest construction. Male and female cooperated in nest construction, sometimes vocalizing (Figure 1A–B). At nest 8, they were first seen on 27 November, when both adults, but especially the male, were pecking clean the tree fern stem where the nest would later be constructed. By 29 November, they had completed the outer globular structure of the nest and were working on the interior. They usually arrived and departed the nest site together and took turns adding material (link to video, https://vimeo.com/306247612; C. A. Ferreyra and M. R. Gómez *in litt*. 2018). In 27 min of video, the male entered 19 times and the female 14. Likewise, in *E. minuta*, *E. imitans*, *E. laniirostris*, and *E. luteicapilla* (Bernard 1954, Skutch 1954, 1972), both male and female are involved in nest construction.

Nest structure and location. Nests were placed against the surface of tree trunks or tree ferns (Cyatheaceae: *Alsophila setosa*), supported from below or above by epiphytic plants or thin branches, 0.9–5.3 m above the ground (Table 1, Figure 1C). These nesting sites seem similar to those reported previously for *Euphonia pectoralis* and different from most other species of *Euphonia*, which were (1) between thin branches of a tree (Barnard 1954), (2) among the pine needles of a lateral branch in a *Pinus elliottii* (de la Peña 2016), (3) in abandoned nests of other bird species, including a woodpecker-excavated cavity in a tree (Skutch 1954, Saibene et al. 1996), (4) in abandoned insect nests (Perella et al. 2017), or (5) within tree cavities, ravines, or open extremes of fence posts (Bertoni 1919, Skutch 1972, Castelino & Saibene 1989, Sargent 1993, Pizo 2000, Lopes et al. 2013, Crisologo et al. 2017, Hilty 2018).

According to the classification of Simon & Pacheco (2005), all nests we found were closed-globular-lateral, with a small lateral entrance (Figure 1D). They were built with plant materials of various origins. In general they were formed by rachises of various species of trees, fronds and stem fibers of ferns (Cyatheaceae: *Alsophila setosa*, *A. procera*), dry twigs, and fine roots. Bamboo (Poaceae: *Guadua trinii*, *G. chacoensis*) leaves and mosses were intertwined with the structure, camouflaging the nests with their surroundings. In nest 4 (a, b, and c) the chamber was comprised almost entirely of rachises and covered with many rhizomorphs of *Marasmius* spp. fungi. Nest 4 (Figure 1D) measured 8.5 cm x 10 cm (width x height) in external diameter of the sphere, and its entrance was 4 cm x 3 cm (width x height). The nest chamber measured 3 cm in vertical depth (from the bottom edge of the entrance to the floor of the nest chamber) and 5 cm in internal diameter (from the edge of the entrance to the back wall). The roof extended 2 cm beyond the entrance in the form of an eave.

In general, nest structure and materials coincided with those mentioned for *E. pectoralis* and other genus members (Bertoni 1919, Snethlage & Schreiner 1929, Castelino & Saibene 1989, Pizo 2000, Hilty 2018). However, all of these nests differ from the possible *E. pectoralis* nest found by dos Anjos & Schuchmann (1999), which had a smaller entrance and was elongated at the bottom with fine compact rootlets.

Figure 1. A–B. Male and female Chestnut-bellied Euphonias (*Euphonia pectoralis*) carrying nesting material near the campsite of Cruce Caballero Provincial Park in September 2016. C. Nesting environment of nest 4; the white arrow indicates where the nest was located. D. Structure of nest 4, supported by an epiphytic bromeliad. Photographers: M. Lammertink (A–B); F. Di Sallo (C–D).

Considering the shape of this nest and the lack of details to confirm nesting, we suggest that it may have belonged to another species.

Eggs and incubation. Complete clutches contained two (n = 1) or three (n = 5) eggs (Table 1). The eggs were white with scattered chestnut speckles, which were concentrated towards the largest pole of the egg, forming a crown (n = 15 eggs; Figure 2A). Egg measurements were 18.7 ± 0.5 x 13.0 ± 0.5 mm (mean ± SD; range: 18.3–19.8 x 12.2–14.0 mm, n = 9). Eggs weighed 1.8 ± 0.1 g (range: 1.7–1.9, n = 6).

The pattern of coloration found in eggs of *E. pectoralis* was similar to that reported for other species in the genus (Hilty 2018). The clutch size of two or three eggs is consistent with previous reports for the species (Castelino & Saibene 1989, Pizo 2000) but smaller than many *Euphonia* clutches at lower latitudes (Table 2), supporting Perella et al.'s (2017) observation that clutch size of *Euphonia* declines with latitude, contrary to the general pattern for birds (Lack 1947, Sargent 1993, Jetz et al. 2008).

Construction was completed at nest 8 on 5 December, and the adults were not observed again until 7 December, when the pair arrived at the nest and the female entered for 2 min. Laying occurred on consecutive days: the first egg was laid between 15:00 h on 9 December and 16:14 h on 11 December, the second by 12:28 h on 12 December, and the third by 12:27 h on 13 December. In the genus *Euphonia*, laying may occur on successive days (*E. luteicapilla* and *E. imitans*, Skutch 1954, 1972; *E. chlorotica*, Perella et al. 2017) or on alternate days (*E. hirundinacea*, Sargent 1993; *E. chlorotica*, Perella et al. 2017). The adults were not seen entering nest 8 during the laying period, but the female was incubating by 12:27 h on 13 December.

Nest 4b was empty at 11:35 h on 20 October, and contained three eggs at 16:50 h on 24 October. One egg hatched between 13:30 h on 7 November and 10:09 h on 9 Novem-

Figure 2. A. Three egg clutch of Chestnut-bellied Euphonia (*Euphonia pectoralis*) at nest 4b. B–D. Development of nestlings in nest 4a on September 17 (approximate age 2 or 3 days, B), September 22 (7 or 8 days, C), and September 28 (13 or 14 days, D). Photographer: F. Di Sallo.

ber, another egg was found on the ground on 3 November, and the remaining egg was removed, presumably by an adult on 10 November. Assuming that incubation began on 23 October and hatching occurred on 8 November, the incubation period would be 16 days, which would fall within the range indicated for other species of *Euphonia* (Table 2). Incubation period varies considerably among different species of *Euphonia* (Table 2), possibly because of inconsistencies in calculation, or possibly because of ecological factors, which could be elucidated in comparative studies involving more nests and species.

Only the female incubated the eggs, and she was in the nest 82% of the time, with complete incubation bouts of 40, 50, and 63 min. This level of nest attentiveness is among the highest reported for the genus *Euphonia* (Table 2).

One time only, during the incubation stage in nest 4a, we observed the male feeding the female in the nest. The male approached from the bottom of the nest. With a short flight he reached the base of the bromeliad that held the nest, and fed the female by regurgitating a gelatinous mass of fruit material while she was incubating the eggs. The male also feeds or accompanies the female during incubation breaks in *E. hirundinacea* (Skutch 1954, Sargent 1993) and *E. minuta* (Skutch 1972).

Nestling development. In nest 4b, a nestling hatched on November 8 or 9. On November 9 (nestling day 0 or 1) it had closed eyes, pink skin, and grey natal down on the back, wing, and head. On November 12 (nestling day 3 or 4), it had closed eyes, light bill with black tip and yellow gape flanges; greyish legs and wings; eyes closed; pink skin with grey natal down on the back, wings, and head; pins under the skin on the ventral flanks, wings, scapulars, thighs and back. On November 17 (nestling day 8 or 9) it began to open its eyes. It had a dark bill with yellow gape flanges, greyish legs, pink skin; a remnant of natal down on the back, head, and scapulars; and unopened black pin feathers on the wings, back, ventral flanks, thighs, and head. On November 19 (nestling day 10 or 11) it had open eyes with black irises; a dark maxilla, yellow mandible and gape flanges; and a naked appearance with black and open pins (few mm) on back, wings, tail,

Table 2. Summary of the reproductive parameters for species of the genus *Euphonia*, where known, given as: mean (range). We report sample size [n] where known. Latitude is given for each study location; where the locality was not specified, we used the state, province, or species' distribution to determine a latitudinal range. Species are listed in order of latitude. Sources: 1 - Isler & Isler, 2 - Sargent 1993, 3 - Blake 1956, 4 - Skutch 1972, 5 - Skutch 1954, 6 - Bernard 1954, 7 - Collins 2006, 8 - Pizo 2000, 9 - this study, 10 - Perella et al. 2017, 11 - Di Giacomo 2005. Empty cells indicate that no information is available. Eleven species of *Euphonia* are omitted from the table because we could find no information on clutch size, incubation, or nestling periods: *E. anneae* (11°–8°N), *E. fulvicrissa* (9°–1°N), *E. concinna* (5°N), *E. finschi* (5°N), *E. plumbea* (8°–0°N), *E. saturata* (5°N–3°S), *E. chrysopasta* (13°N–16°S), *E. xanthogaster* (10°N–19°S), *E. rufiventris* (8°N–16°S), *E. mesochrysa* (5°N–16°S), *E. chalybea* (22°–30°S).

Species	Latitude	Clutch size	Incubation period (days)	Incubation bouts (min)	Nestling period (days)
E. affinis[1]	27°–10°N	2.7 (2–3) [4]			
E. musica[1]	20°–12°N	4 [1]			
E. jamaica[1]	18°N	(3–4)			
E. gouldii[1]	18°–8°N	(2–4)			
E. hirundinacea[2]	10°N	4.4 (3–5) [36]	15 (14–16) [17]	43 (27–58) [5]	19 (18–20) [4]
E. trinitatis[1]	11°–7°N	(3–4)			
E. elengatissima[3]	9°N	2 [1]			
E. imitans[4]	9°N	2.6 (2–3) [6]	18 [1]	87 (77–108) [5]	
E. luteicapilla[5]	9°N	2.9 (2–4) [6]	(13–14) [1]	29 (12–42) [5]	
E. minuta[4]	9°N	3 [2]	17 [1]	25 (7–38) [17]	20 [1]
E. laniirostris[6]	9°N	4.1 (4–5) [7]	(13–16) [2]		(18–21) [2]
E. violacea[1,7]	12°N–4°S	(3–5)			(16–20) [1]
E. cyanocephala[1]	10°–3°N	2			
E. cayennensis[2]	4°S	(3–5)			
E. pectoralis[1,8,9]	27°S	2.8 (2–3) [10]	(16–17) [1]	51 (40–63) [3]	(17–21) [2]
E. chlorotica[1,10]	23°–30°S	2.1 (1–5) [9]	(14) [2]		15 [1] –21 [1]

ventral flanks, and thighs (where the pins were green/yellowish), and some grey pins on the head. On November 24 (nestling day 15 or 16) the nestling was highly developed and had a similar color pattern to the adult female. The nestling fledged between 18:00 h on 26 November and 10:00 h on 27 November, so we calculated a nestling period of 17–19 days. The two nestlings in nest 4a hatched between 14 and 15 September and their development (Figure 2B–D, Table 3) was similar to that of the nestling in nest 4b. The chicks of nest 4a fledged between 08:30 h on 4 October (day 19 or 20) and 09:28 h on 5 October (day 20 or 21). Neither the nestlings at nest 4b nor those at nest 4a were heard to vocalize at any time during their development; their behavior was always extremely silent. At nest 7 we heard very soft vocalizations from three nestlings < 3 days old, in the presence of the brooding female and minutes later when they begged as we inspected the nest.

The development of nestlings coincides with the descriptions reported for *E. hirundinacea* (Skutch 1954, Sargent 1993) and *E. minuta* (Skutch 1972). The nestling period is within the range reported for other species of the genus *Euphonia* (Table 2).

Parental care. Both adults fed the nestlings by regurgitating a gelatinous mass of fruit; the female was observed feeding the nestlings eight times and the male only once. When the nestlings in nest 4a were 2 or 3 days old, the female would enter and feed them inside the nest and then stay brooding the nestlings. When the nestlings in nest 4b were 6 or 7 days old, the female would arrive on the bromeliad and introduce her body into the nest to feed, but she did not stay to brood the nestlings. Disruption of brooding behavior after 6 days was also reported for *E. cyanocephala* (Wright et al. 2017). We observed coordinated misdirection behavior when the pair arrived at nest 4a and 4b to feed nestlings: the female discreetly entered the nest while the male flew onward (Gulson-Castillo et al. 2018). Coordinated misdirection has also been observed for *E. xanthogaster*, *E. hirundinacea*, *E. gouldi*, *E. minuta*, *E. imitans*, *E. chlorotica*, *E luteicapilla*, *E. laniirostris*, *E. rufiventris*, *E. cyanocephala*, and *E. elegantissima* (Skutch 1954, Gulson-Castillo et al. 2018). When the male fed the nestlings, the pair arrived at the nest area, the female fed first while the male remained about 3 m from the nest, and then the male fed while the female remained 40 cm from the nest, perched on other epiphytic plants. The male fed from the nest entrance and never stayed inside the nest.

The feeding frequency for nest 4a (two nestlings) was 1.5 visits/h on 17 September (2 or 3 days old) and 2 visits/h on 3 October (17 or 18 days old). For nest 4b (one nestling) the feeding frequency was 1.3 visits/h on 17 November (8 or 9 days old), 1.5 visits/h on 21 November (12 or 13 days old) and 2.2 visits/h on November 24 (15 or 16 days old). These feeding frequencies are similar to those indicated by Pizo (2000) for *Euphonia pectoralis* (1.1 visits/h for two nestlings).

Nestlings did not form fecal sacs. Their fecal matter was a red or yellow jelly mass. In five samples of this material, we distinguished small seeds but no traces of insects. During our

Table 3. Measurements of two nestlings of Chestnut-bellied Euphonia (*Euphonia pectoralis*) at nest 4a in Cruce Caballero Provincial Park, Misiones, Argentina. Eggs hatched between 13 and 16 September 2015, and chicks fledged between 4 and 5 October 2015.

Measurements	17 Sep (day 2 or 3)	22 Sep (day 7 or 8)	28 Sep (day 13 or 14)
Nestling 1			
Exposed culmen (mm)	3.6	5.0	6.3
Wing chord (mm)	7.5	13.8	16.5
Tarsus length (mm)	7.9	13.2	17.6
Weight (g)	4.0	10.3	11.9
Nestling 2			
Exposed culmen (mm)	3.3	4.6	5.9
Wing chord (mm)	6.8	12.4	16.3
Tarsus length (mm)	7.2	13.4	17.5
Weight (g)	3.8	9.9	12.2

observations, only the female contributed to nest sanitation. In nest 4b, after feeding, the chicks always presented the cloaca in front of the female's beak; she ingested the fecal matter and later she regurgitated it away from the nest (link to video, https://vimeo.com/262885233). Identical behavior was reported for females of *E*. *hirundinacea* (Sargent 1993) and males of *E*. *cyanocephala* (Wright et al. 2017).

The egg coloration, nestling diet, and parental care found for *Euphonia pectoralis* agree with the same parameters for other *Euphonia* species, so we infer that these parameters may be fixed in the genus. However, the natural history and reproductive ecology of most species in *Euphonia* remain poorly known (Table 2).

One of the most studied patterns in bird life history is the increase in clutch size with increasing latitude. Several hypotheses suggest that lower clutch size in the tropics is explained by 1) low food availability (Lack 1947), 2) high nest predation (Skutch 1949), 3) low variation in resource availability, which generates greater survival of adults (Ashmole 1963, Pizarro Muñoz et al. 2018), 4) high risk of adult mortality on the nest (Law 1979, Michod 1979, Martin 2002), or 5) an interaction between intrinsic and extrinsic factors (Jetz et al. 2008). *Euphonia* seems to be an exception to the general pattern, whose study could help to understand the factors influencing clutch size in birds. It would be important to study food availability and seasonal variation, predation rate, and adult survival in *Euphonia* to understand if these parameters also depart from the latitudinal pattern observed in other birds. It should be noted that both *E. pectoralis* (mean clutch size 2.8 eggs) and *E. chlorotica* (mean clutch size 2.1 eggs) occur at the southern range limit of euphonias and of purely fruit-eating birds (Nores et al. 2005). With increasing latitude (away from the tropics), the availability and stability of fruits as a resource declines (Snow 1981), possibly limiting both distribution and clutch size of *Euphonia* and other frugivores.

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