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Capa: Arapaçu-galinha (*Dendrexetastes rufifigula*), fotografado próximo a Manaus, Amazonas, Brasil. Nesse volume, Ferreira *et al.* apresentam uma revisão sistemática do arapaçu-galinha com base em caracteres moleculares. Os autores propõem o reconhecimento de duas espécies adicionais antes consideradas subespécies, *D. devillei* e *D. paraensis*, diagnosticáveis plenamente também por caracteres de plumagem. Autor da foto: Luiz Ribenboim (<http://www.wikiaves.com/1967950>).

Cover: Cinnamon-throated Woodcreeper (*Dendrexetastes rufifigula*) photographed near Manaus, Amazonas, Brazil. In this volume, Ferreira *et al.* present a systematic review of the Cinnamon-throated Woodcreeper based on molecular characters. The authors recommend the recognition of two additional species formerly regarded as subspecies, *D. devillei* e *D. paraensis*, which are also fully diagnosable by plumage characters. Photo author: Luiz Ribenboim (<http://www.wikiaves.com/1967950>).

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Black-collared Hawk *Busarellus nigricollis* in French Guiana: distribution, population size and breeding biology

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ABSTRACT: The Black-collared Hawk *Busarellus nigricollis* is widespread from southern Mexico throughout Central America and east of the Andes in South America. Although rather common in most of its distribution range, little is known about its breeding biology as nests are often built in inaccessible areas. The discovery in 2013 of four nests of this hawk in the coastal region of French Guiana, where it is found near brackish or fresh water in semi-open to open country, allowed us to increase our knowledge of its breeding behavior. The population is estimated at *c.* 200 pairs. Aerial displays of a breeding pair cover a large area around the nest tree. The nest is a large structure of sticks with a shallow cup lined with finer branches and a layer of twigs with leaves. It is mostly built at a height between 15 and 35 m, in the crown of an isolated tree or in a tree crown emerging above the surrounding vegetation. A single egg per nest is laid in French Guiana. The fledgling period for one nest was 55 days. Both male and female incubate and feed the nestling, although the female's share in both activities is more important. During the entire nesting period male and female add fresh twigs with leaves and to a lesser extent, fine dead branches to the nest.

KEY-WORDS: conservation, Neotropical raptor, reproduction biology, status.

INTRODUCTION

The Black-collared Hawk *Busarellus nigricollis* (Latham, 1790) is widespread from southern Mexico to northern Argentina and Uruguay, throughout Central America, northern Venezuela, the Guianas and Brazil, and east of the Andes in Colombia, Ecuador, Peru and Bolivia (Bierregaard-Jr. *et al.* 2016, GRIN 2015). It is a common resident of semi-open to open areas near brackish water (mangroves, tidal marshes) and near fresh water (wooded swamps, marshes, ricefields, dikes, ponds, pools), but also along forest-fringed creeks and rivers and on islands in rivers. It mostly occurs singly, or in pairs during the reproduction period (GRIN 2015). It mainly feeds on fish, but occasionally also on large aquatic insects, mollusks, crustaceans, toads, frogs, lizards, snakes, rodents, waterbird chicks and more rarely a juvenile caiman (Bierregaard-Jr. *et al.* 2016). When watching for prey, it perches low in bushes or trees along or over water. Although widespread, its breeding

biology is poorly known, maybe because it often breeds in extensive, inaccessible areas (mangroves, swampy savannas, tidal marshes) (Evangelista *et al.* 2012, GRIN 2015, Bierregaard-Jr. *et al.* 2016).

Breeding of *B. nigricollis* in French Guiana was first recorded by Tostain *et al.* (1992), reporting three observations of breeding behavior between 1984 and 1989: a pair with a juvenile (30 August 1984, marshes of Kaw, *c.* 04°29'N; 52°02'W), an occupied nest (1 July 1987, marshes of Malmanoury, *c.* 05°20'N; 52°47'W) and a displaying pair (30 April 1989, swampy savannas of Matiti, *c.* 05°07'N; 52°35'W). More recently, four breeding sites were recorded in the database Faune-Guyane (2015): the marshes of Panato (*c.* 05°45'N; 53°56'W), the marshes of Pripris de Yiyi (*c.* 05°27'N; 53°05'W), the swampy savannas of Matiti and the marshes of Leblond (*c.* 04°55'N; 52°20'W) (Figure 1). In this paper, we provide new information on the distribution, population size and breeding biology of Black-collared Hawk in French Guiana.

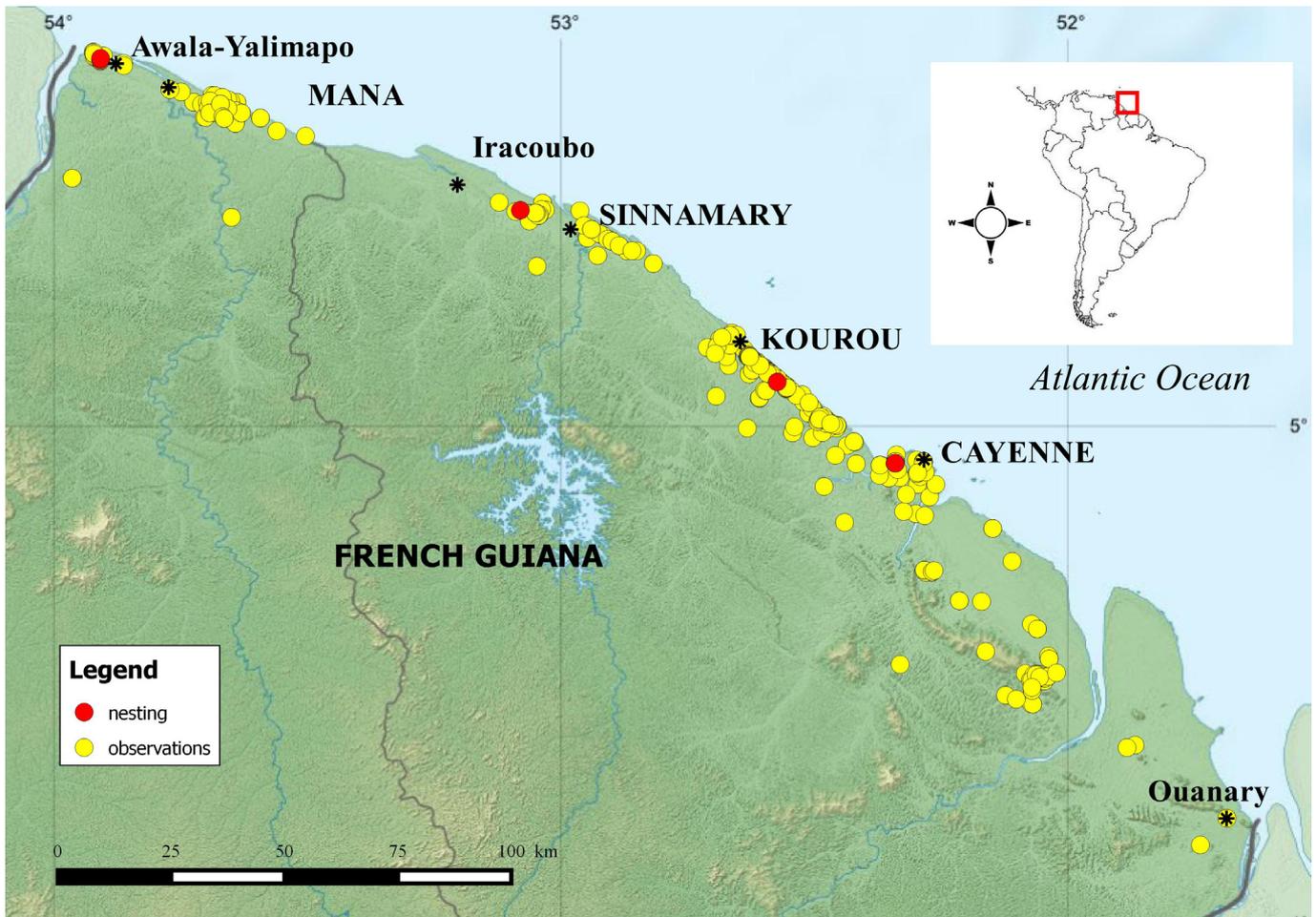


FIGURE 1. Map with distribution of Black-collared Hawk *Busarellus nigricollis* in French Guiana. Yellow dots: observations, red dots: nesting sites (from left to right): marshes of Panato, marshes of Pripris de Yiyi, swampy savannas of Matiti and marshes of Leblond. Nests 1, 2 and 3 were found near Kourou, and nest 4 near Cayenne. All records were obtained between 1984 and 2016.

METHODS

Distribution and population size

The GEPOG association (Groupe d'Étude et de Protection des Oiseaux en Guyane), involved in the study and conservation of French Guianan birds, has developed a citizen science tool, the database Faune-Guyane to report faunal observations by its members. The following data are noted for each observation: date, name of locality and its coordinates, number of individuals observed, behavior, and name of observer. Stored in this database are 815 observations of the Black-collared Hawk collected by birdwatchers and ornithologists between 1984 and 2016. These observations were used to describe its geographical distribution and to estimate the size of the population in French Guiana.

Breeding biology

The study of the behavior during the breeding season was conducted from January to October 2013 at four nests. The first study area was situated in the swampy savannas

of Matiti, also called pastures of Guatemala, because of the local cattle breeding activities. More precisely, the area is situated between road D13 and the RN1 near Guatemala, a landing stage on the right bank of the Kourou River, opposite of the town of Kourou. A survey was carried out in 2010 in the area by the consulting office Biotope in order to estimate the impact of a future sand extraction project of 48 ha on the local avifauna. During that survey, two active nests of *B. nigricollis* were discovered on the site (nest 1 and nest 2, Figure 1). In January 2013, after the opening of the sand quarry, nest 1 was found on the ground, while nest 2 was still on the tree. The distance between both nests was *c.* 450 m. A third nest (nest 3) was found in March 2013 by workers, and was located close to the sand quarry, *c.* 850 m from nest 2 and *c.* 1300 m from nest 1. A second study area was situated in the marshes of Leblond, near the capital Cayenne. Between 1 May and 3 August 2013, an active nest (nest 4) was visited six times by Gil Jacotot to note the presence or the absence of the adults and later of the nestling. For all four nests, we noted: height, dimensions and the species of the tree whenever possible.

From January 2013 on, the behavior of the breeding

pair of *B. nigricollis* was studied at nests 2 and 4. Aerial displays, courtship behavior and general activities were regularly observed with binoculars. This first monitoring was conducted to note the period of egg-laying and the movements of the breeding pair.

Nesting activities were filmed at nest 2 only, using a Panasonic UW-R36 waterproof camera, a MPEG4 PV-1000 format ASF-60 GB digital recorder, a 32 GB HC Class 4 memory card and a 12 V battery. All equipment was installed above the nest during the absence of the breeding pair in order to minimize disturbance. Batteries and memory card were changed once a week. Video recordings were triggered by the movements of the adults (arrival, departure, feeding activities) or by grooming movements of both adults and nestling, and were automatically stopped after 30 sec. During the day, the video sequences were filmed in black-and-white or in color, depending on light conditions. At night, the camera automatically switched to infrared mode.

RESULTS

Distribution and population size

In French Guiana, *B. nigricollis* seems mainly restricted to the coastal region, with rare observations at man-made ponds near inland localities such as Régina (04°19'N; 52°08'W) and Cacao (04°33'N; 52°30'W). Along the coast, *B. nigricollis* were observed at 56 different sites between Awala-Yalimapo (05°44'N; 53°56'W) and Ouanary (04°13'N; 51°40'W) (Figure 1) (Tostain *et al.* 1992, Faune-Guyane 2015). Assuming that one pair is nesting at each site, the population of *B. nigricollis* in French Guiana is at least 50 pairs.

Breeding biology

The four nest sites were quite similar. The nests were located on large trees like a Courbaril *Hymenaea courbaril* (nest 2) and a leafless Ceiba *Ceiba pentandra* (nest 3). They were built in the fork of secondary branches at a height between 15 and 35 m. They can be described as a *c.* 50 cm thick structure of dead branches with a diameter of *c.* 80 cm, and a shallow cup lined with finer material.

As nest 1 was found on the ground in 2013 and no aerial displays or nest building activities were observed, the nesting site was considered abandoned. Yet, nests 2, 3 and 4 were active in 2013.

Collecting data: A camera was installed on 29 June 2013 above nest 2, because it was the most accessible nest. From 29 June to the fledging of the nestling on 30 August 2013, 2618 video sequences were recorded, 1361 during the day and 1257 at night. Among those

2618 video sequences, 286 were collected during the incubation period (113 day and 173 night sequences) and 2332 during the nestling period (1248 day and 1084 night sequences). During the nestling period, video sequences on 19 days, from 3 to 8 August and from 17 to 29 August, were not recorded due to battery issues. Little information was provided by nightly video sequences except for the presence and sex of the adult on the nest.

Pre-breeding behavior: According to our observations in 2013, the pair of Black-collared Hawks of nest 2 first arrived in the area of the nest tree in March. The sex of the adults was distinguished by slight differences in color pattern and the size difference, the female being an estimated 20% larger and heavier, and having less and lighter black shaft streaks on the back than the male (Figure 2).



FIGURE 2. Pair of Black-collared Hawks *Busarellus nigricollis* on nest 2 with one egg (arrow). The female (left) is larger than the male (right), and has less and lighter black shaft streaks on the back. Photo taken on 6 July 2013.

During visits on 16 January, 22 February, 1 and 13 March and 11 April, no *B. nigricollis* were seen in the nest tree. However, on 1 and 13 March, display flights in the nesting area by a pair of *B. nigricollis* were observed by VP. The adults were flying high up in the air, following each other closely in undulating flights and dives, often while screaming. In May, observations were made indicating the beginning of courtship behavior: the presence of an

adult on the nest, a copulation on 7 May (Michel Giraud-Audine, pers. comm.) and a display flight above the nest tree on 11 May. Similar observations were reported at nest 4 in the marshes of Leblond. A pair was observed there on 1 and 11 May 2013 by Gil Jacotot (pers. comm.).

Incubation period: When the camera was installed at nest 2 on 29 June, one egg was found in the nest (Figure 3). At night, the egg was incubated by the female only. In the morning, the female was relieved by the male between 06:51 h at the earliest and 11:24 h at the latest. Change-overs happened twice to four times a day, with the incubating adult flying off just before the arrival of the other adult. Thus the egg was never left alone for extended periods.



FIGURE 3. Nest 2 with one egg of Black-collared Hawk *Busarellus nigricollis*. The nest is neatly lined with leafy twigs. Photo taken on 29 June 2013.

During nine days of the incubation period, 40 video sequences were triggered by the male and 50 by the female. During these nine days, no nuptial feeding of the female was observed. On 7 July, 30 min before the egg hatched, the female brought a fish to the nest. This prey was partly consumed by the female and the leftovers were eaten by the male, after which he resumed incubation. The nestling hatched at 16:45 h while the male was incubating and with the female standing next to him on the nest. After the egg hatched, the adults ate the egg shells and left the nest, leaving the nestling unprotected. However, only ten minutes later, the female returned to the nest and started to brood the nestling. It was not fed the day it hatched.

Similar observations were reported for nest 4. On 1 and 10 May, a pair of *B. nigricollis* was seen standing on the nest. On 23 June, an adult was observed sitting on the nest and appeared to be incubating.

Nestling period: At nest 2, the nestling period lasted 55 days between hatching of the egg (7 July) and fledging of the nestling (30 August). Among the 609 video sequences recorded from 7 July to 30 August in the nestling period of nest 2, 59 were triggered by the male

and 590 by the female. The video sequences triggered by the male were mostly associated with bringing food or leafed twigs and fine branches to the nest. During the entire nestling period, only the female was present on the nest at night. However, the male was probably sleeping in the nest tree. The nestling was never left alone at night, and until the age of 20 days (27 July), the female brooded it. Thereafter, she was still present on the nest but was usually sitting next to the nestling, preferably face to face with it. During hot sunny days, the female sometimes shaded the nestling, or the nestling itself moved into the shadow of the female. During rain showers, she stood close to the nestling or was even brooding it to protect it from the rain.

At nest 4 in the marshes of Leblond, the nestling was seen in the nest on 20 July and again seven days later. On 3 August the nest was empty and neither adults nor juvenile were seen in the nesting area.

Feeding of the nestling: A total of 156 feedings were recorded. Only four feedings were performed by the male, on the morning of 14 and 15 July when the nestling was respectively seven and eight days old. The other 152 feedings were performed by the female.

The nestling was fed by the female for the first time on 8 July at 09:31 h, 12 h after hatching. However at 06:34 h, 3 h earlier, the male had already arrived at the nest with a fish. He ate a few pieces, then the female grabbed the remains and left the nest, followed by the male, without the nestling being fed.

Prey was brought to the nest at any time of the day, with the earliest feeding at 06:22 h on 9 July and the latest at 18:54 h on 22 July. Generally, the number of bits of prey given during a feeding session was less than 10, with an exception of 50 small pieces of a very large fish given in 14 min on 20 July when the nestling was 13 days old. The nestling was never seen to butcher prey itself.

A total of 96 prey items were brought to the nest during the 36 days of the nestling period that the camera was functional. The male brought 26 items and the female 70. Fish of the families Cichlidae, Callichthyidae (*Hoplosternum littorale*, local name: Atipa) and Erythrinidae (*Erythrinus erythrinus*, local name: Coulan), and *Hoplias malabaricus*, local name: Patagaï) represented 68 items. Four items were large tadpoles of the frog *Pseudis paradoxus*, one item a small snake and 23 items could not be identified.

Fledging: On 26 July, the nestling of nest 2 could stand on its feet without support of its wings. On 30 July, the nestling already flapped its wings to exercise its wing muscles. The black flight feathers, a few cm long, were already visible.

On 30 August, the last day that the nestling was in the nest, the female was feeding it from 12:06 to 12:17 h, with bits of fish. Thereafter, the nestling stood on the rim

of the nest and looked actively around. At 13:22 h, the nestling was perching on a branch at 1 m from the nest where it stayed for 38 min. It definitively left the nest at 14:00 h. The camera remained active for a few more days, however neither the fledgling nor the adults returned to the nest.

The nestling was born on 7 July and left the nest on 30 August, which makes a nestling period of 55 days. After fledging, two adult *B. nigricollis*, most probable the nesting pair, were seen in the nesting area with a juvenile on 23 September. Again on 5 October, an adult with a juvenile was seen. Thus, a juvenile seems to stay with the adults at least for two months after fledging.

Nest sanitation and maintenance: The female regularly removed prey remains from the nest, likely to avoid attracting flies. The nestling ejected its droppings sitting on the rim of the nest from 15 July on, when eight days old. From 25 July on, when 18 days old, the nestling moved cleverly around in the nest and it started to stand on the edge of the nest to eject its droppings.

During nine days of the incubation period, six fresh leafy boughs and one dead branch were recorded to be added to the nest, five by the female and two by the male. During 36 days of the nestling period, a total of 52 leafy boughs and dead branches were brought to the nest, 39 by the female and 13 by the male (Figure 3 & 4).



FIGURE 4. Female of Black-collared Hawk *Busarellus nigricollis* with nestling in nest 2 lined with leafy twigs. Photo taken on 12 July 2013.

Hazards for the nestling: On 7 July, the adults left the nest after the egg hatched, leaving the new born nestling unprotected. Immediately, a large blowfly (Calliphoridae) alighted on it, flying off, however, when the nestling made movements.

During four nights, a common vampire bat *Desmodus rotundus* was filmed while attacking the nestling. On 11 and 15 July when the nestling was respectively four and eight days old, the vampire was detected by the female which chased it with wing beats. On 13 and 15 August when the nestling was respectively 37 and 39 days old, the bat arrived without waking up the female and could bite the nestling. The first time, the nestling made movements so that the vampire flew off without feeding. The second time, however, the vampire could feed for 3 min before the nestling made movements so that the vampire flew off.

On 29 July at 15:00 h, the female with feathers ruffled, actively protected the nestling by holding her open wings over it, while screaming several times. She had probably detected a possible predator flying overhead.

Nesting season: At nest 2, display flights already started in March. The egg appeared to be laid in early June and the nestling fledged at the end of August. After fledging, the adults with the juvenile were seen in the nesting area for two more months, September and October. Thus, the nesting season seems to extend from March to October, from the arrival in the nesting area and first courtship activities until the last observations of the adults with the juvenile in the nesting area. At nest 4, the nestling fledged at the end of July.

DISCUSSION

Distribution

In French Guiana, the Black-collared Hawk is rather common in humid zones of the coastal region and absent from the forested interior (Faune-Guyane 2015) (Figure 1). In adjacent Suriname, it is common in the coastal region, uncommon in the northern savannas and rare in the forested interior (Ribot 2015).

At least 50 pairs breed in the coastal region of French Guiana. We suppose, however, that in vast favorable, but difficult to visit areas, such as the marshes of Panato near Awala-Yalimapo, the rice fields of Mana (c. 05°38'N; 53°40'W), the marshes of Pripris de Yiyi, the swampy savannas of Matiti, and the marshes of Kaw, up to 10 pairs may nest. As many parts of the available habitat are inaccessible, an estimated 100 pairs is a reasonable minimum, and the population may even reach as much as 200 pairs.

The population size of *B. nigricollis* in French Guiana is not known to have declined in recent years.

However, its restricted habitat is severely threatened by mining projects, by conversion into farmland or pastures, and by urbanization projects, resulting in reduced food availability and a loss of nesting sites. For these reasons, combined with the small population size, and although *B. nigricollis* is globally evaluated as “Least concern” (LC) by BirdLife International (2016), Claessens *et al.* (2016) propose to classify it as “Vulnerable” (VU) on at French Guiana, according to the IUCN red list criteria. They also estimated the population between 100 and 200 pairs, an estimate equal to, but independent from the one provided by Biotope (2014).

Breeding biology

Nests: As *B. nigricollis* is often nesting in inaccessible parts of mangroves, tidal marshes and swampy savannas, it is not surprising that until now only one nest in French Guiana (Tostain *et al.* 1992), six nests in Suriname (Haverschmidt & Mees 1994), six nests in Argentina (Di Giacomo 2005) and one nest in Brazil (Bertassoni *et al.* 2012) have been described in literature for South America. All these nests were rather large structures of sticks with a low cup lined with finer material, built in a fork of supporting branches (Figure 4), high up in the crown of an isolated tree in a clearing or in a tree crown rising above the surrounding vegetation. The height of six nests in the Chaco province of Argentina varied between 9 and 17 m (Di Giacomo 2005) and the height of a nest in the Brazilian Pantanal was *c.* 15 m (Bertassoni *et al.* 2012). In French Guiana, three nests were built at a height of *c.* 15 m, two others between 20 and 25 m, and one much higher at *c.* 35 m.

Nests seem to be re-used as proven by nest 2 which was used in 2010 and again in 2013. The re-use of old nests was not yet mentioned in literature (GRIN 2015, Bierregaard-Jr. *et al.* 2016). Given the small distance between nests 1 and 3 (1.3 km), nest 3 was probably constructed in 2013 by the breeding pair which used nest 1 in 2010.

Clutch size: In literature, clutch size of *B. nigricollis* is given as 1 or 2 eggs (GRIN 2015, Bierregaard-Jr. *et al.* 2016). Likewise the egg collection of the Western Foundation of Vertebrate Zoology houses two 2-egg clutches collected in Trinidad and Guyana respectively, and three 1-egg clutches collected in Paraguay (René Corado pers. comm.). Another clutch of two eggs was also collected in Guyana (Kreuger 1963). In Suriname, two nests contained one egg, and one nest one nestling (Haverschmidt & Mees 1994). In Argentina, three nests contained one egg and one nest one nestling (Di Giacomo 2005).

In this study, nest 2 contained one egg, nest 4 one nestling and two pairs were observed with one fledgling

(Faune-Guyane 2015). However, one nestling, fledgling or juvenile accompanying a pair of adults does not mean a 1-egg clutch, as sibling competition leading to the death of the youngest nestling (cainism) is widespread among raptors (Newton 1979, Thiollay 1994, Ferguson-Lees & Christie 2001).

Incubation period: The website *Oiseaux d'Argentine* (Canalblog 2011) mentions that only the female of *B. nigricollis* incubates and that the incubation period is 35 to 40 days. It is unclear, however, on what reference(s) these statements are based on. Accipitridae of similar size as *B. nigricollis* such as the Zone-tailed Hawk *Buteo albonotatus* (Kaup, 1847) and the Common Black Hawk *Buteogallus anthracinus* (W. Deppe, 1830), have an incubation period of, respectively, 28 to 34, and 37 to 40 days (Ferguson-Lees & Christie 2001).

From our observations at nest 2, it is also clear that both female and male incubate, although the female's investment is more important. The male incubates for short periods during the day only. However, it is difficult to learn the real share of each adult because of the method used in this study. Indeed, activities like incubation lead to movements that are not sufficient to trigger the camera. Thus, missing video sequences make a quantitative analysis impossible.

Nestling period: The fledgling period for the nestling in nest 2 was 55 days. Our observations of a pair accompanied by a juvenile in the area of nest 2 after the nestling fledged, suggest that juveniles remain with adults for at least another two months. This period was estimated at two nests in Argentina to be between 59 and 66 days (Di Giacomo 2005).

Nest sanitation and maintenance: Nest sanitation is carried out by the female removing food remains from the nest, and from the age of eight days on, the nestling defecated outside the nest, behavior also described for other Accipitridae (Bierregaard-Jr. 1984). Both male and female of *B. nigricollis* add twigs with fresh leaves and, to a lesser extent, fine dead branches to the nest during the entire nesting period, more frequently during the nestling than during the incubation period. This unexplained behavior is rather common among medium-sized and large raptors (Newton 1979, Thiollay 1994).

Nesting season: In Suriname, Ribot (2015) mentions 17 nests with either one egg or a nestling, or two adults with a fledgling, one in May, three each in June, July and August, four in September, two in October and one in December. In Guyana, eggs were collected in April (GRIN 2015) and a clutch of incubated eggs in August (René Corado, pers. comm.). The nesting season seems to extend from March to October in French Guiana. Therefore, it seems that in French Guiana, Suriname and Guyana, where the monthly rainfall pattern is similar (CRU 2015), the breeding season of *B. nigricollis* starts in

the rainy season in the first half of the year. At most nests, however, nestlings, fledglings and juveniles, demanding a constant supply of food, are present during the drier months of the second half of the year. Di Giacomo (2005) also reports six active nests found in Argentina between mid-July and mid-November, which corresponds to the second half of the dry season in the Chaco province. In Paraguay where the dry season in the second half of the year is less pronounced, one clutch was collected in August and two in September (René Corado pers. comm.).

In the HBW Alive account of the Black-collared Hawk *B. nigricollis*, Bierregaard-Jr. *et al.* (2016) mention under “breeding”: very poorly known. The study of four nests discovered in 2013 in the coastal region of French Guiana and especially the monitoring of the activities at one nest with a camera and a digital recorder, greatly add to the knowledge of the breeding biology of this hawk. At this monitored nest, we followed the activities of the male and female during the incubation period, and then the behavior of the male, female and nestling during the nestling period. Recordings also allowed us to identify prey items fed to the nestling, to witness sanitation and maintenance of the nest, and hazards for the nestling. Our observations are consistent with what is already known of the breeding behavior of the Black-collared Hawk.

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Effects of pairing *Thamnophilus ambiguus* males with females on the behavioral responses by males to playback

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ABSTRACT: The behavioral responses of the Sooretama Slaty-antshrike (*Thamnophilus ambiguus*) to playback were tested in a Restinga (sand-coastal plain) area in southeastern Brazil. Field data were collected for seven mornings, from 5:30 h to 11:00 h. Frequency data and the time period between playing the species' song (playback) and the sighting of individuals were recorded by the observer. The following parameters related to behavioral responses to playback were recorded: 1) the bird flew to a visible roost but not sang (sighting); 2) the bird sang as response to playback (vocalization) and; 3) the bird sang and approached to the observer (bird approaching). The time of response to playback of males paired with females was significantly shorter than that of unpaired males, albeit with no significant difference in the sighting and bird approaching frequency. In conclusion, males paired with females become more aggressive and show a faster territorial defense response than solitary males.

KEY-WORDS: restinga, Sooretama Slaty-antshrike, territorial behavior, Thamnophilidae.

Brazil has 1919 bird species recorded, which makes it a mega-diverse country regarding bird species richness (Piacentini *et al.* 2015). Various methods, including linear transects, fixed listening stations, and even walks and direct sighting, are used for bird inventories (Develey 2003). Regardless of the species survey method adopted, the acoustic identification of the species increases the detection efficiency and may also reveal behavioral characteristics of the species.

Vocalization is a form of bird communication among individuals and may be used by researchers as a method for species identification. Vocalization recording and playback the vocalization of the species is another method that is often used to increase the chances of detecting rare species, and is highly effective at detecting territorial species (Bibby *et al.* 1998). For example, given the difficulty in sighting individuals in forest areas, only audio records of different species in these areas may allow the identification of 90% of the species (Mosher *et al.* 1990, Sick 1997). Vocalization patterns may also be used to understand behavioral patterns (Boscolo *et al.* 2006). Thus, the use of playback may be a tool that helps determine the territories of some species and even tests some behavioral patterns, including the movement ability of a species (Sieving *et al.* 1996).

Some species respond to playback more easily than others, and some do not respond at all. Some respond

efficiently, although they are difficult to sight even when attracted to the playback location because they have discrete habits. Conversely, other species show a more pronounced behavioral response to playback and are easier to sight. However, differences in behavioral responses between individuals of the same species are unknown. The present study aimed to evaluate the behavioral responses of the Sooretama Slaty-antshrike (*Thamnophilus ambiguus*) to playback. For this purpose, the behavioral responses to playback of males paired with females and solitary males were analyzed.

The study was conducted at the Paulo César Vinha State Park (PEPCV) located in the municipality of Guarapari, state of Espírito Santo, Brazil. A total of 225 bird species were recorded at the PEPCV in a survey conducted by Venturini *et al.* (1996), accounting for 22.1% of all bird species reported for the Atlantic Forest (MMA 2000).

Fieldwork was conducted from 12 to 18 September 2014. This time period coincides with the beginning of the reproductive activities of several species in the study area, for example, *Formicivora rufa* (Dutra 2014) and *Mimus gilvus* (Araújo 2016). Eighteen *T. ambiguus* males who were previously captured and marked with metal bands provided by the *Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE)* and unique combinations of three colored plastic bands were selected.

Nine individuals were paired with females, and the other nine were solitary males. All individuals were previously sighted defending their territory.

Field data were always collected in the period from 5:30 h to 11:00 h in the morning. A Sony (ICD-PX312) recorder was used to playback *T. ambiguus* vocalizations for 120 s, and 10 × 42 binoculars were used for sighting birds. The playback was used only once a day in each territory. Playback started together with a timer when arriving at the territories of different individuals. Behaviors were recorded by *ad libitum* method (Altmann 1974) from the start of playback. The following parameters related to behavioral responses to playback were recorded: 1) the bird flew to a visible roost but not sang (sighting); 2) the bird sang as response to playback (vocalization) and; 3) the bird sang and approached to the observer (bird approaching). Bird approaching was defined as individuals approaching the observer within 5 m. For each behavioral response, we recorded the time (latency) between the playback and bird response.

Normal distribution was verified with Kolmogorov–Smirnov tests. Differences in the mean times of sighting, vocalization response and approach response were assessed using unpaired t test. All analyses were performed according to Zar (2010) using the Systat Software, version 12.0 (Wilkinson 2007) considering $\alpha < 0.05$ as the significance level.

At least two of the three types of behavioral responses (sighting and vocalization) analyzed were observed every time the species song was played back. Paired males showed the three types of behaviors with a 100% frequency. Solitary males showed a 55.5% response to bird approaching. Females were sighted before males in 33.3% of the responses of the paired males.

No significant differences between mean values of sighting ($t = -1.50$, $df = 16$, $P = 0.15$) and bird approaching ($t = 0.95$, $df = 16$, $P = 0.36$) were found when comparing paired and solitary males. However, paired males responded to vocalizations faster than solitary males ($t = -2.80$, $df = 16$, $P = 0.01$).

Pyriglena leucoptera (Thamnophilidae) individuals responded to playback 75% of the time in the study conducted by Barreiros *et al.* (2008) also testing reaction. This result was similar to the 85% response rate of this species found by Boscolo *et al.* (2006). Response to playback was observed 56% of the time in a study conducted in an urban area, wherein a bird approaching response was observed in only 30% and the birds were sighted in 25% of the attempts (Barreiros *et al.* 2008). The response rate to playback by *T. ambiguus* was 100% in the present study. However, this rate most likely resulted from exclusively testing the playback in territories known to be occupied by individuals of the species.

The faster response of paired males may result from

the threat posed by playback vocalizations perceived as another male invading their territory. Thus, the faster response may be considered a territorial and mating defense strategy. Possibly, this is also a behavior to prevent extrapair copulation, as observed for other territorial species (Møller 1990, Duca & Marini 2014).

Results showed that the responses of males of *T. ambiguus* to playback were faster when paired with a female, which corroborated previous studies on territorial behavior (Araújo-Lima & Duca 2015). Female presence in territories also affected the aggressive behavior to observer approach by territorial males, by increasing the response to playback with an increased frequency. Therefore, *T. ambiguus* can potentially be used in future studies to analyze various physiological, morphological, and behavioral parameters associated with territorial behavior.

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Small territory sizes and high densities of insectivorous birds in an Atlantic Forest secondary fragment, Brazil

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ABSTRACT: Demographic parameters of birds are essential to understand their ecology and delineate conservation and management plans. This becomes especially important in highly altered biomes such as the Brazilian Atlantic Forest, since the few remaining fragments bear mostly secondary forests where demographic parameters might differ from old-growth forests. Few studies about territory sizes and density have been conducted for entire bird communities or groups of species in the Neotropical region, with a bias towards Central America and the Amazon. In this work we determined territories of Atlantic Forest birds in order to assess their size and density. We conducted spot-mapping in a rectangular 40-ha plot within a 384-ha of secondary semideciduous forest fragment in Viçosa region, state of Minas Gerais, Brazil. We identified 260 territories of 30 species of insectivorous birds. Mean territory size of all species was 2.4 ha, ranging from 0.5 to 7.5 ha. The mean density for all species was 21.7 pairs/100 ha, ranging from 2.5 to 72.5 pairs. The sizes of the territories of many Atlantic Forest birds were by far smaller, and the density higher, than those of conspecific or congeneric species from Amazonian or Central American forests. These geographical differences in territory size and density can be explained by at least two non-exclusive hypotheses: 1) higher primary and secondary productivity in advanced successional secondary forest fragments and; 2) density compensation, given the loss of other competitor species.

KEY-WORDS: density compensation, fragmentation, Minas Gerais, Neotropical, secondary forests, territoriality.

INTRODUCTION

Secondary forests are increasingly replacing pristine forests around the world (ITTO 2002) and are, thus, important for conserving the remaining forest specialist species (Wright 2010). Compared to old-growth forests, secondary forests have lower plant species richness and denser and more homogeneous understory (Guariguata & Ostertag 2001). Compared to secondary forests, Neotropical primary forests have more microhabitats, varying from very open understory under a higher and more closed canopy cover, to open vine tangles and bushes in older treefall gaps, and even to virtually impenetrable, shaded vine tangles in more recent treefall gaps (Robinson & Terborgh 1995, 1997). This mosaic of thicker and more open understory in primary Neotropical forests can result in a strikingly different use and distribution by birds in a given area (Robinson & Terborgh 1995, 1997, Jullien & Thiollay 1998).

These secondary forests are also often isolated and even more disturbed by further human activities, and

the question whether they will hold viable populations depends on several aspects of birds' biology and their knowledge is fundamental for conservation planning and actions. Population viability analyses (Shaffer 1981), for example, require estimates of a number of traits, including population density or territory size (Goldingay & Possingham 1995) which might be important for management strategies (Beissinger & Westphal 1998, Duca *et al.* 2009). In addition, the knowledge of the size and distribution of their territories by habitat types allows a better estimation of their population sizes with respect to vegetation characteristics of forest fragments of a given area, and their use in population-based models (Millsbaugh & Thompson-III 2009).

The Atlantic Forest is among the world's top biodiversity hotspots (Myers *et al.* 2000) with only 1% of the original primary (or old-growth) forest remaining. The current forest cover is estimated at 11–16%, considering forest patches older than 15 years, and comprises thousands of remnants, most of them smaller than 50 ha, highly isolated, and consisting primarily of

forests in secondary succession (Ribeiro *et al.* 2009). Bird species richness, and levels of endemic and threatened species (Stotz *et al.* 1996, Marini & Garcia 2005) are extremely high, but their biological parameters, such as life histories, diets, habitat use, habitat selection and social behavior are largely unknown, as is common for many aspects of Neotropical birds (Heming *et al.* 2013). Furthermore, these Atlantic Forest fragments are already facing local bird extirpations (Ribon *et al.* 2003), and complete extinction of many species in the biome are projected for the future although at a rate lower than expected due to a time-lag response (Metzger *et al.* 2009).

Furthermore, within the Neotropics, there is a bias in the geographical distribution of the studies describing basic characteristics of bird territories, such as density and size. Although there are some species-specific studies from the Cerrado (savannah) Biome (Marini & Cavalcanti 1992, Ribeiro *et al.* 2002, Lopes & Marini 2006, Domingues & Rodrigues 2007, Freitas & Rodrigues 2012, Costa & Rodrigues 2013, Duca & Marini 2014, Marini *et al.* 2014) and the Atlantic Forest (Willis *et al.* 1983, Willis & Oniki 2001, Duca & Marini 2005, Duca *et al.* 2006, Lima & Roper 2009) most of them, including all those more comprehensive (*i.e.* encompassing many species), come from Amazonia and Central America (Terborgh *et al.* 1990, Thiollay 1994, Robinson & Terborgh 1997, Robinson *et al.* 2000, Stouffer 2007, Johnson *et al.* 2011).

Considering that still very little is known about territoriality of Atlantic Forest birds, and that most of the remaining Atlantic Forest is composed by fragments of secondary forests, it is very important to know how bird species that persist in these fragments are distributed in different scales if we want to properly manage and conserve them. In this study we focused on insectivorous birds as they have been reported to be highly vulnerable to forest fragmentation and degradation (Stouffer & Bierregaard-Jr. 1995, Barlow *et al.* 2006, but see Anjos 2006). Thus, we studied bird territories in a secondary Atlantic Forest fragment to verify territory size and bird density. Specifically we wanted to know how large are the territories of Atlantic Forest birds still inhabiting a secondary forest of a highly fragmented area originally covered by pristine forest that has suffered many extinctions (Ribon *et al.* 2003). Furthermore, we wanted to determine the abundance and density of territories of each bird species. Additionally, we also used the few literature accounts on territory sizes of Neotropical birds to compare territory sizes and densities with conspecific or congeneric species from pristine and secondary forests from Amazonian or Central American forests as a way to stimulate further studies comparing pristine and secondary forests across the Neotropic within the same biome.

METHODS

Our study was conducted at Viçosa county, a hilly region in southeastern Minas Gerais, Brazil, that consists of a mix of semideciduous secondary forest fragments, immersed in a matrix of pastures consisting of non-native grasses, non-shaded coffee, *Eucalyptus* plantations, small corn and bean plantations, small vegetable gardens and orchards (≤ 0.5 ha), and narrow linear streams often bordered by cattail (*Typha* spp.). Most native forest have been destroyed along the last 200 years (Brant 2004) and the remaining patches (mostly secondary vegetation) cover mainly hilltops and hillsides. These forest patches are mostly < 50 ha in size and the other matrix components occupy the narrow lowlands and ravines (Pereira 1999, Ribon 2003).

Study area

The observations were made in the largest (384 ha) forest fragment in an area of 10,000 ha surrounding Viçosa county (the *Centro de Pesquisas e Educação Ambiental Mata do Paraíso – MP*, 20°48'07.9"S; 42°51'29.5"W, 690–870 m a.s.l.). The fragment suffered from strong selective logging until the middle 1960's and some parts are regenerating from an unshaded coffee plantation and pastureland. The vegetation is nowadays secondary forest with small patches of initial, intermediate and advanced succession stages. The largest forest fragment (~13,000 ha) near MP is the Serra do Brigadeiro State Park located 37 km in straight line to the east. Our study plot reflected the topography of the region and included lowlands, ravines, hillsides, and hilltops (*sensu* Espartel 1977) within its limits.

Studies in different parts of the MP have shown that areas with vegetation in intermediate and advanced successional stages have almost half of the number of trees and shrubs found in the advanced successional stages (Marangon *et al.* 2003, Pinto *et al.* 2007). At an initial forest stage patch at MP (outside our study plot, but very similar to some of its parts), based on their importance value, the most representative species were *Piptadenia gonoacantha* (Mimosaceae), *Vernonanthura diffusa* (Asteraceae), *Miconia cinnamomifolia* (Melastomataceae), *Piptocarpha macropoda* (Asteraceae) and *Luehea grandiflora* (Malvaceae) (Pinto *et al.* 2007). In the same study, in an advanced successional stage section, inside our study plot, *Euterpe edulis* (Arecaceae), *Piptadenia gonoacantha* (Mimosaceae), *Nectandra lanceolate* (Lauraceae), *Myrcia sphaerocarpa* (Myrtaceae) and *Guapira opposita* (Nyctaginaceae) were the most representative species. Intermediate stage inside our study site is less diverse (Shannon diversity index $H' = 3.31$) and has higher evenness (Pielou's $J' = 0.83$) than advanced forest ($H' = 3.46$; $J' = 0.79$) (Pinto *et al.* 2007).

Historically, 298 bird species (of which 177 forest dependent) have been recorded at MP (Ribon *et al.* 2014), but at least 28 were already extirpated from the Viçosa region, including MP, since 1930's (Ribon *et al.* 2003).

Territory mapping

We mapped the territories of birds in a 40-ha grid, with eleven 400 m trails intersecting five 1000 m trails every 100 m in the central portion of MP. Roughly half of the grid is covered by native forest at late succession stage (studied by Pinto *et al.* 2007) with two patches of native bamboo (*Merostachys* sp. and *Olyra* sp., Poaceae). The other half is dominated by native forest at early or intermediate succession with small patches of shaded *Pteridium* (Dennstaedtiaceae) ferns, a half hectare of *Corymbia citriodora* (Myrtaceae) and one hectare of *Pinus eliottii* (Pinaceae) (Figure 1). All vegetation types have a dense understory.

Because understory and insectivorous birds are often considered as negatively affected by forest fragmentation, destruction, and disturbance (Laurance & Bierregaard-Jr. 1997) we focused our study on the following insectivorous families: Momotidae, Thamnophilidae, Conopophagidae, Dendrocolaptidae, Furnariidae, and Tyrannidae, and in one Cardinalidae, the Red-crowned Ant-tanager (*Habia rubica*) an omnivorous mixed-species flock leader consuming large amount of invertebrates.

To map territories we used territory mapping (or spot-mapping) following guidelines in Bibby *et al.* (1997) at the 40 ha grid plot described above (details in Ribon 2005). The plot had 10-m interval contour lines mapped over a grid that were used to plot bird locations in the field (Ribon 2005). This method by itself suffices to estimate territory sizes and bird densities. Territory mapping only requires that the locations of birds observed and vocalizing, especially simultaneous observations of singing males, to be recorded. We followed this standard method, but used pairs of singing, calling, or observed birds to plot territories of some species (Thamnophilidae, Furnariidae, and Tyrannidae) because both males and females sing (pers. obs.; Sick 1997). Such songs are assumed to be related to territory defense and the limits of their territories are assumed to lie in the space between singing birds.

Even though not required by the territory mapping approach, we also color-banded birds to aid in individual identification. We banded 234 individuals of the focus species (85 recaptures) using 6–12 mist nets opened across our grid (1635 net.h) from August 1999 to October 2000. Nets (12 m × 2.5 m) were placed in different parts of the grid to capture as many individuals as possible. Birds were banded with metallic numbered rings from CEMAVE/

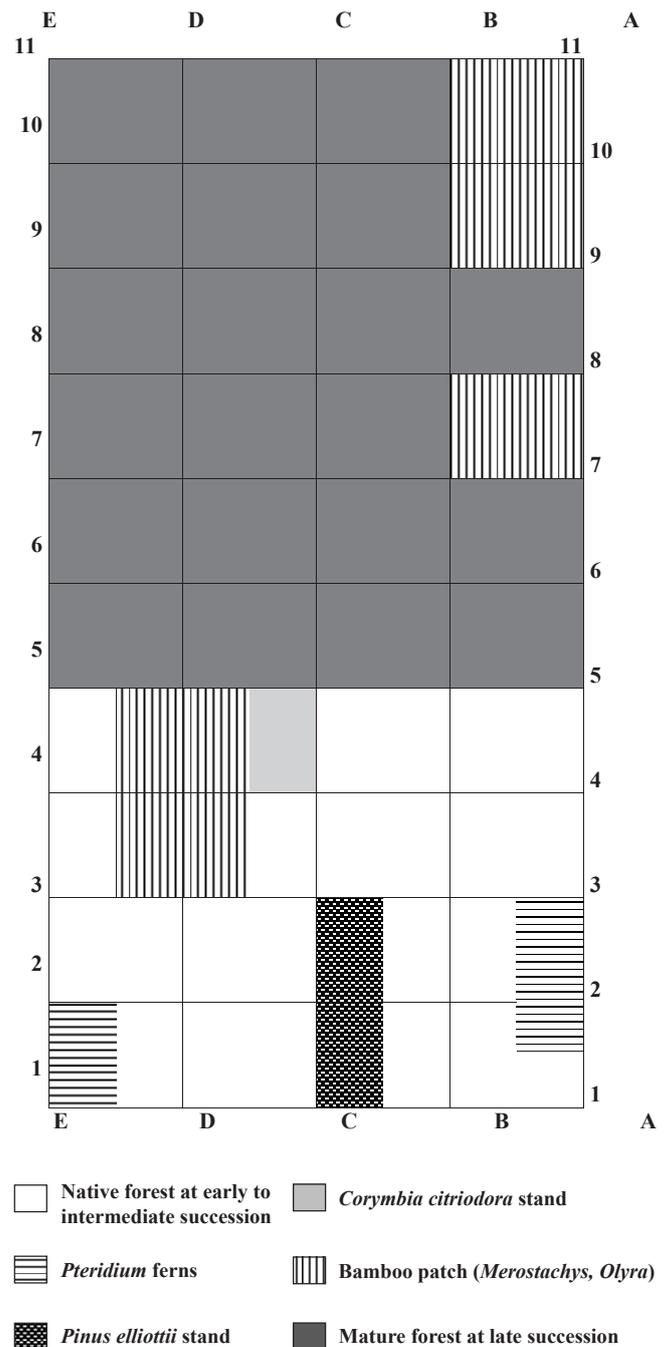


FIGURE 1. Schematic representation of the vegetation at the 40 ha study grid plot established at Mata do Paraíso Research Station, Viçosa, Minas Gerais, Brazil, to map the territories of 30 bird species. Letters and numbers indicate the codes of each of the five 1000 m and eleven 400 m trails opened for the territory mapping.

ICMBio (Permit No. 227) and a combination of two or three color bands.

The entire grid was surveyed 10 times to map bird territories from August to December 2000, each survey occurring at each 10–15 days according to weather conditions. Surveys alternated between 1000 m and 400 m trails. As a morning was not enough to sample all the five 1000 m or all the eleven 400 m trails, two

or three consecutive mornings were spent to survey all the longer or all the shorter trails. All territory mapping was conducted from sunrise to 10:30 h, and birds were observed with a Leica Trinovid 10 × 42 mm binocular. Trails were never left. After 10 visits, we transferred all the locations of each species to a map of the plot, mapped the territories according to Bibby *et al.* (1997), drew each territory contour and further measured them using Autocad 1.4. (by Autodesk). For each territory, we measured its size (in ha). To calculate territory sizes, we used territories entirely inside the plot as well as those that partially overlapped the plot. The exact location of each territory of nine of the species studied along the grid can be found in Ribon (2003).

Among the 76 resident insectivorous bird species at the study site (Ribon *et al.* 2014), we estimated territory sizes of 30 species. Among these, 20 species use the understory and seldom go higher, while 10 species primarily use the mid-story and canopy (Stotz *et al.* 1996, pers. obs.). The sample size for each species varied according to its density and possibility of observation. We used a minimum of three locations (either song, call, visual, or combination of these) to determine the boundaries of bird territories following Bibby *et al.* (1997). However, only one territory each of three different species had three locations, and the general average number of points per territory mapped was 13 (range 3–36). Capture locations and the scarce sightings of banded birds were used to help to solve doubts about territory boundaries obtained after the 10 visits. Recent research suggests that at least 30–40 locations are required for meaningful territory size estimation (Anich *et al.* 2009). Although it is practical to obtain such number of records for species-specific studies (with radio-telemetry or color-banded birds) standard territory mapping still gives accurate estimates and maximize cost-benefit fieldwork effort when a large number of species are studied at the same time (Terborgh *et al.* 1990, Robinson & Terborgh 1995, 1997). Furthermore, the use of territory mapping to estimate bird densities is appropriate if one can distinguish one territory from another. Bird nomenclature and systematic order follow Remsen-Jr. *et al.* (2016).

Comparison with other Neotropical sites

We compared our findings at MP to the few available multispecies territorial studies based on territory mapping in the Neotropics that encompassed several congeneric species found at our study site (Terborgh *et al.* 1990, Thiollay 1994, Robinson & Terborgh 1997, Robinson *et al.* 2000, Johnson *et al.* 2011). All these studies have been conducted in >95–100 ha grids of

primary forest except Robinson *et al.* (2000) that worked on more disturbed forest. To allow a comparison of our densities with those from studies conducted in other Neotropical forests, we estimated the expected number of territories of congeneric species for an area of 100 ha, considering one pair per territory for most species (see above). We did this based in the structural homogeneity of secondary vegetation and in the assumption that birds in these habitats, as at our study plot, are much more evenly distributed than in primary forests (Thiollay 1994, Guariguata & Ostertag 2001, Johnson *et al.* 2011). Although we recognize that territory mapping could lead to less accurate estimates of bird density and smaller territory sizes than radio-telemetry (Streby *et al.* 2012) or detailed following of banded birds (Lima & Roper 2009), we judged it useful for a general comparison to mostly existent data on the Neotropical region (Terborgh *et al.* 1990, Thiollay 1994, Robinson & Terborgh 1997, Robinson *et al.* 2000, Johnson *et al.* 2011) as their data were all based on territory mapping obtained from trail grids. Because of the smaller size of our plot relative to other studies, we considered both birds with territories entirely inside the plot to calculate density, and birds with partial territories inside the plot using a correction factor: densities of birds with partial territories inside the plot were proportional to the part of territory inside it. For example, for a territory that was 50% inside the plot, we assumed a density of 0.5 pairs instead of 1.

RESULTS

We mapped 260 territories of 30 species (Table 1), most of them non-banded. Mean territory size was 2.4 ha (range 0.5–7.5). Mean number of locations to delineate each territory was 12.9, ranging from three to 36 records (Tables 1 and 2). Most territories were smaller than 4 ha (Figure 2). The smallest territory was 0.5 ha (Hangnest Tody-tyrant, *Hemitriccus nidipendulus*; and Greenish Elaenia *Myiopagis viridicata*) and the largest was 7.5 ha (Gray-hooded Attila, *Attila rufus*).

Eleven species were rare and had < 5 territories in our plot. Euler's Flycatcher (*Lathrotriccus euleri*), Rufous Gnateater (*Conopophaga lineata*) and Yellow-olive Flycatcher (*Tolmomyias sulphurescens*) were very abundant, with the largest number of territories demarcated (29, 20 and 19 territories in the 40 ha plot, respectively). General average density for all species was 22 pairs/100 ha, ranging from 2 (Sharp-tailed Streamcreeper, *Lochmias nematura*; and Serra Antwren, *Formicivora serrana*) to 72 pairs/100 ha (Euler's Flycatcher), with 5 species reaching densities of more than 40 pairs/100 ha (Table 3).

TABLE 1. Territory sizes of 30 bird species in a 40 ha Atlantic Forest plot at Viçosa, Minas Gerais, Brazil. N - number of territories of each species; n – mean number of points used to map the territories of each species, followed by the range of points.

Species	N (n; range)	Territory size (ha)	
		Range	Mean ± SE
Rufous-capped Motmot (<i>Baryphthengus ruficapillus</i>)	6 (11.5; 8–14)	1.8–7.8	3.4 ± 0.9
Tufted Antshrike (<i>Mackenziaena severa</i>)	2 (12.5; 7–18)	6.4–6.8	6.6 ± 0.2
Variable Antshrike (<i>Thamnophilus caerulescens</i>)	17 (13.4; 7–22)	0.7–1.7	1.3 ± 0.1
Plain Antwren (<i>Dysithamnus mentalis</i>)	17 (8.4; 5–13)	0.4–1.6	0.9 ± 0.1
Serra Antwren (<i>Formicivora serrana</i>)	1 (8)	--	1.0
Ferruginous Antbird (<i>Drymophila ferruginea</i>)	3 (17.3; 10–29)	0.8–1.3	1.2 ± 0.2
White-shouldered Fire-eye (<i>Pyriglena leucoptera</i>)	16 (15.2; 8–36)	0.3–2.5	1.4 ± 0.1
Rufous Gnateater (<i>Conopophaga lineata</i>)	20 (7.7; 4–12)	0.3–1.2	0.6 ± 0.1
Rufous-capped Spinetail (<i>Synallaxis ruficapilla</i>)	14 (13.9; 6–23)	0.8–2.2	1.6 ± 0.1
Gray-bellied Spinetail (<i>Synallaxis cinerascens</i>)	7 (10.9; 4–19)	1.5–3.5	2.1 ± 0.3
White-collared Foliage-gleaner (<i>Anabazenops fuscus</i>)	9 (18.9; 8–30)	0.7–7.0	3.3 ± 0.6
White-eyed Foliage-gleaner (<i>Automolus leucophthalmus</i>)	3 (21.3; 9–31)	2.1–7.2	5.4 ± 1.6
Streaked Xenops (<i>Xenops rutilans</i>)	4 (15.8; 11–23)	3.7–7.4	6.0 ± 0.8
Sharp-tailed Streamcreeper (<i>Lochmias nematura</i>)	1 (15)	--	2.2
Lesser Woodcreeper (<i>Xiphorhynchus fuscus</i>)	5 (9.6; 5–13)	2.0–4.1	3.3 ± 0.4
Scaled Woodcreeper (<i>Lepidocolaptes squamatus</i>)	8 (9.2; 5–12)	0.7–5.2	2.2 ± 0.5
Black-billed Scythebill (<i>Campylorhamphus falcularius</i>)	5 (9; 3–16)	1.0–4.1	2.8 ± 0.5
Greenish Elaenia (<i>Myiopagis viridicata</i>)	6 (4.6; 3–8)	0.3–1.0	0.5 ± 0.1
Gray Elaenia (<i>Myiopagis caniceps</i>)	3 (7.8; 5–12)	2.0–4.1	3.0 ± 0.6
Sepia-capped Flycatcher (<i>Leptopogon amaurocephalus</i>)	10 (13.5; 9–27)	0.9–3.7	2.3 ± 0.3
Southern Antpipit (<i>Corythopis delalandi</i>)	15 (10.7; 6–19)	0.2–3.0	1.0 ± 0.2
Eared Pygmy-tyrant (<i>Myiornis auricularis</i>)	10 (9.2; 3–16)	0.4–1.9	1.1 ± 0.2
Hangnest Tody-tyrant (<i>Hemitriccus nidipendulus</i>)	3 (7.5; 5–10)	0.3–0.7	0.5 ± 0.1
Yellow-faced Tody-flycatcher (<i>Todirostrum poliocephalum</i>)	8 (19.8; 16–26)	0.3–2.0	1.5 ± 0.2
Ochre-colored Tody-flycatcher (<i>Poecilatriccus plumbeiceps</i>)	2 (12.5; 10–15)	0.9–2.4	1.7 ± 0.8
Yellow-olive Flycatcher (<i>Tolmomyias sulphurescens</i>)	19 (18.3; 8–27)	0.7–2.9	1.6 ± 0.2
White-throated Spadebill (<i>Platyrinchus mystaceus</i>)	12 (15.1; 6–27)	1.2–2.9	2.0 ± 0.2
Euler's Flycatcher (<i>Lathrotriccus euleri</i>)	29 (13.3; 5–31)	0.2–2.0	0.9 ± 0.1
Gray-hooded Attila (<i>Attila rufus</i>)	2 (18.5; 11–26)	3.2–11.7	7.5 ± 4.3
Red-crowned Ant-tanager (<i>Habia rubica</i>)	3 (17.3; 13–21)	2.4–5.7	4.0 ± 1.0

TABLE 2. Territory sizes (ha) of birds at three Neotropical sites. Atlantic Forest birds are aligned at the left.

Species	Viçosa, Brazil ^a	Peru ^b	Panama ^c	Manaus, Brazil ^d
<i>Baryphthengus ruficapillus</i>	3.4			
<i>B. martii</i>			5–8	
<i>Mackenziaena severa</i>	6.6			
<i>Thamnophilus caerulescens</i>	1.3			
<i>T. aethiops</i>		10		
<i>T. schistaceus</i>		8		
<i>T. atrinucha</i>			1	
<i>T. murinus</i>				5.6
<i>Dysithamnus mentalis</i>	0.9			
<i>D. puncticeps</i>			<2	
<i>Formicivora serrana</i>	1.0			
<i>Drymophila ferruginea</i>	1.2			
<i>Pyriglena leucoptera</i>	1.4			
<i>Conopophaga lineata</i>	0.6			
<i>C. aurita</i>				6.3
<i>Synallaxis cinerascens</i>	2.1			
<i>S. ruficapilla</i>	1.6			
<i>Anabazenops fuscus</i>	3.3			
<i>Automolus leucophthalmus</i>	5.4			
<i>A. infuscatus</i>		12		10.6
<i>A. ochrolaemus</i>		11	11	
<i>A. rubiginosus</i>				13.3
<i>Xenops rutilans</i>	6.0			
<i>X. minutus</i>		9	5	13.3

Species	Viçosa, Brazil ^a	Peru ^b	Panama ^c	Manaus, Brazil ^d
<i>Lochmias nematura</i>	2.2			
<i>Xiphorhynchus fuscus</i>	3.3			
<i>X. pardalotus</i>				10.6
<i>Lepidocolaptes squamatus</i>	2.2			
<i>L. albolineatus</i>		14		12
<i>Campyloramphus falcularius</i>	2.8			
<i>C. procurvodes</i>				24
<i>Myiopagis viridicata</i>	0.5			
<i>Myiopagis caniceps</i>	3.0		5–8	6
<i>M. gaimardii</i>		4		5.6
<i>Leptopogon amaurocephalus</i>	2.3	3		
<i>Corythopis delalandi</i>	1.0			
<i>C. torquata</i>		6		5.7
<i>Myiornis auricularis</i>	1.1			
<i>M. ecaudatus</i>		3		
<i>M. atricapillus</i>			3	
<i>Hemitriccus nidipendulus</i>	0.5			
<i>H. zosterops</i>		3		3.9
<i>Todirostrum poliocephalum</i>	1.5			
<i>Todirostrum plumbeiceps</i>	1.7			
<i>T. crysophataphum</i>		7*		
<i>Tolmomyias sulphurescens</i>	1.6			
<i>T. assimilis</i>		6	4	9.1
<i>T. poliocephalus</i>		5		6
<i>Platyrinchus mystaceus</i>	2.0			
<i>P. coronatus</i>		5	6	3.8
<i>P. platyrhynchos</i>		5		5
<i>Lathrotriccus euleri</i>	0.9	5		
<i>Attila rufus</i>	7.5			
<i>A. bolivianus</i>		12		
<i>A. spadiceus</i>		12	8	16
<i>Habia rubica</i>	4	6		
<i>H. fuscicauda</i>			25	
Average	2.4	7.3	7.1	9.2

^a This study. Territory sizes estimated for 100 ha. ^b Terborgh *et al.* (1990). ^c Robinson *et al.* (2000). ^d Johnson *et al.* (2011). ^e Robinson & Terborgh (1997).

TABLE 3. Density of birds (pairs/100 ha) at five Neotropical sites. Atlantic Forest birds are aligned at the left. * – number of individuals.

Species	Atlantic Forest ^a	Peru ^b	Peru ^c	Guyana ^d	Manaus ^e	Panama ^f
<i>Baryphthengus ruficapillus</i>	15					
<i>B. martii</i>						24
<i>Mackenziaena severa</i>	5					
<i>Thamnophilus caerulescens</i>	42.5					
<i>T. aethiops</i>		1				
<i>T. schistaceus</i>		10.5	0.5–21			
<i>T. doliatus</i>			38			
<i>T. murinus</i>				7.75	12.5	
<i>T. amazonicus</i>				4		
<i>T. punctatus</i>				0.25		
<i>T. atrinucha</i>						106
<i>Dysithamnus mentalis</i>	42.5					
<i>D. puncticeps</i>						3.5
<i>Formicivora serrana</i>	2.5					
<i>Drymophila ferruginea</i>	7.5					
<i>Pyriglena leucoptera</i>	40					
<i>Conopophaga lineata</i>	50					
<i>C. peruviana</i>		3				
<i>C. aurita</i>				1	2	
<i>Synallaxis cinerascens</i>	17.5					
<i>S. ruficapilla</i>	35					
<i>S. gujanensis</i>			53			
<i>Anabazenops fuscus</i>	22.5					
<i>Automolus leucophthalmus</i>	7.5					
<i>A. infuscatus</i>		1.5		4.75	7	
<i>A. ochrolaemus</i>		2.5	2–3	1		5
<i>A. rufipileatus</i>			38			
<i>A. rubiginosus</i>					1.5	

Species	Atlantic Forest ^a	Peru ^b	Peru ^c	Guyana ^d	Manaus ^e	Panama ^f
<i>Xenops rutilans</i>	10	4	0.5–4			
<i>X. minutus</i>		6	1.5–7.5	6.5	9	27
<i>X. milleri</i>					4.5	
<i>Lochmias nematura</i>	2.5					
<i>Xiphorhynchus fuscus</i>	12.5					
<i>X. pardalotus</i>					18	
<i>Lepidocolaptes squamatus</i>	20					
<i>L. albolineatus</i>		5			10	
<i>Campyloramphus falcularius</i>	12.5					
<i>C. trochilirostris</i>		0.5				
<i>C. procurvoides</i>			0.5–9	1.25	3	
<i>Myiopagis viridicata</i>	15		5			
<i>Myiopagis caniceps</i>	7.5				5	3
<i>M. gaimardii</i>		4	4–20.5	3.25	12.5	11.5
<i>Leptopogon amaurocephalus</i>	25	2.5	2.5–3	1		
<i>Corythopis delalandi</i>	37.5					
<i>C. torquata</i>		7		3.75	3.5	
<i>Myiornis auricularis</i>	25					
<i>M. ecaudatus</i>		10	10	4	6	
<i>M. atricapillus</i>						3.5
<i>Hemitriccus nidipendulus</i>	7.5					
<i>H. zosterops</i>		5			31	
<i>H. minor</i>				6		
<i>H. josephinae</i>				2		
<i>Todirostrum poliocephalum</i>	20					
<i>Todirostrum plumbeiceps</i>	5					
<i>T. crysophataphum</i>		3.5		3.5–7.5		
<i>T. pictum</i>				3.5	4	
<i>T. nigriceps</i>						0.5
<i>Tolmomyias sulphurescens</i>	47.5					
<i>T. assimilis</i>		4	4–15	2	17.5	15.5
<i>T. poliocephalus</i>		3	3–10		5	
<i>T. flaviventris</i>			4.5–16	0.75		
<i>Platyrinchus mystaceus</i>	30			4		
<i>P. coronatus</i>		7.5	7.5	15	9.5	10
<i>P. platyrhynchos</i>					6	6
<i>P. saturatus</i>					5	3
<i>Latrotriccus euleri</i>	72.5	1.5				
<i>L. virescens</i>						24*
<i>Attila rufus</i>	5					
<i>A. bolivianus</i>		4	4–14			
<i>A. spadiceus</i>		4	2–4	4.5	3	7
<i>Habia rubica</i>	7.5	8.5				
<i>H. fuscicauda</i>						3*
Average	21.7	4.5	12.8	4.3	8.4	15.8

^a This study; density extrapolated for 100 ha from data in Table 1. ^b Terborgh *et al.* (1990). ^c Robinson & Terborgh (1997). ^d Thiollay *et al.* (1994). ^e Johnson *et al.* (2011). ^f Robinson *et al.* (2000).

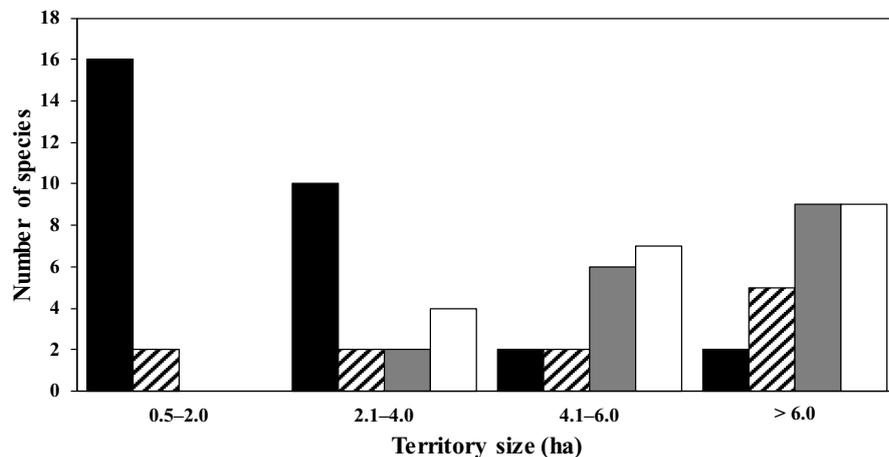


FIGURE 2. Average territory sizes (ha) of birds at the Atlantic Forest (black bars), Panama (Robinson *et al.* 2000) (cross-hatched bars), Manaus (Johnson *et al.* 2011) (grey bars), and Peru (Terborgh *et al.* 1990) (white bars).

DISCUSSION

Small territory sizes (< 5 ha) were common among insectivorous birds in the secondary Atlantic Forest fragment that we studied. Similarly, other species of insectivorous birds found in forested habitats in the Atlantic Forest Biome are known to occupy small territories and occur at high densities, including, Flavescent Warblers (*Basileuterus flaveolus*, 2 ha; Duca & Marini 2005), Variable Antshrikes (*Thamnophilus caerulescens*, 0.9 ha), Plain Antvireos (*Dysithamnus mentalis*, 0.7 ha), White-shouldered Fire-eyes (*Pyriglena leucoptera*, 1.4 ha) (Duca *et al.* 2006), and Black-checked Gnateater (*Conopophaga melanops*, 2.94 ha; Lima & Roper 2009). In addition, the territory sizes of six species of Thamnophilidae in São Paulo varied from 0.8 to 3.0 ha (Willis & Oniki 2001). As ours, all the above studies, carried out in the Atlantic Forest, have been conducted in areas that altered by human activities in the past and, thus, had a vegetation structure similar to that of our study area, although the understory of the area studied by Duca *et al.* (2006) was more open because the forest was older (> 150 years) than ours (*c.* 50 years).

When we compare species among other Neotropical biomes, the average territory size at our study site (2.4 ha) was smaller than that of congeneric birds in Panama (average size = 7.1 ha, Robinson *et al.* 2000), Peru (average size = 7.4 ha, Terborgh *et al.* 1990), and Manaus (average size = 9.0 ha, Johnson *et al.* 2011). When comparing congeneric similarly-sized species, 9 of the 11 species in Panama (Robinson *et al.* 2000) and all the 20 species in Peru (Terborgh *et al.* 1990) had larger territories than those from our Atlantic Forest plot. In Manaus, Stouffer (2007) have found the territories of *Conopophaga aurita* and *Corythopis torquatus* were 2 to about 6 times larger than we found for *C. lineata* and *C. delalandi* at MP, respectively.

As territory sizes were small at our grid, bird densities at MP were high. In their study comparing bird densities in 5000 ha tract of Atlantic Forest that suffered selective logging 25 years before their study, in Paraguay, Cockle *et al.* (2005) applied territory mapping “where possible”. They also have found high densities of territories/100 ha for some of the same species that we studied in Viçosa: Eared Pygmy-tyrant, *Myiornis auricularis* (*c.* 68 territories), Rufous-capped Spinetail, *Synallaxis ruficapilla* (*c.* 24 territories), Eared Pygmy-tyrant, *Myiornis auricularis* (*c.* 40 territories), Euler’s Flycatcher, *Lathrotriccus euleri*, Gray-bellied Spinetail, *Synallaxis cinerascens*, White-throated Spadebill, *Platyrinchus mystaceus*, Plain Antvireo, *Dysithamnus mentalis* and Variable Antshrike, *Thamnophilus caerulescens* (all these five species with *c.* 10–20 territories each). These authors have not obtained their data from a grid in the forest area sampled and territory

mapping is not clearly stated by them as the method used for deriving bird densities. However, their estimates are highly suggestive that the pattern we have found in Viçosa can occur also in pristine areas of the Atlantic Forest. It should be noted, though, that although a small number of large territories in an area often demonstrates low bird density, species with small territories that do not occupy most of the available habitat also have low densities, as have been shown for birds with patchy distribution in primary forests in French Guyana (Thiollay 1994).

The average density at our study site (22 pairs/100 ha) was higher than that for congeneric birds in Guiana (average density = 4.1 pairs/100 ha, Thiollay 1994), Manaus (average density = 8.4 pairs/100 ha, Johnson *et al.* 2011), and the two Peruvian sites (average density = 4.5 pairs/100 ha, Terborgh *et al.* 1990; average density = 12.8 pairs/100 ha, Robinson and Terborgh 1997) (Table 3). In Panama the density of 15.7 birds/100 ha was inflated by a very high density of 106 pairs/100 ha of the hyper-abundant Black-crowned Antshrike (*Thamnophilus atrinucha*) which represented almost 50% of all individual birds reported by Robinson *et al.* (2000). It should be noted, however, that when compared to South American forest bird communities, those in Central America have lower species richness, and this could result in higher densities of some populations such as at the more disturbed secondary forest in Panama (Robinson *et al.* 2000), similarly to our results and to those at successional vegetation in Peru (Robinson & Terborgh 1997). Only four of the 16 species compared in Panama (Robinson *et al.* 2000) and four of the 18 species in Peru (Robinson & Terborgh 1997) had higher densities than those in Viçosa. Also, in an additional study conducted near Manaus, Amazonia (Stouffer 2007), territories were larger (average of 13 ha) and densities were lower (average of 3.4 pairs/100 ha) than those of Atlantic Forest birds.

One important difference among the Neotropical studies compared here is the successional stage of the forest. The lowest bird densities and larger territory sizes were found in the sites with old-growth primary forest in Peru (Terborgh *et al.* 1990), Guyana (Thiollay 1994), and Manaus (Johnson *et al.* 2011). The other study site in Peru had an intermediate average density value and was carried out along a primary successional gradient (Robinson & Terborgh 1997). The second highest bird density was observed in Panama (Robinson *et al.* 2000), at a site of primary forest with plenty of gaps created by natural treefalls and storms. All the Atlantic Forest sites have secondary or selectively logged forests, often with dense understory.

Younger successional vegetation stages have higher productivity allowing higher bird density (Robinson & Terborgh 1997, Aleixo 1999). Birds density and territory size in our study site could be a response to a

denser understory and, consequently, a higher abundance of leaves and insects, as indicated by species-specific (Bechard 1982, Hunt 1996) or community (Robinson & Terborgh 1997, Casenave *et al.* 1998) studies. In fact, studies conducted in secondary forests in Amazonia have shown that territory sizes of birds in these habitats are indeed smaller, and bird density higher, than in the primary forests (Kratzer 1997, Robinson & Terborgh 1997, Kattan & Beltran 2002).

Density compensation, a phenomenon originally described for groups of islands (MacArthur *et al.* 1972, Connor *et al.* 2000), could be occurring in the small forest fragments such as MP. Density compensation results in higher density for those bird species able to colonize islands because of the lack of many species that cannot reach them. The lack of many species would thus trigger “competitor release” and “predator release”, allowing wider niches and much higher densities than in the mainland (Stamps & Buechner 1985, Connor *et al.* 2000). Although density compensation does not always happen (Connor *et al.* 2000) it could help to explain the territory patterns of the Viçosa region since we studied territories in a relatively small forest fragment (roughly 380 ha) from where several birds have already gone extinct (Ribon *et al.* 2003). The extirpation of species with niches similar to those that persisted in our area could make it possible for them to expand their use of resources and achieve higher densities and smaller territories.

Even though territory sizes and bird densities are similar among our study and the few other available studies on Atlantic Forest birds, these results should not be generalized to the biome. This is not only because there are many different vegetation subtypes to be studied (*e.g.* lowland *vs.* submontane *vs.* montane forests; southern *vs.* central *vs.* northeastern forests; old growth *vs.* secondary forests), but also because more studies are needed in order to confirm any pattern. In fact, occasional observations and captures with mist-nets by ourselves in the better preserved parts of primary forest at the Sooretama Biological Reserve (22,000 ha), in the nearby state of Espírito Santo, and at the Rio Doce State Park (32,000 ha), in the state Minas Gerais, have shown to us a very low number of birds per unit area. This suggests that at least Lowland Atlantic Forest birds in pristine forests could have a pattern more similar to that found in the Amazon by Terborgh *et al.* (1990), Thiollay (1994), Robinson & Terborgh (1997), Stouffer (2007) and Johnson *et al.* (2011) and opposite to that found in Viçosa and by Cockle *et al.* (2005) in Paraguay.

We showed here that several understory and midstory insectivorous birds have high density and small territory sizes in a secondary forest fragment of the Brazilian Atlantic Forest. This agrees with other studies of bird territories that have been carried out in

the Atlantic Forest to date. Our estimates might be useful to future conservation and management studies in the biome. However, a comprehensive determination and explanation for this proposed pattern in the biome awaits further tests.

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Waterbirds in a floodplain: influence of spatial and environmental factors through time

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ABSTRACT: Wetlands are rapidly being lost and fragmented around the world, making it imperative to seek an understanding of the drivers of their diversity. Among aquatic assemblages, birds constitute a conspicuous group that provides many ecosystem services. Here, we use a metacommunity approach to understand the influence of spatial (distance among patches) and environmental factors (local characteristics) in wading bird (Pelecaniformes and Ciconiiformes) assemblages in a river-floodplain system through time. We tested the hypothesis that, due to the small scale of our study, spatial factors have no determinant role in waterbird assemblages, and, due to the annual occurrence of flood pulses, the importance of environmental factors varies through time, according to the hydrological cycle. We tested this hypothesis using Partial Redundancy Analysis (pRDA). We used abundance data for the birds in 20 lagoons, sampled quarterly during two years. The spatial factors did not explain variation in community structure in any sampled month, whereas environmental factors explained variation in the assemblages only in two months. Due to high waterbird mobility, the non-significance of the spatial factor is expected among lagoons in the same floodplain. Environmental factors are important in determining the community structure only in two sampled months, evidencing that their importance varies through time in the floodplain, partially agreeing with our hypothesis. The non-conformity between the influence of environmental factors on assemblages and the hydrological cycle may be due to human impacts caused by the operation of upstream reservoirs, which alter the natural flood events, and caused a long drought period previous to this study. A multiscale approach is fundamental to the understanding on how anthropogenic impacts on wetlands affect waterbird assemblages. Thus, this study contributes to the understanding of how seasonality, environmental conditions of lakes, and a local spatial scale act in structuring waterbird assemblages.

KEY-WORDS: Ciconiiformes, metacommunity, Paraná River, Pelecaniformes, variance partitioning.

INTRODUCTION

Wetlands are mosaic-like environments, which generally comprise patches of different types, sizes and distances from other patches (Whited *et al.* 2000). Additionally, wetlands have suffered continuous loss and fragmentation, which has negatively affected the ecosystem services they provide and biodiversity they harbor, including waterbirds (Ma *et al.* 2009). Waterbirds (*e.g.* Pelecaniformes, Ciconiiformes, Charadriiformes, Anseriformes) are highly dispersive birds, moving between favorable areas in search of resources and are dependent on wetlands during most or all of their life cycle (Haig *et al.* 1998). The inherent patchiness and rapid loss of wetlands around the world makes it important to integrate spatial components into analyses of waterbird diversity and distribution (Paracuellos & Tellería 2004, Luis *et al.*

2005). However, few studies have considered space as a structuring factor for local waterbird communities (Pagel *et al.* 2014, Sebastián-González & Green 2014). Here, we used metacommunity theory to better understand the distribution of waterbirds in their patchy environment.

Metacommunity theory is a theoretical and mechanistic framework that serves to explain the interdependence of local and regional processes in structuring communities (Logue *et al.* 2011). As viewed through the lens of this concept, two general types of forces affect community structure: local (biotic interactions and environmental conditions) and regional (spatial dynamics, linked to the dispersal of organisms). These processes interact to produce a local species assemblage (Leibold *et al.* 2004).

Depending on the degree of influence of local and regional processes in structuring the local communities,

four perspectives were defined concerning the organization of metacommunities: neutral model, patch dynamics, species sorting and mass effects. The neutral model assumes environmental homogeneity and species with similar competitive capacities, so that their distribution is influenced only by dispersive capacity. Patch dynamics considers patches also to be homogeneous, but species differ among them, in what constitutes a trade-off between colonization and competition capacities. Species sorting assumes environmental heterogeneity associated with differences among species and with a dispersive capacity that is sufficient for the species to reach different patches, but which does not influence their distribution. Finally, mass effects considers that there is a high dispersive capacity in a heterogeneous environment, which brings to communities affected by source-sink relations, with a greater influence of dispersal than environmental heterogeneity in the structure of communities (Leibold *et al.* 2004). However, the complex dynamics of communities suggests that these models are not discrete or mutually exclusive (Logue *et al.* 2011). Winegardner *et al.* (2012) reviewed the terminology used by Leibold and proposed that the mechanisms underlying these paradigms interact. Thus, they reorganized the models according to the relative importance of dispersal, suggesting that metacommunities can be classified as follows: neutral, species-sorting with limited dispersal (which would be equivalent to patch dynamics, *sensu* Leibold *et al.* 2004), species-sorting with efficient dispersal (equivalent to species sorting), or species-sorting with high dispersal (equivalent to mass effects).

The metacommunity approach contributes to a better understanding of how spatial dynamics and local interactions influence community ecology (Logue *et al.* 2011). Studying metacommunities of waterbirds at different scales is necessary to understand how local communities are structured within and among wetlands. Considering the importance of waterbirds as suppliers of ecological services such as dispersal of seeds and eggs, ecosystem engineering, population control and scavenging, understanding their metacommunity dynamics is essential for wetland management (Green & Elmberg 2013). Knowledge on spatial dynamics for waterbird assemblages enables one to answer questions such as how distances between wetland patches influence assemblages.

As an example of how the metacommunity approach can be used to better explore the mechanisms that shape communities of waterbirds, we evaluated the local and regional drivers of assemblages of wading birds (Pelecaniformes and Ciconiiformes) in a Neotropical floodplain. Floodplains are heterogeneous environments with high biological diversity and are influenced by cyclical variation in river discharge, or flood pulses

(Junk *et al.* 1989). Flood pulses act by connecting and homogenizing the patches of aquatic environments in a floodplain and are a major driver of biodiversity in these ecosystems (Junk *et al.* 1989, Thomaz *et al.* 2007).

Pelecaniformes and Ciconiiformes are medium-to-large waders that occur in most floodplains, and many aspects of their ecology are affected by the hydrologic regime (Kushlan 1986, Dimalexis & Pyrovetsi 1997, Russell *et al.* 2002). The density and vulnerability of prey vary seasonally and spatially (Fernandes *et al.* 2009, Gimenes & Anjos 2011), and depend on the frequency, duration and magnitude of the flooding (Petry *et al.* 2003). Because wading birds forage in shallow waters, prey availability is highest when water is shallower during dry seasons (Gawlik 2002). The seasonal variation in the environment therefore makes it necessary to consider the influence of the hydrological cycle on the local communities of waders.

The goal of this study was to assess the relative importance of regional (spatial) and local (environmental) factors in structuring the wading bird communities in the upper Paraná River floodplain throughout the hydrological cycle. Due to the small scale of our study (a single floodplain spanning *c.* 50 km) and to the vagility and habitat selection capacity of birds (tending to an ideal free distribution, see Fretwell & Lucas-Jr. 1970), we expect that dispersal limitation and mass effects will not play important roles in structuring wader communities in this floodplain. At the same time, due to the cyclic alterations of the water level, we expect that the importance of environmental variables is not equivalent throughout the year. Therefore, we hypothesize that the wader metacommunity of the upper Paraná River floodplain is shaped by species sorting with efficient dispersal (Winegardner *et al.* 2012), and that the role of environmental characteristics in structuring the local communities of waders changes seasonally. Thus, we predict that the regional component will not impact metacommunity structure and that the local component (environmental conditions) will be more important during drier periods, when there is more heterogeneity among the water bodies in the floodplain.

METHODS

Study area

The Paraná River stretches for 4695 km from the Brazilian central plateau southward to the Plate River between Argentina and Uruguay. In Brazil, the Paraná River is affected by dams along most of its length, and only a stretch of 230 km between the Porto Primavera and Itaipu reservoirs remains as a floodplain (22°40'S to

22°52'S and 53°12'W to 53°38'W). The dams installed along the hydrographic basin have modified the natural pattern of magnitude, duration, periodicity and discharge frequency of the Paraná River, increasing the control on the discharge regime, eliminating the highest water level values and causing variability between night and day discharges (Thomaz *et al.* 2004). Thus, the seasonal water level fluctuation in the upper Paraná River floodplain is not continuously sinusoidal, as uninterrupted periods of falling and rising water are rarely observed (Agostinho *et al.* 2000).

The climate of the area is classified as Tropical Subtropical, with an annual average temperature of 22°C (average of 26°C in summer and 19°C in winter). The pluvial regime is marked by a wet summer, with monthly average precipitation greater than 125 mm, and a dry winter, with averages under 80 mm. The high-water period in the Paraná River usually occurs from November/December to April/May and is characterized by an increase in the water level averaging 2.5 m and reaching 7.5 m in years of extreme flood events, with almost no variation observed in years in which the characteristic flood period does not occur. It is quite common for two or three annual flood pulses to be observed during high

water levels, while smaller pulses (< 0.5 m) occur weekly in the dry season, caused by the operation of upstream reservoirs.

The study area, located between the mouths of the Paranapanema and Ivinhema Rivers, encompasses environments with very different characteristics. At this point, the Paraná River has an extensive alluvial plain on its west margin. This floodplain consists of a mosaic of habitats, including rivers, streams, channels, and marginal lagoons with different degrees of hydrological connectivity. Two types of lagoons are used in this study: permanently connected lagoons, which have an above-ground connection with the river all year long, and isolated lagoons, which are disconnected from the river during most of the year and have an above-ground connection only during flooding events.

Data collection

The birds were sampled in 2002 and 2003 (both years on February, May, August and November) in connected (permanently connected to rivers or canals, n = 10) and isolated perennial lagoons (not connected to rivers, except during the flood, n = 10) (Figure 1). The areas

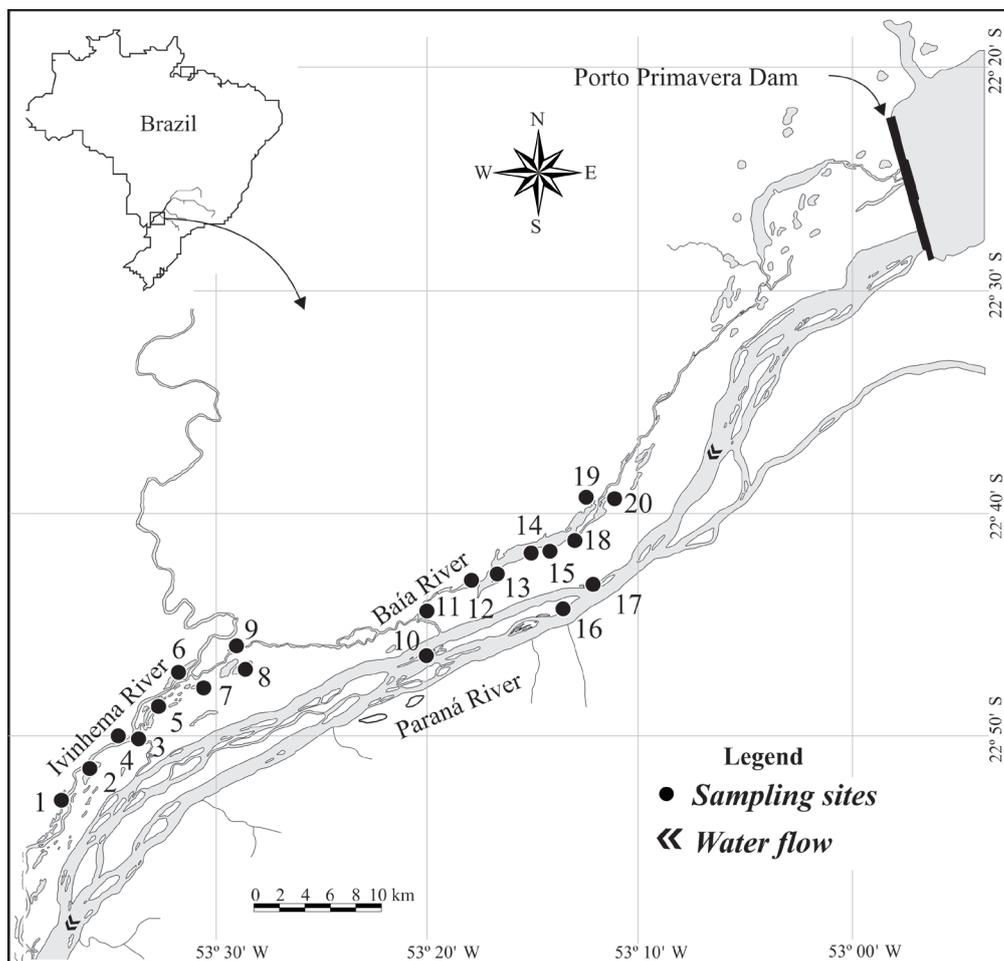


FIGURE 1. Map of the study area. The numbers indicate the sampling units. Connected lagoons: 1, 3, 6, 8, 10, 12, 15, 17, 19, 20; isolated lagoons: 2, 4, 5, 7, 9, 11, 13, 14, 16, 18.

of the sampled lagoons varied from 0.43 to 89.8 ha, and their perimeters from 251.4 to 7151.2 m. These months were chosen in order to sample all the phases of the hydrological cycle. In each month, two visits lasting for 1 h were conducted in each sampling unit, always beginning 1 h after sunrise. In each sampling, a circular transect was performed around the lagoon, through the whole perimeter, either by boat in a constant speed of 30 km.h⁻¹ (connected lagoons) or on foot (isolated lagoons), with identification and registration of each individual sighted (Bibby *et al.* 1992). The entire lagoon was fully visible along transects. Birds observed within a range of up to 5 m from the water were included, but individuals in flight were not recorded, unless they were observed leaving or arriving at the lagoons. In all sampled lagoons only the margins of the water bodies are shallow enough to allow the presence of waders. Birds were identified to species according to Sigrist (2009).

To characterize the environmental component, environmental variables considered important for the distribution of species of Pelecaniformes and Ciconiiformes and possibly related to the vulnerability of prey capture were selected. The recorded environmental variables were: perimeter (in m), average depth (in m), type of dominant vegetation in the surrounding area (forest, grasslands, macrophyte or *Polygonum*), and type of lagoon (connected or isolated). Measurements of water bodies were performed through aerial images. All datasets were obtained from the PELD Technical Report, site 6 (Souza *et al.* 2001, Souza-Filho & Stevaux 2002).

Data analyses

To determine the relative contributions of local (environmental characteristics – E) and regional factors (spatial determinants, or distances between patches – S) to the community structure of Pelecaniformes and Ciconiiformes, we used a variance partitioning technique: partial redundancy analysis (pRDA) (Borcard *et al.* 1992, Cottenie 2005). This method of analysis can be characterized as a multiple regression with multiple response variables. In this case, we used a dependent matrix (species abundance) and two explanatory matrices (spatial and environmental variables) (Legendre & Legendre 1998, Beisner *et al.* 2006). The variation in community structure was decomposed into the following components: E+S - the total variation explained by the analyses; E - environmental variation; S - spatial variation; E|S - the variation explained by the environmental variables, independent of spatial variables, or the pure environmental component; S|E - the variation explained by spatial variables, independent of environmental variables, or the pure spatial component; E∩S - the explained variation shared by environmental and spatial

variables; and the residue, or the variation not explained by any of the above components (Borcard *et al.* 1992) (Figure 2). We considered the adjusted R² values as the results of the variance partitioning procedure (Peres-Neto *et al.* 2006). The significance of each component ($P < 0.05$) was tested by Monte Carlo randomization tests (9999 runs) (Legendre & Legendre 1998).

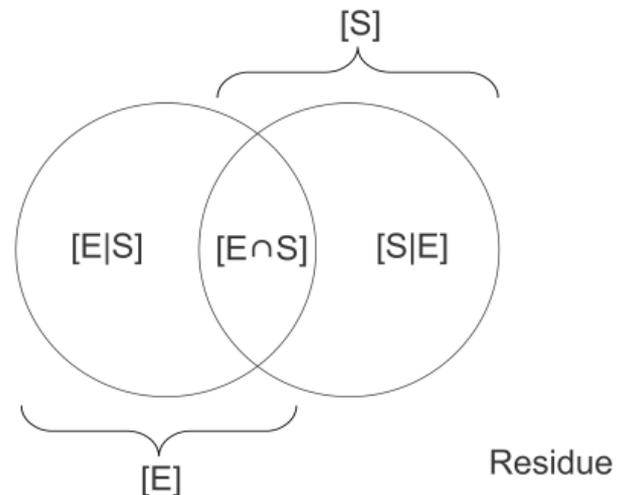


FIGURE 2. Venn diagram representing the decomposition of the community structure into: E = environmental variation or local factor, S = spatial variation or regional factor, E|S = variation explained by environmental variables independent of spatial variables, or pure environmental component, S|E = variation explained by spatial variables independent of environmental variables, or pure spatial component, E∩S = variation explained together by environmental and spatial variables; and residue, variation not explained by any of the previous components.

To construct the spatial matrix, a Euclidean distance matrix was generated between the sampled sites based on their geographic coordinates, measured from the center of each lagoon. From the distance matrix, Moran (MEM) eigenvector maps were created to quantify the spatial arrangement of the sampling points (Dray *et al.* 2006). The eigenvectors (spatial variables) allow one to represent the spatial relationships among the sampling units at different spatial scales. Small eigenvalues indicate the absence of spatial autocorrelation and, therefore, are not suitable for defining spatial structures. We included all eigenvectors with a Moran's I coefficient greater than 0.1 in the spatial predictor matrix (Nabout *et al.* 2009). Variance partitioning was carried out using total abundance data (number of birds recorded per lagoon), which were previously transformed into Hellinger values. The Hellinger distance is a measure recommended for the clustering or ordination of species abundance data (Legendre & Gallagher 2001). We performed eight pRDAs, one for each sampled month, in both years. All analyses were conducted in R software (R Development Core Team 2012) using the packages *vegan* (Oksanen *et al.* 2013) and *PCNM* (Legendre *et al.* 2013).

RESULTS

The water level of the Paraná River was higher between January and April in both the 2002 and 2003 annual monitoring periods. However, it is noticeable that the water levels varied more in the last half of 2003 than in the same

period of 2002. In fact, the water levels reached as high as 3.5 m in November 2003, the level that begins to provide connections between the river and isolated lagoons. The year 2001, which preceded our sampling activities, was markedly dry, showing minimum water level values close to 1 m and maximum values not reaching 4 m (Figure 3).

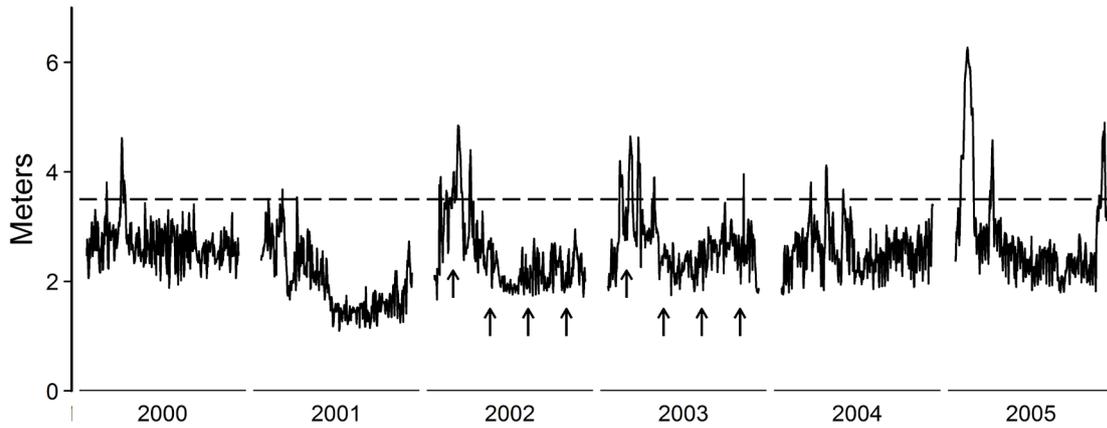


FIGURE 3. Daily fluviometric levels for years 2000–2005. Black arrows represent the sampling months. The line indicates the level at which a connection begins to be established between the environments.

A total of 2028 individuals belonging to 13 species of the orders Pelecaniformes and Ciconiiformes were recorded (Table 1). Six species were common (*Ardea cocoi*, *Butorides striata*, *Egretta thula*, *Ardea alba*, *Tigrisoma lineatum* and *Nycticorax nycticorax*), occurring in almost all sampling months (only in one month, one of the species was absent), with presence in a maximum of 22 sites each month. Other species (*Platalea ajaja*, *Bubulcus*

ibis, *Syrigma sibilatrix*, *Mycteria americana*, *Ciconia maguari*, *Jabiru mycteria*, *Mesembrinibis cayennensis* and *Theristicus caudatus*) were less abundant, occurring in only a few months and sites, mostly in connected lagoons, and present in a maximum of six sites each month. The peak of bird abundance occurred in November 2002. February 2002 and February and August 2003, in turn, were the months with the lowest abundances (Figure 4).

TABLE 1. Species registered in the study area for all the sampled months and according to sampling sites (lagoons). Lagoons are numbered according to the map (Fig. 1). Classification of the species is according to the American Ornithologists' Union (AOU).

	Connected										Isolated										
	Lagoons No.	16	2	8	13	12	7	10	11	17	6	1	14	18	20	15	9	3	5	4	19
Ciconiiformes																					
Ciconiidae																					
<i>Ciconia maguari</i>					x			x		x											
<i>Jabiru mycteria</i>			x					x	x	x											
<i>Mycteria americana</i>			x					x	x										x		
Pelecaniformes																					
Ardeidae																					
<i>Ardea alba</i>		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Ardea cocoi</i>		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
<i>Bubulcus ibis</i>					x													x			
<i>Butorides striata</i>		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x			x
<i>Egretta thula</i>		x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x			
<i>Nycticorax nycticorax</i>		x	x		x		x	x	x	x	x								x		x
<i>Syrigma sibilatrix</i>									x												
<i>Tigrisoma lineatum</i>		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
Threskiornithidae																					
<i>Mesembrinibis cayennensis</i>		x									x										
<i>Platalea ajaja</i>				x				x	x	x											

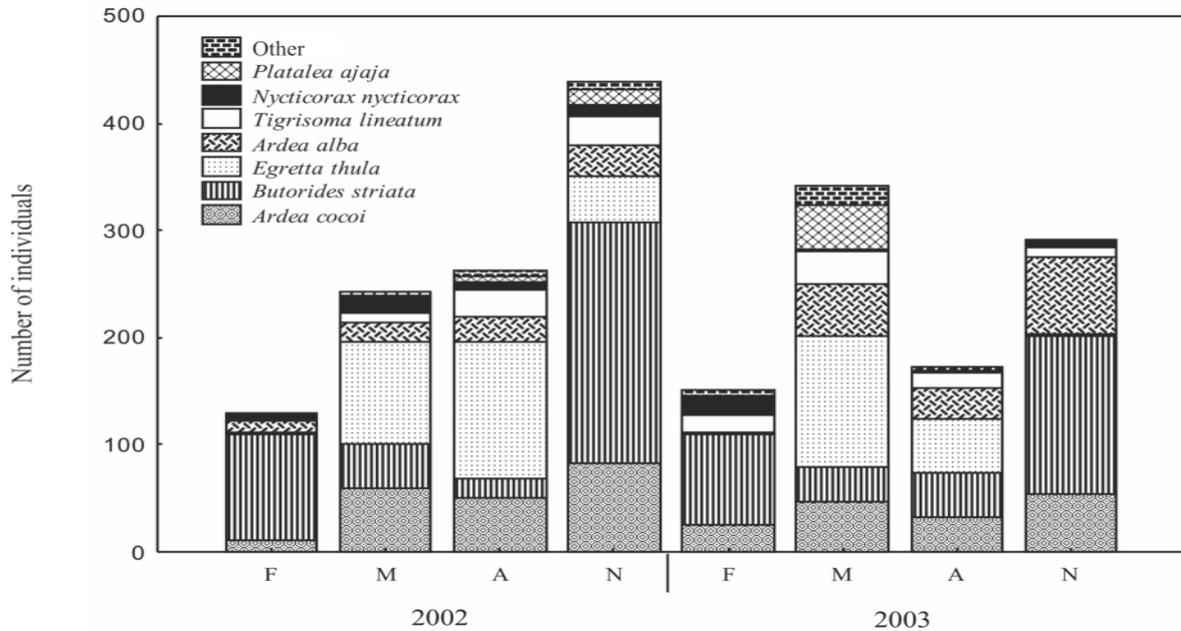


FIGURE 4. Number of individuals of the species of Ciconiiformes and Pelecaniformes recorded in the perennial lagoons of the upper Paraná River floodplain. The letters F, M, A and N stand for the months February, May, August and November, respectively.

The results of the RDA variance partitioning differed between months. In 2002, the environmental factor - E - explained the structure of the bird communities in February ($R^2 = 0.15$; $P = 0.0430$), May ($R^2 = 0.14$; $P = 0.0149$) and November ($R^2 = 0.28$; $P = 0.0001$), whereas the pure environmental factor E|S explained the variability of the communities of birds only in February ($R^2 = 0.22$; $P = 0.0257$) and November ($R^2 = 0.25$; $P = 0.0011$). In 2003, the environmental

factor E explained the structure of the communities in February ($R^2 = 0.14$; $P = 0.0215$) and November ($R^2 = 0.13$; $P = 0.0468$), and the spatial factor S was also important in February ($R^2 = 0.13$; $P = 0.0060$). The pure environmental factor - E|S - did not explain the variation of community structure observed in any month of 2003, and the pure spatial factor S|E showed no importance for the communities in any month of this study (Table 2).

TABLE 2. Variance partitioning of the community structure of Ciconiiformes and Pelecaniformes in different months during the two years of sampling in the 20 lagoons of the upper Paraná River floodplain. E = environmental variation, S = spatial variation, E|S = pure environmental component, S|E = pure spatial component, E∩S = shared variation explained by environmental and spatial variables; residue, or unexplained variation; significance level at $P < 0.05$, Adj. R^2 = adjusted coefficient of determination. Significant values are underlined.

	February		May		August		November	
	Adj. R^2	P	Adj. R^2	P	Adj. R^2	P	Adj. R^2	P
2002								
E	0.15	<u>0.0430</u>	0.14	<u>0.0149</u>	0.03	0.2951	0.28	<u><0.0001</u>
S	0.06	0.7305	0.01	0.3256	0.01	0.3322	0.05	0.0958
E S	0.22	<u>0.0257</u>	0.10	0.0748	0.00	0.7105	0.25	<u>0.0011</u>
S E	0.02	0.3161	0.00	0.6917	0.00	0.8977	0.02	0.2471
E∩S	0.00		0.04		0.07		0.04	
Residue	0.82		0.89		1.00		0.69	
2003								
E	0.14	<u>0.0215</u>	0.06	0.1681	0.00	0.4450	0.13	<u>0.0468</u>
S	0.13	<u>0.0060</u>	0.04	0.1824	0.00	0.5351	0.09	0.0521
E S	0.04	0.2288	0.03	0.3188	0.00	0.6269	0.06	0.1864
S E	0.04	0.1753	0.01	0.3996	0.00	0.7578	0.02	0.2976
E∩S	0.10		0.03		0.03		0.07	
Residue	0.83		0.93		1.00		0.85	

DISCUSSION

Although we have used the metacommunity concept to analyze local communities of waders in a single floodplain, we should emphasize that this approach can be a useful tool, especially to determine the pattern of waterbird communities at larger scales, *e.g.* among different wetlands. Given that human activities often change the spatial structure within and among wetlands, a multiscale approach is essential for understanding how these changes may affect waterbird communities. Therefore, our approach should be viewed as a first step in understanding the importance of the metacommunity concept in structuring local communities of waterbirds.

As we hypothesized, the pure spatial factor S|E did not play an important role in shaping the local communities of waders. Wading birds are highly vagile, which allows them to keep up with the seasonally fluctuating mosaic of suitable habitat (Fretwell & Lucas-Jr. 1968, Haig *et al.* 1998). For this reason, distances between sites may not be important in shaping communities at small spatial scales. Meynard & Quinn (2008) suggested that for bird communities studied on a scale of 1000 km or less, environmental factors will predominate, whereas dispersion will become more important for the structure of local communities at larger scales. Thus, it is expected that space does not play an important role for wader communities within patches of a single floodplain (see Figure 5).

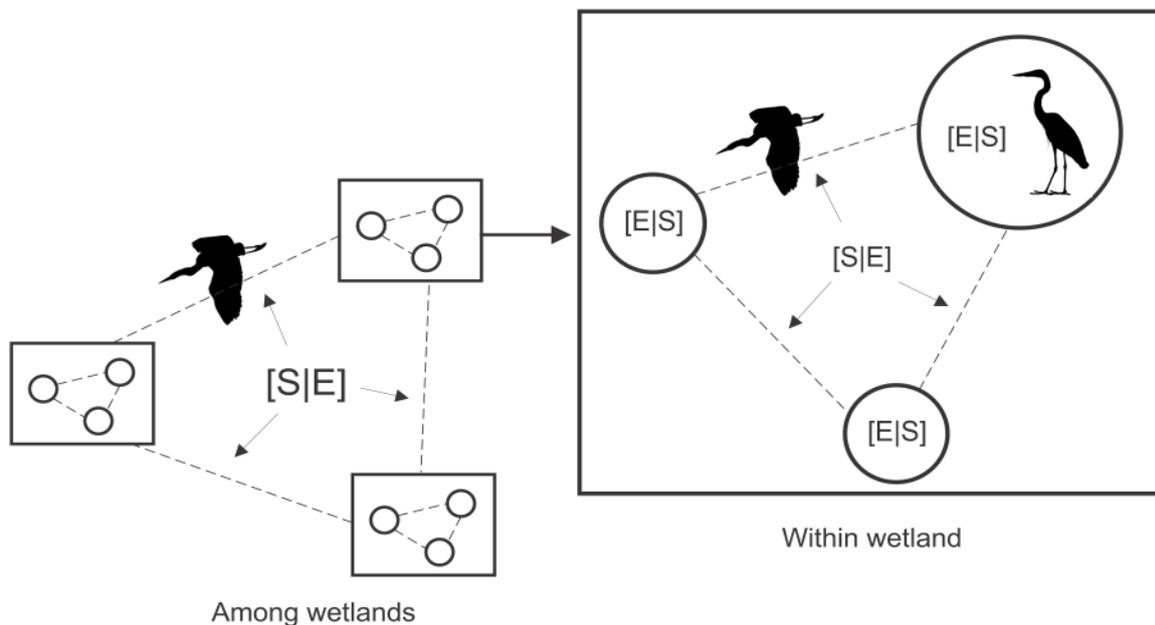


FIGURE 5. Schematic representation of how Local (environmental - LF) and Regional (spatial - RF) factors may influence waterbird assemblages within and among wetlands. Larger distances between sites may imply a more important role of the regional factor in structuring communities.

The significance of the pure environmental component E|S in February and November 2002 shows that these waterbird communities are influenced by local factors and also that the importance of the purely environmental factors varies according to time in the floodplain, partly corroborating our hypothesis. Although we hypothesized that there would be temporal variation in the importance of E|S, we also predicted that the pure environmental factor would be important in most months, being more important during drought. This prediction was not confirmed by data. The pure environmental component was significant only in two months, February and November 2002, the first of which falls within the beginning of the flood period.

The contrasting results found in 2002 and 2003 may be the outcome of human impacts in the Paraná River floodplain. As the Paraná River and its tributaries

are affected by dams, one of the main downstream impacts of the reservoirs is to change the natural water level fluctuations. This change affects the water exchange between the river main channel and the floodplain, and, in extreme years, even the absence of floods is observed. This alteration in the hydrological regime directly impacts wading birds whose life cycles depend on water fluctuation (Agostinho *et al.* 2004). During the two sampled years of this study, the water regime was not consistent. The first year (2002) was typical, with floods occurring from January to April and lower water levels characterizing all other months. The second year of sampling (2003) also had a typical flood period in its first months, but the expected dry period had a higher water level than the same period of 2002, with several flood pulses reaching the level at which the river starts to overflow. Additionally, 2002 was preceded by a dry year, in which the supposed

flood period was characterized by a water level closer to the levels observed in the last months of 2003 (Figure 3).

The variation in the importance of the environmental factor to the local communities of waders is linked to the flood regime of the floodplain. The pure environmental component was important in shaping the community in February 2002, the beginning of the flood, and in November 2002, the end of the dry period. This result might be explained by the differences in water fluctuation among 2001, 2002 and 2003. Wading birds seek optimal foraging habitats given their morphological and behavioral restrictions. They then select habitat based on local conditions. To reflect this, the environmental variables selected for this study are related to the availability of prey to waders, the majority of which are piscivores (Bancroft *et al.* 2002, Gawlik 2002). Previous studies performed in the same floodplain showed that differences among the density of fish in different lagoons increase during the year, becoming more apparent at the end of the dry period (Fernandes *et al.* 2009, Gimenes & Anjos 2011). Additionally, according to Thomaz *et al.* (2007), a time lag is expected after the flood period until the effects of environmental heterogeneity become apparent. Thus, we suggest that there is a tendency for the environmental factor to become more important in shaping communities at the end of the dry period (represented by November in our samples). As we see, 2003 was an atypical year, in which higher water levels caused an interruption in the dynamics of the dry period and thus altered the role of the environment in structuring waterbird communities. In the same way, the significance of the pure environmental factor in February 2002 may be a consequence of the dry year that preceded it. Specifically, as the flood period was still at its beginning in February, it is possible that the effects of the flood pulse were delayed by the long 2001 drought.

The lack of signal from our explanatory variables may be in part due to limitations of our study. The lack of importance of the spatial factor may be associated with the small scale of the floodplain. As wading birds are vagile organisms, the size of the floodplain may be too small for distances between sites to influence the structure of the community. At the same time, environmental characteristics other than those considered in this study are known to influence waterbird assemblages, such as water transparency, productivity, aquatic vegetation and marginal vegetation (Bancroft *et al.* 2002, Guadagnin & Maltchik 2007, Cintra 2015). The addition of such variables could increase the importance of environmental factors or change its seasonal variation. Furthermore, sampling along only two years could not be enough to determine a seasonal variation pattern of the importance of environmental or spatial factors for wading bird community structure. More years of study could bring

better information on the influence of the hydrological cycle for these organisms.

This study is an example of the use of the metacommunity concept as an important tool to better understand the drivers of waterbird diversity in space and time. Knowing the factors driving waterbird distribution in space, as well as the variation in the importance of these factors seasonally is essential to understand waterbird community dynamics. Here, we showed that space is not a strong driver of wading bird assemblages at small scales, considering the area of a floodplain. Furthermore, we showed that there is seasonal variation in the importance of the environmental variables used in this study for this group of waterbirds. Indeed, environmental variables other than those used in this study could be important for these birds in different phases of the flood regime. These additional variables, such as water transparency and aquatic vegetation, could be the focus of future investigations. This approach can be explored to recognize important factors for the maintenance of waterbird communities in recognition of the continuous loss, alteration and fragmentation of wetlands around the world.

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Breeding biology of the Atlantic Least Tern (*Sternula antillarum antillarum*) in a colony of the south of the Gulf of Mexico: new perspectives for its threat status

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ABSTRACT: Although the Atlantic Least Tern (*Sternula antillarum antillarum*) faces the same threats that caused the California Least Tern (*S. antillarum browni*) and the Interior Least Tern (*S. antillarum athalassos*) to be declared threatened, it is considered as “Least concern” globally, mainly because of its wide geographic distribution. However, many populations are threatened and the conservation status of several others is unknown. We evaluate, for the first time, the breeding biology of a colony of Atlantic Least Terns in the southern Gulf of Mexico. During the 2010 breeding season we censused and analyzed some relevant breeding variables for the stability of a colony at Terminos Lagoon. The starting date of egg laying and breeding peak, the clutch size variation during the breeding season and the main causes of eggs loss are similar to those reported for other colonies of this species. However, we found that the size of first (A) and single (S) eggs did not change throughout the season, but second (B) eggs size decreased. The number of breeding pairs and its higher hatching success in comparison with other colonies allow us to affirm that the colony of the Terminos Lagoon must be taken into account in conservation programs of this species. These results will settle the basis to reconsider its threat status globally and to compare breeding parameters with other colonies from the region.

KEY-WORDS: clutch size, conservation, egg size, hatching success.

INTRODUCTION

Seabirds are one of the most threatened taxon globally, with more than 25% of the species listed in risk categories by the International Union for Conservation of Nature and Natural Resources - IUCN (Croxall *et al.* 2012). This is mainly due to consequences of human activities like pollution, overfishing, egg collection for human consumption, loss of habitat, tourism, invasive species on the breeding grounds and global climate change (Croxall *et al.* 2012). These threats have raised the need of monitoring. However, because of its vulnerability, it is imperative that monitoring techniques to measure reproductive variables are noninvasive and low stress.

Laying start date, egg and clutch size are within the most important variables of reproductive success of birds. Females nesting early in the season mate with good quality males and choose the best nesting sites (Wendeln 1997), which is reflected in bigger eggs and larger clutches (Morris 1987). Larger chicks will hatch

from larger eggs (Parsons 1970, Blomqvist *et al.* 1997, Krist 2011) which is beneficial because a greater size at hatching enhances survivorship (Parsons 1970, Amat *et al.* 2001) at least during the first days of life when chicks are more vulnerable to weather and predators (Galbraith 1988, Williams 1994, Dawson & Clark 1996). Thus, egg size influences fitness (Reviewed in Krist 2011) and clutch size is correlated with breeding success (the combination of hatching and fledging success; Langham 1974). At the present, in some seabird species, clutch and egg size are diminishing through time when compared with long term data sets: *i.e.* Glaucous-Winged Gulls (*Larus glaucescens*: Blight 2011) and Atlantic Puffins (*Fratercula arctica*: Barrett *et al.* 2012).

The Least Tern (*Sternula antillarum*) breeds throughout the coastal beaches and interior rivers of USA, Mexico, the Caribbean, and the coasts of Central and South America. Because of its large range, the Least Tern has been catalogued under the category of “Least concern” by the IUCN (IUCN 2016). However, its steep decline

classifies two of its subspecies, the California Least Tern (*Sterna antillarum browni*) and the Interior Least Tern (*Sterna antillarum atthalasso*), as “Endangered” in the USA (US Fish and Wildlife Service 2013), and under special protection in Mexico (Diario Oficial de la Federación 2010). These new categorizations are a consequence of the loss of their breeding and feeding grounds (Massey 1974), eggs and/or chick predation, tidal floods, human activities, and pollution (Hothem & Zador 1995). The third, nominate subspecies, the Atlantic Least Tern, is facing threats as well. Some states within United States have declared it under threat (*e.g.* Maine Department of Inland Fisheries and Wildlife 2009, Delaware Division of Fish and Wildlife 2013, New Hampshire Wildlife Action Plan 2015, New Jersey Department of Environmental Protection 2015). In addition, the colonies of St. Kitts, West Indies, and the main colony in the Caribbean in the Virgin Islands are also under threat (Lombard *et al.* 2010, Stimmelmayer *et al.* 2014). In Mexico, however, except for some published papers (Ornat *et al.* 1989, Winker *et al.* 1999, Navarro-Sigüenza & Peterson 2007) about their presence in some Mexican states and the sighting of a few nests in the Mexican state of Veracruz (Mellink *et al.* 2007), nothing is known about the conservation status of the Atlantic Least Tern. For this reason, the objective of the present study is to quantify variables related with reproductive success such as number of breeding pairs, number of eggs laid/hatched, eggs size and egg mortality of an Atlantic Least Tern colony in the Mexican part of the Gulf of Mexico. These results will provide a baseline data that will facilitate future research and a possible change of its threat status since it is clear that the Atlantic Least Terns in Mexico are facing the same threats that led the other two subspecies to become threatened.

METHODS

We carried out fieldwork during 2010 in one of the several small islets at the Terminos Lagoon located at the south of the Gulf of Mexico and west coast of the Yucatan Peninsula, Mexico (18°45'10.83"N; 91°29'14.23"W) in a population of Atlantic Least Terns which had not been reported previously. We counted, identified and marked the nests during the breeding season (from late April to the end of June). We started checking the nests on 26 April, when 30 nests were already present. During the first three weeks of our monitoring, nests were visited every 3 days. Because more than 10 new nests were found on each visit after the second week, we started to visit the colony daily from week 3 until 26 June, when the tropical storm Alex hit the islet and destroyed every active nest. We visited the islet again on the days 3 10 and 24 July, and no nest was found.

During each visit to the islet, we walked around

the colony from 6:00 to 8:00 h in search of new nests. Every time we found a new nest, we identified it with a numbered flag and marked the first egg (A- or Single S-egg) with non-toxic red ink. After that, we marked any new eggs with blue (second or B-egg) and green (third or C-egg) to identify them according with their laying order. After marking each egg, we measured their breadth and length using a caliper with a 0.01 mm precision and calculated the egg volume with the equation $V = 0.4866 \times \text{length} \times \text{breadth}^2$ (Coulson 1963). Nest marking and egg checking was always done before 10:30 h or after 16:30 h to minimize heat stress. We divided the islet in a central zone of 1 m a.s.l. and a peripheral zone of less than 40 cm a.s.l.

The fate of each egg was defined as successful or failed: predated, overwashed (the main threat to Least Tern nests *sensu* Brooks *et al.* 2013) or abandoned. We considered a successful hatching if the egg completed their incubation time (counting 20–22 days after being laid) and inferred hatching by the presence of eggshells or a recently hatched chick within close proximity (25 cm) to the nest. We registered a nest as tidal flooded, by tidal marks on the beach and signs of the water to have reached or covered eggs (water on the nest cup, eggs moved on the beach). A nest was recorded as predated when eggs disappeared, eggshells were broken with yolk stains, and no evidence of tidal floods was found. We considered an egg as abandoned if it was cold and/or moisture was seen on the eggshell. Every day we conducted observations with binoculars from one of the ends of the islet for at least 3 h (90 min at 6:00 h and 90 min at 16:30 h) to identify the presence of potential predators and we registered the number of direct attacks (*sensu* Rounds *et al.* 2004).

We estimated the hatching date by counting 20–22 days after eggs were laid. We defined hatching success as $(\text{No. of eggs hatched}/\text{No. of eggs laid} - \text{Total No. of eggs lost}) \times 100$. We excluded the eggs lost during the tropical storm because they did not complete incubation. We also calculated the hatching success along the breeding season and for each egg type (A, B or S). For this study we did not attempt to estimate fledging success because we did not have a way to individually marking chicks (*e.g.* colored rings) in order to recognize them, as they are cryptic and mobile since the first 1–2 days of hatching.

We performed statistical analyses using STATISTICA version 8.0 for Windows (StatSoft 2007).

RESULTS

We found 240 nests during the 2010 breeding season on the studied islet. However, 30 of them were not included in the analyses because we could not estimate the laying date and laying order. From the 210 marked nests, 120 had two eggs (57.1%), 83 had a single egg (39.5%)

and seven had 3 eggs (3.3%). Clutches were not laid in a continuous way, *i.e.* there were three laying waves: 1) from 6 May to 13 May; 2) from 23 May to 30 May; and 3) from 10 June to 18 June. During the first (55 nests) and second (118 nests) waves, all nests were located in the central area. On the contrary, during the third wave (37 nests), all of them were in the periphery. Because there were few three-egg clutches, they were not included on the analyses of egg size variation (Table 1).

Clutch size variation

Clutch size ranged from one to three eggs (Mode, $M_o = 2$, mean \pm standard error SE = 1.64 ± 0.04 eggs per nest). Clutch size decreased along the breeding season ($\chi^2 = 24.37$, $df = 4$, $n = 210$, $P < 0.001$). First wave clutches were larger than clutches in the second ($\chi^2_1 = 15.36$, $P < 0.001$) and third waves ($\chi^2_1 = 12.42$, $P = 0.001$). Clutches in the second and third waves were similar in size ($\chi^2_1 = 0.11$, $P = 0.74$) (Table 1).

Egg size variation

Egg size varied accordingly with egg type (A-, B- and S-eggs), as well as the clutch size (GLM Factorial ANOVA: type of egg: $F_{1,314} = 84.12$, $P < 0.001$ clutch size: $F_{1,314} = 26.56$, $P < 0.001$). A significant interaction was found between wave number and egg type ($F_{2,314} = 4.23$, $P = 0.015$). Tukey HSD *post hoc* tests showed that A- and S- eggs were similar in size along the breeding season, but B-eggs were smaller in the third wave than B-eggs in the first and second waves ($P < 0.001$; Figure 1). B eggs were smaller than both A- and S- eggs during the second and third waves ($P < 0.001$; Figure 1). Through the Wilcoxon's test we found that eggs in 2-egg clutches were smaller, in volume, than eggs from single egg clutches during the second ($W = 9996$, $P = 0.047$) and third waves ($W = 825$, $P = 0.025$), but we did not find significant differences in volume between eggs from different size clutches during the first wave ($W = 3858$, $P = 0.51$) (Table 1).

TABLE 1. Reproductive parameters of the three nesting waves of Atlantic Least Terns (*Sternula a. antillarum*), hatching success, and causes of egg loss at Terminos Lagoon, Mexico, during 2010.

Breeding parameters	Wave 1	Wave 2	Wave 3	Total
Number of nests	55	118	37	210
Clutch size (mean \pm SE)	1.9 ± 0.04	1.7 ± 0.04	1.6 ± 0.06	1.64 ± 0.04
Clutch range	1–3	1–3	1–2	1–3
Nests with one egg	8	56	19	83
Nests with two eggs	42	60	18	120
Nests with three eggs ¹	5	2	0	7
S- Eggs (cm ³) (mean \pm SE)	8.07 ± 0.13	7.99 ± 0.07	7.82 ± 0.10	7.96 ± 0.06
A- Eggs (cm ³) Mean \pm SE)	8.3 ± 0.11	8.02 ± 0.07	7.71 ± 0.1	8.01 ± 0.06
B- Eggs (cm ³) (mean \pm SE)	7.68 ± 0.09	7.48 ± 0.08	6.63 ± 0.10	7.43 ± 0.06
A+B Eggs (mean \pm SE)	7.99 ± 0.08	7.75 ± 0.06	7.17 ± 0.12	7.75 ± 0.05
Total eggs laid	107	182	55	344
Total failed eggs (%) ²	7 (6.5)	30 (16)	21 (38.2)	58 (20)
Total eggs hatched (%) ²	100 (93.5)	122 (80.3)	10 (32.3)	232 (80)
S-Eggs (%) ²	6/8 (75.0)	42/51 (82.3)	5/12 (41.7)	53/71 (74.6)
A-Eggs (%) ²	42/42 (100)	43/48 (89.6)	4/11 (36.4)	89/101 (88.1)
B-Eggs (%) ²	40/42 (95.0)	34/47 (66.0)	1/8 (12.5)	75/97 (77.3)
A+B Eggs (%)	82/84 (97.6)	77/95 (80.1)	5/19 (26.3)	164/198 (82.3)
Non-viable (%) ³	0	7 (4.6)	0	7 (12.1)
Predated (%) ³	7 (6.5)	23 (15.1)	10 (32.2)	40 (68.9)
Tidal flooded (%) ³	0	0	11 (35.5)	11 (19.0)
Destroyed by tropical storm "Alex" (%)	0	30	24	54 (15.7)

¹ Eggs do not included in the eggs size variation.

² Eggs lost during the storm were not included to calculate these percentages.

³ Percentage of the total of eggs lost.

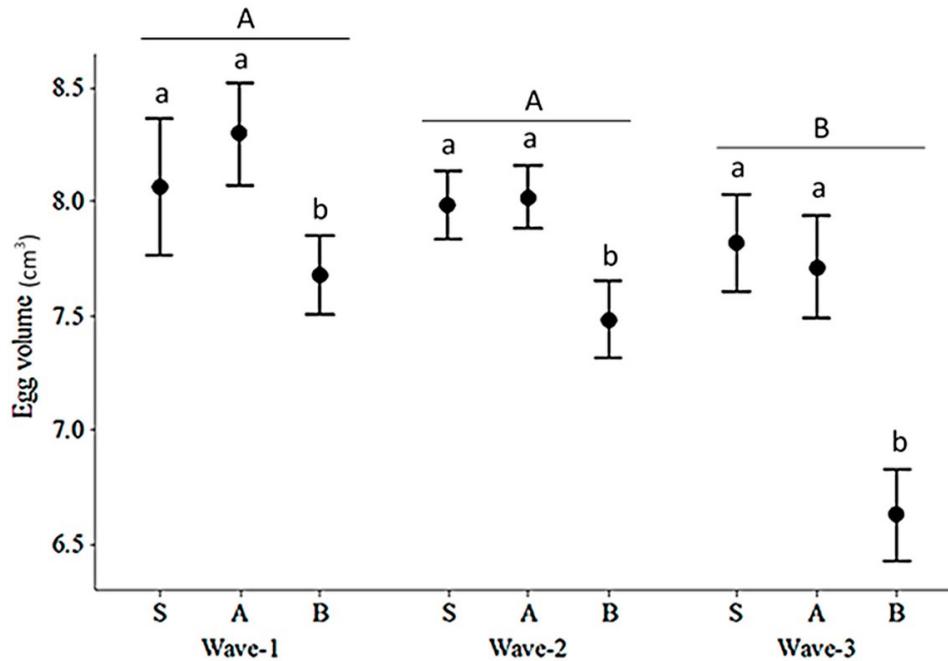


FIGURE 1. Variation in the egg size of Atlantic Least Terns (*Sternula a. antillarum*) between egg types and throughout the breeding season at the Terminos Lagoon, Campeche, Mexico. Points with different letters (a and b) indicate significant differences within waves ($P < 0.05$). Between waves differences were only found in B eggs from the third wave (B).

Predation and tidal floods threats

We observed several egg and chick predators: one Peregrine Falcon (*Falco peregrinus anatum*), two Great Blue Herons (*Ardea herodias*), two Great Egrets (*Ardea alba*), four Laughing Gull (*Leucophaeus atricilla*) pairs breeding on the same islet, and around 80 pairs breeding in nearby islets. Moreover, we registered attacks of Ghost Crabs (*Ocyrode quadrata*), all of them repelled by incubating adults. We estimated that 69% of eggs lost before the tropical storm Alex hit the islet were due to predation, being the main cause of egg lost during the first and second waves. On the other hand, if we estimate the number of eggs lost as a percentage of the total eggs laid during each wave, the third wave was the period with the greatest percentage of predated eggs (Table 1). Tidal floods accounted for the loss of 19% of the eggs during the season. However, all eggs lost by tidal floods were from the third laying wave (Table 1) on peripheral nests. Moreover, 12% of the eggs lost were non-viable and occurred during the second wave (Table 1).

Of the seven non-viable eggs found, 4 were B eggs and a single S, A and C eggs each. Tidal floods accounted for the loss of 5 S, 3 A and 3 B-eggs. Predation was the cause of the loss of 40 eggs, 11 of which were S, 13 B and 5 C-eggs.

Hatching success

Until the arrival of the tropical storm Alex on 26 June, 290 eggs should have completed their incubation period,

but only 232 of them hatched, the rest were lost due to predation, tidal floods or were non-viable, resulting in a pre-storm hatching success for the whole colony of 80%. At that time, all of the 107 eggs laid during the first wave, 152 out of the 182 eggs laid during the second, and 31 of the 55 eggs laid during the third wave should have completed their incubation time (Table 1). Hatching success in the first wave was higher than in the second (Fisher's exact test: $P = 0.003$), while success in the second wave was higher than in the third one (Fisher's exact test: $P < 0.001$). Hatching success was similar between A and S eggs along the season, but decreased in B eggs (Table 1). Two-egg nests were more successful early in the season (Fisher's exact test: $P = 0.04$), while single egg nests were not more successful than 2-eggs nests during the third wave (Fisher's exact test: $P = 0.45$).

DISCUSSION

While the distribution range of the Atlantic Least Tern is vast, there are numerous reports that cast doubt on the viability of populations throughout its range, as a result from reduced breeding success (Lombard *et al.* 2010), a reduction in the genetic diversity in populations (Draheim *et al.* 2012), the decrease of the number of colonies or the population size of the colonies in a given region (Alleng & Whyte-Alleng 1993) and the unknown status of several populations. The 344 nests found in this study are equivalent to the 4.7% of the breeding pairs from Maine to Virginia (between 7000 and 7500; Kress

et al. 1983), 17% of the 2000 pairs nesting on natural beaches in coastal South Carolina, Georgia, and north Florida (Jodice *et al.* cited in Brooks *et al.* 2013) and 15% of the 2250 breeding pairs estimated for the Caribbean (McGowan *et al.* 2006). Therefore, based only on its size, we can affirm that the colony of the Atlantic Least Tern in the Terminos Lagoon, is large enough to be taken into account in the management plans for the species. The present work establishes a baseline for long-term monitoring of this subspecies in the Mexican Gulf of Mexico, taking into account its breeding biology, which will allow a more accurate assessment of the threat status of this subspecies along their geographical distribution.

Early nesting pairs (wave 1) have larger clutch sizes than those who laid on the second and third waves. In addition, adults nesting later (waves 2 and 3) tend to lay single egg clutches and when they lay 2 eggs in the third wave, the second egg is rather small (Figure 1). In the studied colony, early nesting pairs had higher hatching success than pairs nesting at the peak of the breeding season (second wave). Clutch size *per se* may not explain the hatching success variation because we found that clutch sizes were similar between waves two and three, but those from the second wave were more successful. Egg size alone did not explain hatching success: single eggs were as big as A eggs, and bigger than B eggs, but had overall lower hatching success than A eggs and were as successful as B eggs. Resource depletion as the season goes by may not explain our results because pairs nesting late (wave 3) had clutch sizes as large as in the peak of the breeding season, and cannot explain why S and A eggs remained as big as eggs laid early in the season.

However, results indicate that some of the interactions between those variables are important for hatching success. We suggest that those interactions depend on breeding time within a season. Nesting early in the season enable parents to choose the best nesting sites (Sergio & Newton 2003), face low competition for food and reduce the predation or tidal flood risk, so they can lay two or three egg clutches with a high probability of hatching. However, just pairs in good condition can do it (Eising *et al.* 2001). As the season goes on, the capacity of breeding pairs to produce two or more egg clutches decrease, thus, in order to maintain the size of A eggs without reducing the clutch size, they produce ever smaller B eggs or even stop producing them (single egg nests; Perrins 1996). Thus, we suggest that clutch size, egg size and the proportion of each type of egg in each wave during the breeding season should be included in the assessment of the conservation status of this species.

Results from the present study suggest that the Atlantic Least Tern population in the Terminos Lagoon is worthy to preserve. Nonetheless, given the great variation in reproductive success of this species between breeding

seasons (*i.e.* Szell & Woodrey 2003) along with the loss of genetic diversity (Draheim *et al.* 2012), could put the survival of this population at risk. Thus, a periodic evaluation of the breeding biology of this colony is necessary. Reproductive parameters like clutch and egg size, as well as laying date, are altered by stressors such as tourists walking through the nesting sites (Erwin 1989), pollution (Rattner *et al.* 2013) and climate change (Jarvinen 1996, Ancona *et al.* 2011, Munroe *et al.* 2014). The value of this study is that it will serve as a baseline for long term studies on the Atlantic Least Terns breeding in the eastern coasts of Mexico and provide information in order to reevaluate its global status.

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Year-round presence of Slaty Thrush (*Turdus nigriceps nigriceps*) in mountains of central Argentina

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ABSTRACT: The migration patterns of passerine species in the Neotropical region present several gaps of knowledge. The migratory behavior of the Slaty Thrush (*Turdus nigriceps nigriceps*) has been well characterized in their central and northern distribution along eastern slopes of the Andes from Argentina to Ecuador. The Slaty Thrush was historically considered a migrant breeder in the southern extreme of their distribution. In the present study, we show new evidence of the resident status of this species in its southernmost distribution on western slopes of Sierras Grandes and Sierras de Comechingones in Córdoba Province, Argentina. There, the Slaty Thrush has a year-round presence only at sites invaded by fleshy-fruited alien plants. The main invasive plants form dense patches of vegetation and offer an abundant fruit supply that is highly consumed by this bird species during autumn–winter, when there are no native fruits available. We suggest that the Slaty Thrush was a migrant species in past decades, but the recent invasion by fleshy-fruited species could explain its actual year-round presence by providing fruit in a period of the year of food shortage and new suitable habitats.

KEY-WORDS: Chaco Serrano Woodland, Córdoba, nonbreeding season, plant invasion, western Sierras Grandes.

INTRODUCTION

Several species of the Turdidae family are distributed over the different Argentinian ecosystems (Mazar-Barnett & Pearman 2001), but the ecology of some of them is still poorly understood (Collar 2005). Slaty Thrush (*Turdus nigriceps*) is a medium size thrush (21.5 cm). Males are mostly dark gray above, blacker on the crown and have a white throat sharply streaked blackish; females are basically brown where males are gray, though some gray shows on the sides and flanks (Ridgely & Tudor 2009). According to Sibley & Monroe (1993), the Slaty Thrush have a controversial taxonomic status with two currently recognized subspecies distributed allopatrically (Collar 2005, Remsen-Jr. *et al.* 2015; it is considered as two full species for Ridgely & Tudor 2009). Both subspecies are mainly frugivorous and occasionally consume arthropods and earthworms (Rougès & Blake 2001, Collar 2005).

Turdus nigriceps subalaris is an uncommon breeder in humid forests and woodlands in eastern Paraguay, southeastern Brazil and northeastern Argentina. In austral winter, this subspecies migrates to non-breeding areas in northern to southern central Brazil (Ridgely & Tudor 2009, but see Vogel 2014). *Turdus nigriceps nigriceps* is a fairly common breeder in montane forest and woodland

on eastern slopes of the Andes from western Bolivia (Cochabamba and southern Beni) to northwestern Argentina (the southernmost distribution in La Rioja and Córdoba Provinces). The breeding season begins in November–December and ends in January–February, when nestlings leave the nests (Collar 2005). In austral winter (June–September) populations at the southern end of the distribution migrate north following the Andean forests and reach eastern Peru. At the northern end of their distribution, *T. nigriceps* is resident and breeds in montane woodlands and even in scrublands from southwestern Ecuador (mainly Loja) to northwestern Peru (northern Cajamarca and Lambayeque; see Figure 1; Ridgely & Greenfield 2001). In Argentina, *T. nigriceps* is a partial migrant in the southern Yungas of Tucumán, Jujuy and Salta Provinces (Rougès & Blake 2001, Capllonch *et al.* 2008), and Collar (2005) suggests they may undertake altitudinal movements. Details about the migratory behavior of this species in its southernmost distribution remains unclear (see Collar 2005 and Appendix I in Capllonch *et al.* 2008).

In Córdoba Province, the Slaty Thrush was historically considered a scarce summer migrant (Nores *et al.* 1983, Yzurieta 1995) because of the absence of winter records until the last decade of the 20th Century (M. Nores,

pers. comm.). However, recent records during the non-breeding period questioned the actual migratory status of the subspecies in the southernmost area of its distribution (Barri *et al.* 2015). In this area, the Slaty Thrush inhabits humid ravines of the Chaco Serrano woodlands (Yzurieta 1995, Figure 1) from 900 to 1500 m a.s.l. (Luti *et al.* 1979, Cabido *et al.* 1998). Currently, many areas of this region suffer from anthropogenic alterations such as plant invasions, urbanization, and periodic fires (Hoyos *et al.* 2010, Giorgis & Tecco 2014, Argañaraz *et al.* 2015). These alterations modify the environmental physiognomy and food resource abundance and availability (Hoyos *et al.* 2010, Tecco *et al.* 2013). Some invasive plants such as *Pyracantha* spp., *Ligustrum lucidum* and *Morus alba* produce fleshy fruits that are widely consumed and dispersed by birds like Slaty Thrushes (Vergara-Tabares *et al.* 2016). Fruit production by these plants may alter the temporal availability of this resource (Vergara-Tabares *et al.* 2016), because they produce fruits in periods of food scarcity (*i.e.* autumn-winter, Tecco *et al.* 2013). Thus, fleshy-fruited plant invasions may be involved in a switch of Slaty Thrush behavior from migratory to resident. In the present study we (1) report the year-round presence of Slaty Thrush in its southernmost distribution in Chaco Serrano woodlands, and (2) discuss the potential effect of fleshy-fruited invasive plants on the residence status of the Slaty Thrush.

METHODS

Study area

The study was carried out in six sites located on western slopes of Sierras Grandes and Sierras de Comechingones between 900 to 1300 m a.s.l., Córdoba Province, Argentina (Figure 1). The topography of each selected site is characterized by a ravine where runs a stream. All six sites present a plant assemblage corresponding to the Chaco Serrano woodland (Luti *et al.* 1979). Mean annual precipitation in the area is approximately 700–800 mm (concentrated in summer) and mean annual temperature is 17.5°C (data taken at the station La Ventana; Acosta *et al.* 1992). The dominant wood species are *Lithraea molleoides*, followed by *Acacia caven*, *Celtis ehrenbergiana* and *Bougainvillea stipitata*. Among dominant shrub plants are *Heterothalamus alienus*, and species of the genera *Flourensia* sp. and *Baccharis* spp. (Cabido *et al.* 1998). Three sites (Las Calles, San Javier, and Los Hornillos; red areas in Figure 1) are invaded by fleshy-fruited plants. The most abundant invasive shrubs correspond to fleshy-fruited *Pyracantha angustifolia* and *P. atalantoides*, and to a lesser extent *Ligustrum lucidum*, *Morus alba*, and *Olea europea*. Both *P. angustifolia* and *P.*

atalantoides as well as *L. lucidum* and *M. alba* are native from southeast Asia. Some of these species, including *P. angustifolia* and *P. atalantoides*, occasionally form dense patches of vegetation and produce fruit during autumn–winter, when native fruit is scarce or absent (Vergara-Tabares *et al.* 2016). The other three sites (Las Rabonas, Travesia and Luyaba; green areas in Figure 1) do not have fleshy-fruited invasive plants. In order to control for aspects that may affect the presence of Slaty Thrush, we selected the six sites regarding its altitude (between 900 and 1100 m a.s.l.) and similarity in plant community (mountain forests dominated by *L. molleoides*). As the maximal distance between study sites (*i.e.* Las Rabonas to Luyaba) is approximately 50 km, it is probable that climatic conditions (precipitation or temperature) among all sites did not vary greatly.

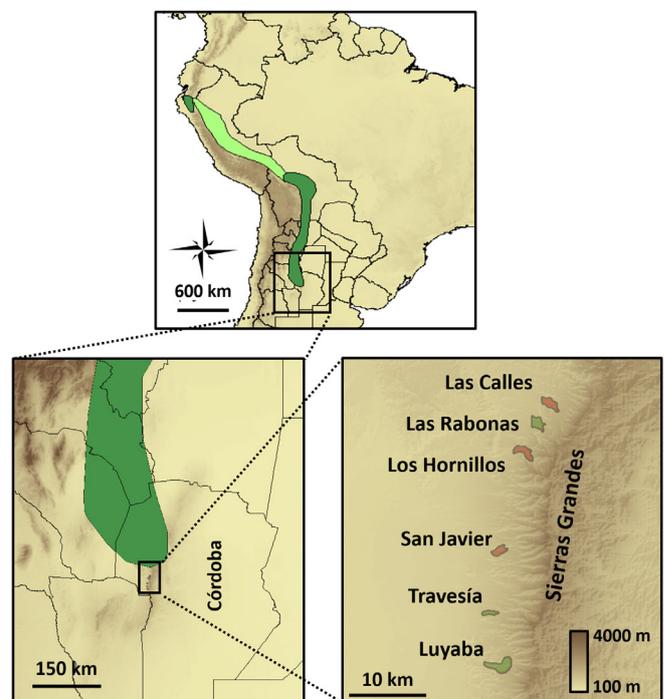


FIGURE 1. Distribution of Slaty Thrush (*Turdus nigriceps nigriceps*) and the southern portion of its distribution where we conducted fieldwork. In the upper frame, we show the distribution of the western subspecies of Slaty Thrush (*sensu* Ridgely & Tudor 2009); dark green in the northern part of the distribution shows the range of resident and breeder populations that inhabit southern Ecuador and northern Peru; light green shows the areas where Slaty Thrush visits during the austral winter; and dark green in the southern part of the distribution indicates the breeding areas during austral spring-summer. In the right frame, we show our six study sites. Red areas indicate invaded sites by fleshy fruited *Pyracantha* shrubs; from north to south: Las Calles, Los Hornillos, and San Javier. Green areas indicate sites that have not been invaded by alien plants; from north to south: Las Rabonas, Travesía, and Luyaba.

Sampling methods

We performed visual and aural searches of Slaty Thrush during April, July and September in 2014 and during January, May, August, October and December 2015.

In both years we looked for Slaty Thrush along an unstructured trail of three km along the ravine of each study site. These searches consisted of 4 h walks along the study sites during the morning or afternoon, and

we recorded the number of individuals of Slaty Thrush detected. During 2014, we sampled three sites (Los Hornillos, San Javier and Luyaba, Table 1), and during 2015 we sampled the remaining six sites mentioned.

TABLE 1. Number of individuals of Slaty Thrush (*Turdus nigricaps nigricaps*) captured using mist nets and number of individuals of this species recorded during unstructured trails in the southern end of their distribution during April, July, and September 2014. The study sites included those invaded by exotic fleshy fruited plants: Los Hornillos and San Javier, and a non-invaded site: Luyaba.

Habitat	Locality	April		July		September	
		Captures	Trails	Captures	Trails	Captures	Trails
Invaded	Los Hornillos	3	7	4	11	3	10
	San Javier	4	15	9	25	12	18
Non Invaded	Luyaba	2	1	0	0	0	0

We also used mist nets during between 20–29 April, 10–19 July, and 20–29 September 2014 at three sites (Los Hornillos, San Javier, and Luyaba; Table 1). Nets were mounted in sites with more intense bird activity and were separated by at least 50 m (*i.e.* near the streams and/or between patches of arboreal vegetation). Once captured, the birds were aged by looking at the bill and leg color that appear with dark irregular spots when the individual is immature. Sex was determined based on plumage, as this species has sexual dichromatism. Birds were ringed on their right leg with a color ring. In addition, feces produced by birds during the captures were collected to identify plants consumed. We opened four 12-m nets from sunrise to 12:00 h and from 16:00 h to sunset during three successive days (approximately 108 h/net per site).

During 2015, we performed a minimum of 20 point counts (a total of 772 point counts) in each of the six sites to detect and count Slaty Thrushes (three among these six sites where the same where we used mist nests in the previous year; Figure 1 & Table 2). At each site, point counts were separated by at least 150 m to avoid double-counts between neighboring points. Point counts were established along the same unstructured trails where we conducted the visual and aural surveys. At each point, the researcher waited 5 min as a settling down period

before starting counts (Bibby *et al.* 1992). Slaty Thrush individuals occurring within a 50-m fixed radius of each point were recorded visually or aurally. Observations were made during 10 min at each point count and we surveyed only under favorable weather conditions, within a 4-h period after sunrise. Point counts were conducted between 6–11 January, 1–6 May, 1–6 August, 10–15 October, and 26–31 December.

Data analysis

To evaluate the effect of presence of *Pyracantha* shrubs and sampling period on Slaty Thrush abundance we used a two way GLM with interaction (Zuur *et al.* 2009). We used the bird abundance obtained from surveys in trails conducted during 2015 as response variable and condition (with two levels: invaded and non-invaded) and the period (with five levels; Table 2) as factors. The six study sites were used as replicates, three invaded (Las Calles, Los Hornillos and San Javier) and three non-invaded (Las Rabonas, Travesía and Luyaba). A negative binomial error distribution was used to deal with overdispersion in abundance data. Analyses were performed using the software R (R Core Team 2014) and the package glmmADMB (Skaug *et al.* 2012).

TABLE 2. Number of individuals of Slaty Thrush (*Turdus nigricaps nigricaps*) registered throughout point counts and unstructured trails during January, May, August, October, and December 2015. In that year the study sites were Las Calles, Los Hornillos, and San Javier (invaded); and Las Rabonas, Travesía, and Luyaba (non-invaded). The number of point counts by month and locality are indicated in parenthesis and the number outside the parenthesis indicates the total number of birds recorded in point counts.

Habitat	Locality	January		May		August		October		December	
		Count points	Trails								
Invaded	Las Calles	0 (30)	1	0 (28)	1	0 (28)	2	0 (20)	0	1 (20)	3
	Los Hornillos	2 (37)	12	3 (30)	18	2 (29)	15	2 (20)	5	5 (20)	9
	San Javier	1 (30)	18	4 (29)	14	12 (30)	21	8 (22)	26	5 (29)	12
Non Invaded	Las Rabonas	0 (29)	2	0 (20)	2	0 (25)	0	0 (20)	0	4 (21)	4
	Travesía	0 (30)	0	0 (29)	0	0 (30)	0	0 (20)	0	0 (20)	0
	Luyaba	0 (39)	0	0 (28)	0	0 (29)	0	1 (20)	0	0 (20)	1

RESULTS

Slaty Thrush was registered during all sampling periods only in two of the sites invaded by non-native plants (Los Hornillos and San Javier) during 2014 and 2015 (Table 1 & 2). During April 2014 we captured and registered thrushes at all study sites (*i.e.* Luyaba, Los Hornillos and San Javier). During July and September 2014, we only captured and recorded thrushes at invaded sites (*i.e.* Los Hornillos and San Javier; Table 1). We captured two individuals with immature plumage only in July at Los Hornillos, and two females in September in San Javier. We collected feces from two individuals from Los Hornillos during July and three individuals from San Javier during September. In all of the feces we found seeds of *L. molleoides* and *Pyracantha* sp.

The GLM analysis showed that only the condition (invaded or non-invaded) affected Slaty Thrush abundance, being the abundance higher at invaded sites ($\chi^2_{1,27} = 34.04$, $P < 0.001$), while the interaction between condition and period, or period alone, did not affect bird abundance (Table 2 & Figure 2).

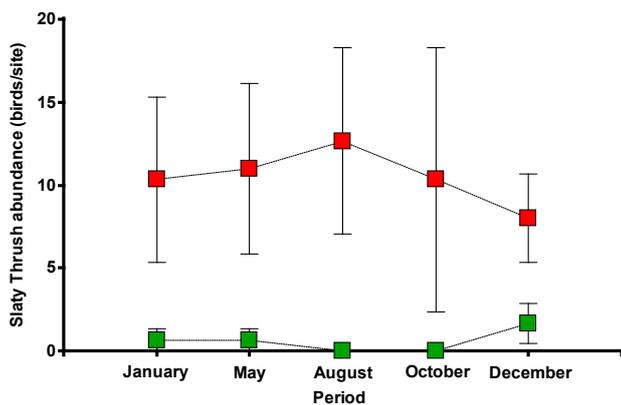


FIGURE 2. Mean abundance of Slaty Thrush per site observed in trails during 2015 in relation to sampling period, and partitioned by invaded and non-invaded condition. Green box indicates non-invaded sites and red box indicates sites invaded by *Pyracantha* shrubs. Boxes show standard error.

DISCUSSION

There is a gap in the current literature about the migratory status of Slaty Thrush in the southern areas of its distribution (Collar 2005). Our observations indicate that Slaty Thrush has a year-round presence in some sites characterized by invasive fleshy-fruit species (mainly *Pyracantha* shrubs) at the southern end of its distribution. Contrary to documented partial migratory behavior in northern Argentina (Capllonch *et al.* 2008), our data supports the recent consideration of Slaty Thrush as a resident species in a reduced area of their southern distribution (Barri *et al.* 2015). Previous records at Córdoba Province (during the 1980's and 90's) were

only obtained during the breeding season (November to February – Nores 1996, Capllonch *et al.* 2008, M. Nores, pers. comm.). If Slaty Thrush was a migrant that left southern areas in past decades, the current resident behavior may be plausibly explained by recent anthropogenic environmental changes, such as invasion by fleshy-fruited exotic plants. Our results show that Slaty Thrush was more abundant throughout the year in invaded *vs.* non-invaded areas, not only during the fruiting period of invasive plants (Table 2), ruling out the suggestion that the presence of the Slaty Thrush may be only related to invasive fleshy fruit during autumn–winter. The pattern of presence observed suggests that plant invasion by *Pyracantha* species would have an effect on resident behavior of Slaty Thrush, maybe due to the generation of adequate micro or mesohabitats and the availability of fruits during periods of fruit scarcity. Although the magnitude of plant invasion in our study sites is lesser than other regions in Chaco Serrano Woodland (*e.g.* Hoyos *et al.* 2010), the density, size and scattered distribution of patches of invasive plants may be sufficient for Slaty Thrush requirements. There is evidence supporting the positive effects of fleshy fruited invasive plants on abundance of frugivorous birds (*e.g.* Gleditsch & Carlo 2011, Vergara-Tabares unpubl. data) and other researches have documented cases where individuals and populations respond rapidly to changing environmental conditions, leading to a modification in their migratory behavior (*e.g.* Berthold *et al.* 1992, Whittington *et al.* 1999).

Slaty Thrush has been considered a partial migrant species, showing high seasonal fluctuations, and being more abundant during the breeding season in spring–summer in the southern Yungas (Capllonch *et al.* 2008, Rougès & Blake 2001). In contrast, we obtained a similar number of records of the species throughout the year during 2014 and 2015, mainly at sites invaded by exotic plants. At non-invaded sites, the presence of Slaty Thrush was variable, occurring mainly during the breeding season, despite at a lower frequency than in invaded areas. In addition, it is important to highlight that our study area was located at the southernmost end of the distribution of Slaty Thrush. This situation allows us to discard the possibility that the Slaty Thrush found here did not belong to a southern locality.

From a general perspective regarding the distribution of Slaty Thrush, previous evidence supports a resident status at the northern end of their distribution (Fjeldså & Krabbe 1990, Best *et al.* 1993, Rasmussen *et al.* 1996), while other studies reveal a uniquely winter presence of the species in the eastern Andes of central and southern Peru (Schulenberg 1987, Walker 2001). Finally, Capllonch *et al.* (2008) analyzing twenty years of data, revealed the migratory behavior of Slaty Thrush mainly in the Yungas

of northwestern Argentina, and Collar (2005) does not rule out altitudinal movements of this species. Our data suggests that Slaty Thrush has a resident behavior in the southern extreme of its distribution, clearly associated with sites invaded by fleshy fruited plants. If Slaty Thrush was a migrant species in past decades, the recent invasion by fleshy fruited plants and environmental changes caused by such invasion may explains the recent year-round presence of this species, through the creation of micro and/or mesohabitats and availability of fleshy fruits during autumn–winter.

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The juvenile plumage of Quebracho Crested-Tinamou *Eudromia formosa* (Aves: Tinamidae)

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ABSTRACT: The first description and images of the chick of the range restricted Chaco endemic Quebracho Crested-Tinamou *Eudromia formosa* are provided. They are essentially similar to adults, but possess a pale mid-dorsal stripe along the body. When crouching in a cryptic defensive posture, this stripe combines with the paler lateral stripes on the head and neck to effectively break up the outline of the bird. The identity of a *Eudromia* chick in the Los Angeles County museum is also confirmed as *E. formosa*.

KEY-WORDS: Chaco, chick, Paraguay, Tinamiformes.

The Chaco endemic Quebracho Crested-Tinamou *Eudromia formosa* occurs in semi-open areas adjacent to dense, xerophytic, thorny forest with open or dense undergrowth (Smith *et al.* 2013) in northwest Argentina, western Paraguay and extreme southeastern Bolivia (Davies 2002, Fernández *et al.* 2009, Capllonch & Allende 2013). Though currently treated as monotypic (Blake 1977, Navas & Bó 1981, Davies 2002, Capllonch & Allende 2013, Smith 2014a), the Paraguayan population has previously been separated as *E. f. mira* (Brodkorb 1938, Short 1975, Banks 1977) on account of its supposedly browner plumage and broader, but less well-defined shaft-streaks on the upperparts.

The natural history of the species is poorly documented. Smith *et al.* (2013) provided data on global distribution, habitat preference, a single egg and vocalizations from Paraguay and Argentina, as well as summarizing the limited available data on breeding throughout the range, and Smith (2014b) provided additional natural history observations on predation, feeding and distraction display. The latest comprehensive monograph of the Tinamidae (Davies 2002) makes no reference to the downy chick of this species and it is apparently undescribed. In this note we provide a description and photographs of a downy chick captured in the Paraguayan Chaco during September 2014 and a discussion of a Bolivian specimen in the Los Angeles County Museum tentatively referred to as *Eudromia elegans intermedia*, but within the known range of *E. formosa* (Banks 1977).

Banks (1977) mentions a downy chick a few days old of a *Eudromia* species that was taken “15 km NE of Capirenda, Tarija state, SE Bolivia; Bolivian Chaco” on 4 August 1957 by Kenneth E. Stager and Stephen C. Bromley (field number 16635) and housed in the Los Angeles County Museum. He tentatively attributed this specimen to *Eudromia elegans intermedia*, but noted that it was conceivable that it may represent an “extreme westward range of *Eudromia formosa mira* of the Paraguayan Chaco or a northwestward extension of *E. f. formosa* of the Argentine Chaco”. Remsen & Traylor (1983) also suspected this chick might be *E. formosa*, and the presence of that species in this area of Bolivia was later confirmed by Fernández *et al.* (2009). However, none of these publications provided any description of the chick. The specimen in question is LACM 35339 (Figure 1A, B), is a male and is indeed referable to *Eudromia formosa*.

LACM 35339 has the following measurements, in mm: exposed culmen (feathering to tip) = 13.3; bill from anterior nares to tip = 6.7; bill depth at anterior nares = 4.0; bill width at anterior nares = 4.1; head length (back of skull, which is intact on the skin, to bill tip) = 34.9; tarsus (heel joint to last undivided scale) = 18.4; wing chord (to tips of flight feather sheaths) = 31.5; maximum length of flight feather sheaths on right wing (no remex has broken the sheath) = 11.7 from skin at tip of “hand”; total length of bird (skin) = 130.

The specimen closely resembles those of *E. elegans* of similar age (*e.g.*, LACM 56997, an avicultural specimen; Figure 1A, B), but is strongly suffused with pale Cinnamon

(Color No. 39 in Smithe 1975) on the breast, belly and flanks and with Mikado Brown (No. 121C; Smithe 1975) on the dorsum and crest. Thin creamy-white feathers along the center of the back are loosely organized into a pale mid-dorsal stripe. Comparative specimens of chicks of *elegans* are colder, near Light Drab (No. 119C; Smithe 1975) above and very pale gray-buff below; no mid-dorsal stripe is present, although some thin whitish feathers are scattered along that region. The chest and sides of the neck are paler (less strongly patterned with dusky) in the *formosa* chick. Additionally, there is a strong white lateral crown stripe (above but parallel to the white supercilium) at the lateral edges of the crest, and extending back to the sides of the hindneck in the *formosa* specimen; examined chicks of *elegans* showed just a few thin white streaks in this area.

An adult (presumably male) with three downy chicks was observed on the southeastern border road of *Parque Nacional Teniente Enciso, Departamento Boquerón* (21°08'57.6"S; 61°31'18.9"W) on 21 September 2014. One chick was captured by hand and is described below (Figure 1C). The chick was subsequently released due to the lack of relevant collection permits.

The banded head pattern recalls that of the adult,

but additional stripes are present (Figure 1D). Crown and forehead are rich chestnut-brown with black flecking, some thin blackish filoplumes on the forehead are longer than the other feathers. A thin lateral crown stripe runs from the base of the bill on the forehead to the base of the crest and fades out on the hind crown without uniting; this stripe is absent in adults. A broad white stripe runs from above the eye and ear coverts to the hind neck and dorsally to the mantle and a third white stripe begins at the gape and runs under the eye and ear coverts, broadening behind the ear and running down the side of the neck. Though both of these stripes are present in the adult bird, they are more conspicuous in the chick than in adults, where they fade out more rapidly on the neck (particularly so in the case of the lower stripe which becomes less obvious shortly after the ear coverts). A rhomboid shaped white loreal spot in front of the eye is not continuous with the stripe above the eye, but forms a pattern with it that helps to break up the form of the head. This is present as a barely visible paler area on the lores in adult birds. The throat is conspicuously white, with scattered elongated plumes giving a slightly bearded impression. The foreneck lacks the bold sagittate markings

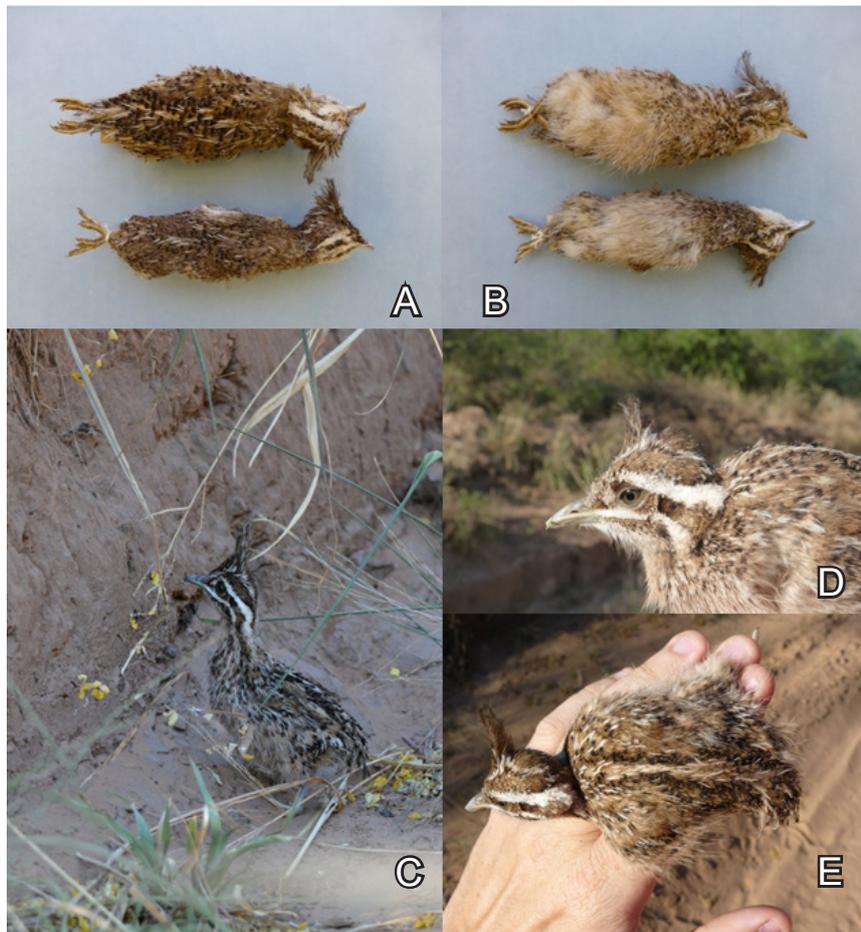


FIGURE 1. *Eudromia formosa* Specimen LACM 35339 “15 km NE of Capirenda, Tarija state, SE Bolivia; Bolivian Chaco” collected on 4 August 1957 (A, above) in direct comparison with a specimen (LACM 56997) of a chick of similar age of *E. elegans* of captive origin (aviary of Harold Schmidt, collected 29 November 1960) (A, below), in dorsal and ventral views. Photo: K. Garrett. Chick of *Eudromia formosa*, Parque Nacional Teniente Enciso, Departamento Boquerón (21°08'57.6"S; 61°31'18.9"W) on 21 September 2014 (C). Photo: J. Lehmborg. Head detail of the same chick (D). Photo: P. Smith. Dorsal pattern of same chick (E). Photo: P. Smith.

of adults and instead shows a more diffuse pattern of pale buffy-white bases, indistinct scattered black spotting and thin white streaking. Dorsally the chick is pale brownish with irregular but heavy black flecking typically associated with broader white streaking that combine to give a poorly defined, but highly cryptic dorsal pattern. The exception to this is a notably paler mid-dorsal stripe which can look almost pure white at certain angles, and is bordered on either side by an irregular dark stripe formed by dense black tips to the down. This pattern is absent in adult birds, which show a more consistent pattern of greyish-brown base color, more or less heavily mottled and vermiculated black and with irregular ochraceous spotting and freckling (Smith 2014a). Laterally the dorsal pattern fades out rapidly, and the underparts are predominately whitish with buffy bases to the feathers, being especially whitish on the belly and more infiltrated by the dorsal pattern on the breast and foreneck. Legs are pale grey-white. The iris is pale brown. The bill is pale greyish-white on the ramphotheca; greyer towards the base and around the nares. Nares are laterally located. With the exception of the paler bill color, bare parts are not notably different from those of the adult (Smith 2014a).

Short (1976) described a “half-sized” immature of *E. formosa* as closely resembling adults but “a bit duller, with a darker neck, and the inner vanes of its outer primaries are barred basally, showing a tendency toward the barred feathers of *E. elegans*”. The downy chicks documented here are in fact as brightly-colored as typical adults, at least on the head neck, and more boldly patterned in general on the upperparts. This may indicate that age-related plumage changes are more complex than is currently understood in this species, or perhaps that individual variation in plumage characters is great.

As is typical of many tinamous when threatened (Sick 1993), downy Quebracho Crested-Tinamou chicks were observed to crouch amongst vegetation with the head resting against the ground and remain motionless. Once in this posture the lateral white head stripes merged with the paler mid-dorsal stripe to effectively break up the outline of the bird (Figure 1E). This cryptic coloration made location of the chicks difficult unless the bird was observed whilst in the process of adopting this posture. Chicks could easily be captured by hand, but made no vocalizations when they were handled. No vocalizations were given by the accompanying adult, which had disappeared into nearby forest with the other chicks during the handling process.

Given the vast geographical distribution of *E. elegans*, its numerous subspecies, and the small number of available specimens of *E. formosa* from a restricted geographical area, we refrain from providing a detailed comparison between the chicks of the two species of the genus. However, in direct comparison with chicks of

E. elegans with a captive origin in LACM, both known specimens of *E. formosa* were noticeably more reddish-brown overall, especially on the head, neck and crest (Figure 1A, B), a plumage difference that is consistent with the differences observed between adult birds of these two species.

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Nest and nestling development of the Sooty-capped Hermit (*Phaethornis augusti*) from Venezuela

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ABSTRACT: In order to improve the previous knowledge about the nest and nestling development of the Sooty-capped Hermit (*Phaethornis augusti*) from Venezuela, a nest was followed from February to July 2015. Details of nest structure (shape, materials, dimensions), nest usage, intervals between breeding attempts, hatch time, fledgling period, as well as nestling development data such as body mass, measures, nestling condition on hatching, pterilia development, and when eyes opened were all recorded in detail. The nest had the typical cup-shape structure that hung by a single stout cable of spiders' silk from a single iron nail 1.90 m above the floor, built with moss and spider webbing, inside a shadowy, fresh, and quiet storehouse. Despite appearing to be bulky and heavy, the nest had a mass of only 9.4 g. After four consecutive breedings by a single female, several hitherto unknown parameters were determined, including intervals between breeding attempts (10–21 days), incubation period (20 ± 0 days), fledgling period (26 ± 0 days), egg mass (0.6 ± 0 g); egg lengths (14.0 ± 0.05 mm), nestling mass at hatching (0.65 ± 0.07 g), and nestling mass at fledging (6.1 g). Breeding season of Sooty-capped Hermit was better understood: December–July, with scant records between September–November. Sooty-capped Hermit reproductive success (87.5%) was higher than that of other related species which nest in more natural conditions (16.7%). This is probably due to the breeding strategy of nesting within man-made constructions that offer protection from most natural predators.

KEY-WORDS: avian development, clutch size, incubation, Trochilidae.

Sooty-capped Hermit *Phaethornis augusti*, like most members of its genus, is characterized by an olivaceous plumage, strong white facial-lines, and a long, typically white tipped tail. The orange-rufous-colored rump and upper-tail coverts are a distinctive species character (Meyer de Schauensee & Phelps-Jr. 1978). This hermit could be considered an almost endemic species from Venezuela, as its distribution area consist mostly of the montane areas both north and south of the country (0–2500 m a.s.l), with additional records in neighboring NE Colombia, N Brazil, and W Guyana (Snow 1973, Meyer de Schauensee & Phelps-Jr. 1978, Hilty & Brown 1986, Schuchmann 1999, Hilty 2003, Restall *et al.* 2006). It has three recognized races: *P. a. augusti*, typical of the northern mountains of Venezuela, and E Colombia; *P. a. curiosus* of the Santa Marta Mountains, Colombia; and *P. a. incanescens* of the southern mountains of Venezuela, north Brazil, and western Guyana (Meyer de Schauensee & Phelps-Jr. 1978, Schuchmann 1999, Restall *et al.* 2006). There, Sooty-capped Hermit is found in a wide variety of habitats, including undergrowth, edges of dry to moist natural forests, second growth habitats, pasturelands (*Megathyrsus maximus*, Poaceae), and

several agricultural lands, from shade plantation (coffee, cocoa) to others sunny cultures such as banana, orange, and peach (Ginés *et al.* 1951, Meyer de Schauensee & Phelps-Jr. 1978, Hilty 2003, Vereá *et al.* 2009a, 2013). It is regularly recorded in urban and suburban areas frequently entering houses and other buildings searching for small insects, spiders and their silk, which accounts for the common name of *Limpacasa* (House-cleaner). Shadowy, fresh, and quiet locations of these houses or other man-made constructions are often selected for a nesting site. A couple nests on these conditions have been previously described in Venezuela (Gilliard 1959). One nest was described suspended from a strand of woven spider webs in a dark culvert, located under the bridge of a roadway. It hung from a pipe-like structure in the ceiling, where small bats roosted some of them even very close to the nest. A second nest was suspended by a spider silk support, from the ceiling of a concrete pump house with a corrugated asbestos sheet roof. In natural conditions, *Phaethornis* nests have been found attached to the underside of *Heliconia bihai* leaves with strands of spider web, hidden from an observer's view (C. Vereá, pers. obs.). Beside spiders' webs, typical materials found

in hermit nests have been moss, rootlets, little stones, and lumps of dry mud (Gilliard 1959, Skutch 1964). The stones and mud are located in the outside walls of the nest, and play an important role as a counterbalance, in order to keep the nest evenly balanced (Gilliard 1959, Hansell 2000).

Some general information about the Sooty-capped Hermit nest structure (shape, dimensions), materials involved, and clutch size is known (Gilliard 1959, Schuchmann 1999). However, information about the nest usage, intervals between breeding attempts, hatch time, fledgling period, nestling development and important data associated to reproductive success are still unknown. This study aims to provide information about these parameters, taken from a Sooty-capped Hermit nest followed from February to July 2015, as well as improve the knowledge on its nest.

Sooty-capped Hermit nest was discovered on 12 February 2015. It held two well developed nestlings that left the nest three days later. The nest was a cup-shape structure build with the most typical materials of moss, spider webbing, and lumps of dry mud. It was hanging by a single stout cable of spider silk from an overhead support (a single iron nail, 1.90 m above the floor), inside a shadowy, fresh, and quiet storehouse located under a stairway, with an open access door toward the exterior garden of a residential house (Figure 1). The opening of the nest faced away from the door and the nest had to be carefully turned around for its contents to be seen. The house is located in the SE suburbs of Caracas, at Los Naranjos farm, El Hatillo County, Miranda state, north Venezuela (10°26'14"N; 66°47'27"W), about 900 m a.s.l. This area used to be an old poultry farm, but is being developed as a residential area. Most of area around the house was covered by pasture (*M. maximus*) and a few fruit trees such as citrus and avocado. A little creek (Quebrada Santa Rosa) runs close the house and nest site (less than 20 m), with a small riparian forest along its edges. Tall trees such as *Erythrina poeppigiana* (Fabaceae), *Bursera simaruba* (Burseraceae), *Hura crepitans* (Euphorbiaceae), and *Cecropia peltata* (Cecropiaceae) emerge above the forest canopy. Shrubbery plants such as *Oyedeaea verbesinoides* (Asteraceae), *Carica papaya* (Caricaceae), and few *Heliconia* (Heliconiaceae) were present. Although the nest resembles that described by Gilliard (1959) the counterbalance section was extended from behind the incubation area of the cup, downward as a long beard (Figure 1A). Thus, counterbalance section had 160 mm long, including 85 mm of "beard" (Figure 1B). Nest dimensions were (mm): total length: 240; support length: 80; counterbalance section length: 160; inner-cup depth: 20; outer-cup depth: 75; cup-rim thickness: 11.5–15.0; cup-rim length: 30; cup-rim wide: 20 (Figure 1A–C). While the studied nest aspect was

bulky and heavy, it only had body mass of 9.4 g. No records of Sooty-capped Hermit nest mass are previously known.

At this time, I thought that Sooty-capped Hermit work had finished. Including Sooty-capped Hermit, other member of the genera has been reported as communal display (lek) birds (Davis 1958, Höglund & Alatalo 1995, Ramjohn *et al.* 2003). Thus, the entire reproduction effort rests on the female: nest construction, eggs laying, incubation, nestling care and feeding. Nonetheless, on 15 March two white eggs were discovered inside the nest. Two nestlings hatched on 20 March and left the nest 26 days later, on 14 April. During the entire period, the female was left strictly undisturbed and only notes about egg laying and nestling departing times were made. Seven days after nestlings left the nest, on 21 April, the female was observed carrying new material to the nest. A single white egg was found in the early morning of 5 May. The next day, a second egg was laid at afternoon time about 36 h later. Skutch (1964) indicated an interval of

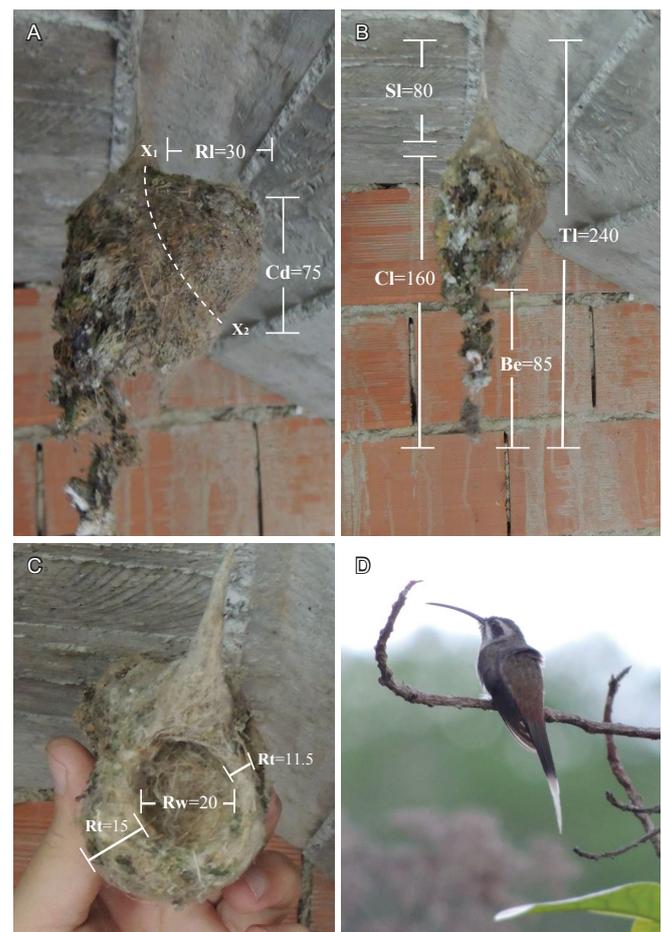


FIGURE 1. Sooty-capped Hermit (*Phaethornis augusti*) nest structure (A–C): total length (TI); support length (SI); counterbalance-section length (CI); “Beard” section (Be); outer-cup depth (Cd); cup-rims thickness (Rt); cup-rim length (RI); cup-rim wide (Rw). Inner-cup depth (20 mm) no represented. Section X₁–X₂: lower cup margin: all arrangement below dotted lines represents the counterbalance-section. All measures in mm. Female Sooty-capped Hermit resting on an avocado twig (D). Photos: C. Vereá.

two days between egg laying in *Phaethornis superciliosus*. After the two previous and successful clutches, detailed notes on the nestlings' development were now taken on a daily basis. An electronic precision balance Acculab EC-211 model, with 0.1 g readability; and a plastic dial caliper Spi 31-415-3 model, with 0.1 mm readability, were used. Notes were taken at 08:00 h every morning recording masses, dimensions and total lengths of bill and tail of both nestlings. Total length was the distance between the bill tip and tail, feathered or not; bill length between the base and the bill tip (culmen); and tail length between the base and tail tip of the two central feathers. Eggs and naked nestling were removed from the nest with a metal spoon, previously sterilized with 100% ethylic alcohol. Once the nestlings were feathered, with eyes open, they were removed by hand. During the last days in the nest, the nestlings became aggressive, and had to be weighed together whilst still inside the nest. To achieve this, the nest with the nestlings still inside was carefully placed on the electronic balance. Once a constant value was recorded, the nest mass (9.4 g) was deducted and the average nestling mass was estimated. Before measurements started, crop condition (empty, occupied) was recorded as it could affect mass accuracy. Notes on particular events of the nestlings' development were recorded, including days when the pteriliae were noticeable, the papillae opened, the eyes opened, and days of mass increase and decrease (Table 1). A photographic sequence of nestling development is shown in Figure 2, including naked, eyes-closed days (Figure 2A–B), pteriliae and papillae development (Figure 2B–E), facial lines and rump color development (Figure 2E–F), and the well-developed nestlings with adult appearance (Figure 2G–H). Previously, the eggs were weighed and measured on the day of laying. Both eggs has mass of 0.6 g each, and were 13.9 and 14.0 mm long respectively (mean = 13.95 mm). Despite *P. augusti* individuals being slightly bigger than *P. superciliosus* (Restall *et al.* 2006), their eggs are shorter. According to Skutch (1964), *P. superciliosus* eggs are 15.9 mm length. No previous data on egg mass of *Phaethornis* are known.

Both eggs hatched on 25 May, after 20 days of incubation; the newly-hatched nestlings had body mass of 0.6 and 0.7 g, respectively. This incubation period was longer than the 17–18 days recorded for *P. superciliosus* (Skutch 1964). When one day old, each nestling oriented itself with its beaks toward the support cable. This position allows them to be located side-by-side in the nest. They have a natural reflex that strongly keeps their toes curled, securing the nestlings to the delicate threads of the nest bottom. They also are able to move backwards toward the edge of the nest to strongly eject excreta. This behavior is known for nestlings of other *Phaethornis* species (Davis 1958, Skutch 1964).

The nestlings were completely naked for the first nine days but the female brooded them for the initial five days only, and only during the afternoon and night time. On day five, nestling pteriliae became noticeable (Table 1), so it probably had a thermal protective effect on nestlings, and female care was no longer necessary. In contrast, Davis (1958) reported no brooding activities on first two or three days in *P. superciliosus*. Skutch (1964) also reports dark skin, sparse down, and tightly closed eyes at hatch time for that species. In the present study of *P. augusti*, the nestlings were naked at time of hatching, had ruddy-colored skin, and the eyes were completely closed until day 10 (Table 1). On day 15, the rump and upper-tail coverts began to turn orange-rufous color (Figure 2E).



FIGURE 2. Sooty-capped Hermit (*Phaethornis augusti*) nestling development. Naked, eyes-closed days (A–B); pteriliae become dark (deep lead gray) with feather papillae (contour, wings) acuminate (B); eyes open day (C) and contour papillae just open, showing a brush-like aspect (C–D); white facial-lines and white papillae on tail appears, wing papillae open, brush-like aspect (E); upper jaw still yellow, but base and tip become fuscous colored (E–F); white papillae on tail open, and wing papillae get a rowing-like aspect; tail exceeds nest edge and nestlings resemble the adult except by short tail and lower jaw base pale-orange colored (G–H). Days 3, 8, 11, 12, 13, 16, 20 and 23, from A to H, respectively. Photos: A, G (E. Pescador), others (C. Vereá).

TABLE 1. Mass, length measurements (total, bill and tail length), and growth observations on a couple Sooty-capped Hermit (*Phaethornis augusti*) nestlings from Venezuela. Day 1: 25 May 2015; Day 26: 19 June 2015. Particular events on nestling development underlined. Crop condition: E: empty; O: occupied. Individual dashes (-) indicate data not collected.

Day	Observations	Mass (g)	Mean	Total length (mm)	Mean	Bill length (mm)	Mean	Tail length (mm)	Mean	Crop
1	Naked; eyes closed, bill yellow.	0.7–0.6	0.65	28.9–29.0	28.95	2.0–2.1	2.05	-	-	E
2	As above.	1.1–1.1	1.10	29.5–29.8	29.65	2.2–2.4	2.30	-	-	O
3	As above.	1.1–1.2	1.15	30.5–31.0	30.75	3.0–3.1	3.05	-	-	E
4	As above.	1.6–1.6	1.60	35.0–35.1	35.05	5.3–5.5	5.40	-	-	O
5	Pteriliae slightly dark.	2.1–2.3	2.20	37.4–37.8	37.60	5.3–5.5	5.40	-	-	O
6	Pteriliae dark.	2.3–2.5	2.40	38.7–39.1	38.90	5.8–6.0	5.90	-	-	E
7	Pteriliae dark (lead gray) and bump.	2.6–2.9	2.75	39.9–40.2	40.05	6.1–6.2	6.15	-	-	O
8	Pteriliae dark (deep lead gray) with feather papillae (contour, wings) acuminate.	2.8–3.1	2.95	43.0–44.2	43.6	6.3–6.7	6.50	-	-	O
9	Well-developed contour feather papillae: imminent opening.	3.7–3.8	3.75	45.0–47.1	46.05	7.0–7.2	7.10	-	-	O
10	Eyes half-closed; <u>contour papillae open</u> .	3.8–3.9	3.85	45.4–47.5	46.45	7.2–7.6	7.40	-	-	E
11	<u>Eyes open</u> ; contour papillae open, brush-like aspect.	4.0–4.2	4.10	46.3–48.0	47.15	7.4–7.7	7.55	-	-	O
12	Wing papillae enlarged: imminent opening; <u>white facial-lines and white papillae on tail appears</u> .	4.3–4.4	4.35	48.5–49.0	48.75	7.8–7.9	7.85	-	-	E
13	Wing papillae open, brush-like aspect; white facial-lines and white papillae on tail conspicuous; upper jaw yellow, base and tip fuscous.	4.7–4.9	4.80	52.0–54.8	53.40	8.0–8.4	8.20	-	-	E
14	Conspicuous white facial-lines; large white papillae on tail.	5.0–5.0	5.00	53.7–55.0	54.35	8.4–8.5	8.45	-	-	E
15	Conspicuous white facial-lines; white papillae on tail enlarged: imminent opening; <u>rump feathers turned orange fuscous colored</u> .	5.5–5.7	5.60	54.5–55.5	55.00	8.9–9.6	9.25	-	-	E
16	Conspicuous white facial-lines; white papillae on tail open; wing papillae rowing-like aspect; <u>upper jaw yellow, fuscous colored</u> .	5.8–6.1	5.95	60.2–61.5	60.85	9.0–10.0	9.50	7.4–9.1	8.25	O
17	As above.	5.9–6.2	6.05	60.3–63.1	61.70	10.0–11.1	10.55	8.2–10.5	9.35	E
18	Nestling large barely fit in nest; tail reaches the nest edge, resembles adult.	5.9–6.2	6.05	67.0–68.2	67.60	11.5–11.7	11.60	10.0–12.2	11.10	E
19	Nestling large resembles adult; open bills when handled; <u>upper jaw totally black; mass decreased</u> .	5.8–6.0	5.90	68.9–69.7	69.3	11.6–12.0	11.80	12.5–13.7	13.20	E
20	Nestling large, adult aspect; tail exceeds nest edge; difficult nestling re-entry on nest; <u>mass decreased</u> .	5.5–5.7	5.60	70.5–71.7	71.10	12.2–13.0	12.55	13.9–15.1	14.50	E
21	Nestlings too large. Weighed in nest together; <u>mass decreased</u> .	-	5.20	72.5–73.2	72.85	13.7–15.0	14.35	17.8–18.4	18.10	-
22	<u>Mass decreased</u> .	-	5.15	72.9–73.4	73.15	13.7–15.1	14.40	18.3–20.7	19.50	-
23	<u>Mass increased again</u> .	-	5.30	76.7–78.4	77.55	15.3–16.9	16.10	20.9–21.5	21.20	-
24	After weighing, one nestling flew away during handling it to take measures.	-	6.10	-	-	-	-	-	-	-
25	One nestling remain in nest late afternoon (17:30 h).	-	-	-	-	-	-	-	-	-
26	Nest empty (08:00 h).	-	-	-	-	-	-	-	-	-

This important detail means that field ornithologists can then identify the nestlings and fledglings to species with no confusion with other similar species. When the nestlings reached 19 days old, they showed a decrease in mass gain. This coincided with an accelerated rate of tail growth. It could be interpreted as an energy limitation due to the spurt in tail feather growth that necessarily must be completed at fledging as it is an important element in Sooty-capped Hermit flight. On the same day nestlings became aggressive, and opened their beaks when handled. Mass and measurements were then taken with the two birds inside the nest together. Nonetheless, one nestling flew away on day 24 while being measured. The second nestling left the nest two days later, 26 days after hatching. This fledgling period was exactly the same recorded previously. Skutch (1964) indicated a shorter time (22–23 days) for fledgling period of *P. superciliosus*. Nonetheless, from two *P. superciliosus* nests followed by Davis (1958), one matched with Skutch (1964) data; the other was an estimate of at least 18 and possibly as much as 27 days. The last body mass recorded was 6.1 g, similar to the adult mass (mean = 6.0 ± 0.8 g; n = 10) reported by Dunning-Jr. (2008). At time of fledging, the juvenile resembles the adult plumage almost exactly, except for a slightly short tail and lower mandible base pale-orange colored (Figure 2H).

Three days after nestlings left the nest, I saw the female carrying new material to the nest once again. Seven days later, on 29 June, one white egg was laid in the nest, and a second appeared the next day. Both eggs had mass of 0.6 g and measured 14.0 mm in length. Both eggs hatched on 19 July, after 20 days incubation and each nestling had mass 0.7 g. Three days later, one nestling had disappeared. There was no corpse on soil or nearby areas. Similar occurrences have been reported in other *Phaethornis* nests (Skutch 1964). For nestling safety the nest was no longer disturbed. The solitary nestling was raised without incident and left the nest 26 days later, on 13 August. These data represent the evidence of four continuous reproduction cycles in Sooty-capped Hermit. Disarranged plumage and resting behavior at same avocado twig (Figure 1 D) were unmistakable signs that the female involved was always the same. The nest was never visited again once abandoned.

The results add significant data on the nesting of Sooty-capped Hermit, including repeated nest usage (four consecutive periods), intervals between breedings (10–21 days, n = 2), incubation period (20 ± 0 days, n = 2), fledgling period (26 ± 0 days, n = 3), egg mass (0.6 ± 0 g; n = 4), egg length (14.0 ± 0.05 mm; n = 4), nestling mass at hatching (0.65 ± 0.07 g, n = 2), nestling mass at fledging (6.1 g, n = 1), nestling development and other aspects of Sooty-capped Hermit natural history. The primary breeding season previously recorded as the

December–May period (Schäfer & Phelps 1954, Hilty 2003, Vereá *et al.* 2009b), is extended up to July, with sparse additional records between September–November (Vereá *et al.* 2009b). Sooty-capped Hermit studied here had a higher reproductive success rate (87.5%) than other related species (*P. superciliosus*) which nest in more natural conditions (16.7%) (Skutch 1964). It is probable that man-made constructions provide protection from natural predators.

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Biometrics and body masses of some birds of prey of Argentina

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ABSTRACT: We present data from 97 live specimens from 20 different taxa of diurnal raptors from Argentina. Data were obtained from bird banding campaigns conducted by the *Centro Nacional de Anillado de Aves (CENAA)*, Universidad Nacional de Tucumán, Argentina. Another important source of data was the *Centro de Rehabilitación de Aves Rapaces (CeRAR)*. We used mist nets and bal-chatri traps to catch birds during CENAA campaigns in central and northern Argentina, in order to band them and study their migration. During fieldwork, we measured total body length, bill length (exposed culmen and culmen with cere), wing chord, and body mass of each bird. The biometric information of raptors in Argentina is scarce. These measurements can therefore be useful for a variety of topics such as conservation, ecology, biology, taxonomy and phylogeny.

KEY-WORDS: Accipitridae, Cathartidae, diurnal raptors, Falconidae, measurements.

In Argentina, 40 species of diurnal raptors, 20 species of nocturnal raptors and five scavengers are present, but very little is known about their biology and ecology due to their low population abundance and the difficulties associated with their study (Trejo *et al.* 2007). Previous studies reporting body masses of birds in the region include Belton (1984) and Dunning-Jr. (1992, 2008). However, in general, biometric data of raptors in Argentina is scarce (Trejo 2007). These measurements can be useful for a variety of topics such as conservation, ecology, biology, taxonomy and phylogenetic studies.

Few studies on austral raptors present morphometric data, and these are mostly based on specimens housed in collections, instead of live birds. Therefore, certain measurements such as body mass or total body length are nonexistent or inaccurate (Jiménez 1995). Here, we present information on body measurements and body mass of 20 species of scavengers and raptors belonging to the families Cathartidae, Accipitridae and Falconidae.

Data were obtained from bird banding campaigns conducted by the *Centro Nacional de Anillado de Aves de Argentina (CENAA)*, Universidad Nacional de Tucumán. Another important source of data was the *Centro de*

Rehabilitación de Aves Rapaces (CeRAR) of *Reserva Experimental de Horco Molle (REHM)*, which is part of the *Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán*. The CeRAR, created in 2008 and under authorization from the *Departamento de Flora y Fauna* of Tucumán Province, rescues, rehabilitates, and releases raptors. These interventions are conducted according to international protocols and guidelines of the International Union for Conservation of Nature and Natural Resources (IUCN), taking into account both conservation and animal welfare. Many of these birds, especially of *Geranoaetus polyosoma*, were part of the undergraduate thesis work of Aráoz (2012).

We also used mist nets and bal-chatri traps (Bloom *et al.* 2007) to catch birds during CENAA campaigns in central and northern Argentina, in order to band them and study their migration. The bal-chatri traps, a handmade box of thick wire with numerous plastic wire ties on its exterior, upper surface, were baited with live laboratory mice. These plastic ties slide and entangle the legs of the raptors that attempt to take the mice, without causing injury to the birds. A heavy weight tied to the trap prevents birds from lifting the trap off the ground.

The two capture methods are different: mist nets catch prey at random, while bal-chatri traps deliberately aim to capture a particular individual. The later method presents some difficulties, for example, the capture success of the bal-chatri with *G. polyosoma* is usually very low, with only a few individuals captured in dozens of attempts.

The capture of birds of prey with nets was only occasionally possible, as several hawks, Barred Forest-falcons and American Kestrels (*Accipiter bicolor*, *A. striatus*, *Micrastur ruficollis*, and *Falco sparverius*, respectively) were entangled as they tried to feed on small birds caught in the nets; all of these captures occurred in dense forest. However, bal-chatri traps were specifically effective for Variable and Savanna Hawks (*G. polyosoma*, *B. meridionalis*, respectively) and Black-chested Buzzard-Eagles (*Geranoaetus melanoleucus*). We found that these traps operated better in open landscapes, such as at 3000 m high pastures composed of tall grasses.

During fieldwork, we measured the total body length, bill length (exposed culmen and culmen with cere), and wing chord of every captured bird. We used a caliper to measure the bill, a metal ruler to measure wing chord and total body length, and 100 g, 500 g and 1000 g Pesola® scales to measure body mass. For heavier birds, a 50 kg digital scale was used. Birds were banded with bands from the *Instituto Miguel Lillo, Universidad de Tucumán*, and later released. Many birds were also banded with colored bands.

Age of *G. polyosoma* and *G. melanoleucus* was determined by plumage (Cabot & De Vries 2004, Seipke 2007). For the nomenclature of raptor species, we followed the list of species proposed by Remsen-Jr. *et al.* (2016).

We distinguish between captive birds and those captured in the field. Raptors raised from young might be smaller, and although measurements may be similar to those found in natural conditions if they have been in captivity for a longtime, their masses may be inaccurate (*i.e.*, they may be either very thin or very fat in comparison to natural conditions). Some specimens were sexed by plumage (*F. sparverius*, *G. polyosoma*, *Vultur gryphus*), while others that died at the CeRAR were sexed by gonad examination during necropsy. The sex of some birds with no sexual dimorphism in plumage remained undetermined; although females are usually larger, small females can frequently have measurements that overlap with smaller males.

The localities in Argentina (Figure 1) where specimens were obtained, by province, were: **Salta:** Orán (23°08'S; 64°19'W), Rosario de la Frontera (25°48'S; 64°58'W), Gaona (25°12'S; 64°05'W), Potrerillos (26.08°S; 65.46°W), Tolombón (26°12'S; 65°55'W); **Jujuy:** Caimancito, Calilegua (23°48'S; 64°47'W), Aguas Negras, Calilegua (23°55'S; 64°50'W); **Formosa:**

Comandante Fontana (25°20'S; 59°41'W); **Tucumán:** Ruta 9, Tapia (26°13'S; 65°16'W), Burruyacu (26°29'S; 64°44'W), Altos de Medina (26°36'S; 65°05'W), Amaicha del Valle (26°36'S; 65°55'W), Tafi Viejo (26°43'S; 55°33'W), San Javier (26°43'S; 65°22'W), Pinar de Velárdez (26°43'S; 65°22'W), Horco Molle (26°45'S; 65°23'W), El Infiernillo (26°45'S; 65°40'W), Villa Mariano Moreno (26°46'S; 65°12'W), Cebil Redondo (26°47'S; 65°17'W), Alderetes (26°49'S; 65°08'W), Yerba Buena (26°49'S; 65°19'W), Country Las Yungas (26°49'S; 65°19'W), Villa Amalia (26°51'S; 65°12'W), San Pablo (26°52'S; 65°18'W), Los Vallistos (26°59'S; 65°15'W), Tafi del Valle (26°52'S; 65°41'W), Lastenia (26°52'S; 65°09'W), Las Cejas (26°53'S; 64°44'W), La Aguadita (26°69'S; 65°12'W), Famaillá (27°03'S; 65°24'W), Río Colorado (27°09'S; 65°21'W), Simoca (27°16'S; 65°20'W), Concepción (27°20'S; 65°35'W), Reserva Provincial de Santa Ana (27°26'S; 65°46'W), Escaba (27°39'S; 65°45'W); **Misiones:** Posadas (26°55'S; 54°31'W); **Catamarca:** Santa María (26°41'S; 66°02'W), Capital (28°28'S; 65°46'W); **Santiago del Estero:** Rapelli (26°23'S; 64°30'W), Guasayán (27°06'S; 64°16'W), Pozo Hondo (27°10'S; 64°29'W), Capital (27°47'S; 64°16'W), Loreto (28°18'S; 64°12'W), Sumampa (29°22'S; 63°28'W); **San Luis:** Bajo de Véliz (32°18'S; 65°24'W); **La Pampa:** Guatraché (37°40'S; 63°32'W).

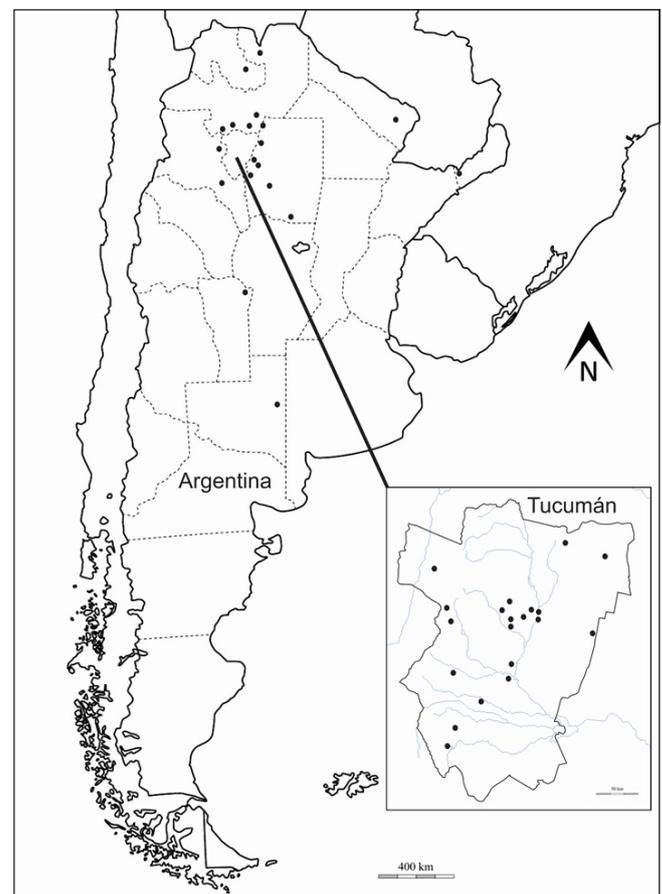


FIGURE 1. Sampling sites in Argentina where specimens were captured (black dots). Tucumán Province is displayed at the bottom right.

At El Infiernillo, Taquí del Valle, Tucumán Province, we captured 17 specimens during the impressive migration of birds of prey that takes place in fall, and which belongs to an Andean migratory route (Capllonch *et al.* 2011). The area is a true migratory corridor that acts as a “funnel” for soaring birds (Trejo *et al.* 2007, Capllonch & Ortiz 2009). This region constitutes the first site with a migration of such magnitude, in terms of number of birds, described for migrating raptors in Argentina (Capllonch *et al.* 2011), especially for *G. polyosoma* (Aráoz 2012). The valley, which reaches 2000 m a.s.l. and has an extension of 20 km between 27°S and 65°W, acts as a connection between two mountain chains, Aconquija and Cumbres Calchaquíes, and thus, specimens are able to acquire greater speeds when crossing the valley in a N-S direction.

We obtained data from 97 live specimens from 20 different taxa. The most captured species were *G. polyosoma*, *G. melanoleucus*, *Buteo magnirostris*, and *F. sparverius*. Three subspecies of Roadside Hawk (*B.*

magnirostris) were captured: *saturatus* from the Yungas, *pucherani* from the eastern Chaco, and *magniplumis* from the Atlantic Rainforest (Table 1). Regarding *G. p. poecilochrous*, which is common and resident in Taquí del Valle, it was earlier considered a distinct species, with some authors still considering it as a full species, but later genetic studies placed it subspecifically (Riesing *et al.* 2003). This subspecies coexists during winter months with *G. p. polyosoma* in valleys between 2000 and 3500 m a.s.l.

For *F. sparverius*, all of which belong to the same subspecies in Argentina, individuals captured in the southern area of Argentina are larger than those in the north, confirming Bergmann's Rule. Specimens captured in La Pampa Province (Guatraché) and in Bajo de Véliz, at 32°S, in San Luis Province (the two most southerly points in Figure 1), are strikingly larger than those captured in Tucumán Province, at 26°S. The same applies to some specimens caught at 2000 m a.s.l. in Taquí del Valle, Tucumán Province, which are larger than those captured on the plains.

TABLE 1. Body mass, total body length, wing chord, tail, bill, and tarsus length measurements of 97 live specimens. CERAR = data provided by Centro de Rehabilitación de Aves Rapaces; CENAA = data obtained from bird banding campaigns conducted by the National Bird Banding Center; M = male; F = female; A = adult; SA = subadult; - data not obtained.

Species Place	Location	n	Sex and age	Body mass (g)	Total body length (cm)	Wing chord (cm)	Tail (cm)	Culmen with cere (cm)	Culmen without cere (cm)	Tarsus length (cm)
Cathartidae										
<i>Vultur gryphus</i> CeRAR	Taquí del Valle	1	AF	10000	107	77.4	40	7.1	4.6	14.5
<i>Sarcorhamphus papa</i> CeRAR	Catamarca	1	A	3100	75	51	22	-	-	-
<i>Cathartes aura</i> CeRAR	Taquí Viejo	1	A	1460	66.5	54.6	-	5	-	7.6
Accipitridae										
<i>Geranoetus melanoleucus</i> CeRAR	Santa María, Guasayán, Las Cejas, Yerba Buena, Rapelli, Alto de Medina, Concepción, Santiago del Estero, Burruyacú	7/9/10	A	2125.5 (n = 10)	68.75 (n = 9)	52.25 (n = 9)	29 (n = 10)	5.12 (n = 10)	3.68 (n = 7)	11.85 (n = 10)
<i>Spizastur melanoleucus</i> CeRAR	Orán	1	SA	1030	60	38	28	5.5	4	8
<i>Rupornis magnirostris pucherani</i> CENAA	Comandante Fontana	1	AF	340	37	25.6	17	3.7	1.9	8
<i>Rupornis magnirostris magniplumis</i> CeRAR	Posadas	1	A	365	31	-	-	2.5	1.9	7
<i>Rupornis magnirostris saturatus</i> CENAA CeRAR	Agua Negras, Reserva Santa Ana, Reserva La Florida, San Javier, Tucumán, San Pablo, Yerba Buena, Banda del Río Salí, Famaillá	10/12/ 14/15	A	311.92 (n = 14) (215–410)	39.33 (n = 14) (37–44)	26.60 (n = 15) (24–28)	18.55 (n = 14) (16–21)	2.85 (n = 12) (2.5–3.5)	1.83 (n = 10) (1.7–2.3)	7.5 (n = 14) (7–8.4)
<i>Geranoetus polyosoma</i> CENAA	Calilegua, Caimancito, Valle de La Sala, Taquí del Valle Tucumán, Amaicha del Valle	3	M	738.33 (720–770)	46.3 (43–47)	36.8 (41–32)	22.1 (21–23)	3.3 (3.1–3.5)	2.4 (2.2–2.6)	9.23 (8.7–9.8)

Species Place	Location	n	Sex and age	Body mass (g)	Total body length (cm)	Wing chord (cm)	Tail (cm)	Culmen with cere (cm)	Culmen without cere (cm)	Tarsus length (cm)
<i>Geranoaetus polyosoma</i> CeRAR, CENAA	Tolombón, El Infiernillo, Tafi del Valle	7	SA	797.85 (660–900)	48.6 (46.5–50)	38.5 (34–42.5)	22.1 (21.5–23)	3.3 (3.1–3.5)	2.3 (2.2–2.5)	10.1 (9–10)
<i>Geranoaetus polyosoma poecilochrous</i> CENAA	El Infiernillo	2	SA	-	49.25 (49–49.5)	44.25 (43.5–45)	22.65 (22.5–22.8)	3.5	2.5	10.5 (10–11)
<i>Buteogallus urubitinga</i> CeRAR	Simoca	1	SA M	-	64	42	27	4.5	3.2	13
<i>Buteogallus meridionalis</i> CENAA, CeRAR	Comandante Fontana, Guachula, Loreto	2/3	A	840 (n = 3) (740–895)	49.8 (n = 3) (48–53)	40.6 (n = 3) (38–43)	21.6 (n = 3) (21–23)	3.7 (n = 3) (3.3–4)	2.8 (n = 2) (2.6–3)	12.25 (n = 2) (12–12.5)
<i>Parabuteo unicinctus</i> CeRAR	Agua Amarga	1	A	880	53	33	24	3.5	2.5	10
<i>Accipiter striatus</i> CENAA	Potrerrillos	1	A	100	26	16.4	13.7	-	1	4.6
<i>Accipiter bicolor</i> CENAA	Rosario de la Frontera	1	A	149	31.5	25.5	16.8	-	-	5.1
CeRAR	Tafi Viejo	1	A		42	32	21	2.5	2.0	7
Falconidae										
<i>Falco sparverius</i> CENAA, CeRAR	Pozo Hondo, Tucumán, Guatrache, Tafi del Valle.	5/8/9	AM	105.5 (n = 9) (80–120)	25.3 (n = 8) (22.5–27.2)	18.1 (n = 8) (16–19)	12.6 (n = 8) (11–13.4)	1.5 (n = 8) (1.5–1.6)	1.1 (n = 5) (1.1–1.2)	4.2 (n = 8) (4/4.6)
<i>Falco sparverius</i> CENAA, CeRAR	Gaona, Bajo de Véliz, Alderetes, Cebil Redondo, Tucumán, Tafi del Valle, Tafi Viejo	11/12	AF	116.8 (n = 11) (90–152)	26 (n = 12) (23–28)	19 (n = 11) (17–21)	13.2 (n = 12) (10.9–15)	1.5/1.2 (n = 12) (1.5–1.8)	1.2 (n = 11) (1.2–1.4)	4 (n = 12) (3.8–4.5)
<i>Falco femoralis</i> CeRAR	Villa Mariano Moreno	1	A	230	32	24	10	2.2	1.6	6
<i>Caracara plancus</i> CeRAR	La Aguadita, Tucumán, Banda del Río Salí, Escaba, Lastenia.	3/4/5/6	A	811.25 (n = 4) (700–960)	53.1 (n = 5) (50–57)	37.1 (n = 6) (32–40.1)	23 (n = 6) (20.5–25)	4/3 (n = 6) (3.5–4.3)	3 (n = 3) (3–3.1)	9.84 (n = 5) (9.1–10.2)
<i>Caracara plancus</i> CeRAR	Tucumán, Capital	1	SA	835	52	36	22.4	5	2.7	7.5
<i>Milvago chimango</i> CeRAR	Villa Amalia, Yerba Buena, Río Colorado, Los Vallistos, La Aguadita, Ruta 9, Tucumán	6/7/8/9	A	226.87 (n = 8) (170–260)	35.3 (n = 8) (32–39.4)	27.7 (n = 7) (25–29.9)	18.5 (n = 8) (10–19.5)	2.6/1.8 (n = 9) (2.5–3.1)	1.8 (n = 6) (1.7–2.1)	5.6 (n = 9) (4.8–6.7)
<i>Spizapteryx circumcincta</i> CENAA	Sumampa, Bajo de Velis	2	A	157.5 (155–160)	28.7 (28.3–29.2)	17.2 (17–17.4)	15 (14.8–15.5)	1.9	1.6	4.8 (4.5–5.1)
<i>Micrastur ruficollis</i> CENAA	Reserva Santa Ana, Pinar Velárdez, Santa Lucía.	2/3	A	190 (n = 3) (180–207)	37 (n = 2) (35–39)	18 (n = 2) (18.5–19)	18.5 (n = 2) (18–19)	1.8/1.5 (n = 2) (1.7–1.9)	1.5 (n = 2) (1.4–1.6)	6.1 (n = 2)

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First description of the nest and notes on parental care of Oustalet's Tyrannulet, *Phylloscartes oustaleti* (Passeriformes: Tyrannidae)

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ABSTRACT: A nest of *Phylloscartes oustaleti* (Sclater, 1887), collected in the state of Santa Catarina, southern Brazil, is described as an ovoid structure with a dome-shaped lateral entrance supported laterally by thin twigs of a shrub. Building material was slender plant fiber interwoven with strands of live moss, which was growing also on twigs around the nest, thus serving to camouflage it. Egg cup was lined by silky material, probably seed down. This nest was found on 13 December 2007 when an adult was spotted carrying food to the nest, located 2.3 m above ground on the edge of secondary forest. Only arthropods were identified in the provisioned food, including mainly insects, but also spiders. General features of this nest conform to those of the few other species of the genus whose nests are known. Available records of Oustalet's Tyrannulet nests are consistent with the previously postulated September to December breeding season for the species, although one record of a bird carrying nest material in early August suggests the breeding season may extend earlier. Detailed nest descriptions are needed from a larger number of species before intra- and interspecific variation in nesting can be adequately appreciated in evolutionary or purely taxonomic contexts in this genus.

KEY-WORDS: Atlantic Forest, breeding, *Pogonotriccus*, systematics, taxonomy.

Phylloscartes oustaleti (Sclater, 1887) is a small bird (12 cm, 8 g) endemic to the Atlantic Forest in eastern Brazil, ranging from southern Bahia to eastern Santa Catarina, where it occurs in humid tropical and upper tropical forests, usually foraging with mixed-species flocks in canopy and subcanopy (Fitzpatrick 2004). In the absence of a comprehensive phylogenetic analysis to allow a proper delimitation of the genus *Phylloscartes*, it has been treated as consisting of 15–23 species, with different authors including or not species of other related genera (Fitzpatrick 2004, Ridgely & Tudor 2009, Clements *et al.* 2015). The nests of thirteen of these species are known, but only some of them have been described, in varying levels of detail (taxonomy following Clements *et al.* 2015): Marble-faced Bristle-tyrant *P. ophthalmicus* (Taczanowski, 1874), Spectacled Bristle-tyrant *P. orbitalis* (Cabanis, 1873), Southern Bristle-tyrant *P. eximius* (Temminck, 1822), Mottle-cheeked Tyrannulet *P. ventralis* (Temminck, 1824), Restinga Tyrannulet *P. kroniei* Willis & Oniki, 1992, Bahia Tyrannulet *P. beckeri* Gonzaga & Pacheco, 1995, Olive-green Tyrannulet *P.*

virescens Todd, 1925, Alagoas (Long-tailed) Tyrannulet *P. ceciliae* Teixeira, 1987, Cinnamon-faced Tyrannulet *P. parkeri* Fitzpatrick & Stotz, 1997, Minas Gerais Tyrannulet *P. roquettei* Sneath, 1928, Oustalet's Tyrannulet *P. oustaleti*, and Serra do Mar Tyrannulet *P. difficilis* (Ihering & Ihering, 1907), and Bay-ringed Tyrannulet *P. sylviolus* (Cabanis & Heine, 1859) (see Kirwan *et al.* 2010, Lombardi *et al.* 2010, Londoño 2014, Crozariol 2016).

Here we provide the description and report observations of an Oustalet's Tyrannulet nest discovered in a privately owned resort near Salto do Pirá, 18 km from Joinville, in the state of Santa Catarina, southern Brazil. Geographic coordinates taken at nest location, with a GPS receiver, were 26°17'20.8"S; 49°00'37.6"W (Datum WGS 84); elevation was 200 m a.s.l.

Nest location and dates: The nest was discovered at 16:10 h (BRST) on 13 December 2007, when L.P.G. spotted an adult carrying food to the nest. It was situated at the edge of tall secondary forest, about 2.5 m from a trail that is intensively used during sunny weekends by

people heading to waterfalls nearby (Figure 1A). At the nest location, this hiking path was cut into the ravine slope *c.* 50 m above the river. The nest was supported by thin twigs of a shrub growing on the bank by the trail side. The nest was 2.3 m above ground (at the trail level), and the vertical and horizontal distances from the bottom and left side of nest to the sloped ground (at the adjacent

bank) were 1.1 m and 0.5 m, respectively. The nest was collected by V.Q.P. two weeks later, when it was empty, and deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP 2282). Measurements were taken (with calipers) by L.P.G. on 12 February 2008, when he noticed the nest was "slightly compressed antero-posteriorly, possibly due to storage position".

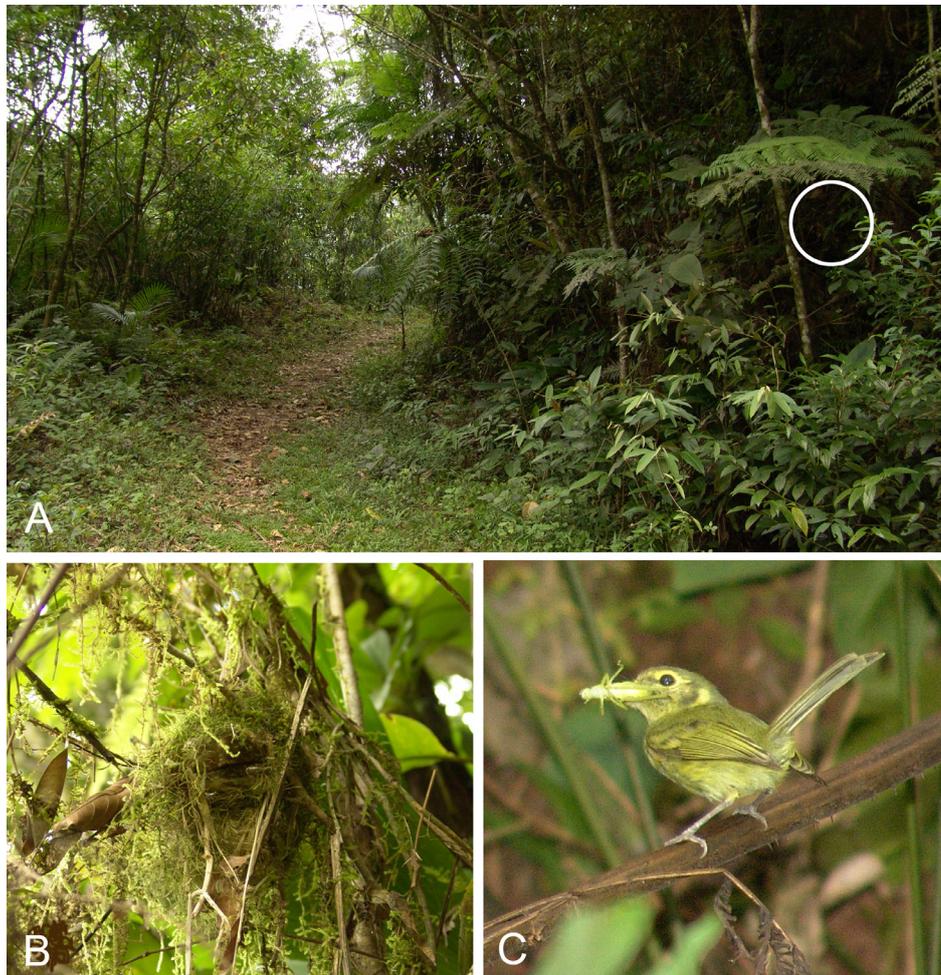


FIGURE 1. (A) Location (white circle) of the nest of Oustalet's Tyrannulet (*Phylloscartes oustaleti*) in the shade of Atlantic Forest trailside understory near Salto do Pirai, Joinville, Santa Catarina state, Brazil. (B) Entrance view of the enclosed nest camouflaged by green moss and dry leaves. (C) Adult Oustalet's Tyrannulet sitting on a favored perch (a dry leaf petiole of a tree fern) before delivering a male katydid to nestlings. Photo: C. Ozanick.

Nest description: the nest was a closed structure, with a dome-shaped lateral entrance situated slightly above the vertical midpoint of the nest opening directly into the nest chamber (Figure 2). The nest wall was thin, constructed mainly of very slender (*c.* 0.1 mm thick) light straw-colored plant fibers interwoven with strands of live moss. These moss strands were spread loosely around the nest between supporting twigs and also hung below the nest together with some dry leaves, forming an appendage-like structure *c.* 30 cm long and giving the whole a general appearance of a natural, unkempt mass of epiphytes (Figure 1B). Some light straw-colored dry plant material stands below the entrance and is the most exposed part of the nest. The incubatory chamber (below entrance level) was lined with soft, beige, silky cotton-

like material, probably seed down. When the nest was collected, this lining was swollen and filled the entire nest cavity below its entrance, perhaps due to expansion after being soaked by recent rainfall.

The nest was supported laterally by three twigs stemming from two branches (Figure 2). Two of these twigs, forming a fork, were attached to the nest entrance. The slenderer one (2 mm thick; Figure 2 t3) was parallel to ground and firmly tied with many fibers to the bottom edge of the entrance, forming its doorsill; the other (5 mm thick; Figure 2 t1) was attached to the left and upper margins of the entrance with only a few fibers, thus being almost entirely exposed. Another twig (2 mm thick; Figure 2 t4), stemming from the same branch, was situated several cm below the nest without touching it. The third

supporting twig (2 mm thick; Figure 2 t2) originated from an independent branch and intersected the nest wall at two points 5 cm apart, passing horizontally through the nest near the top of the chamber.

Parental behavior: we observed the nest with binoculars and a spotting scope for about 6 h from 16:35 h to 19:10 h on the day of discovery and from 05:30 h to 08:43 h on the following day. During this period, we recorded (1) the frequency of adult visits to the nest, (2) the types and relative size of food items delivered to nestlings, and (3) adult behavior. We did not use a blind to observe activity at the nest, and despite our presence only *c.* 6 m (occasionally less) from the nest, the adult continued to regularly attend it. To avoid disturbing the nestlings or damaging the nest, we did not attempt to see or count nestlings or inspect the nest more closely.

Only one adult at a time was ever observed at the nest. Because sexes are alike in this species, we were unable to know the sex of the bird attending the nest or to verify the presence of a second adult. An adult usually arrived silently with a food item and spent some time at one of a few favored perches within *c.* 2 m of the nest (always facing its entrance side) before flying straight into the nest. Most often (69%), time spent waiting at the perch was < 30 s (range 5–270, mean = 37.4, *n* = 29), and only on four occasions 60 s or more. Adult remained inside the nest very briefly, apparently only long enough to feed young and collect fecal sacs. We never observed the adult perching on the outside of the nest, either for delivering food or to collect fecal sacs. No brooding

was evident during our observations. The adult usually vocalized only after leaving the nest (17 times, *vs.* 5 times upon arrival), while flying away across or along the trail toward the stream valley, but sometimes it stayed foraging and eventually vocalized on the canopy of treelets situated on the nest vicinity. The only occasion when the adult vocalized more continuously, for *c.* 2 min., was during the early morning of the second day after mobbing a female White-shouldered Fire-eye *Pyriglena leucoptera* (Vieillot, 1818; *Thamnophilidae*) *c.* 1 m from the nest, having apparently remained alarmed with the continued presence of this antbird nearby.

Feeding visits to the nest occurred at an average rate of 9.3/h, and were about 2.3 times more frequent during the morning (12.4/h) than during the previous afternoon (5.4/h; *n* = 54). At no time did we hear begging calls. All of the large and conspicuous prey items we were able to identify in the provisioned food (*n* = 18) were arthropods (Figure 1C). These included three adult lepidopterans, two lepidopteran larvae (caterpillars) (*Lepidoptera*), three adult flies (*Diptera*) (including one horsefly: *Tabanidae*), two cockroaches (*Blattaria*), two katydids (*Ensifera: Tettigoniidae*), one praying mantis (*Mantodea*), one cicada (*Hemiptera: Cicadidae*), one stink bug (*Hemiptera: Pentatomidae*), one longhorn beetle (*Coleoptera: Cerambycidae*), and two spiders (*Araneae*). Fecal sacs were removed at an average rate of 2.1/h, almost four times more often in the morning (3.1/h) than in the previous afternoon (0.8/h; *n* = 12).

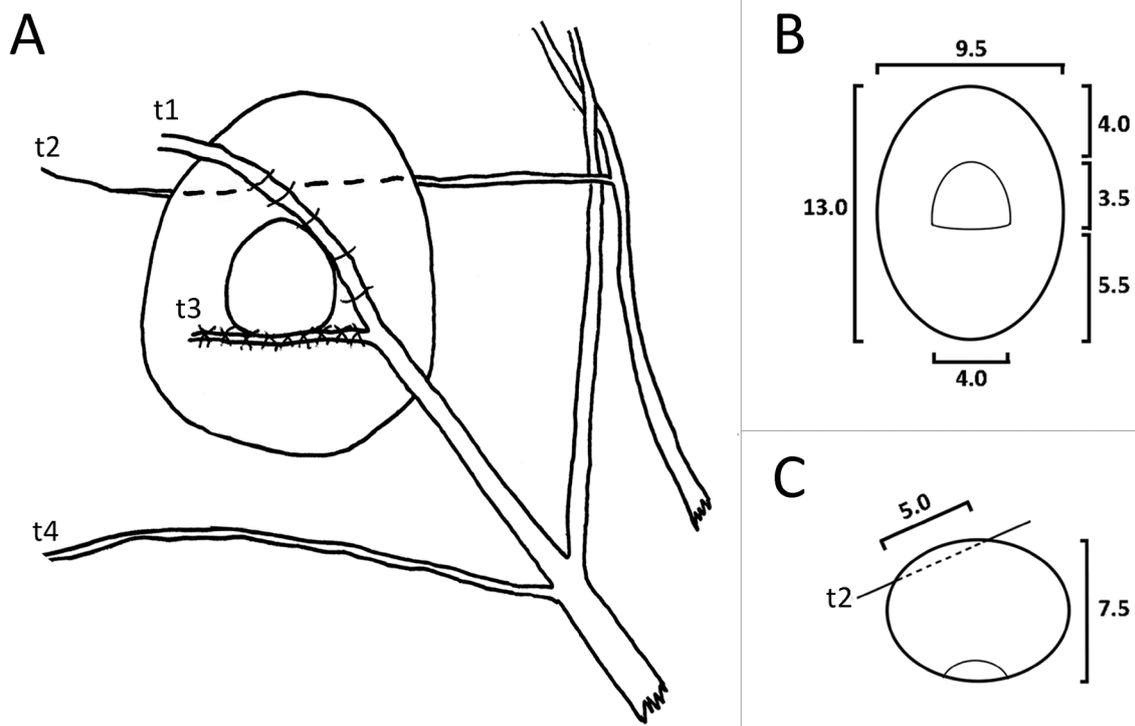


FIGURE 2. (A) Attachment to substrate and (B–C) External measurements (cm) of the nest of Oustalet's Tyrannulet. A, B – entrance view; C – top view; t1–t4 – twigs. Drawing: Juliana Machado.

In addition to the detailed nest description and associated observations presented above (among them what seem to be the first specific data on the diet of this species, which has been recorded only as “arthropods”: Fitzpatrick 2004), a limited amount of information on the nesting of Oustalet's Tyrannulet is available from other sources. Another nest of Oustalet's Tyrannulet was discovered by C.E.C. on 7 December 1986 in forest edge habitat at Augusto Ruschi (then Nova Lombardia) Biological Reserve (c. 19°50'S; 40°33'W; 900 m a.s.l.) in Espírito Santo state, southeastern Brazil. It was also a closed structure, placed c. 4 m above ground amidst a clump of dead leaves wrapped around twigs of a small tree. The nest appeared to be made mostly of green material (possibly live moss), which contrasted with the surrounding brown dry leaves. Two adults were foraging in the foliage around nest site when one of them, without carrying any food or building material, entered the nest, thus leading to its discovery. The nest location precluded a closer inspection at the occasion, and a big treefall at nest site precluded its collection when C.E.C. returned one month later, so that no further details on its shape and attachment became available. A third nest of the species, discovered in Espírito Santo by F. Costa in October 2010 (image available at <http://www.wikiaves.com/223181>), was also a closed structure with a lateral entrance, made of straw-colored fibers interwoven with live moss.

All these three nest records of Oustalet's Tyrannulet are consistent with the previously postulated September to December breeding season for the species (Fitzpatrick 2004). However, a bird photographed by F. Costa (image available at <http://www.wikiaves.com/178584>) carrying nest material in early August in Espírito Santo state suggests the breeding season may extend earlier. Two additional records of birds of this species carrying nest material are from November, in Espírito Santo and Paraná states (images available at <http://www.wikiaves.com.br/1519229> and <http://www.wikiaves.com.br/1154692>). This timing follows the general pattern of breeding bird activity occurring mostly during spring and early summer in southeastern Brazil (Euler 1900, Davis 1945, Marini & Durães 2001).

The general form and attachment of the nest of *P. oustaleti* agree with those found in the few other species of *Phylloscartes* whose nests are known. All these species construct closed structures with lateral entrances, and most of them include live moss as building material and have nests firmly attached to substrate instead of pensive (see Kirwan *et al.* 2010, Londoño 2014). Given its architecture, measurements and way of attachment, the Oustalet's Tyrannulet nest described here conforms to the closed/ovoid/lateral type of Simon & Pacheco (2005). Although the form of nests in this genus has usually been identified as “globular” (*e.g.*, Kirwan *et al.* 2010), strict

adherence to the classification scheme proposed by Simon & Pacheco (2005) in this case leaves no doubt that it is better to include the nest described here in their variant “ovoid”, in which “the length is up to twice the width”, and not with external diameters approximately identical as in their “globular” type. Since the vast majority of available descriptions lack any measurements, we predict that other species in this genus may also be found to build ovoid nests as more information becomes available or when existing information is reviewed. We concur with Kirwan *et al.* (2010) in their encouragement of nest finders and describers to use the system proposed by Simon & Pacheco (2005), as a way to render comparisons more objective across taxonomic levels. However, some features of nests that are required for such standardized descriptions cannot be assessed by photographs only, so we recommend that in addition to clear photographs and detailed field notes, nests be collected and deposited into museum collections whenever possible, in which we also concur with Russel *et al.* (2013).

The potential importance of nest architecture and other features related to breeding behavior in the understanding of phylogenetic relations among tyrant flycatchers (and other bird families) has been claimed by many authors along time (*e.g.*, Lanyon 1984, 1988, Kirwan *et al.* 2010, Crozariol 2016). Unfortunately, current knowledge is still unsatisfactory to be of any help in solving the puzzle of relationships among the members of *Phylloscartes* and related genera. Clearly, nest descriptions are needed in greater detail from a larger number of species before any intra- or interspecific variation can be adequately appreciated in evolutionary or even purely taxonomic contexts, because homoplastic and symplesiomorphic features may be a considerable source of noise. But not only data on nesting are scarce: existing DNA-based phylogenies of tyrant flycatchers have included barely a few species of this group (*e.g.*, Tello *et al.* 2009). Consequently, not even a preliminary understanding of the possible phylogenetic signal in the few known nesting features is possible at this systematic level. However, as molecular techniques have recently advanced many times faster than even the rapidly growing number of field ornithologists in the Neotropics, we expect this gap can be filled as soon as the attention of molecular phylogeneticists is focused on this particular group of birds, so that we can speed up learning on the evolution of their nesting habits.

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Mouth troubles: possible outcomes for three bird species with deformed bills

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ABSTRACT: Bill deformities occur with low frequency among birds (0.5–2%). The deformity degree may influence several phases of the birds' life, from feeding to feather maintenance, the latter affecting thermoregulation, parasite proliferation, courtship and mating. We recorded three bird species, a pigeon, a hummingbird and an ovenbird, with similar bill deformity (crossed bill). This deformity affected a female Brazilian Ruby (*Clytolaema rubricauda*) with lower mandible skewed to the left, an unsexed individual and a probable female of the Picazuro Pigeon (*Patagioenas picazuro*) with similar deformity, and an unsexed individual of the Rufous Hornero (*Furnarius rufus*) with upper mandible strongly twisted to the left. We hypothesise that possible outcomes due to crossed bill vary with the deformity degree, and the species, sex, and general habits of the affected birds.

KEY-WORDS: crossed bill, detrimental effects, non-Passeriformes, Passeriformes.

Bill deformities seem rare among birds, with recorded occurrence of about 0.5–2% (Craves 1994, Vereá & Vereá 2010). These deformities may be due to injuries and diseases, malformations, malnutrition and possibly genetic factors and pollutants (Craves 1994), although evidences for any of these causes are inconclusive (Fox 1952, Pomeroy 1962, Sharp & Neill 1979). The deformity degree may influence several phases of the birds' life, from feeding to feather maintenance, the latter affecting thermoregulation, parasite proliferation, courtship and mating (Pomeroy 1962, Sharp & Neill 1979, Thompson & Terkianian 1991, Zampiga *et al.* 2004). We describe and illustrate herein three bird species, a hummingbird, a pigeon, and an ovenbird, from southeastern Brazil, which share a similar deformity (crossed bill) but have different habits. Additionally, we comment on the possible consequences of this deformity, as the outcomes probably vary according to the deformity degree, species, sex, and general habits of the affected birds. We are unaware of such comparative reports, less so about the possible outcomes depending on the birds' habits.

The hummingbird was recorded in the Parque Nacional do Itatiaia (22°26'20"S; 44°36'28"W), Rio de Janeiro, 23–24 April 2015. There are hummingbird feeders at this site, as well as introduced and native flower species. The pigeons were recorded in Campinas (22°48'42"S; 47°04'21"W), São Paulo, 09 August 2011 and 28 April and 03 May 2015. There is food provisioning (corn kernels,

poultry feed, and bran) for the domestic waterfowl raised at the study site (Corbo *et al.* 2013). The ovenbird was also recorded in Campinas (22°49'59"S; 47°04'41"W), 08 July 2010. We observed the birds with bare eye and through a 70–300 mm telephoto lens mounted on a camera at a distance of 1–5 m. Throughout the observational sessions, we used the “*ad libitum*”, “sequence”, and “focal animal” samplings (Altmann 1974), which are adequate to record fortuitous or rare events. Voucher digital photographs of the birds with bill deformities are on file at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

We recorded a Brazilian Ruby (*Clytolaema rubricauda*) female with the lower mandible distinctly skewed to the left (Figure 1A). The bird regularly visited hummingbird feeders, perching on a nearby twig afterwards (Figures 1A, B). Besides taking the sweetened water from the feeders, the bird sought nectar from flowers in the vicinity. The visited flowers had short corollas (10–15 mm) and the bird was able to extend her tongue into the corolla to take nectar. The distinctly crossed bill (Figure 1A) did not impair the intake of liquids, as the tongue could be drawn out entirely (Figure 1B). However, we recorded no hawking for insects by this individual, a common foraging mode in this species (I.S., pers. obs.).

Two Picazuro Pigeon (*Patagioenas picazuro*) individuals were recorded with bill deformities. An unsexed bird had its lower mandible strongly skewed to the left (Figure 1C). Another individual had a similar bill

deformity (Figure 1D). The first individual was recorded picking corn kernels and poultry food pellets (Figure 1C), which it handled with more effort than individuals with normal bill. The pigeon with deformed bill pecked at each kernel or pellet up to five times before it was able to secure and ingest it, whereas pigeons with normal bill habitually pecked at the food once to ingest this food type. Despite its preening, this pigeon displayed a somewhat untidy plumage (Figure 1C). The second individual

was recorded brooding (Figure 1D) and, occasionally, rearranging sticks in the nest.

We recorded an unsexed Rufous Hornero (*Furnarius rufus*) with its upper mandible strongly twisted to the right (Figures 1E, F). The bird perched on a dead branch sunning itself, resting, and stretching. Additionally, the bird preened the plumage repeatedly, but its deformed bill made it incapable to arrange the feathers adequately, as these were clearly unkempt (Figures 1E, F).



FIGURE 1. Three instances of birds with distinct habits and similar deformities (crossed bill). The lower mandible of the Brazilian Ruby (*Clytolaema rubricauda*) female is skewed to the left (a); the unkempt plumage on her chest indicates an inability to rearrange the feathers properly, and the drawn out tongue makes possible the intake of sweetened water from feeders and nectar from flowers (b); provisioning of corn kernels and poultry feed pellets are awkwardly picked by this Picazuro Pigeon (*Patagioenas picazuro*) with its lower mandible strongly skewed to the left – notice untidy back plumage and wing feathers (c); a similar bill deformity did not prevent the reproduction of another individual, probably a female due to her behavior – brooding and rearranging sticks on the nest (d); the untidy feathers on the chest of the Rufous Hornero (*Furnarius rufus*), with the upper mandible strongly twisted to the right, indicates the importance of the bill to feather maintenance (e); the misaligned wing feathers show the troubles the bird had with plumage maintenance (f). Photos: I. Sazima (a, b, e, f), J. V. Hipolito (c), G. B. D'Angelo (d).

The three deformity instances recorded herein are similar (crossed bill) but occur in species with distinct habits. The deformity degree varies from moderate in one non-passerine (hummingbird) to great in a non-passerine (pigeon) and a passerine (oven-bird).

The crossed bill did not impair taking flower nectar by the Brazilian Ruby female, but apparently restricted her to flowers with shorter corollas than those visited by individuals with normal bill (corollas up to 80 mm, see Sazima *et al.* 1996). In addition, the crossed bill likely hampered hawking for insects, which is an important component in the diet of hummingbirds (Schuchmann 1999). This protein source would be missing by the recorded female. Additionally, the plumage of this female was unkempt, a probable consequence of the crossed bill (Sharp & Neill 1979, Vereá & Vereá 2010). Untidy plumage has the potential to negatively affect thermoregulation (Burton 1985, Gill 2007) and may contribute to parasite proliferation (Pomeroy 1962, Arendt & Arendt 1986, Thompson & Terkianian 1991). Also, the untidy plumage has the potential to negatively affect reproduction, as males could be less prone to court a female in such condition (Burton 1985, Zampiga *et al.* 2004, Amat *et al.* 2011). Moreover, the misaligned mandibles likely hamper gathering and arranging nest material, as nest in hummingbirds is made exclusively by females (Schuchmann 1999). Thus, this deformity type could negatively affect nest construction and, consequently, her reproduction. In addition, her apparent inability to catch insects by hawking and the consequent lack of protein prior to reproduction possibly affects her whole reproductive cycle.

Picking corn kernels and poultry food pellets by the Picazuro Pigeon with crossed bill went with more handling effort that would be displayed by individuals with normal bill. We suppose that without the food provisioning (Corbo *et al.* 2013), the deformed pigeons would not thrive as well as at the studied site. Both the Picazuro Pigeon we observed had untidy plumage, with the consequences cited above for the hummingbird. However, plumage condition seemed not to affect this pigeon species strongly, as one individual with crossed bill bred at least once (present paper). Gathering sticks to for the nest is a male issue in the life of the Picazuro Pigeon, whereas the female arranges the sticks in the platform she already sits (Baptista *et al.* 1997). A male with deformed bill probably would have trouble to breed, since a crossed bill probably would hamper gathering of nest material. Thus, we suppose that the brooding and nest arranging individual was a female.

The strongly twisted bill of the Rufous Hornero (*Furnarius rufus*) likely hindered its feeding, as this bird species picks with its bill tip the insects and other arthropods that are its staple food (Schubart *et al.* 1965,

Corbo *et al.* 2013). On the other hand, for birds that are used to feed in garden and backyard in bird-feeders (Stiteler 2008) feeding troubles are probably lessened. Additionally, this individual would have trouble to gather and work the mud for the construction of its characteristic nest (Sick 1997). The more unkempt plumage of the ovenbird as compared with the precedent species possibly increases the disadvantages already mentioned for the other recorded birds. Additionally, the bill deformity and the untidy plumage probably hamper the reproduction, as the Rufous Hornero calls in duets and the mated pair builds the nest together (Sick 1997, Corbo *et al.* 2013). Thus, the bill deformity degree we recorded for this ovenbird individual most likely reduces its survival altogether.

The same deformity type (crossed bill) would affect a bird in different ways and degrees, according to the general habits of the afflicted bird. For instance, the Brazilian Ruby female had the least deformity degree among the recorded birds, but would be more affected than the Picazuro Pigeon female, whose deformity was comparatively more prominent. This difference would be related to courtship and nest building (Baptista *et al.* 1997, Schuchmann 1999), as already pointed out above. The most impaired bird in several fundamental phases such as feeding, feather maintenance, and reproduction seemed to be the Rufous Hornero. However, all the three species reported herein may have their life cycle abbreviated due to their bill deformity. We hypothesise that the possible outcomes vary according to the degree of the deformity, and the species, sex, and general habits of the recorded birds (Fox 1952, Pomeroy 1962, Vasconcelos & Rodrigues 2006, Vereá & Vereá 2010).

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Systematic review of the Cinnamon-throated Woodcreeper *Dendrexetastes rufigula* (Aves: Dendrocolaptidae) based on a multilocus phylogeography

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ABSTRACT: The Amazon is one of the most speciose regions in the world. Yet there are still undescribed and misidentified species, and scarce information about the biology of the described species in the region. Here, we evaluate for the first time the existence of genetically differentiated lineages within the polytypic species *Dendrexetastes rufigula*, an endemic Amazonian lineage. We identified three major evolutionary independent units using both mitochondrial (Cytb and ND2) and nuclear (G3PDH, BF5 and MUSK) markers that roughly corresponded to currently recognized subspecies. Although we found strong statistical support for the reciprocal monophyly of *D. r. rufigula* and *D. r. devillei*, we did not find reciprocal monophyly between *D. r. moniliger* and *D. r. paraensis*, which were paraphyletic. However, these two taxa grouped together in a clade with Bayesian but not bootstrap support. Moreover, clades *D. r. rufigula*, *D. r. devillei*, and *D. r. moniliger/paraensis* differed from each other by much higher mitochondrial genetic distances (between 1 and 2%), than that separating *D. r. paraensis* from *D. r. moniliger* ($0.3 \pm 0.1\%$). We add molecular evidence to the morphological data supporting that *D. r. rufigula* and *D. r. devillei* are highly diagnostic taxa that could be regarded as two distinct species. Conversely, although *D. r. moniliger* and *D. r. paraensis* are both genetically and morphologically distinct from either *D. r. rufigula* or *D. r. devillei*, *D. r. moniliger* and *D. r. paraensis* cannot be considered mutually independent evolutionary lineages. This result is particularly important from a conservation perspective, since *D. r. paraensis* is considered threatened in Brazil. Our results support that at least three main evolutionary lineages deserving evolutionary species status exist in the Cinnamon-throated Woodcreeper, and that the endangered lineage in the Belém area of endemism is a morphologically slightly distinct subset of a more widespread lineage endemic to southeastern Amazonia east of the Madeira River.

KEY-WORDS: Amazonia, conservation, *Dendrexetastes rufigula paraensis*, leapfrog pattern, species limits, taxonomy.

INTRODUCTION

Growing evidence highlights that global biodiversity levels are higher within the Amazon region than previously acknowledged (plants: Kier *et al.* 2005; mammals: Ceballos & Ehrlich 2006; birds: Jetz *et al.* 2012; several examples: Jenkins *et al.* 2013). Overall, birds are one of the best known taxonomic groups within the region, with fewer bird species discovered since the 1950s in comparison to mammals, and amphibians (Jenkins *et al.* 2013). Yet, a considerable percentage of the latest “new” bird species described from the Amazon resulted from the recognition of widespread species as species complexes (*e.g.* Carneiro *et al.* 2012, Whitney & Cohn-Haft 2013). Molecular analytical tools have been

particularly important in the assessment of species limits for these geographically widespread species complexes in Amazonia (see revision by Bickford *et al.* 2007; and recent examples, such as D’Horta *et al.* 2013, Fernandes *et al.* 2013, Sousa-Neves *et al.* 2013, Thom & Aleixo 2015). This hidden diversity, as described by Bickford *et al.* (2007), results from the inability to distinguish two or more species, cryptic species, due to their morphological similarities, and so they are treated as the same nominal species. Thus, currently, despite being a well-known group, the Amazonian avifauna still suffers from a chronic under-estimation of its diversity, namely needing an accurate assessment of its cryptic diversity (see Bates & Demos 2001, Aleixo 2009, Whitney & Cohn-Haft 2013, Barrowclough *et al.* 2016).

The Cinnamon-throated Woodcreeper *Dendrexetastes rufigula* (Aves: Dendrocolaptidae) is a widespread and polytypic Amazonian endemic species, which occurs in both upland *terra-firme* and seasonally flooded forests, such as *várzea* and *igapó* (Figure 1A). The genus is considered monospecific, and four subspecies are currently recognized (Marantz *et al.* 2003): *D. r. devillei* (occurring west of the Negro River to the west bank of the Madeira River in Brazil, and across southern Colombia, eastern Ecuador, eastern Peru, and northwestern Bolivia); *D. r. moniliger* (found from the east bank of the Madeira River to the west bank of the Tocantins River in Brazil, and northeastern Bolivia); *D. r. paraensis* (found east of

the Tocantins River in the Brazilian states of Pará and Maranhão); and *D. r. rufigula* (occurring on the Guiana shield from eastern Venezuela, the Guianas, and Brazil east of the Negro River to Amapá state). Vocalizations are very similar among subspecies, but each is distinguishable by discrete plumage characters, which prompted their recognition as separate taxa (Marantz *et al.* 2003). In fact, *D. r. devillei* had been treated as a separate species by some sources (Hellmayr 1907, Sneath 1908), but later subsumed under *D. rufigula* as a subspecies (Hellmayr 1910), an arrangement that has been followed ever since (Cory & Hellmayr 1925, Peters 1951, Marantz *et al.* 2003).

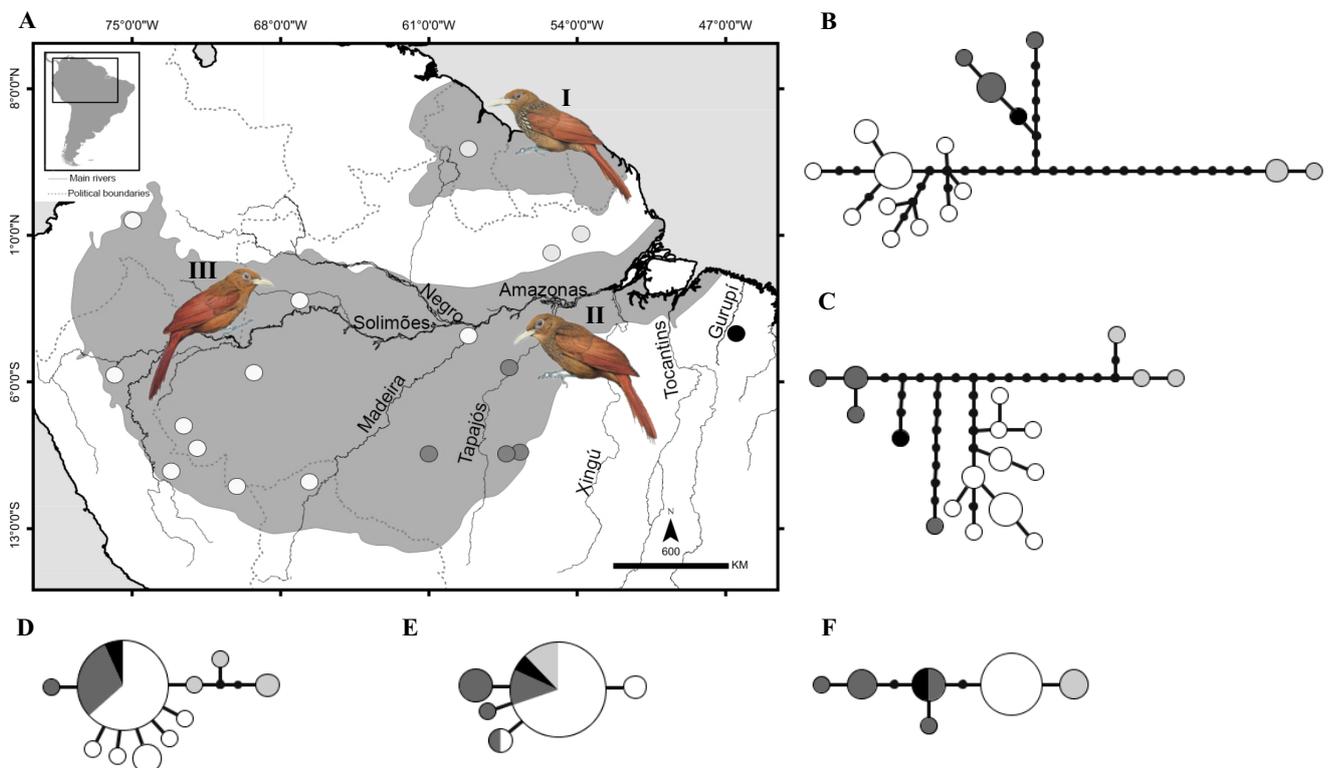


FIGURE 1. Putative distribution range of *Dendrexetastes rufigula* (modified from Marantz *et al.* (2003), sampling localities for each subspecies (A); and haplotype networks for NADH dehydrogenase (B), cytochrome *b* (C), β -fibrinogen intron 5 (D), glyceraldehyde-3-phosphate dehydrogenase intron 11 (E) muscle, skeletal, receptor tyrosine kinase intron 3 (F). In the haplotype networks, circle areas are proportional to haplotype frequencies. I and light grey *D. r. rufigula*, II and dark grey *D. r. moniliger*, III and white *D. r. devillei*, and black *D. r. paraensis*.

Given the species wide range and putative large population size, the Cinnamon-throated Woodcreeper is evaluated as Least Concern by IUCN, yet deforestation might be affecting its populations, and leading to a demographic decrease (Bird *et al.* 2012, BirdLife International 2012). Indeed, the most recent version of the Brazilian list of threatened species included *D. r. paraensis* from the Belém area of endemism (Da Silva *et al.* 2005) under the status “Vulnerable” (MMA 2014). The species is thought to have gone locally extinct in the Belém metropolitan area over the last 70 years, due to habitat destruction and fragmentation (Moura *et al.* 2014).

So far, no phylogeographic study exists for the Cinnamon-throated Woodcreeper, which prevents the

assessment of the degree of evolutionary independence among its taxa, including the endangered *D. r. paraensis*. Here, we estimate for the first time the evolutionary history and degree of genetic differentiation among subspecies of the Cinnamon-throated Woodcreeper based on a multilocus approach, and discuss the systematic and taxonomic implications of these data.

METHODS

Specimens analyzed

Tissue samples of 28 specimens of Cinnamon-throated Woodcreeper *D. rufigula* were sequenced (Table 1; Figure

1A), as follows: *D. r. devillei* (n = 17), *D. r. rufigula* (n = 3), *D. r. moniliger* (n = 7), and *D. r. paraensis* (n = 1). A sample from *Nasica longirostris* was used as outgroup following Derryberry *et al.* (2011). For comparative purposes with the genetic data, we inspected plumage variation patterns of 31 Cinnamon-throated Woodcreeper study skins housed at the Museu Paraense Emílio Goeldi (MPEG) bird collection (Appendix I), as follows: *D. r. devillei* (n = 15), *D. r. rufigula* (n = 5), *D. r. moniliger* (n = 8), and *D. r.*

paraensis (n = 3); of these, a total of 18 specimens were the same individuals used in the molecular analyses (Appendix I). We searched for any plumage characters diagnosing any taxon or recovered clade of the Cinnamon-throated Woodcreeper. Each specimen examined was scored qualitatively for the color and shape of any marks on the plumage of its different body parts. Alphanumeric color designations were determined through direct comparison with Smithe (1975).

TABLE 1. Voucher information of *Dendrexetastes rufigula* and *Nasica longirostris* tissue samples. M – Male; F – Female.

Museum	Taxa	Sex	Locality
FMNH 395555	<i>Dendrexetastes rufigula devillei</i>	M	Brazil, Acre, Reserva Extrativista Alto Juruá, River Tejo
LSUMZ B-1159	<i>Dendrexetastes rufigula devillei</i>	M	Bolivia, La Paz Department
LSUMZ B-103621	<i>Dendrexetastes rufigula devillei</i>	?	Peru, Loreto Department
LSUMZ B-28077	<i>Dendrexetastes rufigula devillei</i>	M	Peru, Loreto Department
LSUMZ B-4329	<i>Dendrexetastes rufigula devillei</i>	M	Peru, Loreto Department
LSUMZ B-11084	<i>Dendrexetastes rufigula devillei</i>	M	Peru, Ucayali Department
ANSP 183229	<i>Dendrexetastes rufigula devillei</i>	M	Equador, Imuya Cocha
ANSP 183230	<i>Dendrexetastes rufigula devillei</i>	F	Equador, Imuya Cocha
MPEG 58872	<i>Dendrexetastes rufigula devillei</i>	F	Brazil, Acre, ESEC River Acre, Acampamento 2 (11°00'53.4"S; 70°13'02.7"W)
MPEG 58873	<i>Dendrexetastes rufigula devillei</i>	M	Brazil, Acre, ESEC River Acre, Acampamento 2 (11°00'53.4"S; 70°13'02.7"W)
MPEG 62041	<i>Dendrexetastes rufigula devillei</i>	F	Brazil, Acre, Porto Walter, Igarapé Cruzeiro do Vale, Colônia Dois Portos (08°20'35.7"S; 72°36'19.7"W)
MPEG 62670	<i>Dendrexetastes rufigula devillei</i>	M	Brazil, Amazonas, Japurá, River Acanauí (01°56'12.4"S; 66°36'18.8"W)
MPEG 60145	<i>Dendrexetastes rufigula devillei</i>	M	Brazil, Amazonas, RDS Cujubim, E bank River Jutai (05°38'19"S; 69°10'59"W)
MPEG 62669	<i>Dendrexetastes rufigula devillei</i>	M	Brazil, Amazonas, Japurá, River Acanauí (01°56'12.4"S; 66°36'18.8"W)
MPEG 73774	<i>Dendrexetastes rufigula devillei</i>	F	Brazil, Amazonas, Autazes (03°46'52.8"S; 59°03'23.8"W)
LSUMZ B-39873	<i>Dendrexetastes rufigula devillei</i>	M	Peru, Loreto Department
LSUMZ B-35686	<i>Dendrexetastes rufigula devillei</i>	M	Peru, Loreto Department
ANSP 187812	<i>Dendrexetastes rufigula rufigula</i>	M	Guyana, Iwokrama Reserve Surama, Kurupukari Base Camp
MPEG 65390	<i>Dendrexetastes rufigula rufigula</i>	F	Brazil, Pará, Alenquer, ESEC Grão-Pará (00°09'S; 55°11'W)
MPEG 66217	<i>Dendrexetastes rufigula rufigula</i>	M	Brazil, Pará, Almeirim, REBIO Maicuru (00°49'N; 53°55'W)
FMNH 389808	<i>Dendrexetastes rufigula moniliger</i>	F	Brazil, Rondonia, Waterfall Nazare, W bank River Jiparana
FMNH 389815	<i>Dendrexetastes rufigula moniliger</i>	F	Brazil, Rondonia, Waterfall Nazare, W bank River Jiparana
LSUMZ B-35540	<i>Dendrexetastes rufigula moniliger</i>	M	Brazil, Mato Grosso
MPEG 69376	<i>Dendrexetastes rufigula moniliger</i>	F	Brazil, Mato Grosso, Paranaíta, River Teles Pires, left margin (09°24'51.4"S; 56°33'39.7"W)
MPEG 67351	<i>Dendrexetastes rufigula moniliger</i>	M	Brazil, Mato Grosso, Paranaíta, River Teles Pires (09°25'310"S; 56°33'753"W)
MPEG 67350	<i>Dendrexetastes rufigula moniliger</i>	F	Brazil, Mato Grosso, Paranaíta, River Teles Pires (09°25'310"S; 56°33'753"W)
MPEG 76624	<i>Dendrexetastes rufigula moniliger</i>	M	Brazil, Pará, Itaituba, River Tapajós left margin, Penedo (05°27'21.61"S; 57°04'12"W)
MPEG 76873	<i>Dendrexetastes rufigula paraensis</i>	F	Brazil, Maranhão, Centro Novo, REBIO Gurupi (03°42'12.8"S; 46°45'44"W)
MPEG 73862	<i>Nasica longirostris</i>	M	Brazil, Amazonas, Autazes, Uricurituba, Ilha (03°35'31.2"S; 58°56'35.6"W)

Institution acronyms: ANSP - Academy of Natural Sciences of Drexel University, Philadelphia, USA; FMNH - Field Museum of Natural History, Chicago, USA; LSUMZ - Louisiana State University Museum of Natural Science, Baton Rouge, USA; MPEG - Museu Paraense Emílio Goeldi, Belém, Brazil.

Genetic analyses

Total genomic DNA was extracted using the Genomic DNA Purification Kit (Promega; Wizard®). Two mitochondrial molecular markers were amplified: cytochrome *b* (Cytb) using primers L14841/H16065 (Kocher *et al.* 1989, Sorenson *et al.* 1999), and NADH Dehydrogenase Subunit 2 (ND2) using primers L5215/H6313 (Hackett 1996, Sorenson *et al.* 1999); two nuclear autosomal markers: β -fibrinogen Intron 5 (BF5) with primers S713/AS767 (Marini & Hackett 2002), and Glyceraldehyde 3-phosphate Dehydrogenase Intron 11 (G3PDH) using primers G3PD-13b/G3PD-14b (Fjeldså *et al.* 2003); and a Z-linked marker Muscle Skeletal Receptor Tyrosine Kinase Intron 3 (MUSK) using primers 13F/13R (Clark & Witt 2006). Polymerase chain reaction (PCR) amplifications were performed using an initial denaturation at 94°C for 5 min, followed by 33 (ND2 and BF5) or 35 cycles (all the other loci) of a denaturation at 94°C for 1 min, annealing for 1 min at temperatures between 50°C and 70°C according to the marker, and an extension at 72°C for 1 min; and the final extension was at 72°C for 5 min for all markers. Master Mix (Promega, Inc.) was used to perform PCR for Cytb and MUSK with the following concentrations: 6.25 μ l of Master Mix, 10 pmol of each primer, 50 ng/ μ l of DNA, in a final volume of 12.5 μ l. Taq DNA polymerase recombinant kit (Invitrogen, Inc.) was used to amplify all the other loci using 1 \times buffer; 0.4 mM DNTTP; 10 pmol of each primer, 0.5 U Taq DNA polymerase; 2 mM, 1.4 mM or 1.5 mM MgCl₂ (for ND2, BF5 and G3PDH, respectively) and 50 ng/ μ l of DNA in a final volume of 12.5 μ l. PCR products were visually inspected in a 1% agarose gel, after electrophoresis; and positive results were purified using PEG8000 2.5 M (Hawkins *et al.* 1994). After sanger sequencing reactions using the Big Dye Terminator v3.01 kit, sequence products for both strands were electrophoresed on an ABI 3130 automatic sequencer, following the manufacturer's protocol (Applied Biosystems, CA).

Sequences were visually inspected in BioEdit, and aligned using Clustal W (Hall 1999). Sequences from nuclear molecular markers were phased using the PHASE algorithm (Stephens & Scheet 2005), implemented in DnaSP 5.0 (Librado & Rozas 2009). A threshold of 80% was used. For all loci and subspecies, standard genetic diversity indices (*e.g.*, haplotype and nucleotide diversity) were estimated, and mismatch distribution plots were obtained in DnaSP 5.0 (Librado & Rozas 2009). Neutrality (Tajima's *D* and *R*₂; Tajima 1989, Ramos-Onsins & Rozas 2002), and recombination tests were also performed (Hudson & Kaplan 1985, Hudson *et al.* 1987, Rozas *et al.* 2001) using the same software, and the coalescent simulation test therein implemented (Rozas

2009). One thousand replicates were run to estimate statistical significance ($P < 0.05$) of the tests. Insertions/deletions detected in nuclear markers were coded as (-) and considered a fifth state.

Mean uncorrected P-distances, between and within subspecies, were estimated for mitochondrial markers, using concatenated datasets, in MEGA 5.0 (Tamura *et al.* 2011).

Haplotype networks for each molecular marker were constructed in haplotype viewer (Blake *et al.* 2012). Haplotype viewer requires the input of a maximum likelihood tree, which was obtained in raxmlGUI (Silvestro & Michalak 2012, Stamatakis 2014), using the mutation model that best fit the data (GTR-GAMMA) as determined by PartitionFinder (Lanfear *et al.* 2012). A more thorough phylogenetic analysis was obtained using raxmlGUI (Silvestro & Michalak 2012, Stamatakis 2014), by running 10 independent runs with 1000 slow bootstrap pseudo-replicates (Felsenstein 1985).

Species limits in the Cinnamon-throated Woodcreeper were tested using BPP3.2 (Yang 2015). This method considers gene tree/species tree conflicts, and the possible occurrence of incomplete lineage sorting (Yang & Rannala 2010, Rannala & Yang 2013). A joint species delimitation and species tree analysis was conducted (Yang 2015) to test the delimitation of the three clades recovered by ML analyses (*D. r. rufigula*, *D. r. devillei* and *D. r. moniliger/D. r. paraensis*; see results section for more details). We ran the reversible-jump Markov Chain Monte Carlo (rjMCMC) analysis, with algorithm 0 and $e = 2$, for 500,000 generations (sampling interval of five), and a burnin of 100,000 generations. Priors for ancestral population size and divergence times might influence the posterior probability distributions (Yang 2015), so we tested different combinations for these priors, considering relatively large and small ancestral population sizes: θ -G(1,10) and θ -G(2,2000), respectively; and shallow and deep divergence times: τ -G(2,2000) and τ -G(1,10), respectively. The other divergence time parameters were assigned the default Dirichlet prior (Yang & Rannala 2010). A heredity file was input to account for the different inheritance patterns in the dataset. Each analysis was run twice to confirm consistency of results.

RESULTS

We sequenced a total of 3564 base pairs (bp), respectively 1015, 997, 571, 556 and 425 from ND2, Cytb, MUSK, BF5 and G3PDH. All generated sequences have been deposited in GenBank under accession numbers KY510693 to KY510809. Standard sequence summary statistics are presented in Table 2. For *D. r. devillei*, mismatch distributions for G3PDH and BF5 genes fit

well with expected curves of population growth (data not shown). For *D. r. moniliger*, mismatch distribution analyses also detected signs of expansion for BF5 (data not shown). All other mismatch distributions did not support demographic expansions. Recombination tests did not detect recombination events.

TABLE 2. *Dendrexetastes rufigula* genetic diversity and neutrality tests results for the (A) full dataset and (B) by subspecies for each locus. bp – base pairs, S – number of segregating sites, H – number of haplotypes, Hd – haplotype diversity, π – nucleotide diversity, D – Tajima's D, SD – standard deviation, n – number of sequences analysed, Cytb – cytochrome *b*, ND2 – NADH dehydrogenase 2, BF5 – β -fibrinogen intron 5, G3PDH – Glyceraldehyde-3-phosphate dehydrogenase intron 11, MUSK – muscle, skeletal, receptor tyrosine kinase intron 3. * $P < 0.05$. *D. r. paraensis* only included in Table A, because only one sample was available.

Locus	bp	S	H	Hd \pm SD	$\Pi \pm$ SD	D	R ₂
A							
Cytb	997	43	18	0.967 \pm 0.024	0.01001 \pm 0.00131	-0.819	0.16
ND2	1015	42	15	0.934 \pm 0.030	0.00941 \pm 0.00122	-0.765	0.27
G3PDH	425	4	5	0.377 \pm 0.092	0.00097 \pm 0.00026	-1.319	0.06
BF5	556	10	10	0.490 \pm 0.094	0.00165 \pm 0.00047	-1.791	0.02*
MUSK	571	6	6	0.714 \pm 0.080	0.00321 \pm 0.00059	0.426	0.71
B							
<i>D. r. devillei</i>							
Cytb	15	13	10	0.924 \pm 0.053	0.00340 \pm 0.00054	-0.784	0.04*
ND2	17	19	8	0.912 \pm 0.056	0.00357 \pm 0.00053	-1.455	0.02*
G3PDH	26	2	3	0.218 \pm 0.103	0.00053 \pm 0.00026	-1.224	0.11
BF5	26	5	6	0.465 \pm 0.116	0.00094 \pm 0.00027	-1.709	0.06
MUSK	14	0	1	0.000	0.00000	-	-
<i>D. r. moniliger</i>							
Cytb	5	13	4	0.900 \pm 0.161	0.00593 \pm 0.00291	-0.978	0.91
ND2	7	7	4	0.810 \pm 0.130	0.00391 \pm 0.00074	0.952	0.82
G3PDH	10	3	4	0.733 \pm 0.101	0.00221 \pm 0.00048	-0.431	0.15
BF5	10	1	2	0.200 \pm 0.154	0.00036 \pm 0.00028	-1.112	0.71
MUSK	7	3	4	0.810 \pm 0.130	0.00284 \pm 0.00052	1.459	0.83
<i>D. r. rufigula</i>							
Cytb	3	3	3	1.000 \pm 0.272	0.00208 \pm 0.00073	-	0.27
ND2	3	1	2	0.667 \pm 0.314	0.00066 \pm 0.00031	-	1.00
G3PDH	4	0	1	0.000	0.00000	-	-
BF5	4	4	3	0.833 \pm 0.222	0.00420 \pm 0.00109	0.650	0.18
MUSK	2	0	1	0.000	0.00000	-	-

TABLE 3. Uncorrected genetic P-distance (%) between and within *Dendrexetastes rufigula* subspecies estimated using cytochrome *b* and NADH dehydrogenase 2 (Cytb e ND2) sequences.

	<i>D. r. devillei</i>	<i>D. r. moniliger</i>	<i>D. r. rufigula</i>
<i>D. r. devillei</i>	0.4 \pm 0.1		
<i>D. r. moniliger</i>	1.2 \pm 0.3	0.4 \pm 0.1	
<i>D. r. rufigula</i>	2.0 \pm 0.5	1.8 \pm 0.4	0.1 \pm 0.1
<i>D. r. paraensis</i>	1.0 \pm 0.3	0.3 \pm 0.1	1.6 \pm 0.4

Haplotype networks for both mtDNA gene fragments (Cytb and ND2) recovered three totally distinct haplogroups, corresponding to *D. r. devillei*, *D. r. rufigula*, and *D. r. moniliger* plus *D. r. paraensis* (Figures 1B–C). These three haplogroups are also depicted in nDNA networks (although some haplotype sharing among subspecies is present; Figures 1D–F); and in both

Mean uncorrected P-distances within and between subspecies are presented in Table 3. These indices ranged within subspecies between 0.1% (*D. r. rufigula*) and 0.4% (*D. r. moniliger*), and between subspecies from 0.4% (*D. r. moniliger*/*D. r. paraensis*) to 2.0% (*D. r. devillei*/*D. r. rufigula*).

maximum likelihood (ML) trees obtained (Figure 2). In the ML trees, *D. r. devillei* and *D. r. rufigula* clades were recovered with high bootstrap values ($\geq 94\%$). The mtDNA tree was obtained with the full sampling (n = 28; Figure 2B), whereas the combined mtDNA and nDNA inference was obtained with 21 *D. rufigula* samples, including all subspecies, from which all the molecular markers could be amplified (Figure 2A).

All species delimitation and species tree tests, irrespective of the demographic and divergence time model considered, supported the existence of three reciprocally monophyletic clades (posterior probability, PP = 1.0), and the following species tree (*D. r. rufigula*, (*D. r. devillei*, *D. r. moniliger*/*D. r. paraensis*)), 0.986 > PP > 0.577. The second most likely species tree was (*D. r. moniliger*/*D. r. paraensis*, (*D. r. rufigula*, *D. r. devillei*)), 0.224 > PP > 0.00828.

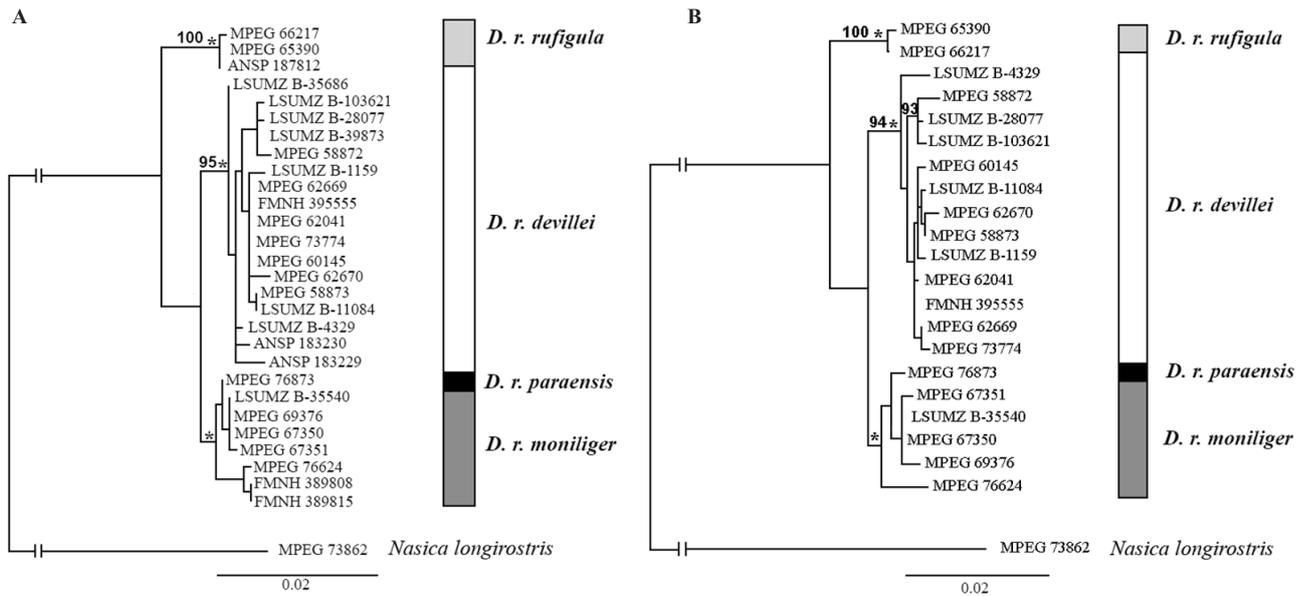


FIGURE 2. Maximum likelihood phylogenetic trees for *Dendrexetastes rufigula* inferred from mitochondrial (A) and both mitochondrial and nuclear molecular markers (B). Only bootstrap values above 90% are represented. * Clades supported by BPP analysis (PP = 1.0).

Our plumage analyses did not detect any sexual dimorphism and consistently confirmed the diagnoses of all currently recognized subspecies of the Cinnamon-throated Woodcreeper (Figure 3). With no exception, all examined specimens from each subspecies differed consistently from those of the other subspecies based on the following features: a) throat color; b) size and shape of pectoral stripes; c) size and shape of nuchal and upper dorsal stripes; and d) presence or absence of a superciliary stripe (Figure 3). *Dendrexetastes rufigula rufigula*, with its Robin Rufous (#340) colored throat with few markings is readily distinguished from the remaining subspecies. *D. r. moniliger* and *D. r. paraensis* share a brown (Buff #124) spotted throat, and *D. r. devillei* has a lower throat colored True Cinnamon (#139), which is barely marked by thin light brown stripes (Figure 3A). In contrast, the size and

shape of pectoral stripes appear to follow a “leapfrog” pattern (*sensu* Remsen, 1984) whereby the more boldly patterned *D. r. rufigula* from the Guianan shield approaches the distantly related and allopatrically distributed *D. r. paraensis* from the Belém area of endemism, with the geographically intermediate and more closely related *D. r. devillei* and *D. r. moniliger* distinguishing themselves by narrower stripes, which are much narrower in *D. r. devillei* (Figure 3A). With respect to the dorsal stripes, the same “leapfrog” pattern is observed, with the nominate form from the Guiana shield approaching *D. r. paraensis* in having wider and longer stripes than *D. r. devillei* and *D. r. moniliger*, with *D. r. devillei* having nearly unmarked upperparts (Figure 3B). Finally, *D. r. paraensis* distinguishes itself from all remaining taxa by the presence of a faint and interrupted superciliary stripe.



FIGURE 3. Ventral (A) and dorsal (B) views of representative specimens illustrating plumage diagnoses among *Dendrexetastes rufigula* subspecies, as recognized in Marantz *et al.* (2003). From left to right: *D. r. rufigula* (MPEG 65390), *D. r. devillei* (MPEG 58872), *D. r. moniliger* (MPEG 67350), and *D. r. paraensis* (MPEG 76873). Note the three characteristic distinct throat color patterns diagnosing unequivocally *D. r. rufigula*, *D. r. devillei*, and *D. r. moniliger/paraensis*, which correspond to the main evolutionary lineages in *Dendrexetastes*. The size and shape of pectoral, nuchal, and upper dorsal stripes follow a “leapfrog” pattern whereby the more boldly patterned *D. r. rufigula* approaches the distantly related and allopatrically distributed *D. r. paraensis*, with the geographically intermediate and more closely related *D. r. devillei* and *D. r. moniliger* distinguishing themselves by smaller markings.

DISCUSSION

Species limits and taxonomy

Our phylogeographic analyses identified three major evolutionary independent units in the Cinnamon-throated Woodcreeper that roughly corresponded to currently recognized subspecies. Although we found support for the reciprocal monophyly and consequent evolutionary independence of *D. r. rufigula* and *D. r. devillei*, the same did not occur between *D. r. moniliger* and *D. r. paraensis*,

which were paraphyletic, but grouped together in a single clade without significant statistical support in ML analyses. In this clade, our lone sample of *D. r. paraensis* was nested within *D. r. moniliger* and their pairwise mitochondrial distance ($0.3 \pm 0.1\%$) indicates a level of differentiation slightly lower than that verified within other subspecies, such as *D. r. devillei* (i.e., $0.4 \pm 0.1\%$; see Table 3). This suggests that *D. r. paraensis* is a morphologically slightly distinct subset of a more widespread lineage endemic to southeastern Amazonia east of the Madeira River that includes *D. r. moniliger* (Figures 3 & 4).



FIGURE 4. Ventral (A) and dorsal (B) views of specimens showing plumage variation within *Dendrexetastes paraensis*, as defined herein (grouping *D. r. paraensis stricto sensu* and “*D. r. moniliger*”). From left to right (specimens were organized from west to east): “*D. r. moniliger*” (MPEG 39641, 39640, 76624, 69376, 67350, 67351, 51404, 54679), and *D. r. paraensis stricto sensu* (MPEG 26817, 17214, 76873). Note the trend of *D. r. paraensis stricto sensu* specimens to have broader lower throat and pectoral spots (A) as well as wider and longer nuchal and dorsal stripes (B) than those of “*D. r. moniliger*”. The faint and interrupted superciliary stripe distinguishing all *D. r. paraensis stricto sensu* specimens examined cannot be seen in these pictures.

The species delimitation analysis indicated with high support that clades *D. r. rufigula*, *D. r. devillei*, and *D. r. moniliger/paraensis* are separate evolutionary species (de Queiroz 2007) and that gene flow, even if present, has not affected their mutual diagnoses. The same could be inferred from the plumage data based on the specimens analyzed, whereby each clade was characterized by a unique combination of characters, and no intermediate specimens were found. Despite these findings, the relatively small sampling of specimens and molecular

markers screened by the present study did not allow for a more detailed evaluation of levels of gene flow among the three main evolutionary lineages of the Cinnamon-throated Woodcreeper, preventing an assessment of whether they are separate biological species. Nevertheless, Gill (2014) points out, based on recent advances on the genetics of speciation, reproductive isolation, directional selection, and hybridization dynamics, that “distinct and reciprocally monophyletic sister populations of birds exhibit essential reproductive isolation and would not

interbreed freely if they were to occur in sympatry". In other words, in instances such as documented herein for the Cinnamon-throated Woodcreeper, the burden of proof should now stand in demonstrating that levels of gene flow are actually high enough among its three main lineages so that they cannot be regarded as reproductively isolated from each other, in strong contrast with the data shown herein. Given the apparent allopatry of these three divergent Cinnamon-throated Woodcreeper clades, this approach to assessing species limits seems appropriate. Similarly, our study provides the first assessment ever of the evolutionary history within this lineage, which had otherwise been treated as a polytypic species based on the purported morphological intermediacy of the population later named *D. r. moniliger* between *D. r. rufigula* and *D. r. devillei* (Hellmayr 1910, Zimmer 1934). As we discuss below, plumage evolution in the Cinnamon-throated Woodcreeper complex has involved some degree of convergence, which can obscure the inference of true evolutionary relationships and species limits.

Rather than recognizing a single polytypic species, the results obtained in this study support the following three taxa should be treated as species diagnosable by molecular and plumage characters (Figures 2 & 3) – a possibility already indicated by Piacentini *et al.* (2015): 1) Cinnamon-throated Woodcreeper - *Dendrexetastes rufigula* (Lesson, 1844). Unequivocally diagnosable from all remaining *Dendrexetastes* taxa by a Robin Rufous (#340) colored and nearly unmarked throat (Figure 3); it is distributed on the Guianan shield north of the Amazon River and east of the Negro River in Venezuela, Brazil, Guyana, Surinam, and French Guiana (Marantz *et al.* 2003); 2) Deville's Woodcreeper - *Dendrexetastes devillei* (Lafresnaye, 1850). Distinguished from the remaining species by a dark True Cinnamon (#139) throat and much shorter and narrower pectoral and nuchal stripes, resulting in nearly unmarked upperparts (Figure 3); found west of the Negro River in Amazonian Brazil westward towards the base of the Andes in Colombia, Ecuador, and Peru both north and south of the Amazon River, northern Bolivia and east to the west bank of the Madeira River (Borges *et al.* 2001, Marantz *et al.* 2003); 3) Pará Woodcreeper - *Dendrexetastes paraensis* Lorenz, 1895. Told apart from the other species by a Buff (#124) and heavily spotted throat, which has an overall squamate appearance (Figure 3); it occurs from the east bank of the Madeira River to easternmost Amazonia in the Belém area of endemism. The name *D. r. paraensis* Lorenz, 1895 has priority over *D. r. moniliger* (Zimmer, 1934), and thus should be used to identify the clade grouping specimens of these taxa (Figure 2). Some variation in plumage within *D. paraensis* has been detected (see Figure 4, as well as Cory & Hellmayr 1925) and is discussed in more detail below.

Plumage evolution

When contrasted with the molecular phylogeny estimated for the *Dendrexetastes* taxa, plumage patterns such as the size and length of pectoral, nuchal, and upper dorsal spots followed a "leapfrog" pattern (Remsen 1984), whereby the more boldly patterned and allopatrically distributed *D. paraensis* and *D. rufigula* approached each other despite their more distant phylogenetic affinities, to the exclusion of the overall concolor and more closely related *D. devillei*, which is in contact via parapatry with both of these taxa along the middle-upper courses of the Negro (*D. rufigula*) and Madeira Rivers (*D. devillei*). Despite the fact that the sister relationship between *D. paraensis* and *D. devillei* is poorly supported in our estimated phylogeny, it nevertheless suggests that they are sister taxa and hence that plumage characters may not have evolved in concert with the history of diversification in this group (Figures 2 & 3). This conclusion is reinforced by the observed differentiation in plumage between the taxa *paraensis* (*stricto sensu*) and *moniliger* (Figure 4), despite their little genetic divergence, which is even lower than that found within *moniliger* alone (see above; Table 3), and the fact that they are nested within the same clade. Our results are then consistent with either a scenario of convergent phenotypic change or retention of ancestral traits among geographically distant lineages, that is typically associated with a "leapfrog" pattern (Remsen 1984). Understanding the underlying causes of "leapfrog" patterns of geographic variation are difficult, but several studies documented similar scenarios of parallel evolution or retention of ancestral traits in geographically and phylogenetically distant tropical and temperate avian lineages, with differentiation of geographically intermediate populations (Norman *et al.* 2002, Pavlova *et al.* 2005, Cadena *et al.* 2011). In the case of *Dendrexetastes*, both parallel evolution and retention of ancestral traits remain valid hypotheses behind the documented "leapfrog" pattern of plumage variation. The first split in the *Dendrexetastes* tree involves the separation between the more boldly patterned *D. rufigula* and the more concolor-like *D. devillei* plus *D. paraensis*, so it can be assumed that bigger pectoral, nuchal, and upper-dorsal stripes represent more ancestral rather than derived character states, which appeared more conspicuously in the easternmost *D. paraensis* population. Alternatively, as supported by Cadena *et al.* (2011), selection could produce convergent or parallel evolution in plumage characters to maximize the fitness of local populations. Both boldly patterned *Dendrexetastes* taxa are found in eastern Amazonia, which is significantly drier and more seasonal than western Amazonia, where the least marked species *D. devillei* occurs (Davidson *et al.* 2012, Cheng *et al.* 2013); therefore, selection along an environmental gradient running from western to eastern

Amazonia could influence convergent plumage types in *Dendrexetastes*. Future studies with more powerful datasets, both in terms of specimens and number of loci, could test between these two hypotheses.

Conservation implications

Our study did not support a separate evolutionary species status for the “Endangered” *Dendrexetastes paraensis stricto sensu* (MMA 2014), since it failed to uncover significant genetic differentiation between this population and “*D. r. moniliger*”. This contrasts with previous taxonomy and patterns of plumage variation, which allow for the distinction of a more boldly patterned population (to which the name *paraensis* originally applies) distributed east of the Tocantins River and a less marked group found between the Madeira and the west bank of the Tocantins River (to which the name *moniliger* applies; Zimmer 1934; Figure 4). The phylogenies obtained showed that these populations are paraphyletic, and hence that they cannot be treated as independent evolutionary lineages, despite some morphological differentiation (Figure 4). Despite this mismatch between plumage patterns and the phylogeny, three geographically structured sub-clades were recovered within *D. paraensis*, each associated with a major Amazonian interfluvium, as follows: a) Madeira-Tapajós (grouping samples MPEG 76624, FMNH 389808 and 389815); Tapajós-Xingu (grouping specimens LSUMZ 35540, MPEG 67351, 67350 and 67351); and east of the Tocantins (MPEG 76873). Interestingly, this same degree of geographic structure is not observed in *D. devillei*, whose populations north and south of the Amazon were not recovered as reciprocally monophyletic (Figure 2), although their degree of genetic differentiation is comparable to that found in the clade joining *D. paraensis stricto sensu* and “*D. r. moniliger*” (Table 3). This demonstrates that important phylogeographic structure exists in *D. paraensis*, yet to a smaller extent than that verified among the three main *Dendrexetastes* lineages. Unfortunately, our small sampling of specimens and molecular markers does not allow for a more in-depth phylogeographic analysis of *D. paraensis*, which includes three sub-clades apparently endemic to the most deforested sectors of Amazonia (Da Silva *et al.* 2005, Bird *et al.* 2012). Therefore, while we recommend that *D. paraensis* as defined herein is treated as an independent species whose conservation status should be evaluated separately from other *Dendrexetastes* species, we also stress the importance of evaluating threat levels for each of its three sub-clades, particularly during national and regional conservation assessments. This cautious approach is justified from a conservation standpoint, and we suggest that Next Generation Sequencing methodologies be used in the future as a stronger test of

the genetic distinctiveness among *D. paraensis* sub-clades. Unfortunately, only a few specimens of *D. paraensis* exist in collections worldwide, and the great advantage of these methods is that they work well for suboptimal samples, such as study skins collected dozens and even hundreds of years ago (McCormack *et al.* 2015).

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APPENDIX I

Study skins of *Dendrexetastes rufifigula* analyzed in this study. All specimens are deposited at the Museu Paraense Emílio Goeldi, Belém, Brazil (MIPEG). Specimens marked with asterisks (*) were also included in the molecular analyzes.

Specimen number	Taxon	Locality, in Brazil	State	Sex
03034	<i>Dendrexetastes rufifigula devillei</i>	Boca do Acre, Rio Purus, Bom Lugar (08°43'S; 67°20'W)	Amazonas	F
03589	<i>Dendrexetastes rufifigula devillei</i>	Boca do Acre, Rio Purus, Ponto Alegre (08°57'S; 67°50'W)	Amazonas	F
18310	<i>Dendrexetastes rufifigula devillei</i>	Estrão do Equador, Rio Javari (04°27'S; 71°30'W)	Amazonas	M
43099	<i>Dendrexetastes rufifigula devillei</i>	Maraá, Lago Paricá, Santa Rita (02°23'S; 66°10'W)	Amazonas	M
43100	<i>Dendrexetastes rufifigula devillei</i>	Maraá, Rio Japurá, right bank, opposite to Maguari (02°30'S; 65°40'W)	Amazonas	F
52093*2	<i>Dendrexetastes rufifigula devillei</i>	Marechal Thaumaturgo, Rio Tejo, c. 5 km from mouth (09°00'S; 72°42'W)	Acre	M
55213	<i>Dendrexetastes rufifigula devillei</i>	4,5 km NE São Paulo de Olivença, Rio Solimões, north bank (03°25'S; 68°57'W)	Amazonas	M
58872*	<i>Dendrexetastes rufifigula devillei</i>	Assis Brasil, ESEC Rio Acre, Acampamento 2 (11°00'53.4"S; 70°13'02.7"W)	Acre	F
58873*	<i>Dendrexetastes rufifigula devillei</i>	Assis Brasil, ESEC Rio Acre, Acampamento 2 (11°00'53.4"S; 70°13'02.7"W)	Acre	M
60145*	<i>Dendrexetastes rufifigula devillei</i>	RDS Cujubim, margem E Rio Jutai (05°38'19"S; 69°10'59"W)	Amazonas	F
62041*	<i>Dendrexetastes rufifigula devillei</i>	Porto Walter, Igarapé Cruzeiro do Vale, Colônia Dois Portos (08°20'35.7"S; 72°36'19.7"W)	Acre	F
62669*	<i>Dendrexetastes rufifigula devillei</i>	Japurá, Rio Acanauí (01°56'12.4"S; 66°36'18.8"W)	Amazonas	F
62670	<i>Dendrexetastes rufifigula devillei</i>	Japurá, Rio Acanauí (01°56'12.4"S; 66°36'18.8"W)	Amazonas	M
73774*	<i>Dendrexetastes rufifigula devillei</i>	Autazes (03°46'52.8"S; 59°03'23.8"W)	Amazonas	M
79707*	<i>Dendrexetastes rufifigula devillei</i>	Jutai, ESEC Jutai/Solimões, Capivara (03°10'56.3"S; 67°22'47.1"W)	Amazonas	M
39640*	<i>Dendrexetastes rufifigula moniliger</i>	Cachoeira Nazaré, margem oeste do Rio Ji-paraná (10°13'S; 62°28'W)	Rondônia	F
39641*	<i>Dendrexetastes rufifigula moniliger</i>	Cachoeira Nazaré, margem oeste do Rio Ji-paraná (10°13'S; 62°28'W)	Rondônia	F
51404	<i>Dendrexetastes rufifigula moniliger</i>	Rio Teles Pires, Alta Floresta, Reserva Florestal Cristalino (09°42'S; 55°55'W)	Mato Grosso	F
54679*	<i>Dendrexetastes rufifigula moniliger</i>	32 km NE Alta Floresta, margem W Rio Teles Pires (09°38'01"S; 55°56'21"W)	Mato Grosso	M
67350*	<i>Dendrexetastes rufifigula moniliger</i>	Paranaíta, Rio Teles Pires (09°24'S; 56°33'W)	Mato Grosso	M
67351*	<i>Dendrexetastes rufifigula moniliger</i>	Paranaíta, Rio Teles Pires (09°24'S; 56°33'W)	Mato Grosso	F
69376*	<i>Dendrexetastes rufifigula moniliger</i>	Paranaíta, Rio Teles Pires, margem esquerda (09°24'51.4"S; 56°33'39.7"W)	Mato Grosso	M
76624*	<i>Dendrexetastes rufifigula moniliger</i>	Itaituba, margem esquerda Rio Tapajós, Penedo (05°27'21.61"S; 57°04'12"W)	Pará	F
17214	<i>Dendrexetastes rufifigula paraensis</i>	São Miguel do Pará, Rodovia Belém-Brasília km 36 (01°37'S; 47°29'W)	Pará	M
26817	<i>Dendrexetastes rufifigula paraensis</i>	Belém (01°27'S; 48°29'W)	Pará	?
76873*	<i>Dendrexetastes rufifigula paraensis</i>	Centro Novo Maranhão, REBIO Gurupi (03°42'12.8"S; 46°45'44"W)	Maranhão	M
30118	<i>Dendrexetastes rufifigula rufifigula</i>	Manaus, Reserva Ducke (03°08'S; 60°02'W)	Amazonas	M
53020	<i>Dendrexetastes rufifigula rufifigula</i>	Manaus, km 24 ZF-3, c. 80 km N de Manaus, Fazenda Esteio (02°30'S; 60°00'W)	Amazonas	M
53021	<i>Dendrexetastes rufifigula rufifigula</i>	Manaus, km 24 ZF-3, c. 80 km N de Manaus, Fazenda Esteio (02°30'S; 60°00'W)	Amazonas	F
65390*	<i>Dendrexetastes rufifigula rufifigula</i>	Alenquer, ESEC Grão-Pará (0°09'S; 55°11'W)	Pará	M
66217*	<i>Dendrexetastes rufifigula rufifigula</i>	Almeirim, REBIO Maicuru (0°49'S; 53°55'W)	Pará	M

First record of *Anous minutus* in the state of Amapá, Brazil

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ABSTRACT: We present the first record of *Anous minutus* for the state of Amapá, Brazil, and only the second for the whole Amazonian region. Within Brazil *A. minutus* is restricted as a breeder to Fernando de Noronha, Atol das Rocas, São Pedro and São Paulo and Martin Vaz/Trindade archipelagos, with records of vagrants from the states of Ceará and São Paulo. We photographed a single bird at the Maracá-Jipioca Ecological Station, on the 10 December 2015, west of the Maracá do Sul Island in an area known as Ponta Sul. To our knowledge this is the first record from Amapá and only the second from northern Brazil and the Amazon region.

KEY-WORDS: black noddy, Maracá-Jipioca Ecological Station, seabirds, vagrancy.

The Black Noddy *Anous minutus* Boie, 1844 has a wide distribution, occurring in tropical and subtropical islands in the Caribbean, mid-Atlantic, western and central Pacific, northeast Indian Ocean (Gauger 1999). In Brazil, it breeds on Fernando de Noronha, Atol das Rocas, São Pedro and São Paulo, and Martin Vaz, near Trindade Island (Murphy 1915, Antas 1991, Sick 1997, Both & Freitas 2004, Mancini *et al.* 2016). Along the Brazilian coast there are records of vagrants from Fortaleza, state of Ceará and the Ilha Comprida in the state of São Paulo (Girão *et al.* 2008, Barbieri *et al.* 2010). The only record for the Amazon region is a male, collected at Vigia Beach, Pará state, in 20 January 1926, and housed at the Museu de Zoologia, Universidade de São Paulo (MZUSP No. 12096).

We discovered the first *A. minutus* for the state of Amapá (Figure 1) during a survey of vertebrates at the Maracá-Jipioca Ecological Station. This station (*Estação Ecológica Maracá-Jipioca - EEMJ*) is a Conservation Unit under full protection and consists of Maracá Island, which is divided into Maracá do Norte and Maracá do Sul by the Igarapé do Inferno Channel and the Jipioca Island, which receives a high diversity of migratory birds (Xavier & Boss 2011). The individual was sighted west of Maracá do Sul Island in an area known as Ponta Sul (01°52'09"N; 050°26'03"W), on 10 December 2015 at 11:00 h and observed for 17 min. During this time, the bird was observed in flight and resting on the water as well as along the margins of the island (Figure 1). Separation from Brown Noddy (*Anous stolidus*) was based

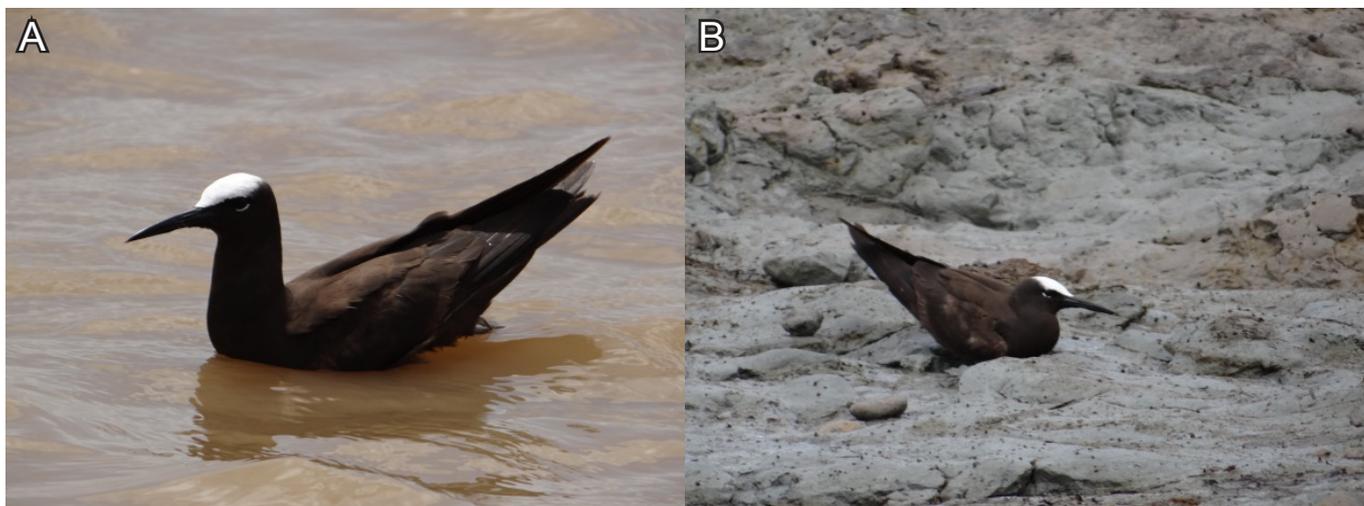


FIGURE 1. Black Noddy *Anous minutus* recorded at Maracá-Jipioca Ecological Station, Amapá state, Brazil, on 10 December 2015, roosting on water (A) and on land (B).

on its extremely long, slender and droopy bill, its white cap with its rear border well-defined without fading.

It seems likely that this first sighting of *A. minutus* for Amapá represents a storm-driven vagrant. It is unclear at present whether the species may be regular over the continental shelf in the Amazon region as there is a lack of pelagic bird surveys.

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The following *abbreviations* should be used: h (hour), min (minute), s (second), km (kilometer), m (meter), cm (centimeter), mm (millimeter), ha (hectare), kg (kilogram), g (gram), mg (milligram), all of them in lowercase (not capitals) and with no “periods” (“.”). Use the following *statistical notations*: *P*, *n*, *t*, *r*, *F*, *G*, *U*, *df* (degrees of freedom), χ^2 , ns (non-significant), CV (coefficient of variation), SD (standard deviation), SE (standard error). With the exception of temperature and percentage symbols (*e.g.*, 15°C, 45%), leave a space between the number and the unit or symbol (*e.g.*, $n = 12$, $P < 0.05$, 25 min), also in figures and tables.

Latin words or expressions should be written in italics (e.g., *i.e.*, *c.*, *et al.*, *in vitro*, *in vivo*, *sensu, a priori*). The same rule applies to words in a language distinct from the manuscript language, *i.e.*, English, but does not apply to references, which follow distinct format rules, as indicated below. Numbers one to ten should be written out, unless a measurement (e.g., four birds, 6 mm, 2 min); from 11 onwards use numbers.

Author citations in the text must follow the pattern: (Pinto 1964) or Pinto (1964); two publications of the same author must be cited as (Sick 1985, 1993) or (Ribeiro 1920a, b); Two authors are cited in text with "&" (e.g. Aleixo & Pacheco 2006). Three or more authors must be presented as the first author followed by *et al.* (e.g. Aleixo *et al.* 2013). Avoid multiple citations in text, such as more than 3 references to support an idea or information. Multiple references should be listed in chronological order (e.g. Sick 1997; Narosky & Yzurieta 2003; BirdLife International 2015). Unpublished information by third parties must be credited to the source by citing the initials and the last name of the informer followed by the appropriate abbreviation of the form of communication: (H. Sick, pers. comm.) or V. Loskot (*in litt.*); unpublished observations by the authors can be indicated by the abbreviation: (pers. obs.); when only one of the authors deserves credit for the unpublished observation or another aspect cited or pointed out in the text, this must be indicated by the name initials: "... in 1989 A.S. returned to the area...". *Unpublished manuscripts* (e.g., technical reports, Undergraduate Monographs, M.Sc. Dissertations and Doctoral Thesis) and *meeting abstracts* should be cited only exceptionally, in cases they are absolutely essential and no alternative source exists. The *reference* list must include all and only the cited publications (titles written in full, not abbreviated), in alphabetical order by the authors' last name:

Articles

- Fargione J., Hill J., Tilman, D., Polasky S. & Hawthornez P. 2008. Land clearing and the biofuel carbon debt. *Science* 319: 1235–1238.
 Santos M.P.D. & Vasconcelos M.F. 2007. Range extension for Kaempfer's Woodpecker *Celeus obrieni* in Brazil, with the first male specimen. *Bulletin of the British Ornithologists' Club* 127: 249–252.
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Books and Monographs

- Sick H. 1985. *Ornitologia brasileira, uma introdução, v. 1*. Brasília: Editora Universidade de Brasília.

Book Chapters

- Thiollay J.M. 1994. Family Accipitridae (hawks and eagles), p. 52–205. In: del Hoyo J., Elliott A. & Sargatal J. (eds.). *Handbook of birds of the world, v. 2 (New World vultures to guineafowl)*. Barcelona: Lynx Editions.

Theses and Dissertations

- Novaes E.C. 1970. *Estudo ecológico das aves em uma área de vegetação secundária no Baixo Amazonas, Estado do Pará*. Ph.D. Thesis. Rio Claro: Faculdade de Filosofia, Ciências e Letras de Rio Claro.
 Cavalcanti L.M.P. 2014. *Sazonalidade na estação reprodutiva de aves de uma área de Caatinga e sua relação com a precipitação*. Bachelor's Monograph. Mossoró: Universidade Federal Rural do Semiárido.

Web-based References

- IUCN. 1987. A posição da IUCN sobre a migração de organismos vivos: introduções, reintroduções e reforços. <http://iucn.org/themes/ssc/pubs/policy/index.htm> (access on 25 August 2005).
 Dornas T. 2009a. [XC95575, *Celeus obrieni*]. <http://www.xeno-canto.org/95575> (access on 25 February 2012).
 Pinheiro R.T. 2009. [WA589090, *Celeus obrieni* Short, 1973]. <http://www.wikiaves.com/589090> (access on 05 March 2012).

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