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Original paper

Nesting behavior of the Elegant Euphonia (*Euphonia elegantissima*, Aves: Fringillidae) in urban and suburban sites of east Mexico

Conducta de anidación del monjito (*Euphonia elegantissima*, Aves: Fringillidae) en sitios urbanos y suburbanos del este de México

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ABSTRACT. Between 2005, 2014–2017, we studied six Elegant Euphonia (*Euphonia elegantissima*) nests from two sites (urban and suburban) in the city of Xalapa, Veracruz. They were located in a macadamia tree crown, under epiphytic bromeliads, and under hanging fern and *Euphorbia* pots. The two nests we extracted and measured (7.2 x 7.5 x 5.6 cm; 10.1 x 8.6 x 11 cm), were closed and globular, with a lateral entry and mainly made of plant fibers, leaves, and cobwebs. Our observations included nest construction, egg incubation and chick care (nestling phase). Nest construction took at least 10–11 days, while egg incubation took 14–18 days. Incubation was done by the female in all but one observation, and the male escorted the female to the nest on every occasion. Time of incubation sessions ranged from 36–88 min (mean = 62 min) with shorter out nest sessions (3–18 min, mean = 9 min). There were three eggs in two of the nests, and in one only two eggs hatched; four chicks were observed in another nest. The nestling phase lasted 20 days in two nests, with the male spending more time (35–300 s, mean = 109 s) than the female taking care of the chicks (25–99 s, mean = 53 s). Reciprocal escorting was observed during the nestling phase, with the male always arriving first. Breeding occurred in January, April, May (two nests), June, and July. Observing the



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male of the Elegant Euphonia escorting the female during the incubation period, corroborates previous observations of this behavior in genera *Euphonia* and *Chlorophonia*. Incubation and nestling time periods were similar to other species of these genera.

Key words: egg incubation; escort behavior; fledgling; nests; tropical birds

RESUMEN. Durante los años 2005, 2014–2017, estudiamos seis nidos del monjito (*Euphonia elegantissima*) en dos sitios urbanos y suburbanos de la ciudad de Xalapa. Los nidos se localizaron en la punta de un árbol de macadamia, debajo de bromelias epífitas y debajo de macetas colgantes con helechos o euforbiáceas. Los dos nidos que fueron colectados fueron cerrados y esféricos (7.2 x 7.5 x 5.6 cm; 10.1 x 8.6 x 11 cm), con una entrada lateral y estuvieron fabricados principalmente de fibras vegetales, hojas y telarañas. Las observaciones incluyeron la construcción del nido, la incubación de los huevos y el cuidado de los polluelos. La construcción de los nidos tardó al menos entre 10 y 11 días. La incubación de los huevos duró entre 14 y 18 días. En todos los casos con excepción de uno, la incubación fue hecha por la hembra y en todas las observaciones el macho escoltó a la hembra al nido. El tiempo de incubación por sesión fue de 36–88 min (media = 62 min) con sesiones fuera del nido más cortas (3–18 min, media = 9 min). En dos nidos se encontraron tres huevos, en uno de los cuales sólo dos huevos eclosionaron; en otro nido se observaron cuatro polluelos. En dos nidos la fase de polluelos duró lo mismo, 20 días, presentando los machos un mayor tiempo de cuidado de los polluelos (35–300 s, media = 109 s) que las hembras (25–99 s, media = 53 s). Se observó una escolta recíproca durante la fase de polluelos, siendo el macho el primero en llegar siempre. La reproducción ocurrió en los meses de enero, abril, mayo (dos nidos), junio y julio. Al registrarse para el monjito la escolta de la hembra por el macho durante la fase de incubación, se corroboran observaciones previas en los géneros *Euphonia* y *Chlorophonia*. Los tiempos observados para las fases de incubación y polluelos fueron similares a valores previamente publicados para las especies de ambos géneros.

Palabras clave: incubación de huevos; conducta de escolta; empollamiento; nidos; aves tropicales

INTRODUCTION

Formerly considered part of the family Thraupidae, Neotropical bird genera *Euphonia* and *Chlorophonia* are now within the family Fringillidae (Donsker & Rasmussen, 2019); some authors even propose to include them in their own subfamily, Euphoniinae (Zuccon *et al.*, 2012). Recently, Imfeld *et al.* (2020) clearly showed that the blue hooded group of *Euphonia* species, are more related to *Chlorophonia* than to the extant *Euphonia* species. Both genera share two main behavioral and physiological characteristics: i) a closed dome nest and ii) a simplified digestive system adapted to feed mainly on mistletoe fruits (Isler & Isler, 1999; Hilty, 2011). Apparently, their fruit diet has conditioned a series of breeding modifications aimed at protecting eggs and chicks that, compared to tanagers, develop at a much slower pace. Although this particular breeding system has been documented for some species of both genera, and a renewed interest has recently emerged (Perrella *et al.*, 2017; Wright *et al.*, 2017; Di Sallo *et al.*, 2019), there is still a dearth of knowledge in several species regarding breeding behavior.

Of the 27 recognized species of *Euphonia* (Hilty, 2020; Imfeld *et al.*, 2020), Mexico harbors five species, being Elegant Euphonia [*Euphonia elegantissima* (Bonaparte, 1838)] the third most common species with *ca.* 7,550 records from 23 states, obtained in the Trans-volcanic Mountain System, the Sierras Madre Oriental and Occidental, and the mountains of Oaxaca and Chiapas (GBIF, 2019). Its altitudinal range is 1,000–2,500 m a.s.l. The species is also known as Blue-hooded Euphonia or Elegant/Blue-rumped Euphonia and is a small bird (10 cm) with a clear color sexual dimorphism (Hilty, 2011; 2020), the male having an easily recognized orange chest.

The Elegant Euphonia has three subspecies distributed in Central American mountains and in Mexico's west and central highlands (Hilty, 2011; 2020): *E. elegantissima elegantissima*, *E. elegantissima rileyi* (van Rossem, 1942) and *E. elegantissima vincens* Hartert, E, 1913.

Notwithstanding the amount of records and observations, including descriptions and location of some nests (Sclater, 1859; Robins & Heed, 1951; Blake, 1956; Stiles & Skutch, 1989; Table 1), there is still little information on the natural history and nesting behavior of this species.

This study reports our observations on some Elegant Euphonia couples (corresponding by its distribution to the subspecies *elegantissima*) observed during nest construction, egg incubation and chick care. We also include a description of their nests and photographs of adults, nests, chicks, and escorting behavior. These observations were conducted in urban and suburban places near cloud forests remnants, where tree infestation by mistletoe (*Psittacanthus schiedeana*) has increased in recent years. Our aim was to obtain more data on their breeding system and to compare our records with other *Euphonia* and *Chlorophonia* species that have been more thoroughly investigated.

MATERIALS AND METHODS

Observations were carried out during 2005, 2014, 2015, and 2017 at two sites in the city of Xalapa, state of Veracruz, Mexico.

Sites

U-Urban: In the backyard of a house located in a small southeastern canyon, SW oriented and facing towards the forests of Coapexpan in the foothills of the Cofre de Perote volcano. The site is highly urbanized although close to the SW limit of the city, so that it faces remnant patches of disturbed cloud forest (19° 31' 48.01" N, 96° 56' 12.78" W, 1,387 m a.s.l.). One nest observed.

SB- Suburban: On a southern-oriented porch of a house located in Xalapa's suburbs; the house is still surrounded by patches of low to highly disturbed cloud forest (19° 32' 20" N, 96° 56' 52" W, 1,413 m a.s.l.). Five nests observed. Both sites were located above low hills.

Observations

Site U. Nest U1. Observations covered 27 days, from 19 April to 16 May 2014. However, detailed, systematic sightings did not begin until 27 April. They were generally carried out from 06:00 to 10:00 (CST), but not every day; some sightings took place in the afternoon. All observations were

made at a distance of 8 m from the nest and 1 m above it. Photographs and videos were made with a Fuji digital camera (Finepix Z110). Low-quality photographs were improved using Microsoft office 2010 tools for images. Several low-quality videos of escorting behavior were recorded. Detailed observations covered a total of 23.3 hours along the period of observations. On average, duration of observation sessions in this nest was 40.18 min (SD 31.3, $n = 54$).

Site SB. Observations of perched birds were made at a distance of c. 6 m, whereas nests were observed at 3–4 m and, when parents were out, at a distance of under 50 cm. Photographs and videos were obtained with Canon and Sony digital cameras (models PowerShot SX510 Hs and DSC-H50, respectively). Five nests were observed in different years:

Nest SB1. Only observations of a nest carried out in the month of January, 2005; no further activities recorded.

Nest SB2. Another nest occasionally observed in June–July, 2014.

Nest SB3. Observations included nest construction, incubation, and chick care; the most detailed records corresponded to the nestling phase. The observation period covered 48 days, from March 28 to May 15, 2015, until chicks left the nest. Of the 27 sessions, 35% were taken before noon (06:20–10:30) and 65% in the afternoon (11:30–18:00).

Nest SB4. Intermittent records of construction, egg incubation and the nestling phase were obtained during March and April, 2017.

Nest SB5. In the same place of former nest; some aspects of incubation and nestling were observed during May and June, 2017.

RESULTS

Structure and location of nests

Nest U1. On 19 April 2014, we realized that an *E. elegantissima* female (Fig. 1A) and male (Fig. 1B) were constructing their nest on a fork of the tallest *Macadamia integrifolia* branches (Fig. 1C). We observed that both male and female contributed to nest construction by transporting thin organic fibers, and both genders entered to the nest. The nest was like a concave bowl, roofed with dead and live *M. integrifolia* leaves, with a lateral entrance and an internal diameter of 5.5 cm (Fig. 1D; Table 1); externally, the nest had a more elliptical shape of 7.2 x 7.5 cm. At the center, the nest measured 5.6 cm in height, but as the roof was slightly sloping, it measured 5.7 cm on one side and 5.5 on the other. The entrance, located 3.2 cm from the floor, was 4.5 cm wide and 2 cm high. The internal walls consisted of thin plant fibers or even plastic threads no more than 0.5 mm thick; there were two layers of these fibers, one tightly cemented and the other made of looser threads. Externally, the nest consisted of organic debris and twigs captured by a cobweb. This cobweb also trapped and fixed the roof leaves and completely covered all external nest; only the entrance was left free (Fig. 1E). After removing this nest and examined it at night, we found no less than 50 tiny, live spiders of the genus *Metepeira*, probably recently emerged from an egg sac. We assume that the cobweb belonged to this spider species. The nest was supported by a fork of five *M. integrifolia* branches, at a height of 5 m aboveground, on the south side of an east-west oriented canyon, now full of houses. The nest entrance faced away from the slope. Following the terminology of Simon & Pacheco (2005), it was a closed-globular-fork nest.

Nest SB1. On 23 January 2005, a nest was observed under the epiphyte bromeliad *Tillandsia usneoides* (Spanish moss) growing over oak *Quercus germana*, in a house next to site 2.

Nest SB2. During June and July of 2014, we observed in site 2 a nest under the hanging pot cultivated plant *Acalypha reptans* (Euphorbiaceae).

Nest SB3. During the months of April and May of 2015, we observed an *E. elegantissima* couple at site 2 (Fig. 2A) nesting under the sword fern *Nephrolepis exaltata*, planted in a hanging pot (Fig. 2B, Table 1). Nest material consisted mainly of roots, very thin and blackish in the internal lining and wider and brown on the exterior, white cotton-like fibers, big and small leaves, and other organic debris externally cemented with cobwebs (Fig. 2C, D). The nest was like a concave bowl, with a lateral entrance and with an internal diameter of 4.5 cm. Externally, it measured 10.1 cm long, 11 cm high and 8.6 cm wide. The nest was 1.9 m above the porch and 4.8 m above the garden floor. It corresponded to a closed-globular-base nest (Simon & Pacheco, 2005).

Nest SB4. During March and April of 2017, a couple was observed in the same site where couples had appeared in previous years. Their nest was also under a sword fern (*Nephrolepis exaltata*) growing in a hanging pot only 3.5 m from nest SB3.

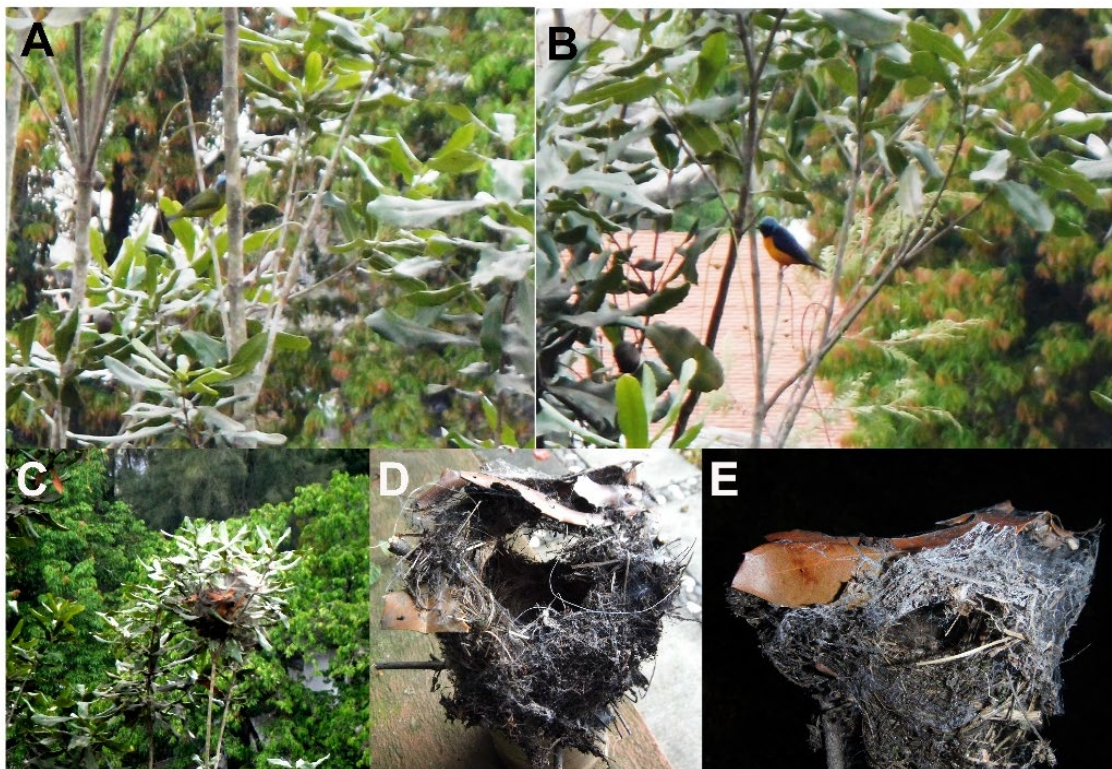


Figure 1. *E. elegantissima* female (A) and male (B) observed close to their nest, perching on a macadamia nut tree (*Macadamia integrifolia*) in the environs of the city of Xalapa (urban site U). C) Nest U1 located between *M. integrifolia* branches and leaves. D) Supra-posterior view of nest U1; small *M. integrifolia* branches and leaves removed to show their structure. E) Frontal view of nest U1 showing the entry and the cobweb that joined roof leaves. Photographer: C. Fragoso.

Nest SB5. Corresponds to nest SB4 that was occupied again, only 48 days after the juveniles' flight and quite probably by the same couple.



Figure 2. A) *E. elegantissima* female and male observed during the nestling phase, perching on a *Euphorbia cotinifolia* shrub at suburban site SB (April 2015). B) Nest SB3 constructed by this couple under hanging potted fern *Nephrolepis exaltata*, showing lateral entrance. C) Supra-posterior view of SB3 extracted nest. D) Superior view of the same nest after roof removal, showing an injured egg that never hatched. Photographers: C. Fragoso (A) and V. Sosa (B-D).

Nest construction

Nest U1. The first confirmed observation of nest construction was made on 19 April 2014, although the birds were seen fluttering around the tree five days before. Both male and female were observed alternatively entering the nest (Fig. 3A), always with thin threads of some material in their beaks. They displayed the same behavior throughout the day until 24 April. It can be assumed that nest construction took at least six days, but probably closer to eleven (Table 2).

Nest SB3. The male and female were first observed to begin nest construction on 28 March 2015, and practically finishing it by the following day.

Nest SB4. The couple was first observed on 11 February 2017 (Fig. 6A). On 6 and 9 March, the male and female were observed constructing the nest, with almost the same amount of time spent in it (male 27, 30 s; female 25 s). On 10, 11 and 12 March, we observed the male and female taking turns entering the nest, the construction of which lasted at least 10 days (Table 2).

Table 1. Data on nests, eggs, and breeding dates of Elegant Euphonia (*E. elegantissima*) obtained in this (Xalapa, Veracruz, Mexico) and other studies.

Location and Reference	Nest ublication	Nest shape and materials	Nest size	No. and size of eggs	Breeding dates
Joya de Salas, Tamaulipas (1,760 m asl), Mexico Robins and Heed (1951)	One over leafage of an oak branch, 6.6 m height; others in Spanish moss	Made of plant fibers and pine needles	-----	-----	March, May
Volcan de Chiriqui (1,800 m asl), Panama Blake (1956)	In the crown of a tree, 5 m above ground	Pouch-shaped cup made of green moss	10.1 x 8.9 x 12.7 cm, 7.6 cm in depth but only 2.5 cm in diameter at the rim	2; spheroidal and thickly dotted. Size: 1.76 x 1.38 and 1.8 x 1.4 cm	May
Costa Rica Stiles & Skutch (1989)	In a niche on a vertical bank (2 m); hidden amid green moss, <i>Tillandsia</i> and other epiphytes, or in tree crotch, (5–18 m height)	Globular, side entrance, finely woven of slender rootlets and dry grass stems, lined with finer grasses	-----	3, with reddish-brown spots	April
Juquila, Oaxaca, Mexico Sclater (1859)	-----	-----	-----	Rounded, creamy with scattered brown spots and blotches. Size: 1.6 x 1.3 cm	May
Xalapa. U1	Over a fork of <i>M. integrifolia</i> branches; 5 m above ground; south side of an east-west oriented canyon	Concave bowl, lateral entry. Made of <i>M. integrifolia</i> leaves and thin fibers of plants and plastic threads. Externally with organic debris and twigs captured by cobwebs	7.2 x 7.5 x 5.6 cm; internal diameter (i.d.) 5.5 cm; lateral entry (l.e.) 4.5 cm	-----	April-May
Xalapa. SB1	Under bromeliad <i>T. usneoides</i> growing on <i>Q. germana</i>				January
Xalapa. SB2	Under plant <i>A. reptans</i>			4 (Chicks)	June-July

Location and Reference	Nest ublication	Nest shape and materials	Nest size	No. and size of eggs	Breeding dates
Xalapa. SB3	Under fern <i>N. exaltata</i>	Concave bowl, lateral entry. Made mainly of roots. Roofed with silky seeds and coiled small fiber threads	10.1 x 8.6 x 11 cm; i.d. 4.47 cm; l.e. 5.3 cm	3, spheroidal, creamy with scattered brown spots. Size: 1.8 x 1.3 cm	April-May
Xalapa. SB4	Under fern <i>N. exaltata</i>			3	March-April
Xalapa. SB5	Under fern <i>N. exaltata</i>			3	May-June

Eggs Incubation (Table 2)

Nest U1. As of 24 April 2014, two different behaviors were recognized. The first was observed over three days once nest construction was finished. During this period, the female remained in the nest for a few minutes: 2, 4, and 5 minutes in two morning observations, from 06:35–07:35, and one in the afternoon at 17:50. We also observed the male escorting the female (Fig. 3B; Supplementaryvideo2), and in one of three observations, the female returned to the tree only 30 seconds after leaving the nest. This behavior probably corresponds to the female's egg-laying period.



Figure 3. A) *E. elegantissima* female observed flying towards nest entry while the male is perched below (nest U1 construction phase); the nest is on a macadamia nut tree (*Macadamia integrifolia*) five-branch fork. B) The same female flying towards nest, closely followed (escorted) by male (nest U1 incubation phase). In both figures, the female is within a black ellipse. Photographer: C. Fragoso.

Table 2. Summary of nest construction, incubation, and nestling behavior data recorded in the studied nests of Elegant Euphonia (*E. elegantissima*).

		Studied Nests	
		UI	SB3, SB4
Nests	Time of building (days)	At least 11	10
Incubation	Total time (days)	11	18, 14
	Duration of sessions (min)	36–88, mean = 61.8 (n=19)	-----
	Duration of recess (min)	3–18, mean = 8.7 (n=23)	-----
	% of time incubating ((total sessions min/total recess min + total sessions min) *100))	85.6	-----
	Incubating gender	Female (100%)	Female; male?
	Female escorted by male	Yes, 100% of 27 female entries	-----
Nestling	Total time (days)	Failed, apparently due to predation	20, 20
	Male sessions time (sec)	-----	35–300, mean = 109 (n=9)
	Female sessions time (sec)	-----	25–99, mean = 52.6 (n=7)
	Gender reciprocal escorting	-----	Yes, male always arrived first
	Total time (incubation + nestling; days)	-----	38, 34

The second type of behavior occurred from 28 April to 8 May 2014 (11 days) and was recorded in greater detail. The main observed aspects were as follows: i) The male and female arrived together and perched on tree branches for a few seconds before the female entered the nest. We were unable to clearly recognize which of the two arrived first, so we considered their arrival simultaneously. Once in the tree, both male and female jumped from branch to branch, getting closer to the nest with each jump (Supplementaryvideo1). The female was always above the male and closer to the nest. On average, both birds remained on the branches for 23.6 seconds (SE = 1.96 s, range = 7–45 s, N = 27). ii) The male escorted the female to the nest (Fig. 3B; Supplementaryvideo1 and Supplementaryvideo2). This behavior was observed on 27 occasions, whenever the two birds arrived together. By reviewing video recordings, it was clear that the female always flew towards the nest first and was closely followed by the male that, once the female entered, stopped in front of nest entrance, and then returned to tree branches. When flying together, the male's bright yellow chest was more conspicuous than the female's colors (Fig. 3B). iii) Only the female entered the nest. iv) After escorting the female to the nest, the male remained in the tree for less than a minute (mean = 23.8 s, SE = 3.39 s, range = 5–40 s, N = 16). v) The female remained in the nest an average of 61.8 min (SE = 3.24 min, range = 36–88 min, N = 19). vi) The female left the nest flying down the tree very quickly and then far away towards the forest at the

other side of the canyon. vii) On average, the female returned to the nest 8.7 minutes after leaving it (SE = 0.80 min, range = 3.4–18 min, N = 23).

Nest SB3. After 10 days without observations, the female was seen entering the nest on 9 April 2015. Two days later (15 days after nest construction had begun) three eggs were found (ca. 1.5 cm long, two whitish and one a spotted sandy color). On 21 April just before noon, the male was observed within the nest incubating the eggs. On 23 April, the three eggs were still there; at 9 am the next morning, two chicks were observed. Thus, egg incubation lasted at most 16 days. In this nest, one egg (the spotted sandy colored one) (Fig. 2D) never hatched and was left in nest after the two chicks had flown away. This egg was found fixed to the floor and ventrally broken; it measured 1.8 cm long x 1.3 cm wide.

Nest SB4. On 16 March 2017, one egg was observed in this nest; two days later (March 18), the number of eggs had increased to three (probably laid on three consecutive days). On 22 March, the female entered the nest to brood the three eggs; the same behavior was recorded on 30 March. Chicks were first seen on 2 April; egg incubation took place over 17 days.

Nest SB5. On 20 May 2017, the female was observed incubating three eggs; on May 24, that was still the case.

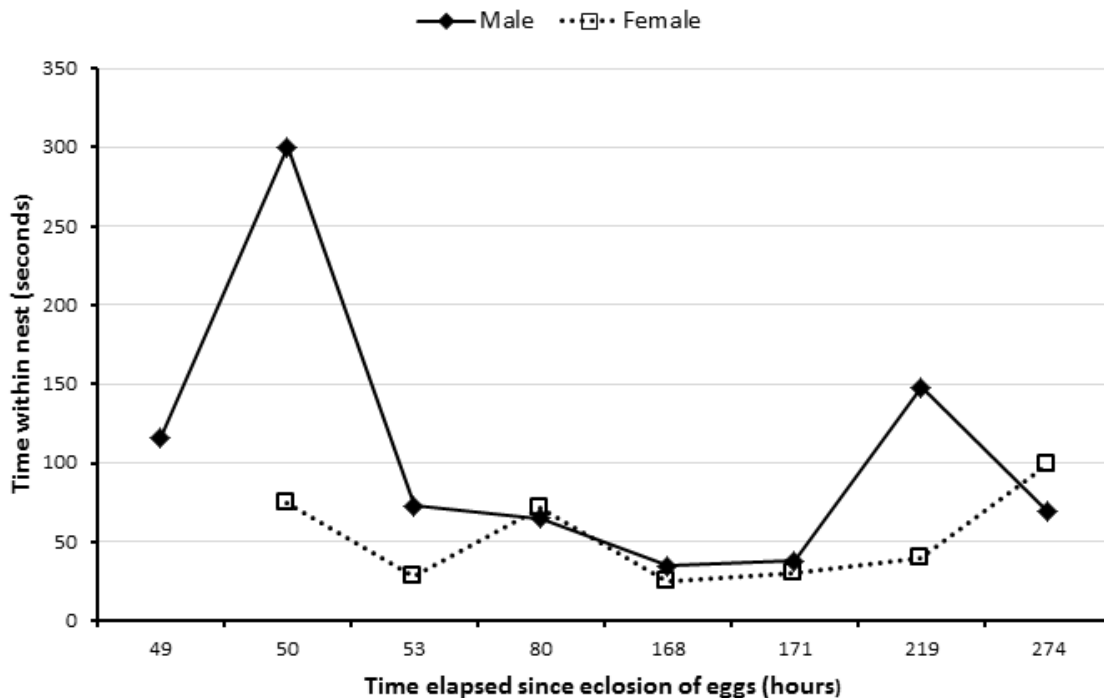


Figure 4. Variation of time spent by *E. elegantissima* male and female within nest in function of the time elapsed since egg eclosion (nestling phase; nest SB3, April 2015).

Chick brooding and feeding (Table 2)

Nest SB2. Four chicks were observed in July 2014 (Fig. 5A).

Nest SB3. Throughout the day of 25 April 2015, the two parents alternated visits to the nest, the male always visiting first. Apparently, the male performed no brooding and only fed chicks: in all observations, rather than entering the nest it remained perched near the entrance. Escorting behavior was observed in both parents, either when the female visited the nest (escorted by the male; Supplementaryvideo3) or vice versa (Supplementaryvideo4). Both parents perched in neighboring trees and plants before visiting the nest. The following behavior occurred several times (27 april-1 may): the male perched on a tree vocalizing and pecking at a twig several times during 20–30 s, until the female arrived and, once quite close to him, made a fluttering. After that, the female flew to another tree and the male repeated the “twig pecking” behavior three times; then the female returned and fluttering again. The couple then flew to the nest; the male entered first being replaced by the female after a few seconds. Once the female left the nest, both parents flew away.



Figure 5. *E. elegantissima* altricial chicks. A) Four chicks from nest SB2 (July 2014) constructed under hanging potted *Acalipha reptans*. B-D) Two chicks from nest SB3 (April 2015) built under the hanging potted sword fern *Nephrolepis exaltata*, of three (B), nine (C), and ten (D) days old. Photographer: V. Sosa.

On average, the male spent more time in the nest (mean = 109 s, range = 35–300 s, N = 9) than the female (mean = 52.6 s, range = 25–99 s, N = 7), although differences were not significant (t-test, $P = 0.10$). When time in nests was related to the time elapsed since hatching (Fig. 4), a reduction in nest time was observed in both the male and the female after two days (50 hours), with a recovery in both genders after 7 days (171 hours). Although three eggs were laid, only two chicks were observed throughout the nestling phase (Fig. 5B, C, D). Three days after hatching, two chicks with down were observed (Fig. 5B). They began to develop feathers after nine days (Fig. 5C, D). On 15 May the nest was empty. In summary: i) Both, male and female cared for chicks, feeding them while standing outside the nest at its entrance. ii) Escort to the nest during feeding was done by both genders, the male always flying first. iii) On average, the male spent more time in the nest than female (Fig. 4). iv) Feeding and brooding of chicks lasted 21 days.



Figure 6. Suburban nest SB4. A) Male and female perched close to the nest. B) Female escorting male during a visit to the nest to feed chicks. Photographer: Melisa Sosa.

Nest SB4. The first observation of three chicks took place on 2 April 2017. On 8 April, chicks still had closed eyes and were covered with grey down; by 13 April they had opened their eyes. The same day, we observed the female escorting the male (Fig. 6B). On 16 April, chicks had almost all their feathers. Two of the chicks flew away on 20 April, while the last one abandoned the nest on 21 April at almost noon. Feeding and brooding of chicks lasted 19 days.

Nest SB5. At midday of 1 June 2017, the female was observed within the nest brooding; five hours later (16:40), a chick and two eggs were observed. Seven days later (7 June) only one chick was observed; the two extant eggs never hatched. On 12 June, the single chick had feathers; it abandoned the nest, sometime between June 17–19.

DISCUSSION

Information about nests and nesting behavior is patchy for most *Euphonia* and *Chlorophonia* species, with quantitative data on incubation and nestling behavior absent in nearly half of the species (Supplementarytable1).

With the Elegant Euphonia (*E. elegantissima*) data presented in this study, the number of species with qualitative and quantitative data on nest construction, incubation, and nestling behavior in *Euphonia* and *Chlorophonia* genera increases to 14 (twelve *Euphonia* and two *Chlorophonia*; Supplementarytable2).

Data from this study support previous observations of Elegant Euphonia regarding how the male escorts the female during nestling and about the number of eggs laid; it adds new information on nest shape, measurement, and location (Table 1). Its main contributions, however, relate to quantitative recorded data on the frequency with which the male escorts the female and the time she spends incubating, away from her nest, and perched outside the nest before entering it. Additional observations indicate that during nestling, both genders feed chicks, although the male allocates slightly more time than female, and that escort is performed by both male and female during nestling.

Nests

As observed in the majority of *Euphonia* species (Isler & Isler, 1999; Hilty, 2011) and formerly recorded for the Elegant Euphonia (Robins & Heed, 1951; Stiles & Skutch, 1989), the two extracted and detailed observed nests (U1, SB3) were domed with a lateral entry (i.e. close-globular). Four of the observed nests in Site SB were built on the roots of epiphyte plants (ferns and bromeliads), a common pattern observed in several Euphonias (Isler & Isler, 1999). The measurements of nest SB3 are comparable to those of the only nest with measures (recorded in Panama; Blake, 1956; Table 1); size of U1 nest, being constructed on the fork of a tree tip branch, was smaller. The leaves of U1 nest roof were bound with cobwebs, whereas in SB3 nest, cobwebs were used on the outside to fix twigs and cotton-like fibers. In the first case, spiders apparently joined leaves to make their own nests, and that birds took advantage of this to do the same. Cobweb use by *Euphonia* and *Chlorophonia* species in nest construction has been recorded in Yellow-throated Euphonia (*Euphonia hirundinacea* Bonaparte, 1838), Yellow-crowned Euphonia [*E. luteicapilla*, (Cabanis,

1861]], Blue-crowned Chlorophonia [*Chlorophonia occipitalis* (du Bus de Gisignies, 1847)] (Skutch, 1954), White-vented Euphonia (*Euphonia minuta* Cabanis, 1849), Spot-crowned Euphonia [*E. imitans* (Hellmayr, 1936)] (Skutch, 1972), and Purple-throated Euphonia [*E. chlorotica* (Linnaeus, 1766)] (Perrella *et al.*, 2017) but never in the Elegant Euphonia (*E. elegantissima*); in all these nest descriptions, cobwebs were carried to the nests by parents. As we did not begin observing the construction of nest U1 until the birds had almost finished it, we failed to see whether or not cobwebs were carried to the nest to use in its construction; it could be that birds simply take advantage of spiders' nests. Considering that no adult spiders were found, their identification (genus *Metepeira*) was accomplished with juveniles. Nests constructed using the cobweb of an active spider nest has not been recorded before in *Euphonia* or *Chlorophonia* and has barely been recorded in other birds (e.g. in the African bird of prey *Micronisus gabar*, Henschel *et al.*, 1991).

Ridgely (in Volcán de Chiriqui, Panamá, quoted in Wetmore *et al.*, 1984) mentioned that in nest construction, the Elegant Euphonia female always preceded the male, something that we were unable to corroborate.

Egg laying

Previous records indicated that Elegant Euphonia laid between 2–3 eggs (Table 1), which was similar to the three eggs observed in SB3, SB4 and SB5 nests. The four chicks recorded in SB2 are comparable to records of other species of this genus where variability in egg number has been observed, i.e. Purple-throated Euphonia (*E. chlorotica*) 3–5 eggs, Trinidad Euphonia (*Euphonia trinitatis* Strickland, 1851) 3–4, Violaceous Euphonia [*Euphonia violaceae* (Linnaeus, 1758)] 3–5, Thick-billed Euphonia (*Euphonia lanirostris* (d'Orbigny and Lafresnaye, 1837) 2–5, Olive-backed Euphonia (*Euphonia gouldi* Sclater, 1857) 2–4, Golden-sided Euphonia [*Euphonia cayennensis* (J.F. Gmelin, 1789)] 3–5, Jamaican Euphonia [*Euphonia jamaica* (Linnaeus, 1766)] 3–4, Yellow-crowned Euphonia (*E. luteicapilla*) 2–4, White-vented Euphonia (*E. minuta*) 3–5, Chestnut-bellied Euphonia [*Euphonia pectoralis* (Latham, 1801)] 2–3 and Golden-rumped Euphonia [*Euphonia cyanocephala* (Vieillot, 1819)] 2–3 (Isler & Isler, 1999; Hilty, 2011; 2020; Wright *et al.*, 2017; Di Sallo *et al.*, 2019). The laying of one egg per day presumably observed for nests SB4 and SB3 has been recorded previously for other *Euphonia* species, e.g. Yellow-crowned Euphonia (*E. luteicapilla*) (Skutch, 1954) and Yellow-throated Euphonia (*E. hirundinacea*) (Sargent, 1993) in Costa Rica, Thick-billed Euphonia (*E. lanirostris*) in Panama (Isler & Isler, 1999), and Chestnut-bellied Euphonia (*E. pectoralis*) in Argentina (Di Sallo *et al.*, 2019). Also, the non-hatching of one (nest SB4) or two (SB6) of the three laid eggs has been recorded in the Golden-rumped Euphonia (*E. cyanocephala*) (Wright *et al.*, 2017) and Chestnut-bellied Euphonia (*E. pectoralis*) (Di Sallo *et al.*, 2019), respectively.

Egg incubation behavior

In our observations, males were consistently seen escorting females during egg incubation. This behavior has been previously recorded in Golden-browed Chlorophonia [*Chlorophonia callophrys* (Cabanis, 1861)] (Skutch, 1954) and six other *Euphonia* species: Golden-rumped Euphonia (*E. cyanocephala*), Yellow-throated Euphonia (*E. hirundinacea*), Spot-crowned Euphonia (*E. imitans*), Yellow-crowned Euphonia (*E. luteicapilla*), White-vented Euphonia (*E. minuta*) and Orange-bellied Euphonia (*E. xanthogaster* Sundevall, 1834) (Sutton *et al.*, 1950; Skutch, 1954; 1972; Sargent, 1993; Cisneros-Heredia, 2006; Wright *et al.*, 2017) (Supplementarytable2). It could be that the behavior

observed by Ridgely (quoted in Wetmore *et al.*, 1984) during Elegant Euphonia nest construction, actually corresponded to egg incubation, as we observed no escorting during the construction of nest U1 (Fig. 3A). For the other species (21 *Euphonia* and four *Chlorophonia*) such male escorting has not yet been recorded, although it is likely present in all the species of both genera. Such escorting has been called “flybys” (Wright *et al.*, 2017) or, more generally “coordinate misdirection behavior”, CMB (Gulson-Castillo *et al.*, 2018). These authors recognized a general behavioral pattern in which both adults perch close to the nest, fly together towards it, but only one enters the nest while the other loops in flight and returns to the perch site. Two variants of this behavior are recognized: CMB1) As both birds fly towards the nest (sometimes departing from the same site), one enters the nest whereas the other stops their flight in front of nest entrance, obscuring the entry of the other gender, and changes direction to return to its perch site; CMB2) The bird which did not enter nest abruptly changes its direction when it is halfway to the nest. During incubation, CMB1 was observed in 13 of the 14 observations (93%); the only time when escorting did not occur was due to the fact that the male never appeared, and the female entered the nest alone. When both birds were more or less close to each other (85% of observations), the female always flew first, followed by the male; only on two occasions, when both genders were separated by a distance of more than one meter, the male did fly in front.

Our observations of nest U1 also confirm that incubation in Elegant Euphonia (*E. elegantissima*), as in other *Euphonia* and *Chlorophonia* species (Supplementarytable2) is carried out only by the female. The single observation of the male incubating in nest SB3 needs to be supported by further observations of other nests. Female-only incubation in *Chlorophonia* and *Euphonia* has been observed in Golden-browed Chlorophonia (*C. callophrys*), Golden-sided Euphonia (*E. cayennensis*), Purple-throated Euphonia (*E. chlorotica*), Golden-rumped Euphonia (*E. cyanocephala*), Yellow-throated Euphonia (*E. hirundinacea*), Spot-crowned Euphonia (*E. imitans*), Yellow-crowned Euphonia (*E. luteicapilla*), White-vented Euphonia (*E. minuta*), Trinidad Euphonia (*E. trinitatis*), and Violaceous Euphonia (*E. violaceae*) (Skutch, 1954, 1972; Sargent, 1993; Isler & Isler, 1999; Wright *et al.*, 2017); it is probably the common pattern for the other species as well. In our study, the percentage of time females spent incubating turned to be the highest recorded for this group of birds (85.6% of observed time within nest vs. 65–74.4% in the case of other *Euphonia* species; Supplementarytable2). Only in Chestnut-bellied Euphonia (*E. pectoralis*) have similar percentages been observed (82%, Di Sallo *et al.*, 2019). Whether this reflects a species difference or an individual pattern (as it was only observed in one nest, U1) should be determined by further observations of other Elegant Euphonia (*E. elegantissima*) couples from different locations (i.e. it could be due to the fact that *E. elegantissima* is located in the north limit of this genus distribution).

Chick feeding and brooding

After eggs hatch, parents take care of chicks by brooding and feeding. We were unable to clearly recognize which of these two activities were carried out within nests by each parent. Our observations, however, showed that the male never entered the nest, while the female did. Thus, quite probably males only feed chicks, whereas females feed and brood them. We also observed that males devoted more time than females to this activity, a pattern also observed in Yellow-throated Euphonia (*E. hirundinacea*) (Sargent, 1993) but not in White-vented Euphonia (*E. minuta*) (Skutch, 1972) nor Golden-rumped Euphonia (*E. cyanocephala*) (Wright *et al.*, 2017).

CMB behavior was also observed during this phase of chick care. In all recorded observations, parents approached the nest together and, after a few seconds, the male flew to the entry first followed by the female (Fig. 6B and Supplementaryvideo4). The male perched outside the nest, while the female stopped their flight at the entrance and returned to the perch site. After nearly a minute, the male left the nest and at the same time, the female flew towards it; when they met, the male stopped and returned to escort the female (Supplementaryvideo3). This behavior was observed on four occasions without variations. Thus, in Elegant Euphonia (*E. elegantissima*) only the male escorts during incubation, but during feeding and brooding both genders escort. More research is needed to determine if this is the typical pattern in all *Euphonia* and *Chlorophonia* species.

Duration of incubation and nestling

Recorded incubation times (14 days, SB4; 18 days SB3) and nestling times (20 days in both SB3 and SB4) are comparable to those observed in other species of the genus (Supplementarytable2). Observed times from egg laying to chick flight were 34, 38 days, very similar to times observed in all species of the genus (32–38 days; Supplementarytable2).

Although *Euphonia* is known to have a digestive system specialized to feed primarily on mistletoe and other fruits (see Hilty, 2011 for a detailed discussion), and that Elegant Euphonia (*E. elegantissima*) eats only fruits (mainly mistletoe, Hilty, 2011), it seems that some of these birds also consume insects. Isler & Isler (1999) and Hilty (2011) summarize information on the feeding habits of all *Euphonia* and *Chlorophonia* species, showing that only nine *Euphonia* species [Elegant Euphonia (*E. elegantissima*), Olive-backed Euphonia (*E. gouldi*), Jamaican Euphonia (*E. jamaica*), Thick-billed Euphonia (*E. lanirostris*), Antillean Euphonia (*Euphonia musica* (J.F. Gmelin, 1789)), Plumbeous Euphonia (*Euphonia plumbea* du Bus de Gisignies, 1855), Rufous-bellied Euphonia (*Euphonia rufiventris* (Vieillot, 1819)), Orange-crowned Euphonia (*Euphonia saturata* (Cabanis, 1861)) and Violaceous Euphonia (*E. violaceae*)] feed exclusively on fruits and seeds. In the case of the other *Euphonia* (18 species) and all *Chlorophonia* species it has been mentioned that they occasionally or “probably” feed on insects. The discovery of small spiders living in the cobweb of nest U1 (probably hatchlings from a spider sac) could be related to a close and high-energy food source to feed offspring. Spider consumption has been recorded in Green-throated Euphonia [*Euphonia chalybea* (Mikan, 1825)] (Bertoni, 1901: 101 “...recorre las ramas en busca de orugas, arañas, cogollos, etc.”), White-vented Euphonia (*E. minuta*) (Skutch, 1972: 182 “White-vented Euphonias seem to subsist on small insects and spiders to a greater extent than many of their congeners.”) and Orange-bellied Euphonia (*E. xanthogaster*) (Hilty, 2011: 296 “...noted also as picking insects and/or spiders (Araneae) from spiders webs...”). Moreover Thick-billed Euphonia (*E. lanirostris*) chicks in captivity were fed with live spiders, whereas in the case of Blue-crowned Chlorophonia (*C. occipitalis*) adults accepted spiders only as food (Isler & Isler, 1999). More research is needed on this and other *Euphonia* species with nests that contain cobwebs, with special attention paid to the use of insects and/or spiders as food.

The fact that of the six observed nests only urban nest U1 failed could be an indication that Elegant Euphonia (*E. elegantissima*) cannot breed successfully in urban zones, as it may depend

on urban green areas or suburban zones for reproduction. González-García *et al.* (2014) recorded the presence of Elegant Euphonia (*E. elegantissima*) and Yellow-throated Euphonia (*E. hirundinacea*) in four green urban areas (including the forests of Coapexpan, close to the two study sites) and one suburban area of Xalapa. It is thus clear that both species are common in the city; however, it remains to be seen if reproduction is common in all these areas or limited only to suburban regions. In this regard, the presence of urban predators (cats) at urban site U could have been a significant factor, as it has been previously documented (Bonnington *et al.*, 2013).

This study is another contribution to a renewed interest in the breeding characterization of *Euphonia* species (Perrella *et al.*, 2017; Wright *et al.*, 2017; Di Sallo *et al.*, 2019). We hope that this recent interest and the results of our study will promote future research on the breeding behavior and other little understood aspects of the peculiar *Euphonia* and *Chlorophonia* bird clades.

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