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LONGITUDINAL AND CYCLIC POLEWARD MIGRATION OF A SOUTH AMERICAN INTRA-TROPICAL MIGRANT FLYCATCHER, THE LESSER ELAENIA (*ELAENIA CHIRIQUENSIS*)

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Abstract · Research on terrestrial migratory birds is incipient in Brazil. Geolocators have recently allowed tracking of small migratory passerines and such data, combined with intrinsic markers such as stable isotopes, have become invaluable in revealing migratory behavior. Here, we used data from a long-term banding program in a *cerrado* reserve in central Brazil, where we also deployed geolocators to track adults of a 15 g flycatcher, the Lesser Elaenia (*Elaenia chiriquensis*). The literature defines it as a resident or migrant that may overwinter in the Amazon or central Brazil. We combined newly collected tracking data from geolocators with long term banding data to assess the migratory connectivity of the studied population by documenting the breeding site fidelity, migratory behavior, and wintering grounds of tracked individuals. Recapture data showed that individuals lived for at least 12 years and that ~15% of all marked birds returned to a ~200 ± 185 m radius from where they were recorded in a previous breeding season. Tracking data revealed low migratory connectivity of the studied population. One individual remained resident and the other two individuals migrated through distinct routes: one made a longitudinal northeast-southwest route and the other a cyclic migration consisting of a poleward section to south Brazil, a NW flight to the *Pantanal* surroundings and ending with a longitudinal NE spring migration. These are the first detailed data of the migratory movements of individual Lesser Elaenias, supporting its partial rather than obligatory migration in central Brazil. Moreover, we found that migrants overwintered in savanna-like areas, as indicated by previous studies. We end by discussing a list of hypotheses we expect to guide further studies on this and other intra-tropical migrant species, thus contributing to improve knowledge on this complex and understudied migratory system within South America.

Resumo · Migração longitudinal e direcionada ao polo de um Tyrannidae migrante intratropical sulamericano, o chibum (*Elaenia chiriquensis*)

Pesquisas sobre migração de aves continentais são incipientes no Brasil. Recentemente, geolocalizadores têm permitido rastrear pequenas aves migratórias, e esses dados combinados com marcadores intrínsecos como isótopos estáveis têm se tornado inestimáveis para revelar comportamentos migratórios. Usamos dados de um longo programa de anilhamento em uma unidade de conservação no Cerrado do Brasil central onde também acoplamos geolocalizadores para rastrear adultos do Tyrannidae chibum (*Elaenia chiriquensis*). Esta espécie é definida como residente ou migratória que passa o período não-reprodutivo na Amazônia ou no Cerrado. Nós combinamos novos dados de rastreamento usando geolocalizadores com dados de longa duração de anilhamento para avaliar a conectividade migratória da população estudada, documentando a fidelidade ao sítio reprodutivo, o comportamento migratório e os sítios de repouso reprodutivo dos indivíduos rastreados. Os dados de recaptura dos indivíduos mostram que eles viveram por pelo menos 12 anos e que ~15% dos indivíduos anilhados retornaram para um novo território em um raio de ~200 ± 185 m do local onde foram registrados na estação reprodutiva anterior. Os dados de rastreamento revelaram baixa conectividade migratória da população estudada. Um indivíduo permaneceu residente. Os outros dois indivíduos migraram por rotas distintas: uma longitudinal nordeste-sudoeste e uma cíclica com um trecho para o sul do Brasil, um para noroeste até as proximidades do Pantanal e um trecho final longitudinal nordeste. Estes são os primeiros dados detalhados dos movimentos migratórios de indivíduos de *E. chiriquensis*, corroborando sua migração parcial e não obrigatória no centro do Brasil. Ademais, encontramos que os migrantes passaram o período de repouso reprodutivo em áreas semelhantes a savana, conforme indicado por resultados de estudos anteriores. Nós concluímos discutindo uma lista de hipóteses que esperamos guiem outros estudos sobre esta e outras espécies migratórias intratropicais, contribuindo assim para aprimorar os conhecimentos sobre este sistema ainda pouco estudado na América do Sul.

Key words: Brazil · Geolocators · Migratory connectivity · Migration route · Wintering ground

INTRODUCTION

Bird migration is a longstanding area of research (e.g. Walter 1908, von Schweppenburg 1917, Steinfatt 1932), but only in the last 20 years this subject has been facing a marked increase in studies in South America (Jahn et al. 2020). A recent and com-

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Table 1. Sample size and average body mass of Lesser Elaenia individuals marked with light-level geolocators in a breeding site in Central Brazil (Estação Ecológica de Águas Emendadas – ESECAE, Brasília/DF).

Sex	N	Mean body mass ± SE (g); range
Female	11	14.9 ± 1.0; 13.8 – 17.4
Male	2	16.5 ± 0.8; 15.9 – 17.0
Unknown	27	15.6 ± 1.2; 13.6 – 17.8
Total	40	15.5 ± 1.2; 13.6 – 17.8

prehensive review showed that 198 bird species are migratory in Brazil (~10% of all species), including 79 Passerines (Somenzari et al. 2018). Nevertheless, this review yielded almost no detailed information about migration or connectivity. Despite the fact that studies of bird migration in Brazil date back to the late 1960s (e.g., Sick 1968, Negret & Negret 1981, Antas 1986, Negret 1988), basic life history information is lacking for all but a few terrestrial migratory species, including the Fork-tailed flycatcher (*Tyrannus savana*) (Wang & Finch 2002, Jahn et al. 2016, Jahn & Guaraldo 2018), the Lesser Elaenia (*Elaenia chiriquensis*) (Marini & Cavalcanti 1990, Paiva & Marini 2013, Guaraldo et al. 2016, Guaraldo et al. 2019), and the White-crested Elaenia (*Elaenia albiceps*) *chilensis* (Marini & Cavalcanti 1990, Capllonch et al. 2011, Jiménez et al. 2016, Bravo et al. 2017). Even after recurring calls for studies on the long-standing neglected intratropical migration system (Levey 1994, Faaborg et al. 2010b), current knowledge is limited for most Brazilian species (Erickson 1982, Lanyon 1982, Antas 1994, Cabanne & Seipke 2005, Efe & Filippini 2006, Areta & Bodrati 2010, Ruiz-Esparza et al. 2011, Castro et al. 2012, Lees 2016, Pinho et al. 2017, Somenzari et al. 2018).

Because we lack distribution and movement data with sufficient resolution, it is a challenge to address even some of the most basic questions about migratory species in Brazil. Among these questions are the following: (1) Do they show a within-population variation in migratory behavior (i.e., partial migration)? (2) What are the degrees of site fidelity and connectivity among different populations? (3) Where do individuals go during the non-breeding period? (4) Are there well-established migratory routes and stop-over sites? It is widely recognized that populations of many migratory bird species are declining worldwide (Faaborg et al. 2010a, Faaborg et al. 2010b, Vickery et al. 2014, Xu et al. 2019), and answering these simple questions is paramount to support and guide the conservation of migratory species. The annual cycles of migratory birds in Brazil likely provide a biological conduit that connects increasingly threatened biomes, such as the Atlantic forest (Andreacci & Marenzi 2020), the Amazon rainforest (Carvalho et al. 2019), and the *cerrado* (Françoso et al. 2015, Sano et al. 2019). Therefore, detailed information about bird connectivity would be an important asset to landscape level conservation plans.

The Lesser Elaenia (*Elaenia chiriquensis albivertex,* Tyrannidae) is one of many Brazilian birds for which we lack even the most basic migratory behavior data. It has an ample distribution range in tropical South America and is one of the most abundant birds during the breeding season (September–December) in some *cerrado* areas in central Brazil (Medeiros & Marini 2007, Paiva & Marini 2013). The known migratory behavior of this subspecies is controversial and inconclusive. Some field-based studies concluded that this subspecies migrates north to winter (June–August) in the Amazon (Fry 1970, Sick 1983, Nunes & Tomas 2008), whereas a subsequent study based on museum and literature data states that the species is found year-round in the Brazilian Amazon (Sanaiotti & Cintra 2001). In relation to the southern area of occurrence, a study based on museum and field data suggests that Lesser Elaenia populations are present only during the breeding season below 15°S (i.e., central Brazil; Marini & Cavalcanti 1990).

More than 20 years after Marini & Cavalcanti (1990), a field study documented overwintering individuals (N = 17) in central Brazil during the non-breeding season (December–March; Silveira & Marini 2012), suggesting that the species may be a partial migrant in that area (i.e., some members of the population migrate while others stay behind during the winter; Newton 2008). In this paper we used data from a long-term banding program and a three-year tracking study to attempt to answer the basic life-history questions listed above. Specifically, we collected data to document the site fidelity, wintering areas, migratory connectivity, and the potential partial migration behavior of a Lesser Elaenia population breeding at 15°S.

METHODS

Study site. We developed this study as part of a long-term banding and nest monitoring program held between 2002–2014 within a 100 ha plot located within the Estação Ecológica de Águas Emendadas (ESECAE; 15°33'S 47°36'W), a 10,500 ha *cerrado* reserve in central Brazil approximately 40 km northeast from Brasília/DF (Marini et al. 2012). A very large breeding population of the Lesser Elaenia at this site has served to reveal much about the life-history of the species (Medeiros & Marini 2007, Lobo & Marini 2012, Paiva & Marini 2013, Guaraldo et al. 2019). The study area has east-west trails at every 50 m, with marker poles every 50 m; thus, distances between any two points were easily assigned trigonometrically. Vegetation in the area ranges from grasslands to dense shrubby vegetation with emergent trees (Marini et al. 2012). The local climate is seasonal, with a hot and rainy season from October to April (Gottsberger & Silberbauer-Gottsberger 2006).

Banding and geolocator deployment. Much of our work with Lesser Elaenias was part of a series of year-round banding and monitoring efforts that took place from 2002 to 2014 and involved capturing and banding numerous bird species (e.g., Lopes & Marini 2005, Medeiros & Marini 2007, Manica & Marini 2012, Silveira & Marini 2012, Paiva & Marini 2013, Guaraldo et al. 2019). In 2011 and 2012, we deployed light level dataloggers (hereafter geolocators) on randomly captured adult Lesser Elaenias during the last days of their breeding season (i.e., 01 to 09 December; N = 4 in 2011 and N = 36 in 2012). These individuals received a unique combination of three plastic color bands plus a metal numbered band (ICMBio/CEMAVE), and we performed a standard set of measurements for body size and mass (IBAMA 1994) for both the initial and subsequent capture of each tagged indi-

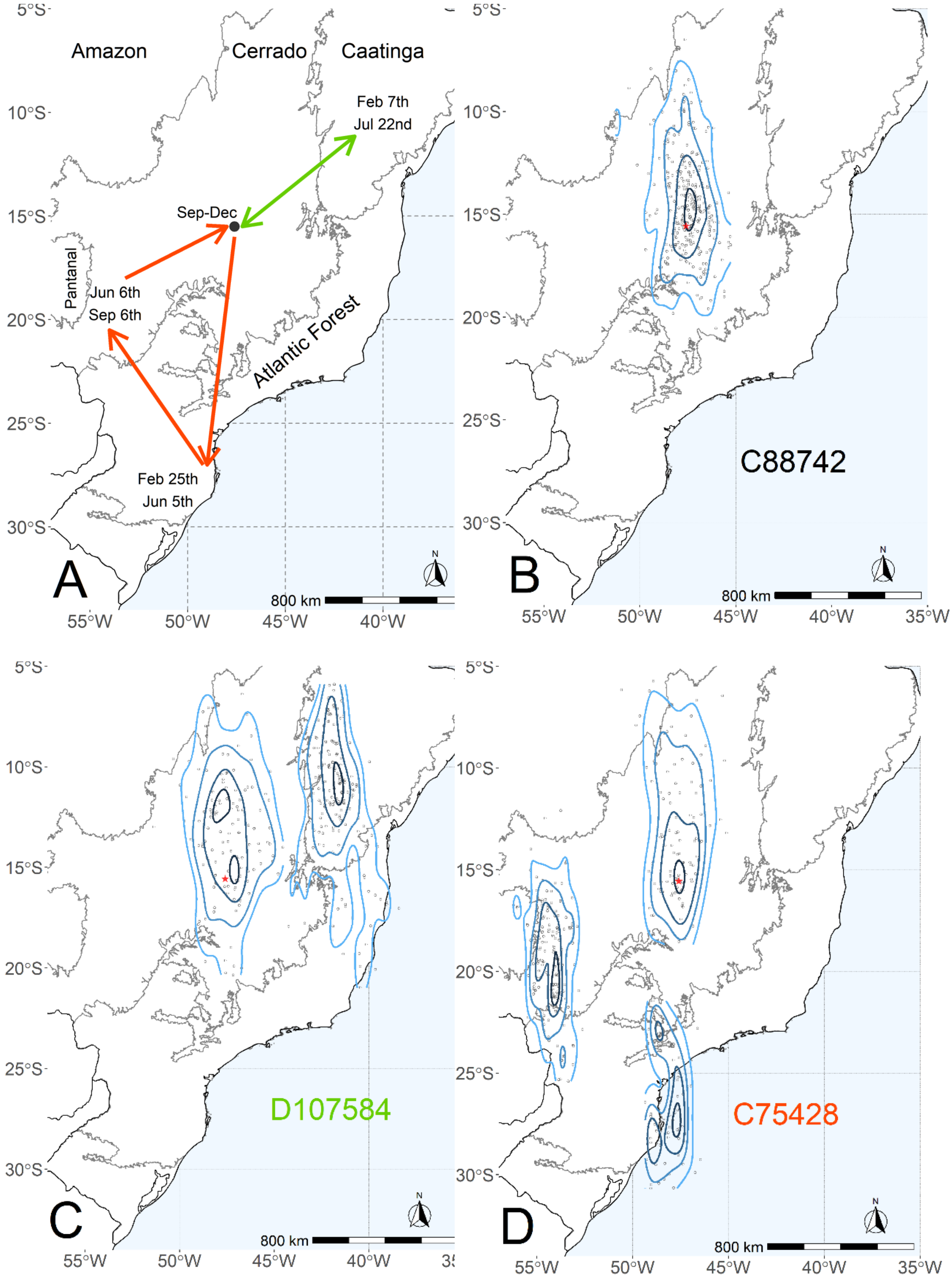

Figure 1. A) Schematics of migration routes through the Brazilian biomes of two Lesser Elaenia individuals (colors refers to individuals in C and D). Breeding season in our study site in central Brazil (black dot) and individuals routes and wintering periods derived from geolocators data. B) Winter ranges and kernel densities (10%, 11-40%, 41-70% 71-90%) from geolocator data revealing the resident behavior of a Lesser Elaenia individual. C) Longitudinal to-and-fro route to wintering grounds in the dry *caatinga* biome. D) Cyclic migration route including a poleward, a latitudinal, and a longitudinal movement to the wintering grounds in the Atlantic Forest and *cerrado* biomes.

vidual. From past banding efforts, we were able to determine a minimum age for each of these birds (the range was from one to nine years), and assigned sex to 466 individuals by molecular sexing analysis (Machado-Filho et al. 2010) or detection of a brood patch, which designates nesting females (Davis 1945, Jones 1971). The geolocators we used were custom made by ESB and were attached with a Rappapole leg loop harness made from stretch magic beading thread (see Bridge et al. 2013). The total mass of each geolocator, including harness, was ~0.7 g, and geolocator load never exceeded 5% of an individual's body mass (Caccamise & Hedin 1985) (Table 1). To check for likely effect of tags on birds' morphology, we ran paired t-tests between body mass, and wing and tail length at the time of tag deployment and at the time of bird recapture for tag retrieval. We also ran a one-way repeated measures ANOVA to check for the tags' effect on bird

Table 2. Data of Lesser Elaenia individuals successfully recovered with geolocator in Central Brazil. -: data missing due to tag malfunction.

Capture	Recapture	Id	Sex	Weight (g) (deployment;	Behavior (direction)	Flight distance (Km) (legs)
09/12/2011	12/09/2012	D76221	M	17.0; 17.0	-	-
01/12/2012	11/09/2013	C88742	F	14.9; 14.5	resident	-
03/12/2012	10/10/2013	C75428	F	13.9; 15.3	cyclic migration (S-NW-NE)	~3,300 (1,340, 1,360, 815)
03/12/2012	09/09/2013	D107584	I	15.5; 16.0	to-and-fro migration (E-W)	~1,500 (750, 750)
09/12/2012	09/09/2013	C71696	I	17.1; 16.7	-	-
09/12/2012	09/10/2013	C88758	I	14.9; 14.8	-	-
09/12/2012	09/09/2013	D107769	I	16.0; 15.8	-	-

masses, considering our study site dataset on captured and recaptured non-tagged birds from 2011–2013 as a control group.

Geolocators must be recovered to collect the data they have recorded. During the 2012 and 2013 breeding seasons (September to December), we devoted five days per week to resighting and recapturing birds with geolocators through our study area. We made additional resighting efforts from July to August in both years (three to five days per week) as part of a parallel study. Because the Lesser Elaenia had never previously been tracked using geolocators, we followed recommendations by Geen et al. (2019).

We assessed home-range fidelity at the breeding grounds by compiling the recapture coordinates for 3730 Lesser Elaenia individuals, excluding within-year recaptures. We did so using our long-term database (2002 to 2014) that includes banding data from systematic annual netting efforts and banding data after multiple studies developed at our study site, many of them focused on the Lesser Elaenia (e.g., Medeiros & Marini 2007, Machado-Filho et al. 2010, Lobo & Marini 2012, Silveira & Marini 2012, Paiva & Marini 2013, Pereira & Marini 2015, Guaraldo et al. 2016, Guaraldo et al. 2019). We then calculated the approximate distance between the last capture of an individual in a given breeding season and the first recapture in the following year. With the recapture distances we tested for sex differences in site fidelity and for effects of geolocators using two Mann-Whitney tests.

Movement tracking. For the geolocator data analysis, we established sunrise and sunset times based on an average sun elevation angle of 4.2° using embedded functions in the GeoLight package (Lisovski et al. 2012) in R (R Core Team 2020). Previous research indicated that Lesser Elaenia begin fall migration in mid to late December (Paiva & Marini 2013); thus, we used the first 10 days of data after geolocator deployment as a calibration period. With these settings, the average geolocation error at the breeding site was 70 ± 20 km (standard error). We used the GeoLight package (Lisovski et al. 2012) to estimate all occurrence coordinates. In identifying the wintering area, we filtered out from the analysis 30 days of data prior to and after the fall equinox (21 February to 21 April). We also excluded from the analysis all data with more than three degrees of difference between the previous or next record. To visualize the location data we generated four kernel density levels: 10%, 11-40%, 41-70% and 71-90%, which were calculated and plotted using the following packages in R (R Core Team 2020): geobr (Pereira and Goncalves 2020), geosphere (Hijmans 2019), ggplot2 (Wickham 2009), ggspatial (Dunnington 2018), rgdal (Keitt 2010), rgeos (Bivand & Rundel 2019), reshape (Wickham 2007), rnaturalearth (South 2017), and sf (Pebesma 2018).

RESULTS

Breeding season: site fidelity and longevity. From 13 years of banding and recapturing efforts, we calculated an average longevity of 3.8 ± 1.9 years (mode = 3 years; N = 381) for Lesser Elaenia in our study site, with one individual that survived for at least 12 years. To assess site-fidelity, we compiled 556 between-year recaptures (89.5% of all recaptures; N = 89 females; N = 7 males; N = 460 unknown sex). Recapture intervals ranged from one (N = 442) to seven (N = 2) years with a mean of 2.3 ± 0.7 years. On average, individuals returned within a 200 ± 185 m radius (range = 0–955 m) from where they were in the previous breeding season with no differences between sexes (W = 586.5, P = 0.32) and whether birds were bearing geolocators (W = 3995, P = 0.20). We detected no significant body changes in tagged birds for body mass (t = 0.47, df = 6, P = 0.66), and wing (t = 1.53, df = 4; P = 0.20) and tail length (t = 0.03, df = 4, P = 0.97). Body mass was unaffected by tags in comparison to our control group (F = 2.28, P = 0.12).

Non-breeding season: wintering areas and migration routes*.* During the 2011 breeding season, we deployed only four geolocators as a pilot project and we recaptured one of these individuals in 2012 (Table 2). This individual was initially resighted in 2012 approximately 270 m from its release point of the previous year. Prior to recapture, it was observed for a total of approximately four hours in two consecutive mornings, when it showed regular singing and foraging behavior within an area of approximately 1.5 ha, without nesting or agonistic interaction with conspecifics. Although the tag failed to record any data, its successful recovery, and the absence of apparent negative effects on the bird prompted us to continue deploying the additional 36 tags by the end of that breeding season. The following breeding season was right after a major fire in August 2013, but we successfully recovered another six tags from September to October that year. Hence, the overall geolocator recovery rate was 7 of 40, or 17.5%, which is similar to the return recapture rate of 16.7% from our long-term banding efforts.

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Only three geolocators recorded useful data, but they confirm partial migration in the studied population and revealed considerable variability in individual migration behavior. First, the geolocation data showed that two individuals migrated, whereas one remained within the study region (Figure 1A), indicating that the study population exhibits partial migration. The migratory individuals departed the breeding grounds by late February heading in different directions. Individual D107584 made an approximately 1,500 Km to-and-fro migration, flying northeast at an average 150 km/day from 12 to 17 February, until it reached a wintering area in what was most likely a dry *caatinga* biome (centroid: 11°8'S, 41°27'W; Table 2; Figure 1B). This individual stayed in this region for five months until 22 July, when it departed southwest on a single day 750 km journey back to its breeding area in central Brazil (arrival by 23 July). Nevertheless, it is likely that the bird was not at the breeding site until early September, when the species was first recorded in our daily field observations (ACG, pers. observ.). The second migratory individual made a more complex cyclic migration through a longer route (approximately 3,335 km) that included two different wintering areas (Table 2; Fig. 1C). The first migration leg was a southern movement of approximately 1,340 km from 23 to 25 February (approximately 447 km/day) to an area within the Atlantic Forest biome, likely within the state of Santa Catarina. Since staging in this area occurred mostly during the equinox, there is considerable uncertainty about this location estimate, and centroid estimates are at sea (26°39'S, 48°7'W). Between 05 and 06 June, this individual flew 1,160 km northwest (approximately 580 km/day) to reach its second wintering ground back in the *cerrado* (centroid = 20°27'S, 53°57'W) in the state of Mato Grosso do Sul, east of the *Pantanal*. After three months, on September 06, this individual headed back approximately 815 km northeast towards the breeding grounds, arriving by 09 September (approximately 204 km/day).

DISCUSSION

The Lesser Elaenia is, to the best of our knowledge, the smallest flycatcher (15.5 ± 1.2 g) ever successfully tracked with geolocators and one of the lightest in South America, together with *E. albiceps chilensis* (Bravo et al. 2017). Though not a main goal of this study, our data reinforces previous findings that tags have no apparent effect on survival or site fidelity of small birds (Brlík et al. 2020). Our findings fill some long-standing knowledge gaps in this species' life history, longevity, and site-fidelity. Besides revealing a partial migration behavior in our study population, we also found two unusual variations in migration routes. Namely, birds made a longitudinal to-and-fro migration and a cyclic migration composed by a poleward, a latitudinal, and a longitudinal displacement (Figure 1D). To our knowledge, a cyclic migration route is unique among Neotropical bird species. Our data also revealed rough flight speeds of migratory individuals ranging from approximately 150 to 750 km/day, which appear to be consistent across spring and fall migrations. The tracking data identified three different wintering locations from the two migratory individuals (Figure 1), suggesting that the Lesser Elaenia population in central Brazil consists of partial intratropical migrants with low migratory connectivity, i.e., individuals from a same breeding population migrate to distinct wintering grounds (Salomonsen 1955, Marra et al. 2006).

Although limited to three individuals, our tracking data have several implications with regard to our current understanding of the distribution of Lesser Elaenia. In particular, there is a longstanding consensus that the Lesser Elaenia is a migratory species that primarily winters in central western Brazil and in the Amazon region (Fry 1970, Sick 1983, Marini & Cavalcanti 1990, Nunes & Tomas 2008) but may also occur within gallery forests borders in central Brazil in April and May (Marini & Cavalcanti 1990). Nevertheless, stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) recently indicate that individuals from a central Brazil population migrate mainly within the *cerrado* (Guaraldo et al. 2016), which was reinforced by our geolocator-tracking data. Altogether, we must stress that further studies should evaluate if the known wintering records in the Amazon (Marini & Cavalcanti 1990) belong to different migratory populations or to residents.

A Lesser Elaenia individual overwintering in the state of Santa Catarina (Figure 1D) is noteworthy because this area is over 300 km south of the widely recognized species distribution in Brazil, as noticeable in the large citizen-science databases eBird (eBird.org) and WikiAves (wikiaves.com.br), and although it occurs in a similar latitude (~26°S) in Missiones, Argentina (BirdLife International 2020, Hosner et al. 2020). Although geolocators are prone to error, we think that the Lesser Elaenia is present in Santa Catarina, but goes undetected especially because Elaenias get very secretive during their non-breeding period (e.g., the Plain-crested Elaenia *E. cristata*; ACG, pers. observ.). Vocalization is the main diagnostic trait for Elaenia species; thus, we argue whether the species has been historically overlooked in Santa Catarina due to identification difficulties. Alternatively, the species may have had only recently expanded into the Santa Catarina coastal region due to ongoing fragmentation of the Atlantic Forest for agricultural purposes (Ribeiro et al. 2009). Such poleward changes of species' distributions have been proposed for several other *cerrado* species due to climatic changes (Marini et al. 2009) and distributional shift might underlie observations of Lesser Elaenia at increasingly higher latitudes in Brazil. Increased joint banding efforts, citizen science observations, and museum data analysis should aid in solving this conundrum and perhaps leading to revising the Lesser Elaenia geographic range.

The cyclic migration documented in one individual, and especially its initial poleward movement in the fall, are unparalleled by any species of the South American migratory systems (Chesser 1994) and is currently known for only one species (though not a circular route), that of the Israeli Longlegged Buzzard (*Buteo rufinus*; Friedemann et al. 2020). Why birds may perform this poleward fall migration is still unknown, but may relate to food availability during fall and winter. The Lesser Elaenia is known to switch to a mainly frugivorous diet while wintering (Guaraldo et al. 2016). The period when the tracked individual was in its southern wintering site coincides with the fruiting season of zoochorous plants in that area, such as *Schinus terebinthifolius* (Lenzi & Orth 2004), mistletoes (Guimarães 2006), and species associated with regenerating (Mantovani et al. 2003) and riparian forests (Cascaes et al. 2013), thus suitable microhabitats for this species. By June, temperature and rainfall levels reach their lowest in this region (~16°C and ~80 mm; INPE - Instituto Nacional de Pesquisas Espaciais 2020). We thus hypothesize that these environmental parameters compelled the bird to depart to its second wintering area back in the *cerrado*, where it was warmer (~22°C; INPE - Instituto Nacional de Pesquisas Espaciais 2020), and where the mistletoe, a zoochorous species frequently consumed by Elaenias (Guerra & Pizo 2014), is fruiting in the region (Caires et al. 2009). Future *in loco* observations may reveal whether the species is simply following food resources or if the cycling migration relates to an integrated molt-migration "strategy" (e.g., Jahn & Guaraldo 2018).

The large geographic spread of the wintering grounds identified by our tracking efforts suggests *synhiemy* of the studied breeding population (Salomonsen 1955) –i.e., a discrete breeding population spread out over a large wintering area and with weak migratory connectivity (Marra et al. 2006). The concept of migratory connectivity has not yet been broadly applied to intratropical South American migrants (Marra et al. 2006). Revealing whether *synhiemy* is the rule or exception for the Lesser Elaenia populations (and other intratropical migrants), as well as revealing their flyways and wintering grounds, is thus a cornerstone for understanding the evolutionary history of Neotropical birds and their migrations. Achieving such goal will demand vast individual-level tracking studies on multiple species, which is a daunting but also exciting challenge. Like recently found for the Snail Kite (*Rostrhamus sociabilis*) (Jahn et al. 2021), the Lesser Elaenia is widely distributed in Brazil (BirdLife International 2020, Hosner et al. 2020) and is often locally abundant, especially in *cerrado*, *sensu strictu* (Tubelis & Cavalcanti 2001, Paiva & Marini 2013). If future studies support the apparent *synhiemy* within our study population, then this population may serve as a monitoring hub to guide management and conservation of its multiple and widespread wintering grounds and syntopic species.

Longevity estimates for South American species are rare –especially for migrants– and greatly vary among species (Scholer et al. 2018). Our long-term data indicated that average longevity for the Lesser Elaenia is 3.8 years, but some individuals can survive for at least 12 years. In this sense, the Lesser Elaenia has greater longevity than the closely related austral migrant Fío-Fío (*E. albiceps*; average ± SD = 2.2 ± 1.5 years; Brown et al. 2007), which may show reduced longevity due to their breeding grounds being under harsher climate (at 55°S, thus approximately 40° south from our study site), and because their two to four times longer migratory journey from the breeding to the wintering grounds (approximately 6,000 km). In comparison to residents, migrants are expected to live shorter than residents (Robinson et al. 2020). Nevertheless, the estimated Lesser Elaenia longevity is similar to those known for other resident Brazilian species, based on Tables 1 and 2 in Lopes et al. (1980) and Table 1 in Silva-Jr et al. (2021). These sources document two migratory species that lived an average of 3.5 ± 1.5 years and 47 resident species that lived 4.2 ± 2.1 years on average. Though beyond the scope of this study, we clearly need further investigation on the role of climate and migratory status on neotropical bird longevity, a vital life history trait for generating accurate population dynamics models (Hostetler et al. 2015).

Breeding site fidelity is another relevant life history parameter rarely documented for intratropical migrants. We found site fidelity to be relatively high among Lesser Elaenia in our study population. Many migrants are faithful to their breeding grounds, which is hypothetically one of the main adaptive drivers for the evolution of migration (Winger et al. 2019). Thus far, site-fidelity data applies exclusively to the breeding grounds in South America and is known for only few species: 10 neotropical austral migrants (Jahn et al. 2009, Presti et al. 2018) and only two South American intratropical migrant Passerines, namely the Lined Seedeater (*Sporophila lineola*) (Ferreira & Lopes 2017), and the White-throated Kingbird (*Tyrannus albogularis*) (Lopes et al. 2018). Unfortunately, details on fidelity are too rare to provide a thorough discussion (Lopes et al. 2018). Thus, we hope that our findings and quantitative data stimulate additional studies focused on intratropical migratory species and its due comparison to migrants from other migratory systems, specifically the ones that would test hypotheses on breeding-site fidelity and its effect on longevity, breeding success and population dynamics.

Many of the likely causes for the South American intratropical migration system remain largely understudied (Levey 1994, Faaborg et al. 2010b), including its wide geographic span and thus complex and expensive logistics, on top of the long-standing problem of limited access of local researchers to technology and funding. Therefore, even though restricted to a single Lesser Elaenia breeding population, our findings reveal critical life-history features, such as the cyclic poleward migration, the general activity schedule, flight speeds, migratory connectivity, and wintering grounds of tracked individuals. The hypotheses we proposed based on our data may guide studies on the migratory ecology of the many understudied intratropical migrants listed in Somenzari et al. (2018). In a highly connected world where animal-borne pathogens may globally spread in a few weeks (e.g. avian influenza and West Nile Virus; Altizer et al. 2011, Canavan 2019), efforts to better understand the underlying patterns and mechanisms of intratropical migration and connectivity may reveal paramount to both bird and human conservation. Moreover, it is vital that we devote efforts to ensure that research on intratropical bird migration keeps thriving. This is the only way we will be able to answer more intricate questions on the ecology of these migrants and ultimately conduct adequate interhemispheric comparisons of migratory systems that are needed to advance the study of bird migration as a whole.

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